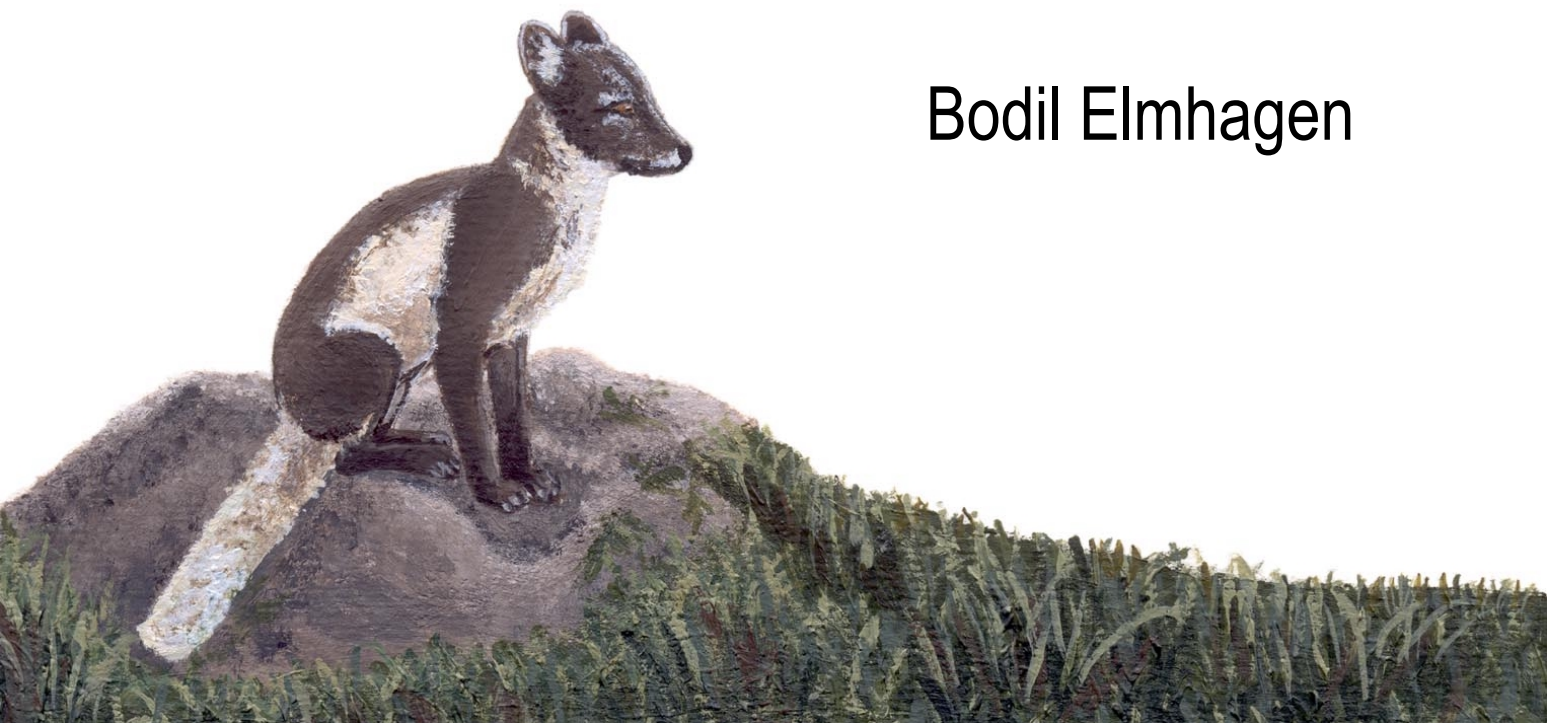




Interference Competition
between
Arctic and Red Foxes

Bodil Elmhagen



Summary of the DPhil thesis

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2003

Doctoral dissertation 2003

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Abstract

In this thesis, I investigate the relationship between arctic foxes *Alopex lagopus* and red foxes *Vulpes vulpes* in Swedish mountain tundra habitat (fjällen). The arctic fox population was severely reduced by hunting in the early 20th century. It has not recovered despite protection since 1928 and it is endangered, while the red fox population increased in 1930-1960.

I found a high food niche overlap between arctic and red foxes and they responded similarly to changes in the prey base, indicating similar prey preferences. Hence, arctic and red foxes should compete for the same territories; more precisely the ones in low altitude areas close to the tree-line where prey abundance is relatively high. In the 19th century, arctic foxes bred in all tundra habitats. An analysis of present den use showed that arctic foxes have retreated to higher altitudes as they rarely used the lower parts of their former range. Instead, red foxes did. Arctic foxes were highly dependent on the availability of Norwegian lemmings *Lemmus lemmus* for reproduction, while red foxes at lower altitudes had better access to alternative prey.

Interference competition imply that there are behavioural interactions between competing species, e.g. fighting or predation, but interactions can also be more subtle and imply that inferior species avoid encounters with stronger competitors by changing their habitat use. Red foxes are larger than arctic foxes. Hence, they have an advantage in direct fights and arctic foxes may either be driven away from their dens when red foxes establish in the vicinity, or they avoid habitats where they risk encounters with red foxes. I found that arctic foxes almost exclusively used dens situated farther than 8 km from inhabited red fox dens. In two out of three cases when they bred closer to red foxes, there was red fox predation on arctic fox cubs. Further, simulations of arctic fox avoidance of areas surrounding inhabited red fox dens in a spatially explicit population model, indicated that relatively small numbers of red foxes might have a large impact on arctic fox population size and distribution.

Thus, the results of this thesis indicate that interference competition with red foxes has hampered arctic fox recovery after the initial population decline, by causing a substantial reduction in arctic fox habitat. Further, red foxes have taken over the most productive areas and remaining arctic fox habitats is of such low quality that it is uncertain whether it can maintain even a small arctic fox population.

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The complete version of this thesis includes all the above and the following papers, which are referred to by their Roman numerals in the summary.

Papers I – V

- I Dalerum F, Tannerfeldt M, Elmhagen B, Becker D, Angerbjörn A. 2002. Distribution, morphology and use of arctic fox dens in Sweden. *Wildl. Biol.* **8**: 185-192.
 - II Elmhagen B, Tannerfeldt M, Verucci P, Angerbjörn A. 2000. The arctic fox (*Alopex lagopus*) – an opportunistic specialist. *J. Zool.* **251**: 139-149.
 - III Elmhagen B, Tannerfeldt M, Angerbjörn A. 2002. Food-niche overlap between arctic and red foxes. *Can. J. Zool.* **80**: 1274-1285.
 - IV Tannerfeldt M, Elmhagen B, Angerbjörn A. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**: 213-220.
 - V Shirley MDF, Elmhagen B, Lurz PWW, Rushton SP, Angerbjörn A. 2003. Modelling the spatial population dynamics of arctic foxes (*Alopex lagopus*): the effects of red foxes and microtine cycles. Submitted manuscript.
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INTRODUCTION

The effects of competition between individuals of different species may extend to population levels where population densities and distributions are affected. The arctic fox *Alopex lagopus* was abundant in Swedish mountain tundra areas in the late 19th century. At the turn of the century, excessive hunting was followed by a drastic population decline (Lönnberg 1927). Despite protection since 1928, there are now only about 70 arctic foxes left. The red fox *Vulpes vulpes* population increased dramatically in the 1930-1960's (Lindström 1989a) and interspecific competition may be a factor which has hampered arctic fox recovery (Hersteinsson et al. 1989). This thesis investigates the relationship between arctic foxes and red foxes, especially what consequences red fox competition may have on the arctic fox population.

When do species compete?

All species require specific environmental conditions and resources to be viable. They require a niche (Hutchinson 1957). Interspecific competition occurs when individuals of different species use the same resource, i.e. when there is an overlap in a niche dimension, and supply of that resource is limited. When all individuals are equally good competitors, interspecific competition leads to decreased reproductive success or decreased survival in both species. However, it is more common with asymmetrical competition, where individuals of one species are more affected than those of the other are (Connell 1983).

A high overlap in a niche dimension may indicate severe competition, but there is no simple relationship between the degree of niche overlap and competition. Competition can cause an individual to change its use of resources, and intense competition can therefore be associated with low niche overlap

(Colwell and Futuyma 1970, Abrams 1980). Further, a high overlap in one niche dimension is often associated with a low overlap in another dimension (Schoener 1974). For example, if two individuals with similar food niches also compete for territories, dietary overlap may remain high while spatial overlap decreases.

It is useful to distinguish between the fundamental and the realised niches of a species. The fundamental niche is its broadest possible niche, which comprises all environments where the species would be viable in the absence of interspecific competition and predation. The realised niche is the part of the fundamental niche where the species remains when competitors and predators are present (Hutchinson 1957). A high overlap between the fundamental niches of two species indicate that they will compete when they are sympatric, while a relatively lower overlap between their realised niches indicate that one or both species have changed their use of resources as a response to competition. If the distribution or density of a superior competitor decrease, the inferior species will experience a competitive release which allows it to expand its realised niche and increase in density or distribution. On the contrary, when an inferior competitor no longer has access to necessary resources, it has lost its realised niche and will go extinct due to competitive exclusion.

Fundamental and realised niches are concepts which apply to an entire species, but some species are found in many different environments. In such cases, it can be useful to identify also the niches of local populations, using the concepts virtual and actual niches as equivalents of fundamental and realised niches (Colwell and Futuyma 1970).

Competition, Predation & the Ecology of Fear

Competition is usually classified as either exploitation or interference competition (Park 1962). Exploitation competition occurs when

one individual uses a resource and thereby deprives another individual of the opportunity to do so. For example if food availability for one individual is affected by other individuals' consumption of that food resource. Interference competition involves behavioural interactions between the individuals, such as fighting and predation. It may also be more subtle and individuals of a species may avoid stronger competitors of other species rather than risk losing a fight or being killed. Exploitation and interference competition are both common among terrestrial animals (Schoener 1983).

A guild can be defined as a group of species which uses similar resources and therefore may compete. When such competition involves predation, so-called intraguild predation, the predator will benefit both by an immediate energetic gain and by decreased exploitative competition (Polis et al. 1989). Predators can kill more than a "doomed surplus" of their prey, thereby affecting prey abundance (e.g. Lindström et al. 1994). However, prey respond to the presence of predators by changing their feeding behaviours and habitat selection. They prefer safe habitats, "predation refuges", rather than productive ones. Hence, the fear of predators may affect both predation rate and prey fitness. The behavioural response in fear-driven interactions may even be more important for prey abundance than predation itself (Brown et al. 1999). Interspecific killing is common among mammalian carnivores and the combined effects of competition and intraguild predation can cause inferior species to change their habitat use or activity patterns (Palomares and Caro 1999). Thus, "competition refuges" may be important for the co-existence of competitors just like predation refuges are important for co-existence of predator and prey (e.g. Durant 1998).

In some carnivores, intraguild predation has a considerable impact on mortality rates. For example, predation by coyotes *Canis latrans* was the major cause of death for kit

foxes *Vulpes macrotis* and swift foxes *Vulpes velox* (Ralls and White 1995, Sovada et al. 1998). Despite this, there was no indication of spatial segregation between coyotes and either fox species (White et al. 1994, Kitchen et al. 1999). However, other carnivores show behavioural responses to predator presence. Avoidance patterns has been found in coyotes which avoid wolves *Canis lupus*, red foxes which avoid coyotes and lynx *Lynx lynx*, and cheetahs *Acinonyx jubatus* which avoid lions *Panthera leo* and hyenas *Crocuta crocuta* (Harrison et al. 1989, Thurber et al. 1992, Durant 1998, Fedriani et al. 1999). Intraguild predation on the inferior species occurs in all these cases (Sargeant and Allen 1989, Thurber et al. 1992, Palomares and Caro 1999, Sunde et al. 1999). However, predation appears to be rare, and avoidance by the inferior species may be more important for the overall effect on distributions and population sizes. Coyote densities were higher in areas where wolf densities were low and coyote home ranges were found outside or near wolf pack territory borders (Fuller and Keith 1981, Thurber et al. 1992). Further, the reduction in wolf numbers in North America was followed by an increase in coyote abundance (Mech 1970). Likewise, red foxes established home ranges outside or close to coyote territory borders, with minimal spatial and temporal overlap (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). Reductions in coyote or lynx populations have also been followed by increased abundances of red foxes (Linhart and Robinson 1972, Palomares 1996).

Arctic and Red Foxes

Evolution, morphology and distribution

The arctic fox is closely related to North American swift and kit foxes. The species diverged as glaciations became more common in the late Pleistocene and the arctic fox evolved in an arctic environment (Geffen

et al. 1992, Mercure et al. 1993). The current distribution of the arctic fox is circumpolar and includes tundra areas in the Arctic, North America and Eurasia, and the mountain tundra in Fennoscandia (Audet et al. 2002).

The arctic fox has several adaptations to tundra climate, such as a short, rounded body with short ears and legs. It has the best insulative winter fur of all mammals and it does not have to increase its metabolic rate significantly to maintain homeothermy under normal temperature conditions (above -40°C) (Prestrud 1991). Further, its resting metabolic rate decreases in winter, possibly an adaptation to conserve energy (Fuglei and Øritsland 1999). The arctic fox appears in two colour morphs. The white morph is brownish-greyish dorsally and whitish ventrally in summer, but turns white in winter. The blue morph is brownish all seasons. In general, both morphs are present in a population, but there is a positive correlation between the frequency of white foxes and snow cover. Due to the camouflage effect of their colour, the white morph probably has a selective advantage over the blue in snowy inland habitats, while the opposite is true in coastal areas with less snow (Hersteinsson 1989).

The traditional placement of arctic foxes in a separate genus, *Alopex*, is due to the morphological differences between arctic foxes and the fox species in the genus *Vulpes*. However, genetic data suggest that arctic foxes should not be generically distinguished from *Vulpes* (Geffen et al. 1992).

The red fox evolved in Eurasia and later colonised North America. Its current distribution covers North America, Europe and Russia, but it does not penetrate into the high arctic. It has also been introduced to other areas (Larivière and Pasitschniak-Arts 1996). The red fox is smaller in northern areas than in southern habitats (Englund 1965), but it is still about 60% heavier than the arctic fox at comparable latitudes. It also has more pointed ears and a relatively longer tail and neck (Hersteinsson and Macdonald 1982).

The colour of red foxes is very variable, ranging from light greyish to bright orange. There are also silver (black) and “cross” colour morphs.

Food and Population Dynamics

Arctic and red foxes are opportunistic feeders, but the arctic fox generally has a less varied diet. This is probably related to the low diversity of prey in tundra areas (Hersteinsson and Macdonald 1982). However, arctic fox populations can be divided into coastal and inland (“lemming”) foxes, as the ecology of the species differs between these environments (Braestrup 1941). Most inland areas are barren and small rodents with cyclic population fluctuations dominate the prey base. In years of low food availability, fox reproduction typically fails. When food availability is high, an inland vixen may carry up to 21 fetuses and wean at least 16 cubs, one of the largest litter sizes among Canids (Macpherson 1969, Ewer 1973, Tannerfeldt and Angerbjörn 1998). As a consequence, the population dynamics of inland foxes is characterised by large fluctuations, as the foxes respond numerically to the availability of their cyclic prey (e.g. Elton 1924, Macpherson 1969, Angerbjörn et al. 1995, Angerbjörn et al. 1999, Strand et al. 1999).

Arctic foxes in coastal areas have access to a greater variety of resources than inland foxes, such as sea birds, seal carcasses, fish and marine invertebrates. Prey availability is therefore relatively stable between years. The difference between inland and coastal areas has led to the evolution of different reproductive strategies. Coastal foxes produce relatively small litters of similar size every year and they appear to have lost the capacity to have very large litters. Inland foxes cannot reproduce successfully all years, but have larger mean and maximum litter sizes (Frafjord 1993a, Tannerfeldt and Angerbjörn 1998).

Red foxes can have a maximum of 12 cubs, but most litters consist of 3-6 cubs (Larivière and Pasitschniak-Arts 1996). Red

fox populations are relatively dense and stable in productive habitats and the populations may be socially regulated. On the contrary, populations in less productive habitats may be food regulated (Lindström 1989b). For example, small rodents are cyclic in boreal Fennoscandia and in other Eurasian areas with similar snow conditions, such as Poland and Russia (Hansson and Henttonen 1985). Both the proportion of breeding red fox vixens and litter sizes are related to vole availability (Englund 1970, Lindström 1988). Consequently, the size of red fox populations in areas with cyclic voles fluctuates in relation to vole abundance (Englund 1970, Angelstam et al. 1985, Goszczynski 1989a).

Social organisation

Home ranges of adult arctic foxes are 4-60 km² (e.g. Eberhardt 1982, Birks and Penford 1990, Prestrud 1992, Angerbjörn et al. 1997, Eide et al. 2002a). The smallest home ranges are found in productive coastal habitats, but average home range size increases as habitats become less productive in inland areas (Eide et al. 2002a). Comparing red fox home ranges in different habitats, home range size also increases as productivity decreases (Lindström 1982, Jones and Theberge 1982, Goszczynski 1989b, Meia and Weber 1995).

The basic social unit in arctic and red foxes is a breeding pair where both the male and the female participate in cub rearing (Kleiman 1981, Hersteinsson and Macdonald 1982, Angerbjörn et al. 2003a). Within habitats, the pair establishes a home range of the size necessary to sustain it when food availability is low (Lindström 1989b, Eide et al. 2002a). When food availability in the home range increases, arctic and red foxes increase group size rather than diminish home range size, as older offspring remain in their natal home ranges (Lindström 1989b, Angerbjörn et al. 2003a). In some cases, resident older offspring reproduce and the foxes practice communal breeding with more than one litter in a den (Macdonald 1979, Hersteinsson and Macdonald 1982, Baker et

al 1998, Strand et al. 2000, Angerbjörn et al. 2003a). The resource dispersion hypothesis suggests that the dispersion of food patches and group size determine home range size by the richness of those patches. This might explain the social organisation of both arctic and red foxes (Hersteinsson and Macdonald 1982, Macdonald 1983).

Interspecific relations

Arctic and red foxes are sympatric in a relatively narrow overlap zone in the low Arctic and the similarities between them indicate that they should be competitors (Hersteinsson and Macdonald 1982). Due to its larger size, a red fox needs more food and a larger home range than an arctic fox to sustain its higher energy demands. Thus, the northern limit of the red fox may be determined by resource availability which in turn depends on climate (Hersteinsson and Macdonald 1992). Red foxes are dominant over arctic foxes in direct interactions (Rudzinski et al. 1982, Schamel and Tracy 1986, Frafjord et al. 1989, Korhonen et al. 1997). The southern distribution limit of arctic foxes may therefore be determined by interspecific competition with red foxes. If that is the case, an amelioration of the climate would increase productivity and allow red fox expansion, while arctic fox populations would retreat due to increased competition from red foxes.

As a hypothetical example, northern Fennoscandia experienced a 2°C increase in temperature in 1910-1935. This would have pushed isotherms and the distribution of red foxes up c. 330 m in mountain tundra areas. If the lowest altitude of arctic foxes in 1900 would have been 600 m a.s.l, the new distribution limit in 1935 would be 930 m a.s.l, and the arctic fox population would have lost more than half of its former habitat (Hersteinsson and Macdonald 1992). Archaeological finds indicate that major reductions in the arctic fox distribution range have occurred before, as all Norwegian fox bones from the warm period 9000-5000 B.P

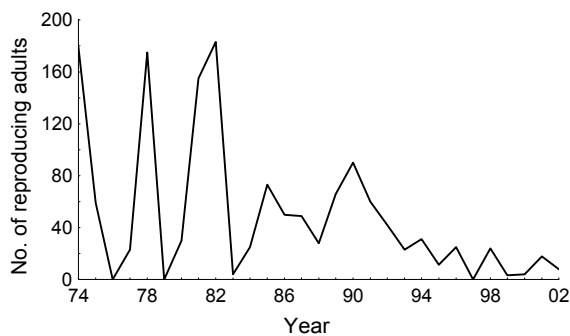


Fig. 1 Estimated number of breeding arctic foxes in Sweden in 1974-2002 (from Angerbjörn et al. 2002).

were from red foxes, while arctic fox bones were either older or younger (Frafjord and Hufthammer 1994).

Arctic and Red foxes in Sweden

The Fennoscandian mountain range stretches from the Kola Peninsula in the north-east to south-western Norway, encompassing areas in Russia, Finland, Sweden and Norway. Due to a combination of relatively high latitudes and altitudes, the area has tundra climate and vegetation, while the rest of Fennoscandia is forested. The habitat can be described as mountain tundra with arctic species like the arctic fox, Norwegian lemming *Lemmus lemmus* and reindeer *Rangifer tarandus*.

Assuming that present densities of breeding arctic foxes in Siberia are comparable to former densities in Fennoscandia, the Swedish population before 1880 consisted of c. 4000 breeding adults (range 730-9430 in 33 000 km² of available habitat; data recalculated from Angerbjörn et al. 1999 and Tannerfeldt pers. comm.). In the late 19th century, increased prices of arctic fox pelts led to excessive hunting and a consequent population decline (Lönnberg 1927). A healthy arctic fox population was regarded as a valuable asset to people in the mountain regions. Hence, the arctic fox was protected in 1928, and protection in Norway (1930) and Finland (1940) soon followed. Despite

this, the population did not recover and peak population sizes in the 1970's were about 180 breeding adults. A further decrease followed from 1980, probably due to food shortage during an absence of lemming peaks (Fig. 1, Angerbjörn et al. 1995). Population estimates for 2002 indicate that there are about 70 adults in Sweden and 10 in Finland. Population densities in Norway and Kola are similar to those in Sweden (Angerbjörn et al. 2002). Low lemming abundances, decreased availability of reindeer carcasses in winter, increased competition with red foxes, inbreeding and Allee effects are factors which may have hampered a recovery (Hersteinsson et al. 1989, Linnell et al. 1999b).

Hunting bags indicate that the Fennoscandian red fox population about tripled in size between 1930 and 1960 (Lindström 1989a, Selås et al. unpublished). The increase coincided with a northward spread of red foxes in North America and Russia (Marsh 1938, Macpherson 1964, Chirkova 1968). There are several factors which may have contributed to the increase. A general amelioration of the climate, decreased interference and exploitative competition with large predators, increased access to food left-overs in human garbage, and changes in forestry practices including large clear-cut areas which favour field voles *Microtus agrestis*, the main prey of boreal red foxes (Hersteinsson and Macdonald 1992, Lindström 1989a).

The red fox population was severely hit by an epidemic of sarcoptic mange in the 1980's (Lindström and Mörner 1985, Danell and Hörnfeldt 1987). Although the epidemic began in northern Sweden, reductions appear to have been largest in the dense populations in southern Sweden. Three Swedish counties have mountain tundra habitat with arctic foxes, Norrbotten, Västerbotten and Jämtland. There was no reduction in red fox hunting bags in Norrbotten and a relatively slight reduction in Västerbotten (Fig. 2; Swedish Sportsmen's Association 1960-2001). Hence, the mange epidemic probably had little effect on the degree of interspecific

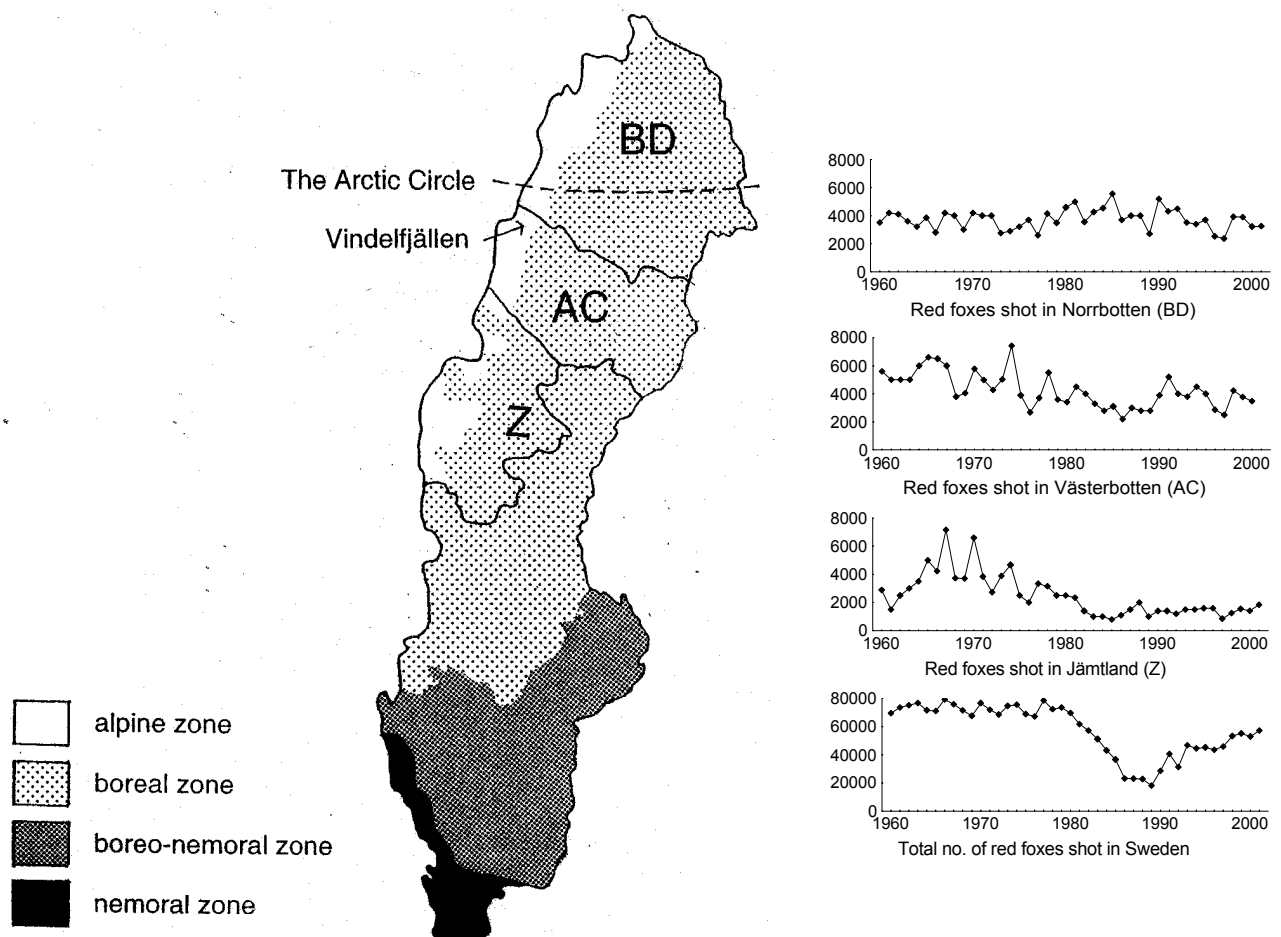


Fig. 2 Biogeographical zones in Sweden. Arctic and red foxes are sympatric only in mountain tundra habitat in the alpine zone of Norrbotten (BD), Västerbotten (AC) and Jämtland (Z) counties. Red foxes are found in all of Sweden, but the population was severely hit by a mange epidemic which started to spread in 1975 (see text). However, estimated numbers of shot red foxes indicate that the epidemic had less serious effects on the northernmost red fox populations compared to the rest of Sweden (figures to the right; data from the Swedish Sportsmen's Association (1960-2001)).

competition between arctic and red foxes in these counties. There is only one observation in Fennoscandia of arctic foxes infested by mange and those foxes were captured, treated and thereafter released (Mörner 1988).

When the red fox population increased after 1930, the number of red foxes also increased in Fennoscandian mountain tundra habitat (Østbye et al. 1978). There is evidence for a parallel redistribution of arctic foxes which retreated to peripheral areas and dens at higher altitudes (Østbye et al. 1978, Linnell et al. 1999a). These findings are consistent with Hersteinsson and Macdonald's (1992) theory on interspecific competition. However, if red foxes have different

habitat or prey preferences than arctic foxes, the retreat could also result from other changes in the environment (Chirkova 1968, Linnell et al. 1999a).

Questions

The aim of this thesis is to investigate the relationship between arctic and red foxes through studies of den use, food niches and interference competition, and to estimate the possible effects of red fox competition on an arctic fox population. The specific questions are:

- Paper I Do arctic and red foxes differ in their use of dens in mountain tundra habitat?
- Paper II The prey base in mountain tundra habitat is restricted. To what extent is the arctic fox dependent on lemmings for food and successful reproduction?
- Paper III Do arctic and red foxes have different virtual food niches?
- Paper IV Is there interference competition causing arctic foxes to avoid red foxes?
- Paper V Using a spatially explicit model to simulate population effects, what is the effect of red fox competition on an arctic fox population?

METHODS

Study area

The study area was located in the nature reserve of Vindelfjällen in Västerbotten county, Swedish Lapland. In total, the study area covered 1300 km² of mountain tundra, but there was a smaller core area of 450 km² (Fig. 3). The major part of the area is situated within the low alpine vegetation zone and the main vegetation types are dry heath, grass heath and dry fen. Most geomorphological structures are of glacial origin and subglacially engorged eskers, kames and other hummocky glaci-fluvial accumulations are common (Ulfstedt 1977). Summers are short with snowmelt in June and first snow in September, but there is no permafrost.

The tree line is situated at about 750 m a.s.l and valleys with birch and coniferous forests intersect the mountain tundra (Fig. 3). Arctic foxes bred only above the tree line. The larger part of the red fox population was found below the tree line, but we have only collected data on red foxes which inhabited dens on the mountain tundra, i.e. those that were most likely to interact with arctic foxes.

All population peaks are by definition “peaks”. However, Fennoscandian lemming and vole cycles generally have amplitudes in the order of 1:200 (Hörnfeldt 1994, unpublished data). As a consequence, there is a popular notion of “peak years” specifically meaning peaks reaching approximately these densities. For lemmings in particular, such peaks are easily distinguished in the field as lemmings suddenly are seen everywhere on the tundra, while they rarely are seen otherwise. In this thesis, I use this qualitative term to distinguish such lemming and vole population peaks from other, relatively small, increases.

Four species of microtine prey were present in the study area, Norwegian lemming, field vole, bank vole *Clethrionomys glareolus* and grey-sided vole *Clethrionomys rufocanus*. Lemming and vole popula-

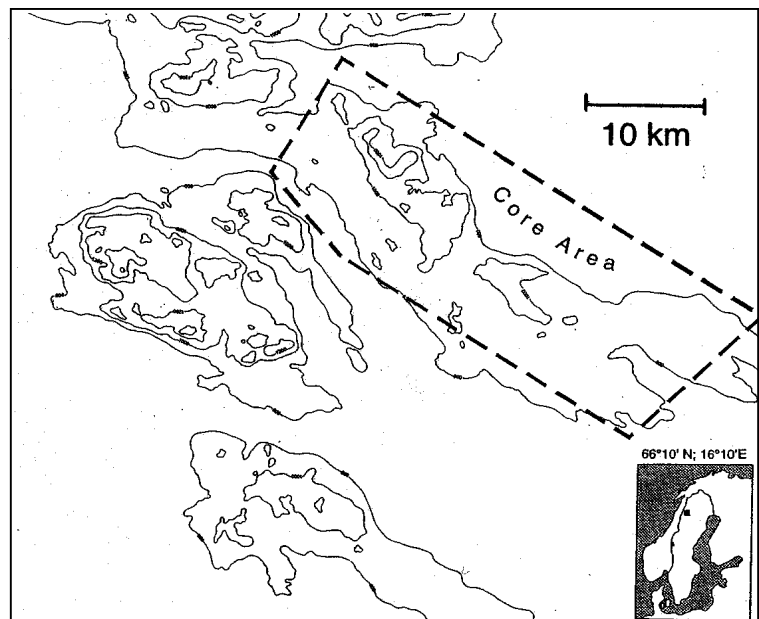


Fig. 3 The study area in Vindelfjällen. Only areas above the tree line where arctic fox dens were surveyed regularly are shown.

tions are generally cyclic in Fennoscandian tundra and boreal forests, but this pattern has been interrupted during the last 20 years (Hansson and Henttonen 1985, Angerbjörn et al. 2001, Hanski et al. 1993, Hörnfeldt 1994). The last lemming peak in Västerbotten before the start of this study occurred in 1982, but fluctuations have continued with a lower amplitude (Angerbjörn et al. 2001). Likewise, densities of grey-sided voles in the forests of Västerbotten have declined drastically and the last population peak occurred in 1985. Forest populations of field and bank voles have continued to peak but there has been a declining trend in peak densities (Hörnfeldt 1994). The declining trends in field and bank vole populations were, at least temporarily, broken in 1998 when there was a large population peak (Hörnfeldt 1998). In 2001, the lemming population finally peaked in all Swedish mountain tundra habitat (unpublished data).

Other species in the study area which arctic and red foxes may prey upon were reindeer *Rangifer tarandus*, mountain hare *Lepus timidus* and shrews *Sorex spp.* There were also rock ptarmigan *Lagopus mutus*, willow ptarmigan *Lagopus lagopus*, passerines *Passeriformes*, ducks *Anseriformes*, gulls and waders *Charadriiformes*.

Other predators which may interact with the foxes were wolverine *Gulo gulo* and golden eagle *Aquila chrysaetos*.

General methods

The arctic fox population in the study area has been surveyed by the Swedish Arctic Fox Project since 1985. The aim of the project has been to study the ecology and behaviour of the arctic fox (e.g. Tannerfeldt 1997).

Dens originally made by arctic foxes are typically large structures that have been in use for hundreds of years. They are covered with lush vegetation which makes them conspicuous and easy to find (Zetterberg 1945, Macpherson 1969). Den surveys dur-

ing the breeding season is therefore the most common method for monitoring of arctic fox populations (Eberhardt et al. 1983, Angerbjörn et al. 1995). Dens originally dug by red foxes are smaller than arctic fox dens. The vegetation on a red fox den does not differ markedly from the surroundings and few dens have more than 5 openings (Østbye et al. 1978). In the early years of the Arctic Fox Project, den surveys mainly covered the core area, but more areas were added as time went on. Most surveyed dens were arctic fox dens, but some red fox dens have also been checked on a regular basis. However, reproducing red foxes were only found in arctic fox dens. Therefore, all dens mentioned in the following are dens originally constructed and used by arctic foxes, but I refer to them as arctic or red fox dens depending on which species that occupied them.

We visited dens in July, when cubs emerge, and searched for foxes or signs of activity such as scats, prey remains wear and tear in the vegetation, fur and newly excavated openings. When we suspected that arctic foxes were using the den, we observed it for at least 24 hours to decide if there were cubs or not and minimum litter sizes were recorded. Within the core area we tagged virtually all cubs and two thirds of the reproducing adults. Red foxes in the area were very shy compared to the arctic foxes, and they often moved even after a short visit at their dens. Hence, we rarely had more than one chance to see them and we only recorded presence or absence of cubs (either visual observation of cubs, or small scats and wear and tear in the grass which indicate that cubs were present). On a few occasions, we did not see any foxes although the dens were clearly inhabited. We then relied on tracks and the size of newly excavated den openings to determine which fox species used the den.

Lemmings build nests under the snow in winter and lemming densities can be estimated by nest counts (Sittler 1995). From 1990 and onwards, we counted the number of

lemming nests per 100 km walked on the mountain tundra and used this as an index for lemming winter population densities. The direction of change in the index between years was used to determine the status of the lemming population in the summer (increase or decrease/low phase).

Fox den use (Paper I)

Most arctic fox dens in the study area were already known by local rangers in the early 1980's, while others have been found during later surveys. In 1999-2000 we gathered morphological data on all dens. We counted the number of openings that were in good condition ("non-collapsed") and measured the distance between the most outspaced openings in two directions (den "length" and "width"). We used the resulting rectangle as an approximation of den area. Altitude and distance from the tree line were estimated from maps.

Survey data showed when dens had been inhabited by foxes. For each den, we used the frequency of litters in relation to surveyed years to analyse and compare the den preferences of arctic and red foxes.

Fox diets and food niches (Paper II, III)

We needed data on fox diets to investigate to what extent arctic foxes depend on lemming availability and to compare the food niches of arctic and red foxes. We collected fresh scats at inhabited den and analysed the contents. Unfortunately, all scats collected in 1991-1992 and some collected in 1993-1995 were lost during storage.

First, we studied arctic fox diets in 1990 and 1994-1997 and tested if there was a numerical response to lemming availability, i.e. if the number of foxes which established and tried to reproduce depended on lemming availability in winter (Paper II).

Second, we compared arctic and red fox diets in 1993 and 1996-1998 (Paper III). The best way to determine if two species compete is to compare their virtual and actual niches by studying resource use under allopatric and sympatric conditions (Colwell and Futuyma 1970, Clode and Macdonald 1995). Arctic and red foxes are sympatric in Vindelfjällen and we have no allopatric populations to compare with in Sweden. However, as lemming and vole populations fluctuate, the composition of the prey base changes between summers. If arctic and red foxes respond similarly to those changes, they should have the same virtual food niches. In that case, percent overlap (Schoener 1970) between their diets should be constant. We tested if this was the case by comparing the degree of overlap between arctic and red foxes diets over four summers.

Interference competition (Paper IV)

If there is interference competition between arctic and red foxes and the arctic fox is the weaker competitor, arctic foxes should avoid contact and not breed close to dens inhabited by red foxes. Although defended territories may be smaller, arctic foxes are often seen up to 6 km from their dens (Angerbjörn et al. 1997, Tannerfeldt pers. obs.). The larger red fox should have a 90% larger home range (Harestad and Bunnell 1979, Hersteinsson and Macdonald 1992). The 6 km radius for arctic foxes should thus be equivalent to an 8 km radius for red foxes. We used den survey data from the core area in 1987-2000 and tested how often high quality dens were inhabited by breeding arctic foxes when breeding red foxes were absent or present within an 8 km distance.

Population effects (Paper V)

Spatially explicit population models can be used to simulate population effects of behav-

ious like interference competition (Rushton et al. 1997, 2000). Hence, we developed a spatially explicit population model to study long-term effects of interspecific competition on the arctic fox population in Vindelfjällen. The model had a GIS component which stored information on den and fox locations. Thereby, we could simulate arctic fox avoidance of red foxes by not allowing them to establish in dens situated within 8 km of dens occupied by red foxes, as described in Paper IV.

The modelled area consisted of the study area in Vindelfjällen and surrounding forests. The forests contained a source population of red foxes from which dispersal to mountain tundra dens occurred. We parameterised the model using available data on arctic and red fox reproduction and mortalities during different lemming and vole population phases (low, increase, peak and crash). We used the observed sequences of lemming and vole phases in the period 1985-2000 as a model input and simulated the corresponding fox population dynamics during this period. Initial fox populations in the simulations were those of Vindelfjällen and surrounding forests in 1985.

We compared model outputs with the observed population dynamics of arctic and red foxes in the core area. We then tested the effect of red fox competition on the arctic fox population by running the model with and without red foxes, comparing population trends.

RESULTS AND DISCUSSION

Fox den use

There were 77 arctic fox dens in the study area, all excavated in glacial fluvial eskers or terrace formations. The lowest lying den was situated 760 m a.s.l, which is only a few meters above the treeline, while the highest den was situated 1160 m a.s.l (Fig. 4, Paper

I). The highest mountain peaks in the study area rise above 1600 m a.s.l, but areas above 1100 m generally consist of boulder fields. Rock dens under boulders are used by arctic foxes in high-arctic Svalbard (Prestrud 1992). We have observed adult arctic foxes use such dens as temporary shelters, but there is no indication that they use them for breeding in Sweden at present low population densities. The average den in Vindelfjällen was situated in an esker on a south-facing slope 915 m a.s.l, 3.5 km from the treeline. It had an area of 277 m² and 44 openings (Paper I). Thus, the dens were among the largest reported for arctic foxes in tundra habitats (e.g. Chesemore 1969, Østbye 1978, Garrott et al. 1983, Anthony 1996, Frafjord 2003).

Unlike many other tundra areas, there is no permafrost in Vindelfjällen and there are many glacial fluvial sand formations. It is therefore possible to dig dens of comparatively high quality. Arctic foxes may dig several new openings in one summer. However, construction of dens with more than 100 openings, as the largest dens in Vindelfjällen, and fertilisation of the den area to an extent where the vegetation differs completely from the surroundings (Österdahl 2003), must be the work of generations of foxes. The dens were constructed before the arctic fox population started to decline in the early 1900:s (Zetterberg 1945) and the distribution of dens should therefore mirror the former distribution of arctic foxes.

Arctic foxes showed a preference for dens with many openings, while red foxes preferred dens which covered large areas. These two measurements were positively related to each other and both species consequently preferred large dens (Paper I). Large dens are equally available at all altitudes (Spearman's $r = -0.054$, $p = 0.97$), which indicates that the former arctic fox distribution reached down to the present treeline (Fig. 4). Zetterberg (1945) worked as a ranger in the area 1904-1929 and also gathered information on the arctic fox from old Sami and settlers. He did not find arctic

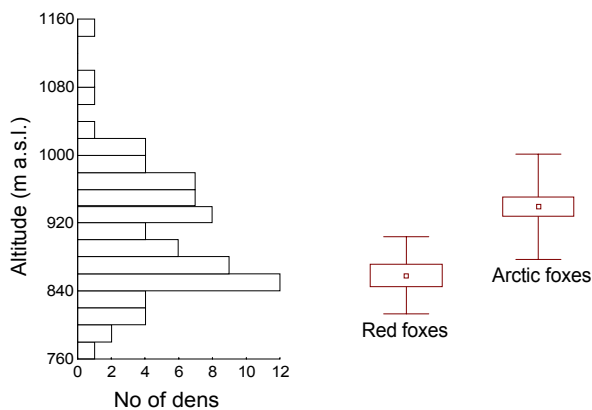


Fig. 4 Distribution of arctic fox dens in Vindelfjällen (n=77) to the left. Median and mean altitudes for the dens were 905 and 915 m a.s.l. respectively. On average, dens used by red foxes were situated 860 m a.s.l. (n=11) and dens used by arctic foxes 940 m a.s.l. (n=30). The right figure show means (small boxes), SE:s (large boxes) and SD:s (whiskers). In the analyses for paper I, we accidentally labelled a den with a red fox litter as having an arctic fox litter, thus n-values differs from the ones presented here. The mistake should not alter the overall conclusions of Paper I as the den was situated 810 m a.s.l, and differences between arctic and red fox den use increase when it is labelled correctly.

foxes breeding below the tree line, but mentions that arctic foxes hunted in the birch forests, which indicates that dens at relatively low altitudes were used. Arctic foxes were also trapped in low altitude dens. Despite this, only 12% of the arctic fox litters born in 1985-2001 were found in dens below the mean altitude of all dens (915 m a.s.l.) and the mean altitude of arctic fox breeding dens was 940 m a.s.l (Fig 4).

A positive relationship between den altitude and density of den openings indicates that dens at lower altitudes disrepair (Spearman's $r = 0.64$, $p < 0.001$). For example, one of the largest dens in Vindelfjällen (den area 800 m²) is situated 900 m a.s.l. It had at least 172 openings in the early 1900:s, but only 40 in 2000. It was inhabited by arctic foxes in 1911 (Zetterberg 1945), but it was only inhabited once (by red foxes) in 1985-2002. Red foxes used dens at lower altitudes, closer to the tree line, than arctic foxes (Paper I). Although they prefer

large dens, they therefore use dens with comparatively less openings than those used by arctic foxes at higher altitudes, which explain why their den use is more related to den area than den openings.

Thus, low altitude dens are rarely used by arctic foxes and they are collapsing, which indicates that the habitat preferences of arctic foxes have changed after the population crashed. Similar patterns of den use have been found in Norway, where radio tracking also has shown that arctic foxes use low altitude tundra less than expected in relation to availability, and that they avoid forested habitats (Østbye 1978, Landa et al. 1998, Linnell et al. 1999a). The retreat of arctic foxes to higher altitudes, and the fact that red foxes use former arctic fox dens at lower altitudes, support the hypothesis that interspecific competition with red foxes determines the distribution of arctic foxes.

Fox diets and virtual food niches

Spatial segregation between arctic and red foxes may be a consequence of different virtual niches rather than interference competition (Chirkova 1968, Linnell et al. 1999a). For example, Chirkova (1968) suggested that parallel changes in arctic and red fox distributions could be caused by changes in prey distributions, as arctic foxes had a strong preference for lemmings, while red foxes preferred voles.

Lemmings, field voles, birds and reindeer were the main constituents of both arctic and red fox diets in Vindelfjällen (Paper II, III). Lemmings were the dominating prey of arctic foxes, while field voles dominated red fox diets (Fig 5). Generally, lemmings occurred significantly more often in arctic fox scats than red fox scats, while field voles and birds occurred significantly more often in red fox scats.

Dens inhabited by arctic foxes were situated at higher altitudes than dens inhabited by red foxes (Paper I, III). For both species and for all years combined, occur-

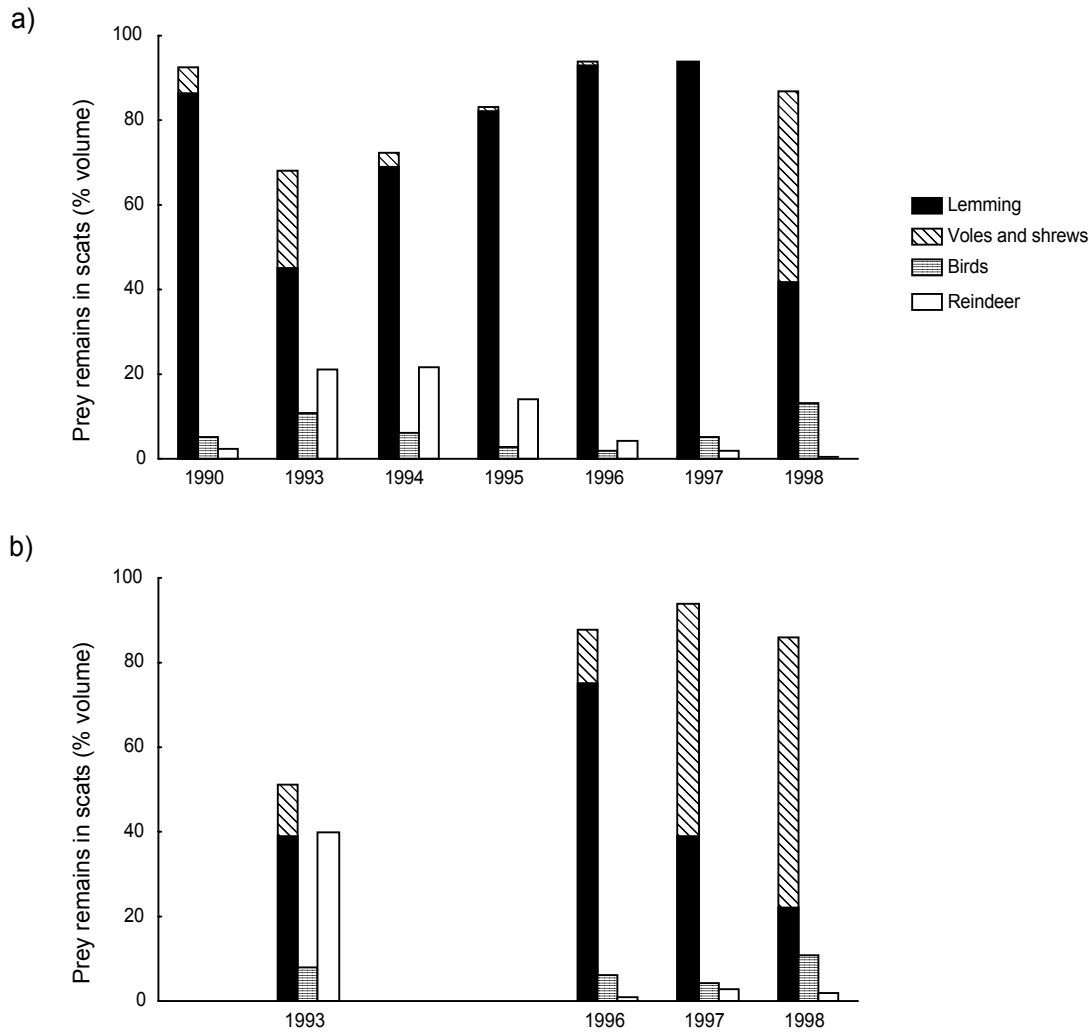


Fig. 5 Summer diets of arctic and red foxes in Vindelfjällen. Food niche overlap between arctic and red foxes was relatively constant in 1993, 1996 and 1998. In 1996, both arctic and red fox diets were dominated by lemmings, while they switched to voles (mainly field voles), birds and reindeer the other years (from Paper II and III).

rence of field voles and birds decreased significantly at higher altitudes, while the occurrence of lemmings tended to increase (Paper III). Productivity generally decreases with increasing altitude and vole densities are higher in productive habitats than in unproductive habitats (Oksanen and Oksanen 1992, Oksanen et al. 1999). There is also a negative relationship between bird abundance and altitude in our study area (Linda Axelsson, unpublished data). Hence, lemmings should typically make up a larger part of the prey base around arctic fox dens compared to red fox dens, while the relative availabilities of field voles and birds should

be higher around red fox dens. Frafjord (1995, 2000) found that lemmings occurred more frequently in arctic fox scats than in red fox scats at comparable altitudes. He suggested that arctic foxes might be less opportunistic than red foxes are, and that they therefore would be more dependent on lemmings also in the same habitat as red foxes. However, the large fluctuations in lemming and vole populations between years imply substantial changes in the prey base. Hence, comparisons between fox diets at similar altitudes should be done in the same year to be completely comparable,

which was not always the case in Frafjord's studies.

We took the effect of temporal changes in the prey base into account by comparing niche overlap between arctic and red foxes in different years. Despite large changes in arctic and red fox diets, food-niche overlap remained almost constant in 3 out of 4 years (75-80%; Fig. 5, Paper III). This indicated that arctic and red foxes switched to the same prey species as the composition of the prey base changed between years, and consequently, that they have the same search images, foraging habitats and diet preferences (Taylor 1984). One year (1997) deviated from this pattern with a relatively low overlap of 44%. Two red fox dens were included in the sample this year and their diets were very different (overlap 29%). Individual variation in red fox diets was consequently larger than that between arctic and red foxes in 1997.

Hence, we conclude that arctic and red foxes generally respond in a similar way to temporal changes in the prey base, and suggest that arctic and red foxes have the same virtual food niches (Paper III).

Specialists, generalists & numerical responses

Arctic foxes are often described as opportunists which readily change their diets to exploit the most profitable food resources (e.g. Garrott et al. 1983, Birks and Penford 1990, Stickney 1991, Frafjord 1993b, Bantle and Alisauskas 1998, Kapel 1999, Anthony et al. 2000, Dalerum and Angerbjörn 2000, Samelius and Alisauskas 2000, Eide et al. 2002b). This was supported by our studies (Paper II, III). Nevertheless, arctic foxes in inland habitats are often strongly dependent on rodent availability for successful reproduction. The number of arctic foxes that occupied dens in our study area was related to lemming availability in spring, i.e. during mating and gestation (Fig. 6) and there was a significant relationship between lemming

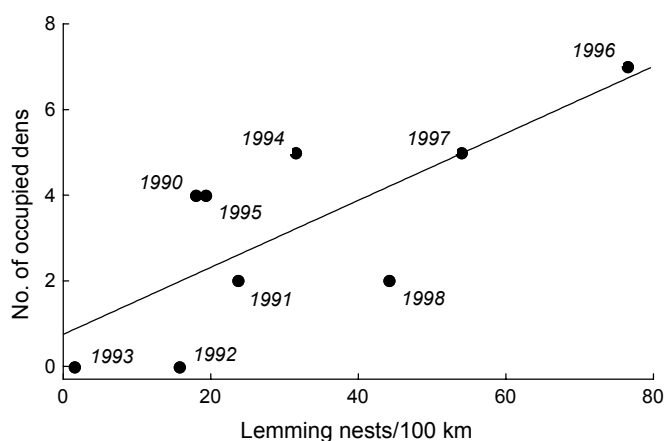


Fig 6 The relationship between lemming densities in the winter and the number of occupied dens in our study area in July ($p = 0,019$, $r^2 = 0.51$; from Paper I).

phase and number of arctic fox litters (Table 1). Other studies have also shown that the number of arctic fox litters and litter sizes are related to rodent abundance (Macpherson 1969, Angerbjörn et al. 1995, Kaikusalo and Angerbjörn 1995, Angerbjörn et al. 1999, Strand et al. 1999).

The boreal red fox population in Sweden preys heavily on field voles and responds numerically to fluctuations in the vole population (Englund 1965, Englund 1970, Angelstam et al. 1985). However, when red foxes establish in mountain tundra areas they readily prey on lemmings. In fact, both arctic and red foxes appeared to prefer lemmings to field voles, unless field voles were far more abundant than lemmings (Paper III). The reason may be that it is more profitable to hunt for lemmings, which are larger and use more open microhabitats than field voles (Heske and Steen 1993). Similarly, red foxes in boreal forests consume more field voles than *Clethrionomys spp.*, although the latter are more abundant. It may be easier and more profitable to hunt field voles than *Clethrionomys spp.* as the latter live in protective shrubs, while field voles move relatively slow and live in more open habitats (Englund 1965).

As red foxes in mountain tundra habitat prey on lemmings, what determines red fox

Table 1 Degree of crosscorrelation between boreal red foxes, tundra red foxes, arctic foxes and field voles/lemmings. The highest correlation coefficient (r) and the corresponding timelag of the foxes are shown for each fox-rodent pair. Significant r -values are bold.

		Boreal field vole (1972–1986)	Boreal field vole (1987–2001)	Tundra lemming (1990–2001)
Boreal red fox	r	0.67	-0.73	0.45
	timelag	0	1	4
	n	15	14	11
Tundra red fox	r		-0.68	0.52
	timelag		1	4
	n		15	12
Arctic fox	r	0.66	-0.44	0.78
	timelag	4	1	0
	n	13	15	12

numbers? A comparison of red fox abundance with (mountain tundra) lemming phase and (boreal) field vole abundance indicated no relationship between lemming phase and the number of red foxes breeding in mountain tundra habitat. Instead, red fox numbers both in mountain tundra and boreal habitats were significantly related to field vole abundance in boreal forests (Table 1, Fig. 7). Thus, different factors determine arctic and red fox abundance in mountain tundra habitat, but the species use the prey base in similar opportunistic manners.

The specialist-generalist concepts are used with two different meanings. Sometimes, they are regarded as immutable, internal characteristic of a species, which implies that a specialist does not switch to other types of prey even when they are readily available. At other times, they are used to describe the functions of predators in specific communities (Reid et al. 1997, Wiklund et al. 1999). Either way, specialists have more pronounced numerical responses to one particular prey species than generalists do, as they cannot fully compensate for declines in that prey by switching to other types of prey (Andersson and Erlinge 1977). Species that are immutably specialised could be described as "virtual specialists", which function as specialists in all environments. An "actual specialist" could also be a "virtual generalist", an opportunist forced into a specialist strategy by a limited prey base. Such species would change strategy and become "actual generalists" in environments with higher

biodiversity.

The red fox is regarded as a generalist (e.g. Englund 1965, Ferrari and Weber 1995, O'Mahony et al. 1999). However, red foxes in southern Sweden have more diversified diets than those in northern Sweden (Englund 1965, Lindström 1982). Red fox populations are also relatively stable in the south and there is no direct relationship between changes in the abundance of any particular prey species and reproduction. On the contrary, northern red fox populations are

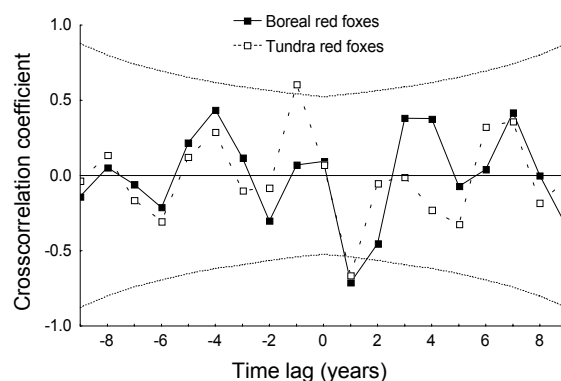


Fig. 7 Correlograms between boreal field vole populations and red fox populations in different habitats in 1987-2001. Both fox populations were significantly correlated with the field vole populations, with a time lag of one year (see Table 1). Data on field vole abundance (no trapped voles/100 trapnights in spring in Västerbotten) was available from the Swedish Environmental Protection Agency (http://www.eg.umu.se/personal/hornfeldt_birger/). Estimated number of red foxes shot in Västerbotten (Swedish Sportsmen's Association 1960-2001) was used as an index of boreal red fox population size, and number of red fox litters in the core area as an index of the number of red foxes in tundra habitat.

food regulated and fluctuate in relation to the vole cycle (Englund 1970). In a transition zone between northern and southern populations, red foxes are food regulated in years of low food availability and socially regulated when vole densities are increasing or high (Lindström 1989). Thus, there appears to be a south-north gradient in the feeding strategies of red foxes. Continuing along the gradient of decreasing productivity from boreal forests to low-production mountain tundra, red foxes should have progressively less varied diets. Thus, red foxes in mountain tundra and boreal habitat can be regarded as actual field vole specialists relative to red fox populations in southern Sweden.

The arctic fox uses a specialist strategy for feeding and reproduction in inland areas and a generalist strategy in coastal areas where there are more types of prey and availability is more stable (e.g. Hersteinsson and Macdonald 1996, Tannerfeldt and Angerbjörn 1998, Dalerum and Angerbjörn 2000). Inland arctic foxes, including the population in Vindelfjällen, function as actual specialists on lemmings as reproduction suffers when lemming availability decreases. Their opportunistic behaviour indicates that they exploit all available resources, but alternative prey is insufficient and does not allow for successful reproduction. Nevertheless, using these resources may facilitate survival of adult foxes during lemming lows, and when lemming popula-

tions start to increase, they respond by producing large numbers of cubs. Some cubs will survive long enough to exploit the next lemming peak and the population will be viable despite drastic fluctuations in population size (Tannerfeldt and Angerbjörn 1996). Thus, the arctic fox is an opportunistic specialist stuck in a world of lemmings (Paper II).

Interference competition

Prey is generally more abundant at low altitudes in mountain tundra habitat. However, both radio-tracking of arctic foxes and patterns of den use indicate that arctic foxes rarely use these areas (Paper I, Landa et al. 1998, Linnell et al. 1999a). This behaviour differs from that in other environments, such as Svalbard, where arctic foxes prefer productive habitats to barren areas (Jepsen et al. 2002). It also differs from previous behaviour in Sweden, as arctic foxes used to hunt also in the birch forests before the population decline (Zetterberg 1945). Arctic and red foxes have the same virtual food niches and they should consequently compete for territories in low altitude areas where prey is most abundant. Observations of encounters between wild arctic and red foxes show that arctic foxes are inferior to red foxes and they avoid close contact when possible (Schamel and Tracy 1986, Frafjord et al. 1989).

We tested if patterns of den use by arctic foxes indicated small-scale patterns of avoidance of red foxes. We found that arctic foxes used dens for breeding more often in the absence of red foxes, than when red foxes were breeding within an 8 km distance. Actually, only three arctic fox litters were born within this distance from red foxes. In two of these cases, arctic fox cubs were killed by red foxes, whereupon the litters were moved to secondary dens, farther from the dens inhabited by red foxes (Fig. 8, Paper IV).

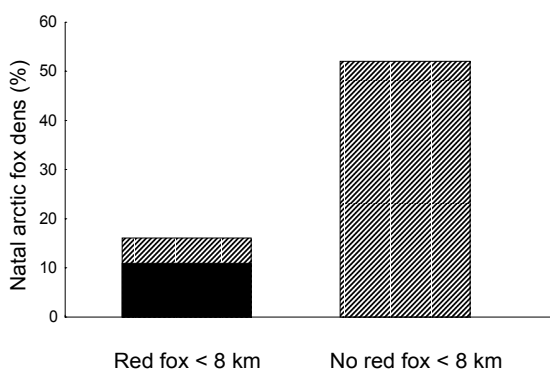


Fig. 8 Arctic fox breeding rate in relation to whether there were reproducing red foxes in the vicinity (within 8 km) or not. Black denotes that there was red fox predation on arctic fox cubs (from Paper IV).

The fact that arctic foxes directly avoid breeding close to red foxes implies that red foxes can affect arctic fox den preferences and distribution patterns. Increased interspecific competition with an expanding red fox population, through territorial and encounter competition (Schoener 1983), may therefore explain why the distribution of the arctic fox in Fennoscandia has shifted and the arctic fox has retreated to higher altitudes. This is similar to the relation between red foxes and coyotes in North America, where interspecific territoriality and predation suppress red fox populations and force red foxes to retreat to coyote territory borders (Sargeant et al. 1987, Harrison et al. 1989, Sargeant and Allen 1989).

It has been suggested that size differences between similar carnivores could lead to coexistence (Rosenzweig 1966). However, this probably requires larger differences in size and food niche than those between arctic and red foxes. For example, despite high mortalities from coyote predation, kit and swift foxes seem able to coexist with coyotes by having a somewhat different food niche and by using dens for protection (White et al. 1994, Kitchen et al. 1999). Interactions between predators of very different sizes and/or niche requirements, as in the kit/swift fox-coyote case, may be similar to those between predators and herbivore prey. Predators would then be able to co-exist as long as there is no hyperpredation on the “predator prey” species. The latter may occur if alternative prey sustain such large top-predator populations that predation pressure on the “predator prey” becomes extremely high (Roemer et al. 2001). As predator species become more similar in size and niche requirements, interactions between them will also involve an increasing amount of competition. In the end, interference competition over territories could have a large impact on the inferior species, which would have little or no habitat left at its disposal.

Population effects

Chirkova (1970) and Linnell et al. (1999) argued that the presence of red foxes could not have a large impact on arctic fox populations, since red fox densities are low in the mountain tundra and there are many vacant dens. However, we have shown that one reproducing red fox can exclude arctic foxes from a relatively large area containing many dens (Paper IV). Thus, red fox reproduction in mountain tundra dens decrease the amount of habitat available to arctic foxes. Such reductions in potential habitat may have long-term consequences for the arctic fox population.

We simulated arctic and red fox population dynamics in the Vindelfjällen area for 15 years, using a spatially explicit population model which incorporated arctic fox avoidance of dens located less than 8 km from dens inhabited by red foxes (Paper V). Lemming and vole population phases during the simulated time period corresponded to those observed in Vindelfjällen in 1986-2000. There was an increasing trend in modelled arctic fox population under allopatric conditions, but the population decreased when interference competition with red foxes was included in the model (Fig. 9). In the latter case, the model recreated the observed population dynamics of arctic foxes in Vindelfjällen relatively well (Fig. 10, Paper V). Thus, these results indicate that a relatively small number of red foxes could have a large impact on the arctic fox population.

Modelled numbers of red foxes reproducing in dens above the tree line was similar to that in the core area in Vindelfjällen, i.e. not exceeding two occupied dens per year (Paper V). It may seem strange that a small numbers of red foxes could have such drastic effect on the arctic fox population in an area encompassing 450 km² and almost 30 dens. However, if two red fox dens would be “strategically” located in the core area, in the central parts of the eastern and western core

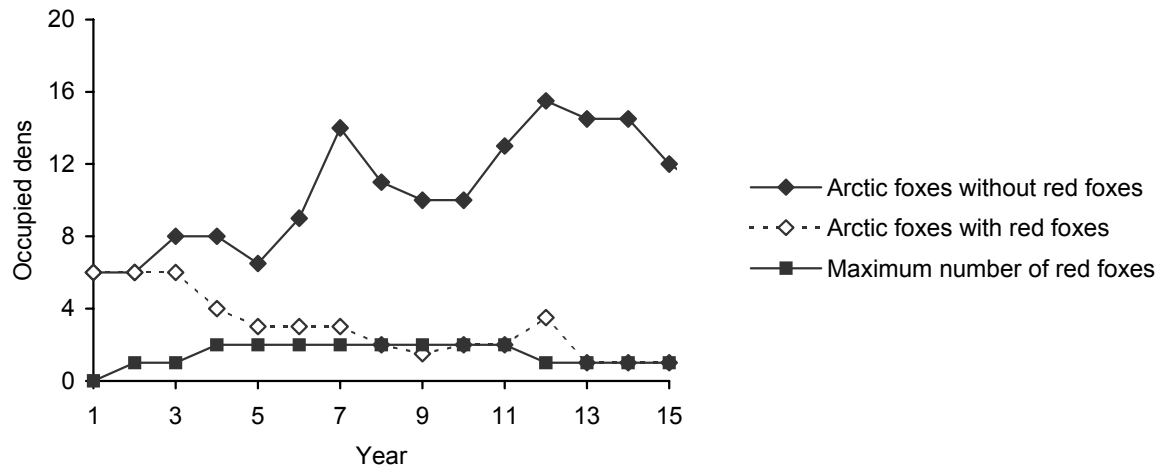


Fig. 9 The simulated effect of red fox competition on arctic fox den occupancy (from Paper V).

area respectively, only two dens would be situated farther than 8 km from either of the red fox dens. Even limited red fox presence may therefore exclude arctic foxes from large parts of their habitat and in that case, arctic foxes would no longer be able to respond to increased lemming availability by increased establishment and reproduction.

Sterilised red foxes were successfully used as biological control agents for arctic fox populations on two islands (Bailey 1992). Arctic foxes were still present on the islands six months after red foxes were introduced, indicating that direct killings of adult arctic foxes were rare, but all arctic foxes disappeared in the following years while red foxes remained. Possibly, the arctic foxes were excluded from the best dens and feeding beaches. In combination with predation on arctic fox cubs, this may have led to their extinction (Bailey 1992). In Norway, the mountain area with the largest and most stable arctic fox population also appears to have the least red fox activity (Frafjord 2003). These examples demonstrate the importance of “competition refuges” for inferior competitors (Durant 1998). Then, could high altitude dens function as competition refuges for arctic foxes in Fennoscandia?

The Swedish arctic fox population decreased from an estimated 180 breeding adults (90 litters) during the lemming peak in 1982, to a total of 18 breeding adults (9 litters) during the lemming peak in 2001 (Angerbjörn et al. 2002). The absence of lemming peaks has therefore been considered as the most acute problem for the arctic fox population. Food shortage has a negative effect on the number of foxes that establish and try to reproduce, litter sizes and juvenile survival in summer (Angerbjörn et al. 1991, Tannerfeldt et al. 1994, Angerbjörn et al. 1995, Paper II). The declining population trend and our model results (Paper V) indicate that high altitude areas were of too low quality to function as competition refuges for Swedish arctic foxes after 1982.

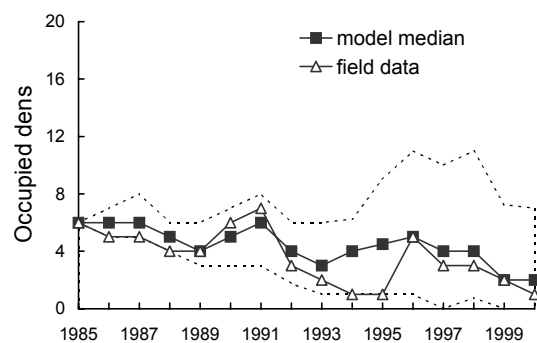


Fig. 10 A comparison between den occupancy in the observed arctic fox population and the predictions of the model. The dotted lines indicate the lower and upper quartiles (from Paper V).

On the contrary, the arctic fox population was relatively small during the period with lemming peaks in 1960-1982, but peak population densities appear to have been relatively stable (Angerbjörn et al. 1995). The higher amplitude of the lemming cycle should have had limited effect on the red fox population as red fox presence in mountain tundra habitat primarily depends on the status of boreal vole populations. Hence, provided that red fox presence in mountain tundra habitat has been relatively constant since 1960, the impact of red fox competition in 1960-1982 may have been ameliorated by two factors:

- 1) A combination of low lemming availability and red fox presence might refrain arctic foxes from establishment in otherwise suitable habitat, while high lemming abundances may increase overall habitat quality to acceptable levels. Arctic foxes have overlapping home ranges in habitats of high productivity, but are strictly territorial in habitats of low quality (Eide et al. 2002a). Interspecific overlap might be explained by arctic foxes paying the cost of predation by using dens close to red foxes during lemming peak years, since the alternative may be not to breed at all.
- 2) A lemming cycle of normal amplitude may increase habitat quality at high altitudes. Hence, arctic foxes in high altitude dens might have had more and larger litters before 1982.

Thus, it is possible that the total reproductive output of arctic foxes, despite red fox competition, was higher when lemming populations peaked regularly. This might have kept the arctic fox population from declining before 1982. Under these circumstances, high altitude areas might have functioned as competition refuges for a small arctic fox population.

CONSERVATION IMPLICATIONS

The arctic fox in Fennoscandia is endangered and the remaining population is fragmented (Angerbjörn et al. 2003b). The low population size is in itself a threat since small, isolated populations are more likely to go extinct (Loison et al. 2001). There has probably been some gene flow between the Fennoscandian population and the large Siberian population in the 1900's, but there is a risk of inbreeding in the small Fennoscandian population (Dalén et al. 2002). Conservation biology is divided into two major fields of research, the small-population paradigm and the declining-population paradigm. The former deals with the persistence of small populations, such as problems related to inbreeding, and the latter with reasons why populations decline (Caughley 1994). However, the ultimate cause of an extinction is usually that the habitat is lost or altered, and problems concerning small populations come into play only during the last generations when a population already is doomed (Thomas 1994). To turn a declining population trend, conservation actions to decrease inbreeding may be necessary, but it is also vital to look beyond these and take measures to restore habitat.

The results of this thesis indicate that interference competition with red foxes has hampered a recovery of the arctic fox population after the initial population decline. Competitive exclusion by red foxes has caused a substantial reduction in arctic fox habitat. Further, red foxes have taken over the most productive areas and remaining arctic fox habitat is of such low quality that it is uncertain whether it can maintain even a small arctic fox population.

In 1998-2002, there was a joint Swedish-Finnish conservation project (SEFALO) to preserve the arctic fox. The aim was to increase population size through supplemental feeding and red fox control. Red fox control, i.e. culling of red foxes in important arctic fox habitats, was intended to facilitate

establishment of arctic foxes and decrease predation on arctic fox cubs. Supplemental feeding aimed to increase establishment and lead to larger litter sizes and higher survival of cubs (Angerbjörn et al. 2002).

In Vindelfjällen, we tried to perform red fox control by hunting at carrion, but the method did not succeed (Paper IV). Instead, rangers began hunting from snow mobiles, which is more efficient, in the county of Jämtland in 2001. They selected a relatively small area of mountain tundra and aimed to keep it free from red foxes. Snow-tracking in spring 2002 indicated that there were fewer red foxes within the hunting area than outside it. There were also fewer red foxes than in Vindelfjällen. There were only four arctic fox litters in Sweden the following summer, but all of them were found within the red fox control area in Jämtland (Angerbjörn et al. 2002). Comparisons with previous den preferences of arctic foxes in Jämtland indicate that the arctic foxes selected dens within the red fox control area rather than previously high-ranked dens (Sverker Dalén, unpublished data). The lemming population peak in 2001 extended through winter 2002, but crashed in late spring. Food availability was consequently low in summer and the arctic fox cubs appeared to be highly dependent on supplemental feeding. However, establishment seemed to have been favoured by red fox control, as feeding did not begin until the dens had become inhabited.

Six dens in Vindelfjällen were inhabited by arctic foxes in spring 2002. In summer, all but one den was abandoned and no arctic foxes were born. Red foxes were observed visiting two of the abandoned dens and a third den was situated close to a den with a red fox litter. We found red fox litters in six arctic fox dens in our study area. Thus, red fox competition probably contributed to the complete reproductive failure of the arctic foxes in Vindelfjällen (Angerbjörn et al. 2002).

The arctic fox was one of the earliest post-glacial colonisers of Fennoscandia. The

increase in the red fox population is likely to be, by large, an effect of human interventions; the green house effect might have caused a warming of the climate, hunting has led to a decrease in populations of large predators, and clear-cutting of forest favoured the field vole and thus indirectly the red fox. In the long run, the future of the Fennoscandian arctic fox population may depend on human activities also outside the mountain tundra.

In a shorter perspective, the relative success of the conservation efforts in Jämtland indicates that it is possible to reverse the declining trend in the arctic fox population. An extensive conservation programme can therefore be used as a temporary measure to overcome the most acute situation. If the lemming peak in 2001 was the first sign that we are entering a new period of regular lemming peaks, we may have a fair chance to, at least, get back to the relatively stable situation we had in 1960-1980.

Perhaps we owe the arctic fox that chance.

CONCLUSIONS

The distribution of the Fennoscandian arctic fox population changed in the 20th century, parallel to an increase in the red fox population. Arctic and red foxes have similar virtual food niches and they should therefore compete for the same territories. Arctic foxes are inferior to red foxes in direct conflicts, and they are consequently ousted from the relatively productive low altitudes areas preferred by red foxes. There were regular lemming peaks in 1960-1982 and high altitude habitats may then have functioned as competition refuges for a small arctic fox population. However, high altitude habitat is not productive enough to support a viable arctic fox population in the absence of lemming peaks, such as the period between 1983 and 2000. Under such circumstances,

the arctic fox might not have a realised niche in Sweden and the population was very close to extinction in spring 2001. In the summer of 2001, the mountain tundra experienced its first lemming peak in almost 20 years and 91 arctic fox cubs were born in Sweden. This has given the arctic fox population some breathing space, but the situation is still grave and the Fennoscandian arctic fox might go extinct within the near future. However, experience from SEFALO, a Swedish-Finnish project to preserve the arctic fox, indicates that a combination of red fox control and feeding of arctic foxes may improve the situation.

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Direkt konkurrens mellan fjällräv och rödräv

För 150 år sedan var fjällräven *Alopex lagopus* en vanlig syn i den svenska fjällkedjan, men mot slutet av 1800-talet sköt pälpriserna i höjden. En omfattande jakt följde och tusentals fjällrävar dödades. I mitten av 1920-talet fanns bara enstaka fjällrävar kvar i Jämtlands och Västerbottens läns fjälltrakter och i Norrbotten var stammen på tillbakagång. Fjällräven betraktades som en viktig resurs för den ofta fattiga fjällbefolkningen och den fridlystes redan 1928 i hopp om att stammen skulle tillväxa och med tiden tåla en viss beskattning. Idag finns det dock bara ett 70-tal fjällrävar kvar i hela fjällkedjan. Det ska jämföras med uppskattningsvis 4000 innan nedgången. I den här avhandlingen har jag undersökt hur fjällrävar påverkas av konkurrens från de större rödrävarna som ökade kraftigt i antal mellan 1930 och 1960. Jag diskuterar också hur detta kan ha bidragit till att den förväntade återhämtningen uteblev.

Konkurrens: När och Hur

Individer som använder samma resurs, t ex en viss sorts föda eller boplats, konkurrerar när tillgången på resursen är begränsad. Ibland kan de konkurrera *indirekt* utan att ha någon kontakt med varandra eller ens veta om varandras existens. Det kan till exempel vara fallet om en individ äter upp en bit föda så att den inte kan ätas av nästa individ som kommer till platsen där födan fanns. *Direkt konkurrens* innebär istället att individer slåss om resurser eller till och med dödar sina konkurrenter. De flesta individer tycks dock ha en ganska god uppfattning om när de riskerar att förlora en konflikt och de ger sig inte nödvändigtvis in i det ena slagsmålet efter det andra. De kan istället välja att undvika kontakt med starkare konkurrenter genom att äta något annat än den föda

konkurrenten föredrar eller genom att välja en boplats någon annanstans. Detta undvikande beteende brukar också betraktas som en form av direkt konkurrens, eftersom den starkare konkurrentens närvaro påverkar den svagares beteende och resursutnyttjande.

I direkt konkurrens vinner stora individer oftast över små, eftersom de är starkare. Om individer av olika art konkurrerar och det råder en generell storleksskillnad mellan arterna, kommer därför individer av den större arten klara sig bäst. Det kan leda till att individer av den mindre arten inte får tillgång till de resurser de behöver. Mellanartskonkurrens mellan enskilda individer kan därigenom leda till att den mindre artens utbredningsmönster minskar och att antalet individer minskar.

Konkurrerar fjällräv och rödräv?

Fjällräven lever i tundraområden i Sibirien, norra Kanada och Alaska, på Grönland, Island och Svalbard samt i den Skandinaviska fjällkedjan. Den är väl anpassad för ett liv i karga miljöer. En vuxen fjällräv väger bara 3-4 kg eller ungefär lika mycket som en liten katt. Det innebär att den behöver jämförelsevis lite mat för att överleva. Dessutom är dess päls den varmaste bland däggdjuren och den har inga svårigheter att hålla sig varm ens då temperaturen kryper ner mot -40° . Rödräven är större än fjällräven och den är inte lika väl anpassad till kallt klimat. Den har därför en sydligare gräns för sin utbredning. Samtidigt innebär rödrävens större storlek att den kan vinna över fjällräven i direkta närkamper om lyor och revir och det har föreslagits att fjällrävens utbredning ner i varmare trakter begränsas av konkurrens med rödräven.

När den svenska rödrävsstammen ökade under 1930-1960-talen så ökade också antalet rödrävar på kalfjället. Norska forskare har tidigare visat att fjällrävens utbredningsområde förändrades under samma tid, men de påpekade att dessa samtida förändringar i

fjällrävens och rödrävens utbredningsmönster också skulle kunna bero på andra förändringar i miljön. Om fjällrävar och rödrävar till exempel föredrar olika bytesdjur och bytesdjurens utbredning förändrats, så skulle rävarna kunna följa sina bytesdjur till andra områden snarare än att konkurrera ut varandra.

För att ta reda på om fjällrävar och rödrävar faktiskt konkurrerar så undersökte jag vilka delar av kalfjället de använder (Artikel I), samt vad de äter (Artikel II, III). Om fjällrävar och rödrävar äter samma föda men inte finns i samma områden, så kan det tyda på att rödrävarna konkurrerar ut fjällrävarna från vissa områden. Om fjällrävar och rödrävar istället är specialiserade på olika slags föda så kan det tyda på att de väljer att leva i olika områden av andra skäl.

Jag utförde undersökningarna i samarbete med andra forskare inom Projekt Fjällräv, ett forskningsprojekt som pågått sedan 1985 i syfte att studera fjällrävens ekologi och beteende i Vindelfjällens naturreservat. Vi hade därigenom tillgång till närmare 20 års inventeringsdata, d v s uppgifter om när olika lyor varit bebodda av fjällräv eller rödräv. Genom att närmare analysera uppgifterna kunde vi få en uppfattning om vilka kalfjällsmiljöer som användes av fjällräv och rödräv, och genom att analysera spillning som vi samlat in på bebodda lyor så kunde vi undersöka om de föredrog olika sorters bytesdjur.

Både fjällräv och rödräv gräver sina lyor i sandkullar (åsar), men fjällrävar har den egenheten att de skapar mycket stora lyor. De tar över lyor som blivit lediga och fortsätter att bättra på dem och hålla dem i skick. De gödslar samtidigt lyorna med sin spillning och bytesrester. Vegetationen på typiska fjällrävslyor är därför mycket frodig och skiljer sig markant från de omgivande hedmarkerna. De största lyorna kan synas på flera kilometers håll och de lyor vi har i Vindelfjällen idag är desamma som användes av fjällräv kring förra sekelskiftet. Fjällrävslyornas utbredning visar därför ungefär

vilken utbredning fjällrävarna hade på den tiden. Rödrävar gräver mindre lyor med bara några få ingångar, men de kan ta över fjällrävslyor och använda dem istället.

I vårt studieområde fanns 77 fjällrävslyor. Den genomsnittliga lyan täckte 277 m² och hade 44 öppningar, men de största lyorna var ungefär 4 gånger så stora med över 100 öppningar. Det fanns även ett antal rödrävslyor, men nästan alla rödrävar som hade valpar bodde i fjällrävslyor. Både fjällrävar och rödrävar föredrog de stora fjällrävslyorna framför små, men fjällrävarna använde lyor som låg högre upp på kalfjället och längre från trädgränsen än vad rödrävarna gjorde. Detta trots att det var gott om stora fjällrävslyor i de lägre liggande områdena. Våra resultat tyder därmed på att fjällräven i princip slutat att använda lågt liggande fjällområden, vilket också stöder resultaten från de norska studierna.

Dietstudierna visade att fjällräv och rödräv åt samma sorts föda, framför allt fjälllämmel, åkersork, fågel och ren. I genomsnitt åt rödrävarna mer sork och fågel än vad fjällrävarna gjorde. Det berodde troligen på att rödrävarna bodde och jagade i lägre liggande områden där tillgången på sork och fågel var relativt god. När tillgången på olika byten förändrades från sommar till sommar, så reagerade nämligen fjällrävarna och rödrävarna på samma sätt. Somrar då det var gott om lämmel åt de mer lämmel, men

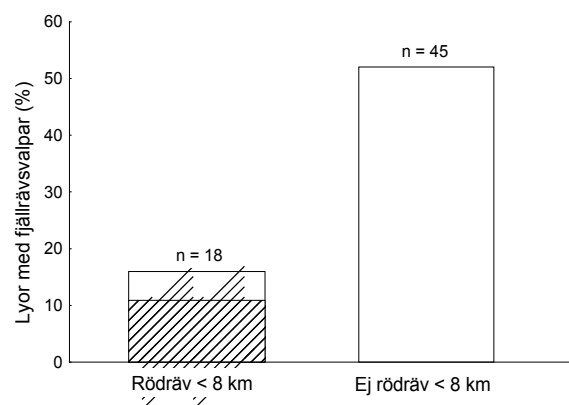


Fig 1 Andelen bra fjällrävslyor som varit bebodda av fjällräv med valpar beroende på om det funnits rödräv i närheten eller ej. Streckade områden visar andelen kullar där valpar blivit dödade av rödräv.

då lämmeltillgången minskade åt de mer sork och fågel. Det här tyder på att det inte fanns någon egentlig skillnad mellan vilka bytesdjur fjällrävar och rödrävar föredrog. Förändringen i fjällrävens utbredningsmönster kan därmed inte förklaras med att fjällräv och rödräv jagar olika slags byten. Istället borde de konkurrera om lyorna i de lågt liggande fjällområdena eftersom tillgången på bytesdjur är störst där.

Hur konkurrerar fjällräv och rödräv?

Som tidigare nämnts så är rödräven större än fjällräven och det skulle kunna få till följd att fjällrävar undviker områden där de riskerar att möta en rödräv.

Vi undersökte hur ofta de 7 bästa fjällrävslyorna i Vindelfjällen var bebodda under en 9-årsperiod (dvs under 63 "lyår") beroende på om det fanns en lya med rödrävvalpar i närheten eller ej (Artikel IV). 45 av lyåren fanns ingen rödrävskull i närheten och vid drygt hälften av dessa tillfällen föddes fjällrävsvalpar i lyorna (52%). 18 lyår fanns det rödrävskullar i närheten och vid dessa tillfällen föddes bara 3 fjällrävskullar i lyorna (17%). Vid 2 av dessa 3 tillfällen dödades dessutom fjällrävsvalpar av rödräv under sommaren, varpå de vuxna fjällrävarna flyttade resten av valparna till en ny lya längre bort från rödrävslan (Fig. 1). Fjällrävarna tycktes alltså undvika att använda lyor i närheten av rödrävar och rödräv kan därmed påverka fjällrävens utbredningsmönster.

Beteendemönster liknande dem vi fann hos fjällräv och rödräv har också observerats hos andra rovdjursarter som konkurrerar med varandra. Till exempel har man sett att prärievargar i Nordamerika undviker de större vargarna, samt att rödräv undviker lodjur och prärievarg. I områden med både varg och prärievarg så håller sig prärievargen undan och den använder framför allt områden i utkanterna av vargarnas revir. I områden med både prärievarg och rödräv så betar sig rödräven på samma sätt gentemot den större

prärievargen. När vargen närapå utrotades i Nordamerika under 1900-talet så ökade antalet prärievargar kraftigt, samtidigt som rödrävarna minskade i antal. I områden där vargen senare har återintroducerats så har antalet prärievargar minskat igen.

Hur påverkas fjällrävsstammen av konkurrensen?

Eftersom fjällräv undviker områden med rödräv så kan ett ökat antal rödrävar på kalfjället leda till att fjällrävarna får allt mindre områden att leva i. På sikt kan det påverka fjällrävsstammens storlek, på samma sätt som exempelvis prärievargsstammen påverkades negativt av konkurrens från varg. Vi ville undersöka hur stor denna effekt var på fjällrävsstammen. Vi konstruerade därför en datormodell där vi kunde simulera fjällrävsstammens utveckling under olika förhållanden (Artikel V).

Modellen var baserad på en karta över fjällrävslyorna i Vindelfjällen. Dessutom placerade vi ut en mängd rödrävslor i de kringliggande skogarna. I fjällrävslyorna placerade vi så många "fjällrävar" som det enligt våra inventeringsdata fanns där 1985 och i rödrävslorna i skogen placerade vi ut så många "rödrävar" som vi uppskattade att där fanns i mitten av 80-talet. Vi programmerade modellen så att varje "räv" skulle ha en viss sannolikhet att få valpar eller dö varje "år". Valparna skulle sedan, i början av varje år, sprida sig till andra lyor på kartan där de i sin tur skulle ha en viss sannolikhet att få egna valpar eller dö. Vi simulerade utvecklingen under 15 år. För varje år berodde sannolikheterna för en räva att få valpar eller dö på lämmel- och sorktillgången i Vindelfjällen under perioden 1986-2000. Vi jämförde därefter den simulerade fjällrävsstammens utveckling med den vilda fjällrävsstammen i Vindelfjällen under samma period. När vi enbart hade fjällrävar med i modellen så klarade sig den simulerade fjällrävsstammen bra. När vi dessutom

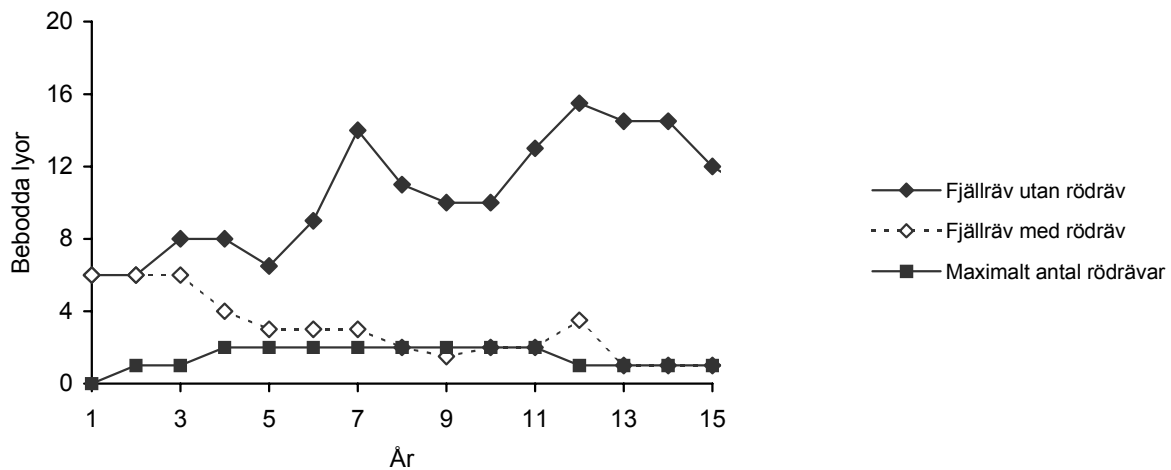


Fig. 2 Den simulerade utvecklingen för fjällrävsstammen (antal bebodda lyor). Om det inte fanns några rödrävar i modellen så tenderade fjällrävsstammen att öka, men om fjällrävarna konkurrerade med rödräv så minskade den istället. Den senare utvecklingen stämmer väl överens med den vi faktiskt observerat i Vindelfjällen 1986-2000.

inkluderade rödrävar och simulerade direkt konkurrens genom att hindra fjällrävarna från att använda lyor nära bebodda rödrävslyor, så gick det däremot sämre (Fig. 2). I det senare fallet var dessutom den simulerade fjällrävsstammens utveckling mycket lik den för de riktiga fjällrävarna i Vindelfjällen 1986-2000. Resultaten av modelleringarna tyder därför på att ett ganska litet antal rödrävar kan ha en betydande, negativ inverkan på fjällrävsstammen.

Att bevara fjällräven

Normalt är det mycket gott om lämmel i den svenska fjällkedjan ungefär vart fjärde år. Under dessa "lämmeltoppar" kan en enda fjällrävshona få upp till 16 valpar. Mellan topparna är det däremot ont om mat och de sämsta åren får fjällrävarna inga valpar alls. Mellan 1960 och 1982 återkom lämmeltopparna regelbundet och under toppåren på 1970-talet föddes ca 90 fjällrävskullar per topp. Mellan 1983 och 2000 uteblev däremot lämmeltopparna och antalet fjällrävar minskade stadigt. När det slutligen blev en ny lämmeltopp år 2001, så fanns det bara ett 30-tal vuxna fjällrävar kvar och det föddes endast 9 kullar. De uteblivna lämmeltopparna har därför betraktats som det mest akuta

hotet mot fjällrävsstammen. Resultaten från våra datorsimuleringar antyder dock att fjällräven kanske skulle ha klarat sig bättre under den här perioden om den inte samtidigt hade varit undanträngd från stora delar av sitt forna utbredningsområde.

Fjällräven fridlystes ungefär samtidigt som rödrävsstammen började öka. Under de följande 30 åren skedde en blygsam återhämtning av fjällrävsstammen i Jämtland och Västerbottens län, men samtidigt minskade fjällrävarnas utbredningsområde. Resultaten i den här avhandlingen tyder på att detta berodde på att fjällräven konkurrerades ut från lågt liggande fjällområden av rödräv. Kring 1960 stannade rödrävsstammens ökning av. Så länge lämmeltopparna återkom regelbundet så tycks de högt liggande fjällområdena, som fjällräven nu var begränsad till, ha försörjt en liten men ganska stabil fjällrävsstam. Då lämmeltopparna upphörde sjönk däremot kvaliteten på dessa områden så mycket att fjällrävsstammen började minska. Läget är nu mycket allvarligt och risken är stor att fjällräven dör ut.

Ett svensk-finskt samarbetsprojekt för att bevara fjällräven startades 1998 och pågick till 2002. De huvudsakliga åtgärderna var att minska konkurrensen mellan fjällräv och rödräv genom en utökad rödrävsjakt i viktiga fjällrävsområden, samt att stödutfodra fjäll-

rävorna vid bebodda lyor. Det var svårt att få rödrävsjakten att fungera effektivt, men det lyckades inom ett mindre område i Jämtlands län där utvalda naturbevakare fick tillstånd att skjuta rödräv från skoter. Jakten pågick 2001-2002 och sommaren 2002 föddes 4 fjällrävskullar inom jaktområdet, medan det inte föddes några fjällrävsvalpar alls i övriga svenska fjällområden. En jämförelse mellan fjällrävarnas val av lyor före respektive efter det att rödrävsjakten inleddes tyder på att fjällrävarna börjat rata tidigare populära lyor för att istället slå sig ner i lyor inom jaktområdet.

Jag drar slutsatsen att konkurrens från rödräv är ett allvarligt hot mot fjällrävsstammen i Sverige, men att det genom effektiva bevarandeåtgärder kan vara möjligt att förbättra situationen.

Tack!

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Bodil

