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Use of dens by red *Vulpes vulpes* and arctic *Alopex lagopus* foxes in alpine environments: Can inter-specific competition explain the non-recovery of Norwegian arctic fox populations?

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Following over-harvest in the early decades of the 20th century, the arctic fox *Alopex lagopus* has declined and failed to recover in Norway. Competition with the red fox *Vulpes vulpes* has frequently been suggested as a possible factor hindering arctic fox recovery. Between 1988 and 1997, a total of 213 former arctic fox dens in four alpine regions of Norway, i.e. Hardangervidda, Dovrefjell, Børgefjell and Dividalen, were checked at least once for occupation by red or arctic foxes. Of these 213 former arctic fox dens, 138 were unoccupied, and 32 and 43 were occupied by arctic and red foxes, respectively. In general, red foxes occupied dens situated at significantly lower altitudes than those occupied by arctic foxes, which supports present ideas of red fox/arctic fox coexistence. As arctic foxes tended to avoid dens at the lowest altitudes, it is possible that arctic foxes to some degree avoid the areas where red foxes are most abundant. This may have disproportionate effects, as the probability of reproduction in arctic fox dens was highest in dens at lower altitudes. Despite this, the large number of unoccupied dens indicates that dens are unlikely to be in limited supply. Therefore, neither our data, nor a review of published data and trapping records, support the hypothesis that inter-specific competition with the red fox is currently preventing arctic fox recovery in the Norwegian alpine environment.

Key words: Alopex lagopus, arctic fox, den, inter-specific competition, population decline, red fox, Vulpes vulpes

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Arctic fox *Alopex lagopus* populations declined rapidly in the early decades of the 20th century throughout Fennoscandia. Although historical harvest data are poor, contemporary commentators generally agreed that the decrease followed a period of high fur prices and state bounties on foxes, which led to very intensive harvest (Lönnberg 1927, Johnsen 1929, Høst 1935, Haglund & Nilsson 1977). By the late 1920s it was suspected that the arctic fox may have been close to extinction in many areas. As a result, the arctic fox was protected from hunting and trapping in 1928, 1930 and 1940 in Sweden, Norway and Finland, respectively. However, despite 68 years (1930-98) of protection in Norway there has been no recovery of the arctic fox populations (Hersteinsson, Angerbjörn, Frafjord & Kaikusalo 1989). In fact, the

trend appears to have been an even greater decline in distribution and density. Today, the arctic fox is found in very low numbers on only a few of the alpine plateaus which they once inhabited (Linnell, Strand, Loison, Solberg & Jordhøy 1999). A similar non-recovery has also been observed in Sweden and Finland (Hersteinsson et al. 1989, Angerbjörn, Tannerfeldt, Bjärvall, Ericson, From, & Norén 1995, Kaikusalo & Angerbjörn 1995).

Many hypotheses have been put forward as explanations for the non-recovery of the arctic fox, but one of the most frequently cited hypotheses is increased competition with the red fox *Vulpes vulpes* in alpine habitats (Skrobov 1960, Hersteinsson et al. 1989, Frafjord & Rofstad 1998). Although data are scarce, it is generally believed that red fox numbers have increased in alpine habitats during the 20th century. The expansion of the red fox has been hypothesised to be due to either a slight warming in climate which makes the alpine environment more productive, or to an increase in lowland red fox density (and therefore in the number of dispersing individuals) following changes in forestry and fox hunting practices. Many confirmed reports of red fox breeding in former arctic fox dens in Norwegian alpine environments exist; a finding which at least appears to strengthen the case against the red fox as a cause of arctic fox non-recovery (Østbye, Skar, Svalastog & Westby 1978).

Based on an energetic model and observed patterns of distribution of the two fox species in Canada, Hersteinsson & Macdonald (1982, 1992) developed a conceptual hypothesis explaining the distribution and interaction of the two species. Their hypothesis states that the northern (and altitudinal) limit of the red fox's distribution is determined by low prey availability, while the southern (and lower) limit of the arctic fox's distribution is determined by inter-specific competition with the red fox. To test their hypothesis we examined the relationship between red fox and arctic fox use of dens, based on the results of 10 years' monitoring of former arctic fox dens throughout the alpine areas of Norway. If the Hersteinsson & Macdonald (1992) hypothesis is correct we would predict that red foxes would occupy the lowest former arctic fox dens (Prediction 1). Accordingly, the remaining arctic foxes should only be found in the higher parts of their former distribution area (Prediction 2).

However, acceptance of the Hersteinsson & Macdonald hypothesis (1992) does not necessarily mean that the red fox is preventing the recovery of Norwegian arctic fox populations. For this to be the case, red foxes should either occupy so many dens that dens had become a limited resource, or interfere (through aggression or predation) with arctic foxes to such an extent that arctic foxes were prevented from occupying even those regions where red foxes do not den. If the first hypothesis (that den sites are limiting) is correct it would be predicted that most available den sites were in use by red foxes, or at least that few potential arctic fox home ranges could exist without including an active red fox den (Prediction 3). Although the second hypothesis is hard to test, if it were correct, we would expect some evidence in the literature that some carnivore species are able to totally exclude other carnivore species from large areas, even outside their reproductive range (Prediction 4). To evaluate this possibility, we reviewed the available literature on the subject. In addition we present some unpublished, turn-of-the-century, trapping records from one alpine area to shed light on the early development of red fox populations in the mountains of Norway.

Study sites and monitoring methods

In Norway, the alpine habitats where arctic foxes live are isolated plateaus, separated by forested valleys, and arctic foxes are always found above the treeline (Landa, Strand, Linnell & Skogland 1998). All these plateaus were once occupied by the arctic fox (Linnell et al. 1999). As arctic foxes commonly occupy large and conspicuous breeding dens for decades (Chesemore 1969, MacPherson 1969, Østbye et al. 1978, Smits, Smith & Slough 1988), their dens can be readily found and monitored. As these dens remain easily visible for many decades, even after they are no longer in use, we believe that the total sum of known dens presents an accurate description of the former distribution of the arctic fox. Many of the dens monitored in our study were originally described in the 1960s or even in the 1930s (Høst 1935, Østbye et al. 1978). For our study, we have used records of den occupation by either red foxes or arctic foxes collected during the last 10 years (1988-1997) in four regions which include a total of eight plateaus (Fig. 1). The Hardangervidda, Børgefjell and Dividalen areas are treated as separate regions, while the Snøhetta, Trollheimen, Knutshø, Forelhogna and Rondane plateaus are pooled into the Dovrefjell region. All records are from above the treeline.

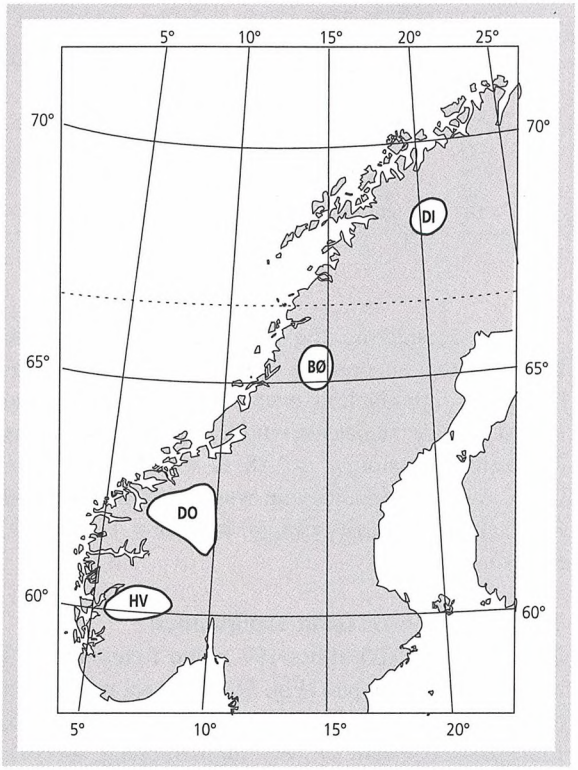

Figure 1. Location of the four Norwegian study regions (DI: Dividalen; BØ: Børgefjell; DO: Dovrefjell; HV: Hardangervidda) where arctic fox and red fox occupation of former arctic fox dens was studied during 1988-1997.

Most records of den occupation come from either our own field research on the Snøhetta plateau (Landa et al. 1998), from systematic records kept by mountain wardens, or from the dens which have been included in the Terrestrial Monitoring Program since 1993 (Directorate for Nature Management 1989, 1997, Linnell et al. 1999). The species of fox using each den was determined either from visual observation, the size of the holes (red foxes enlarge the holes of former arctic fox dens), or from the colour of hairs found in scats or snagged in the vegetation (Østbye, Gullestad & Skar 1976). Each den was categorised either as 'not in use', 'in use, but no breeding' or 'in use for breeding'. Because the location of the treeline varies throughout the length of Norway, and even has changed during the last century (Aas & Faarlund 1995), the altitude of each den was expressed as the vertical height (in metres) above the lowest known former arctic fox den within each of the four regions when pooling data.

One of the main problems in reconstructing the development of red and arctic fox populations in Norway has been the lack of species-specific hunting or trapping records. The only records available are government bounty payments, but they do not distinguish between the two species of fox before 1930, after which time the arctic fox was protected. Fortunately, we were able to obtain trapping records from one professional hunter. Between 1893 and 1956, Kristoffer Haugen (a resident of the municipality of Oppdal in the county of Sør-Trøndelag) trapped foxes each year in the Trollheimen area of south-central Norway. His diary lists the numbers of each species trapped during this period. As far as we know the entries in his diary make up the only species-specific trapping records for foxes from this period in Norway.

Results

Den occupation by red foxes and arctic foxes

In total, 215 dens were monitored at least once during the study period; of these 138 were never occupied by foxes of either species, 32 were occupied by arctic foxes, and 43 were occupied by red foxes at some time during the study period. Two more dens were occupied, but the fox species could not be determined. These latter two dens were excluded from all further analyses.

When including all regions in the same analysis, significant differences in the mean altitudes of the three categories of dens (used by red foxes, used by arctic foxes, not in use) were found (ANOVA, $F = 4.56$, $df = 2, 210$, $P = 0.011$). A Bonferroni post-hoc test identified the difference between arctic fox and red fox den altitudes as being significant (arctic fox dens were situated 84 m higher than red fox dens, $P = 0.009$). Arctic foxes also used dens situated at higher altitudes than the sum of those either unoccupied or used by red foxes (ANOVA, $F = 6.66$, $df = 1, 213$, $P = 0.011$). This confirms that arctic foxes are now confined to the upper portion of their former distribution area. Similarly, red foxes used dens that were situated lower than the sum of those either unoccupied or used by arctic foxes (ANOVA, $F = 4.3$, $df = 1, 213$, $P = 0.039$). This confirms that red foxes were mainly using those former arctic fox dens at the lower end of the distribution area of the arctic fox. Within Hardangervidda and Dovrefjell, there were significant differences in the mean altitudes of the three categories of dens ('used by red foxes', 'used by arctic foxes', 'not in use'; Table 1, Fig. 2) and a post-

Table 1. Altitude of unoccupied dens (not in use) and dens occupied by arctic foxes or red foxes in four regions of Norway. Statistics refer to an overall ANOVA and a post-hoc (PH) Bonferroni test of the difference between red foxes and arctic foxes.

	Not in use			Arctic fox			Red fox			Overall		PH
Region	m a.s.l.	se	N	m a.s.l.	se	N	m a.s.l.	se	N	F	P	P
Hardangervidda	1253	10	73	1507	41	3	1259	13	19	9.8	***	***
Dovrefjell	1168	23	51	1283	28	10	1088	17	20	6.5	**	**
Børgefjell	793	36	10	870	25	9	765	85	2	1.8	ns	ns
Dividalen	750	54	4	823	29	10	730	40	2	1.4	ns	ns

**P < 0.01, ***P < 0.001

hoc test further specified a significant difference between the altitude of dens used by red and arctic foxes. Although arctic foxes were found in dens at higher altitudes within both of the other two regions, this difference was not significant, possibly due to smaller sample sizes.

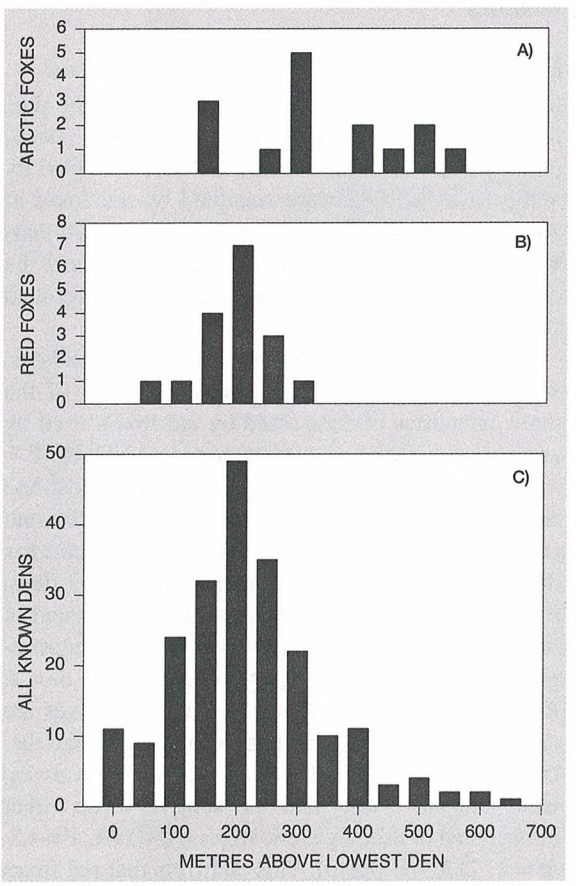

Figure 2. Altitude distribution in metres above the lowest former arctic fox den in which arctic foxes (A) and red foxes (B) have been reported to reproduce during the last 10 years and of all known dens (C) within each of the four Norwegian regions. Arctic foxes used the higher lying dens, but the vast majority of dens were not in use for reproduction by either species. Note the differing scales on the y-axes.

When considering the dens occupied by arctic foxes (all regions pooled), there was a higher probability that reproduction would occur in dens at the lowest altitude, rather than in dens at higher altitudes (Logistic regression, $\chi^2 = 7.18$, df = 1, P = 0.02, $R^2 = 0.27$). A similar relationship was not evident for red foxes (Logistic regression, $\chi^2 = 0$, df = 1, P = 0.9, $R^2 = 0$).

Trapping records from Trollheimen

Between 1893 and 1956, 107 arctic foxes and 172 red foxes were trapped (Fig. 3). The local population of arctic foxes appears to have gone extinct in 1916, following six years of very high trapping success. This corresponds with a period of high fur prices. There are no subsequent records of arctic foxes in the diaries either before or after protection in 1930 which implies that there was no recovery. Although there is an evident increase in the numbers of red foxes trapped after 1935 (in both the Trollheimen series and the records of bounty payments made for 'foxes' in Sør-Trøndelag as a whole), it seems unlikely that this could have influenced the extinction and immediate non-recovery of the arctic fox as it appears 20 years later. Furthermore, the magnitude of the increase in red fox numbers after 1935 is slight. Although trapping records often contain biases associated with trapping efforts, we are convinced that these records obtained from one man, operating within a constant area, and using similar methods throughout the period, provide an accurate illustration of the changes in fox abundance.

Discussion

Support for the Hersteinsson & Macdonald hypothesis

From the combined results of our study and earlier reports (Haglund & Nilsson 1977, Østbye et al. 1978) it is clear that red foxes presently occupy former arc-

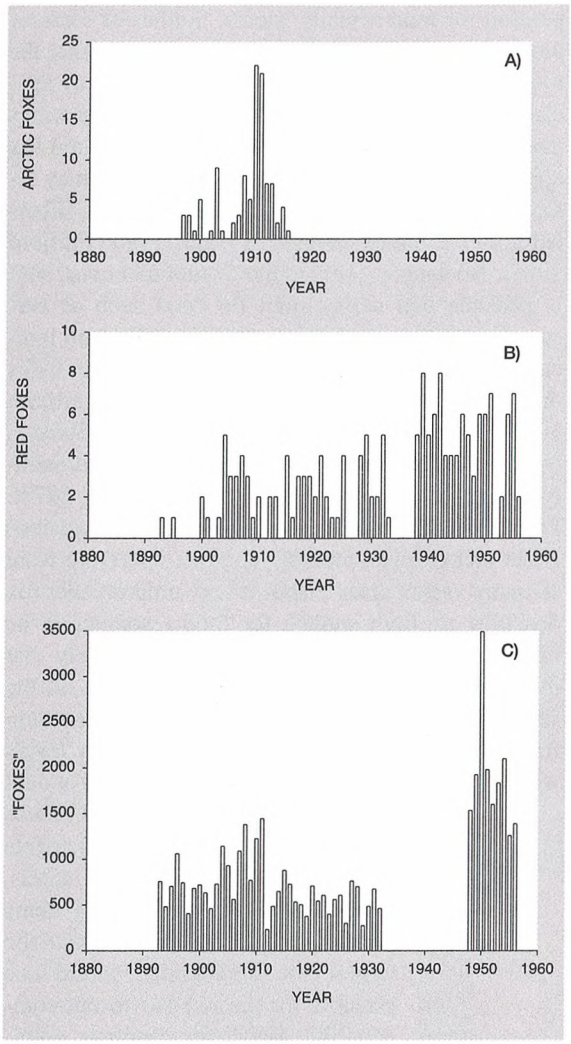

Figure 3. Records of arctic (A) and red (B) foxes trapped by Kristoffer Haugen in the Trollheimen area (part of the Dovrefjell region) between 1893 and 1956. Arctic foxes were protected in 1930 but had become locally extinct 14 years earlier. In his diary Kristoffer Haugen does not mention arctic foxes after 1916. The total number of foxes (before 1930 both red and arctic foxes, after 1930 only red foxes) for which bounties were paid in the surrounding county during the same period is also shown (C). The gap between 1933 and 1947 reflects a lack of records rather than no harvest.

tic fox dens in the alpine habitats of Norway. Our results also provide the first direct support for Hersteinsson & Macdonald's (1992) hypothesis based on European data. As predicted by Prediction 1 red foxes occupy former arctic fox dens at the lower end of their distribution area (see Fig. 2). As temperature is strongly associated with altitude, these dens should be associated with higher primary productivity and therefore higher prey availability. Earlier studies in Norway, Siberia and Alaska (Skrobov 1960, Chirkova 1968, Eberhardt 1977, Østbye et al. 1978) have also shown that red foxes tended to establish at lower altitudes, or in more productive habitats, than arctic foxes. This is consistent with Hersteinsson & Macdonald's conclusion that the red fox is less well adapted to extreme alpine (or arctic) environments, due to the high energetic requirements of their larger body size. Although this may appear to be contrary to expected seasonality/body size trends (e.g. Bergman's rule) it is not uncommon for smaller body sizes to be associated with extremely seasonal environments due to resource limitation. Examples include intra-specific variation in both reindeer/caribou *Rangifer tarandus* and arctic foxes (Frafjord 1993).

Although the arctic fox mainly occupied dens in the central and higher parts of its former distribution area (see Fig. 2), which supports Prediction 2, there was much overlap in the altitude use of the two fox species. In fact, more than half of the dens occupied by arctic foxes were within the range of altitudes used by the red fox, although there was no arctic fox use of dens at the very lowest end of the distribution area. In keeping with Hersteinsson & Macdonald (1992) this can be interpreted as evidence for avoidance of the lowest lying areas because of the greater occurrence of red foxes, although it is hard to distinguish between explanations based on inter-specific avoidance and those based on differential habitat selection. These two hypotheses are virtually impossible to separate, and indeed are not exclusive as red fox presence must be regarded as an autocorrelated habitat characteristic. However, as the now abandoned lowest areas were once arctic fox habitat, an explanation of the separation based purely on habitat selection would imply that some changes had occurred to the lower habitats, possibly due to changes in climate (Aas & Faarlund 1995, Beniston, Daz & Bradley 1997), although direct evidence for this is far from conclusive.

The extent of red fox occupation of former arctic fox dens

On the whole, these results provide evidence that red foxes may have reduced the possibility for arctic foxes of exploiting at least portions of the alpine environment. However, even if arctic foxes avoid the lowest lying den sites because of the presence of red foxes, it is difficult to understand how red foxes could be preventing at least partial recovery of the

arctic fox populations in the remaining areas. In order to have competition for a resource, the resource must be in limited supply (Putman 1994). Our data clearly show that the majority of former arctic fox dens are not used by either species - i.e. there are many vacant dens at both high and low altitudes. In addition, our data are very conservative as we regarded a den as belonging to a given species based on a single documented observation of its use. This implies that many of the dens that were used by red foxes only once, were actually available to arctic foxes in some previous and subsequent years. Therefore, the data do not support Prediction 3. Because of the large distances between active dens, there are very large areas, corresponding to the size of many potential territories (Landa et al. 1998), surrounding former dens where we were not able to document red fox denning activity (Fig. 4). In addition to many dens being vacant, we believe that there may be very many vacant territories with dens, where red foxes are not present, and which are potentially available for arctic foxes.

Potential competition for food

Even in areas of overlap it is unclear how much competition for food actually occurs. Studies of summer diet in Alaska, Canada and Norway indicate that the two fox species appear to favour different prey species. The arctic fox appears to eat more lemmings *Lemmus* sp. and *Dicrostonyx* sp. whereas the red fox appears to prefer *Microtus* sp. rodents which may indicate some degree of dietary niche separation (Eberhardt 1977, Smits, Slough & Yasui 1989, Frafjord 1995). No data on comparative winter diet exist, so it is possible that competition for food such as carcasses may be more intense. Studies in Finland indicate that supplemental winter feeding of arctic foxes only benefited red foxes (Kaikusalo & Angerbjörn 1995), whereas observations at carcasses in Sweden during winter revealed that supplemental food mainly benefited corvids (Haglund & Nilsson 1977). From this it is impossible to draw firm conclusions about diet overlap, although the fact that there were so many vacant areas makes it very unlikely that fox densities are high enough for food resources to be limiting at present, and therefore it is unlikely that the potential for competition for food exists on the scale of the mountain plateaus. Even if competition for food occurred to such an extent that prey levels were depressed, it is likely that arctic foxes would survive better than red foxes because of their lower energy requirements (Hersteinsson & Macdonald 1992). Only if large, defendable prey items such as reindeer carcasses formed the largest part of winter diet, would it be possible for the red fox to out-compete the arctic fox through dominance. Although reindeer are important in arctic fox diet, it is dispersed prey items like small rodents that make up the largest part of their diet, both during summer and winter (Strand, Linnell, Krogstad & Landa in press a) at all stages of the rodent cycle.

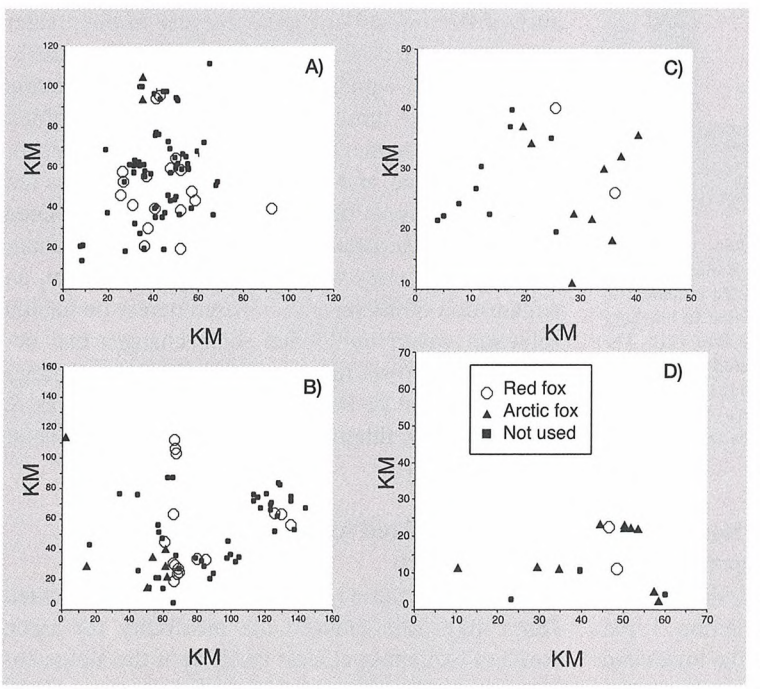

Figure 4. Distribution of dens formerly used by arctic foxes within the four mountain areas in Norway (A: Hardangervidda; B: Dovrefjell; C: Børgefjell; D: Dividalen). Dens are marked according to their present use as either in use by red foxes (○), in use by arctic foxes (▲), not in use by either species (■). Note the differing scale of the axes.

Aggressive interaction between arctic and red foxes

If dens and space are not in limited supply then by what mechanisms could the red fox possibly be preventing arctic fox recovery? As for most pairs of similar-sized canids (Johnson, Fuller & Franklin 1996) existing

data from other studies provide plenty of evidence that red foxes and arctic foxes interact directly (through aggression) in areas of sympatry, and that red foxes are clearly dominant. Reports from experiments carried out with both captive animals and in the field reveal that in most cases arctic foxes simply avoid direct encounters with red foxes (Rudzinski, Graves, Sargeant & Storm 1982, Schamel & Tracy 1986, Frafjord, Becker & Angerbjörn 1989). While this may involve occasional loss of prey items or displacement from a feeding site, encounters do not always lead to fighting, although cases of intra-guild predation (Polis, Myers & Holt 1989) of arctic foxes by red foxes have been documented (Frafjord et al. 1989, O. Strand & J.D.C. Linnell, unpubl. data). In a snow-tracking study in the Finse valley in the northern part of the Hardangervidda plateau, Pedersen (1985) found that the two species were sympatric in the same valley. Though he found some evidence for differences in area use, there was some overlap around an area rich in garbage, indicating the ability of the two species to coexist at relatively close quarters. Records of both arctic foxes and red foxes reproducing in this valley have been made throughout recent decades (Østbye et al. 1978, this study). Both species occur in sympatry in many areas throughout the Holarctic (MacPherson 1964, Chirkova 1968, Hersteinsson & Macdonald 1992). Several authors describe the presence of red foxes within their arctic fox study sites (Eberhardt 1977, Smits & Slough 1993, Anthony 1996) without giving any indication that the presence of red foxes in the area had negative consequences for arctic foxes.

The only evidence that red foxes may have serious effects on arctic fox populations comes from coastal islands off southern Alaska. Both species were introduced onto these islands for fur ranching. However, the arctic fox was never able to establish on these islands if the red fox was also present (Schmidt 1985). The deliberate introduction of sterile red foxes as biological control agents also resulted in the extinction of arctic foxes on two of these islands (Bailey 1992). These latter islands may represent a special case due to their extremely small size (< 10 km^2) relative to arctic fox home range sizes (10-60 km^2; Anthony 1997, Landa et al. 1998), distribution of feeding resources, and the fact that they were never part of the arctic fox's natural distribution area. Winter forage must have consisted of either cached seabirds from the summer or debris washed up on beaches. These patchy resources would be easy for the red fox to monopolise. It is unlikely that such intense competition could occur on a mainland site with more dispersed food resources and lower frequencies of inter-specific encounters.

As the arctic fox and the red fox have coexisted in Scandinavia for at least 8,000 years (Frafjord & Hufthammer 1994) it is not surprising that arctic foxes appear to have coexisted with red foxes for at least two decades of the trapping time series from Trollheimen. No arctic foxes were trapped after 1916 following several years of particularly high harvest of arctic foxes (1910 and 1911). The level of red fox harvest remained constant throughout the whole period, only showing a slight increase in the 1940s, implying that over-harvest was the proximate cause of arctic fox extinction in Trollheimen, rather than any increase in the red fox population. The trapping data from Trollheimen, therefore, support the idea that red and arctic foxes can coexist for a period of decades, and do not support the idea that an increase in red fox density was responsible for the original arctic fox decline and its initial non-recovery after protection.

Precedents from other inter-specific studies

The pattern of coexistence of potentially interacting carnivores at fine spatial scales (within home ranges, or between adjacent ranges, rather than regionally) is typical of that described in the literature. Examples include red foxes and Iberian lynx *Lynx pardinus*, grey fox *Dusicyon griseus* and culpeo fox *D. culpaeus*, red foxes and coyotes *Canis latrans*, coyotes and kit foxes *Vulpes macrotis*, wolves *Canis lupus* and coyotes, and cheetahs *Acinonyx jubatus* and lions *Panthera leo* (Voight & Earle 1983, Harrison, Bissonette & Sherburne 1989, Thurber, Peterson, Woolington & Vucetich 1992, Johnson & Franklin 1994, White, Ralls & Garrott 1994, Palomares, Ferreras, Fedriani & Delibes 1996, Durant 1998). For a species like the red fox, which only occurs at very low densities in alpine/tundra habitats, to have population level effects or to exclude the arctic fox from large areas would be an unprecedented relationship based on what is known from other species (Johnson, Fuller & Franklin 1996). In other words, within alpine/tundra habitats it does not seem likely that the presence of the red fox at low density should cause more than small-scale adjustments in area use by arctic foxes. Besides which, interactions with other predators and scavengers must be considered to be part of the arctic fox's normal environment rather than some recent change (Eberhardt 1977, Haglund & Nilsson 1977,

Garrott & Eberhardt 1982, Ovsyanikov & Menyushina 1986, Frafjord 1991, Menyushina 1994).

In contrast, theory and empirical data (Hersteinsson & Macdonald 1992, this study) indicate that the red fox may set a lower limit on arctic fox distribution close to the treeline where red fox populations occur at much higher population densities and have a virtually continuous distribution. It is unclear if the present occupation of the lower lying alpine areas by the red fox is a result of climate warming (Aas & Faarlund 1995) or a natural expansion of its range. However, if global climate change results in a rising treeline (Aas & Faarlund 1995, Beniston et al. 1997), it would be expected that the red fox population would follow this movement and thus, the area available to arctic foxes would decrease further. How the arctic fox might respond to this potential future threat is of vital interest when planing its future conservation (Skaggs & Boecklen 1996), but an improved understanding of its ecology and interaction with the red fox is required.

Conclusion and alternative hypotheses

In conclusion, our study has confirmed that the red fox has successfully colonised the lower alpine region and in doing so has occupied many former arctic fox dens. The arctic fox is presently absent from these lowest dens of its former distribution area. Together these observations support the Hersteinsson & Macdonald (1992) hypothesis of red fox/arctic fox coexistence. However, because so many dens, presumably with their surrounding territories, remain unoccupied by either species we do not believe that competition with the red fox for either food or dens is sufficient to have prevented at least partial population recovery by the arctic fox. Although interference, and to a lesser extent intra-guild predation, from red foxes may have a disproportionate effect on very small arctic fox populations, it is unlikely to explain non-recovery given the low densities, and resulting low encounter probabilities, which occur in these habitats.

Instead we favour a demographic explanation for the non-recovery of arctic fox populations, where over-harvest lowered the population density to a level where allee effects could cause local extinction during the low years of the rodent cycle on which the foxes are dependent (Loison & Strand 1998, Linnell et al. 1999, Strand et al. in press a, Strand, Landa, Linnell, Zimmerman & Skogland in press b). In this scenario the red fox is just one of a plethora of factors that could possibly have contributed to local extinction of the small arctic fox populations, but which should not affect large populations should they recover.

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