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Lukas Barth, Anders Angerbjörn & Magnus Tannerfeldt

Arctic fox *Alopex lagopus* and red fox *Vulpes vulpes* are close relatives with similar niche demands in the Holarctic. Where they are sympatric, they compete for territories, dens and food. Scat analyses from Fennoscandia have shown different proportions of lemmings and voles in the diets of the two fox species suggesting food partitioning. However, it was not clear if this was due to different food preferences or distinct habitat use. Since the arctic fox is an endangered species in Fennoscandia, it is important to know whether the superior, north spreading red fox can oust it from the tundra habitat, or if food specialisation may prevent displacement. In a feeding experiment at the Lycksele Zoo in northern Sweden, we compared the food preferences of two arctic and two red foxes. Our results show that the four individuals responded similarly to a variety of food items, and particularly that the two species were not distinct in their food preferences concerning lemmings and voles. However, the foxes had considerable individual predilections. Therefore, in the wild, the unequal proportions of lemmings and voles found in scats may reflect different habitat use for hunting.

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In the Holarctic, the red fox *Vulpes vulpes* and the arctic fox *Alopex lagopus* occupy very similar ecological niches. Hersteinsson & Macdonald (1982, 1992) suggested that the circumpolar distribution of the arctic fox is limited southwards by the distribution and abundance of its larger relative. The red fox is reported to be a strong competitor through exploitation of resources, but it is also a predator on arctic foxes (Chirkova 1968, Chesemore 1975, Kaikusalo 1982, Frafjord, Becker & Angerbjörn 1989). However, the red fox is not as well adapted to arctic conditions (Macpherson 1964, Hersteinsson & Macdonald 1982) as the arctic fox and its range is limited to the north by environmental and climatic factors (Hersteinsson & Macdonald 1992). Where the geographical distributions overlap and the two species are locally sympatric, they are likely to compete for resources, i.e. food, territories and dens (Chirkova 1968, Haglund & Nilsson 1977, Østbye, Skar, Svalstog & Westby 1978, Frafjord et al. 1989).

In Fennoscandia, range overlap is found in the mountain tundra at the border between Sweden, Norway and Finland. This overlap has probably been caused by an altitudinal spread of the red fox during the last decades. At present, the local arctic fox population is very small (Angerbjörn, Tannerfeldt, Bjärvall,

Ericson, From & Norén 1995) and despite conservation efforts it is being displaced by the red fox (Löfgren & Angerbjörn 1998). At the turn of the century, intensive hunting reduced the arctic fox population almost to extinction (Lönnberg 1927, Haglund & Nilsson 1977). Since 1928 (Sweden), 1930 (Norway) and 1940 (Finland) the species has been protected by law, but the population has failed to recover.

Several hypotheses explaining the absence of a recovery (reviewed by Hersteinsson, Angerbjörn, Frafjord & Kaikusalo 1989) have been put forward. One possible reason related to food availability is changes in the dynamics of microtine populations (Arvicolinae syn. Microtinae) (Angerbjörn et al. 1995), another is food competition with other microtine predators. Particularly intraguild competition with, and predation from, the red fox is likely to make the situation worse for the arctic fox (e.g. Hersteinsson et al. 1989, Kaikusalo & Angerbjörn 1995).

Although the arctic fox is a food generalist, in tundra habitat it acts as a specialist and shows a strong dependence on microtine rodents in summer (Hersteinsson et al. 1989, Angerbjörn, Arvidson, Norén & Strömgren 1991, Angerbjörn et al. 1995, Angerbjörn, Tannerfeldt & Erlinge 1999, Dalerum & Angerbjörn 2000, Elmhagen, Tannerfeldt, Verucci & Angerbjörn in press). In Fennoscandia, the Norwegian lemming *Lemmus lemmus* is the most abundant microtine species in this habitat type and the state of its local populations is particularly crucial for arctic fox survival and reproductive success. Feeding experiments in the Swedish mountains showed that the number of breeding attempts, litter size and cub survival of arctic foxes are food limited (Angerbjörn et al. 1991, Tannerfeldt, Angerbjörn & ArvidSon 1994, Angerbjörn et al. 1995). As a consequence, the arctic fox population follows the population dynamics of the Norwegian lemming in showing 4-5 year cyclic fluctuations (Elton 1942, Macpherson 1969, Finerty 1980, Kaikusalo & Angerbjörn 1995).

The red fox is also a food generalist and it occurs in a wide range of different habitats showing remarkable adaptability (e.g. Lindström 1989, Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994). However, to sustain its energetic costs the red fox needs a more productive habitat than its smaller relative (Harestad & Bunell 1979, Swihart, Slade & Bergstrom 1988, Hersteinsson & Macdonald 1992). In northern Fennoscandia, red foxes typically inhabit the boreal zone where its diet consists of birds, mountain hares *Lepus*

timidus, invertebrates and berries, but mainly small rodents (Lindström 1982), such as field vole *Microtus agrestis*, bank vole *Clethrionomys glareolus*, greysided vole *Clethrionomys rufocanus* and above the timberline also lemmings.

Analyses of red fox scats from areas above the timberline in northern Sweden suggest that voles are the main food resource of the red fox, constituting 71% of food remains in scats, while the proportion of lemmings constituted only 23% (Elmhagen et al. in press). Arctic foxes living in the same area had 4% voles and 85% lemmings in their diet. In Norway (Finse, Sylane) the red fox diet consisted of 90% voles and 4% lemmings (Frafjord 1995). Birds and their eggs (e.g. ptarmigan *Lagopus mutus*, willow grouse *Lagopus lagopus*, and different passerines), reindeer *Rangifer tarandus*, mountain hare and shrews (Soricidae) were represented in much smaller amounts and were comparable in both species, even in years of low microtine abundance.

Thus, analyses showed that both fox species living in the same habitat are microtine specialists, but with different proportions in their diets. The scat analyses did not show, however, whether this differentiation of realised food niches was associated with resource partitioning by means of distinct preferences, or rather a difference in habitat use (Frafjord 1995, Elmhagen 1997), i.e. habitat segregation on a fine topographic scale. Lemmings are the main prey species of arctic foxes and inhabit the tundra widespread, but primarily at higher latitude and altitude. Voles, on the other hand, are most frequently found in willow rich areas at lower latitude and altitude.

To investigate the mechanisms of food competition between the red and the arctic fox, we tested and compared the preferences of arctic and red foxes for voles and lemmings in a feeding experiment. Further, since birds are a main food resource on coasts and islands and temporally available in the tundra (Larsson 1960), we also ran the same experiments with chicks of domestic hen *Gallus gallus* and house mice *Mus musculus* to study whether foxes discriminate between birds and rodents.

Methods

In a cafeteria experiment, snap trapped lemmings and voles were offered to two white arctic foxes (female AFF, male AFM) and two red foxes (female RFF, male RFM) at the Lycksele Zoo in northern Sweden (64°N,

18°E). The arctic foxes were born in the wild and caught as cubs in summer 1993 in Sweden and may have had contact with lemmings and voles in nature, whereas the red foxes were born in 1994 at the zoo in Järvsö, Sweden (61°N, 16°E) and therefore had no previous experience of lemmings. In the area of Lycksele in the county of Västerbotten, different vole species are found in nature. Therefore, in the enclosures, wild voles were potentially available before the studies, whereas lemmings were not. The arctic foxes were temporally separated in two enclosures (500 m² and 1,000 m²), for reasons of later mating. The red foxes were together in one enclosure (2,500 m²). There was a third red fox, a subdominant female, in the same enclosure, but she was very shy and during the experiment she never participated in the feeding sessions. The experiments were carried out during December 1997 and January 1998. Although the Zoo was open to the public, there was an average of less than one visitor a day during this time of the year.

To run the experiments, we built feeding arenas in all three fox enclosures. The feeding arenas were divided into two zones: distant from (Z1) and close to (Z2) the food (Fig. 1). A 60 cm high wooden wall divided Z2 into a left and a right part with a feeding box on each side (B$_l$, B$_r$). The plastic feeding boxes (20 x 20 x 20 cm) had their openings towards the entrance, so that it was easy to see the food placed in the middle of the boxes from the entrance. However,

Table 1. Sample size and weight (g) of the prey items used in the feeding experiments with arctic and red foxes.

Prey item	Sample size	Weight (g) (mean ± SD)
Lemmus lemmus	110	54 ± 21
Voles	99	31 ± 9
Apodemus sylvaticus	12	21 ± 5
Mus musculus	154	(20 - 30)
Sorex minutus	18	6 ± 2
Gallus gallus (juv.)	96	(50 - 60)

it was difficult to look into the boxes from a flat angle.

The food offered to the foxes were whole carcasses of Norwegian lemmings, field voles, bank voles and grey-sided voles, white and brown house mice and domestic hen chicks. Control samples were made with combinations of wood mice *Apodemus sylvaticus*, pygmy shrews *Sorex minutus*, herring *Clupea harengus*, commercial fox food (CFF) and crispbread (Table 1). *L. lemmus*, *C. rufocanus* and *M. agrestis* were caught in summer 1997 in the Swedish mountains around Abisko (68°N, 18°E) using snap traps. *M. agrestis*, *C. glareolus*, *A. sylvaticus* and *S. minutus* were trapped using the same method near Stockholm (59°N, 18°E) in autumn 1997. *M. musculus* were laboratory inbred lines and originated together with juvenile male *G. gallus* from laboratory experiments. All animals were stored in a -20°C freezer and thawed just before feedings. CFF is a food mixture containing minced fish, slaughter remains, grain and vitamins. Crispbread (Swedish *knäckebröd*) is ignored by wild foxes (L. Barth, pers. obs.) and was therefore used as a control item.

The following food combinations were tested: CFF vs crispbread, shrew vs rodent, lemming vs vole and domestic chicken vs white house mouse. Successive food trials were carried out by randomly alternating the food between B$_l$ and B$_r$. One food unit was defined as one prey individual (see Table 1) or 20-30 cm³ of crispbread, CFF or herring, respectively. For each stage, food was randomly drawn from insulated boxes, the individual lemmings and

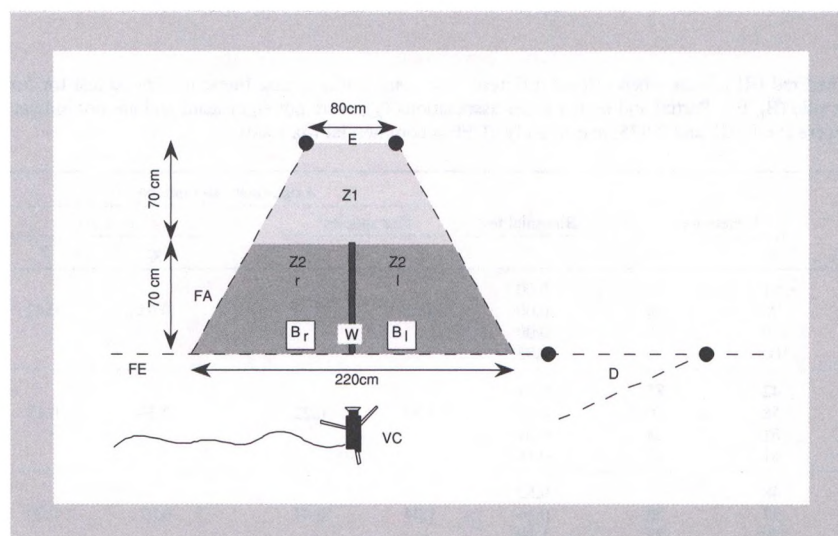Figure 1. Feeding arenas were divided into two zones (Z1, Z2). A 60 cm high wall (W) divided Z2 in a right (r) and a left (l) part with a feeding box on each side (B$_r$, B$_l$). The movements of the foxes were recorded with a video camera (VC) from outside the enclosure. D indicates the door to the enclosure, E the entrance to the arena, FE the fence of the enclosure, and FA the fence of the arena.

voles being packed in separate plastic bags. To min-imise habituation and bias to one side, at least one dummy trial (with no food on either side) was carried out between the actual food trials. Interactions be-tween the two red foxes were minimised by luring one of them with food to a different part of the enclosure. Due to the nocturnal activity of the foxes all feeding occurred at night under artificial light. Food trials were carried out until the foxes lost their interest, i.e. for approximately one hour per individual and feed-ing day. In order to reduce effects involved with the new feeding practice and the feeding arena, all foxes were first trained at least one week with CFF and crisp-bread before carrying out trials with rodents and birds.

All behaviours were recorded with a video camera from outside the enclosures. The feeding arena was enlightened by two 500 Watt lamps. Samples of food choices and time measurements were taken each time a fox entered the arena. A fox entering left or right Z2 (see Fig. 1), with at least the head and both forefeet, was defined as having chosen a side. The behaviour of foxes at the boxes was divided into two groups: 1) eating the food or carrying it out of the feeder - or to the other box (see below) - was defined as having been chosen; 2) looking at, sniffing at, or just chewing on the food without swallowing it was defined as having been refused. Foxes who ate a food unit inside the feed-ing arena were not allowed to take the other food unit. After a fox left the feeding arena the remaining food unit was immediately removed.

We further studied time response with a timer in the video camera (one second intervals) to measure the time between entering the arena and the different events (see a-e in Fig. 2). The following time steps per fox and trial were recorded: a) arrival at the first box, b) contact with first food item, c) switching side, d) arrival at the second food box, e) contact with sec-ond food item and f) leaving the arena. The time re-quired for choosing and eating a food item was meas-ured. Because of the difficulties connected with car-rying out observations in the large enclosures, it was unknown to which extent a fox had eaten, buried or cached the food.

A two-sided binomial test was used to test whether the decisions of foxes were symmetrical or not. Where it was allowed, we approximated binomial distribu-tions by normal distributions. We also tested if there was a sequential trend in choice with logistic regres-sion tests. Between individuals, frequencies of choices were compared using Fisher's exact test or χ^2-test. To check for the presence of interactions between the at-tributes fox species, fox sex and food choice we con-ducted log-linear likelihood tests. For the tests with lemming vs vole we included also the factor micro-tine sex chosen ($\female,\male$) and the offered combination of microtine sex ($\female/\female$, $\male/\male$ or $\female/\male$). Further, the factor choice side (B_l or B_r) was taken into account. Trends in time series were estimated using 'moving propor-tions' following the empirical method of moving aver-ages. Randomness of choice sequences was tested

Table 2. Preference tests of arctic (AF) and red (RF) foxes when offered different food combinations. Log-linear likelihood test for fox species, fox sex, food choice and choice side (B_l, B_r). Partial and higher order associations (χ^2) were not significant and are not indicat-ed. Critical values for the binomial test were P = 0.025 and 0.975, respectively. (CFF = commercial fox food).

| | | | Preferences | | Binomial test | Log linear associations | | | |
| | | | | | | Fox species | | Fox sex | |
Test	Combination	Individual	%	N	P	χ^2	P	χ^2	P
A	CFF-crispbread	AFF	91	96	0.00				
		AFM	96	49	0.00	0.95	0.33	0.65	0.42
		RFF	100	38	0.00				
		RFM	100	6	0.03				
B	Lemming-vole	AFF	42	85	0.19				
		AFM	58	50	0.32	1.50	0.22	2.30	0.13
		RFF	61	28	0.34				
		RFM	61	46	0.18				
C	Microtine-sex	AFF	48	77	0.82				
		AFM	37	38	0.14	1.04	0.31	0.07	0.79
		RFF	50	24	1.00				
		RFM	44	39	0.52				
D	White mouse-chicken	AFF	60	120	0.04				
		AFM	38	28	0.34	1.05	0.31	0.03	0.87
		RFF	50	42	1.00				
		RFM	76	42	0.001				

Table 3. Frequencies of shrews (*Sorex minutus*) preferred (taken or eaten) when tested against: rodents (*Mus musculus*, *Apodemus sylvaticus*), herring (*Clupea harengus*) and CFF by the arctic fox female (AFF), the arctic fox male (AFM) and the red fox female (RFF). P = probabilities from binomial test. χ^2-values were obtained from a logistic regression testing trends over time.

Combination	Individual	% Sorex taken	N	P	% Sorex eaten	N	P	χ^2	P
Sorex - Mus	AFF	63	16	0.45	67	6	0.22	7.12	0.008
	AFM	7	15	0.003	0	7	0.02	1.75	0.19
	Combined	34	31	0.08	31	13	0.27		
Sorex - Apodemus	RFF	20	15	0.04	0	6	0.03	0.60	0.45
Sorex - CFF	AFF	25	16	0.08	0	13	0.000	0.02	0.9
Sorex - Clupea	AFM	0	8	0.008	0	5	0.06		
Sorex - all others	Combined	20	69	0.003	11	37	0.007		

with runs test for dichotomised data. For all time comparisons we ran ANOVAs.

Results

The suitability of the experimental set-up was checked in control tests with CFF and crispbread. None of the four individuals had a significant preference for a particular food box (two-sided binomial test). Further, there were no differences in preferences between the two fox species, between sexes or between individuals (log-linear likelihood test, Table 2a). However, all individuals showed a strong preference for CFF over crispbread (two-sided binomial test: all Ps < 0.05, see Table 2a).

Since shrews are known to be avoided by many carnivores, we wanted to test if our experimental set-up was sensitive enough to identify such trends. In several cases the foxes chewed on or carried shrews away in the shrew vs rodent tests (Table 3). One fox ate four shrews and took 10 out of 16 shrews, but all the others showed significant (or close to significant) preferences to take and eat the alternative food and to avoid shrews. For the fox that took 63% shrews (AFF), there was a significant sequential trend (logistic regression, χ^2 = 7.12, P = 0.008) to take fewer shrews during the experiment (see Table 3). Thus, the experimental set-up gave clear responses for the preferred foot items.

In testing individual preferences for lemmings or voles, none of the four foxes chose significantly more lemmings or voles (see Table 2b). Moreover, in a runs test for dichotomised data the hypothesis of random arrangements could not be rejected, which indicated that all foxes chose lemmings and voles in random sequences. When we combined the individual choices with other factors in a test of independence (log-linear likelihood test, see Table 2b), none of the associations were significant. In particular, the results indicated that there was no difference in preference for lemmings or voles between the two fox species, or between fox sex (see Table 2b). The same held true for the factor microtine sex with no significant differences between fox species or sex (see Table 2c).

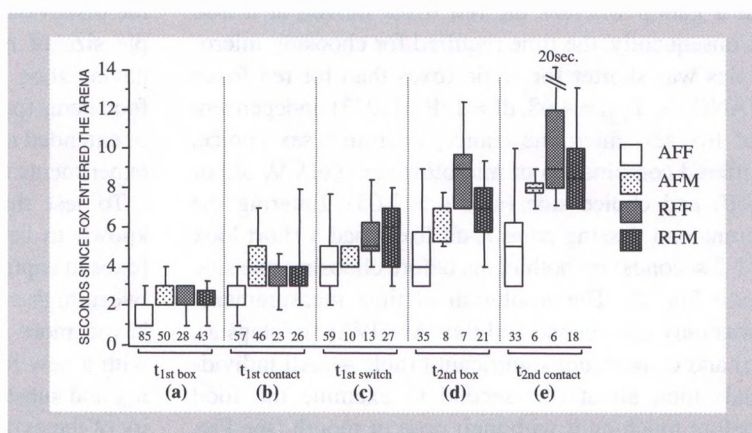Continuing with white mice vs chicken, AFF and RFM chose significantly more white mice than chick-

Figure 2. Time (in seconds) from the moment the foxes entered the arena (t_{in}) until they a) reached the first food box, b) had the first contact with a lemming or a vole, c) switched to the second food box, d) reached the second food box and e) had the second contact with a lemming or a vole. Note that c), d) and e) were no longer of necessity if the first contact b) was a choice. Vice versa, physical contact was not necessary for refusing and side switching. Cases of foxes ordered to go out of the arena were excluded. Bars indicate medians, first and third quartiles and ranges.

Table 4. Time as dependent variable in six two-way ANOVAs (a-f), each with factor 1) fox species (AF, RF), 2) fox sex (F, M) and 3) microtine choice (vole, lemming) as independent variables. Effects by factor fox species are given.

Test		F	df	P
a	$t_{1st box}$	0.48	1	0.49
b	$t_{1st food contact}$	0.06	1	0.81
c	$t_{1st side switch}$	2.48	1	0.12
d	$t_{2nd box}$	4.76	1	0.032
e	$t_{2nd food contact}$	4.66	1	0.035
f	t_{in-out}	8.96	1	0.003

ens (two-sided binomial test, see Table 2d). In a test of independence, food choice was neither associated with fox species or sex (see Table 2d). The significant three-way interaction between fox species, fox sex and food choice was therefore probably a result of individual preferences ($\chi^2 = 12.4$, P = 0.0004).

Since the number of feeding days was too small to reveal trends towards lemming or vole preferences, we investigated if there were any sequential trends in the lemming vs vole trials. For AFF, AFM and RFF the choices fluctuated without any clear trends (logistic regression: $\chi^2 = 0.75$, P = 0.78; $\chi^2 = 0.54$, P = 0.46; $\chi^2 = 0.87$, P = 0.35, respectively). However, for RFM there was a tendency to choose more voles than lemmings over time ($\chi^2 = 3.25$, P = 0.07).

The evaluation of time response in the lemming vs vole trials showed a significant interspecific difference (Fig. 2). The smaller arctic foxes were more agile and acted faster inside the feeding arena. They mostly ran at a gallop whereas the red foxes moved at a trot. Consequently, the time required for choosing microtines was shorter for arctic foxes than for red foxes (ANOVA: $F_{1,92} = 4.68$, df = 1, P = 0.033), independent of fox sex, microtine choice, microtine sex choice, offered combination of microtine sex (i.e. ♀/♀, ♂/♂ or ♀/♂) and choice side (all Ps > 0.05). Entering the arena and passing zone 1, all foxes had a short look (1-2 seconds) on both items before choosing one side (see Fig. 2). The resolution of time measurements was only one second and thus ANOVAs for steps a), b) and c) were not significant (Table 4). All individuals took about one second to examine the food before touching it with their nose or mouth (see Fig. 2b). After that they either started to eat, carried the item away or refused. In the last case they switched straight to the other side, which was most frequently and fastest done by AFF (see Fig. 2c). At box two, the order of events was the same (see Fig. 2d and 2e) and the foxes sometimes switched back again, with or

without having touched the food. Thereby arctic foxes were faster (see Table 4d and 4e) and when leaving the arena they both had spent considerably less time inside the arena than the two red foxes (see Table 4f).

After the choice, all four individuals carried most microtines away, to eat or cache them out of sight. At the latest after having eaten half a dozen, all foxes started to bury the surplus in the snow, dispersed all over the enclosures. All four foxes gathered and cached all kinds of food except CFF and shrews. The CFF was always eaten inside the feeder and the shrews were only eaten four times by AFF. Food items were always consumed totally and with rodents all foxes typically began at the head. RFM was the only fox that, after feeding, was observed to play with dead rodents of different species, pouncing at and throwing them in the air.

Discussion

The results obtained in our feeding experiments did not support the hypothesis that arctic and red foxes have different food preferences. There was no interspecific difference in choice in any offered food combination (shrew vs rodent, lemming vs vole, white mouse vs chicken, CFF vs crispbread). It is difficult to get comparable data directly on the food preferences of the two species in the wild. However, the advantages of controlled conditions in captivity are opposed by the disadvantages of artificiality and the small sample size of non fur-farmed arctic foxes in Scandinavian zoos. We were also limited by the number of food items (particularly lemmings and voles). In favour of extended trials per fox individual, we restricted the experiments to four individuals.

To test the experimental set-up, we used food known to be liked and disliked by wild foxes and foxes in captivity. The foxes clearly distinguished between high and low quality food, and in all tests behaved more cautious and curious when confronted with a new food type, manifested in slow approaching and substantial inspecting and sniffing. The ability of the experimental set-up to detect avoidance acquired by learning was confirmed by the result of the shrew vs rodent tests. Insectivores are known to belong to the dislikes of foxes (Chesemore 1968) and many other carnivores, so shrews are rarely found in scats. In the beginning of our tests, AFF ate several shrews and AFM and RFF repeatedly chewed on

them. However, after repeated trials the tested individuals clearly avoided shrews. The observed avoidance was thus not inherited but developed by learning, and this was detected in the experiment. The most likely mechanism would be repellent odour and taste.

From diet analyses of wild foxes, we expected a preference for lemmings in arctic foxes and for voles in red foxes (Frafjord 1995, Elmhagen 1997). Selection typically favours specialisation where predators live in intimate associations with their prey. In Fennoscandia and elsewhere, arctic fox life history traits are finely tuned to the population cycles of lemming species (Tannerfeldt 1997). The conspicuous colouration and a strong odour of lemmings have been suggested to be an anti-predator strategy (Andersson 1976, Taitt 1993). Since arctic foxes seem to be specialists on lemmings (Angerbjörn et al. 1995, 1999) whereas red foxes act as generalists (Englund 1965), it is possible that the red fox would be affected by such defence strategies. However, there was no evidence in our experiments of any anti-predator effects from the colouration or odour of lemmings, neither for red nor for arctic foxes. Unlike Andersson's live-fed skuas *Stercorarius longicaudus* (Andersson 1976), the foxes in our experiment did not show any preference to voles or lemmings. Moreover, the foxes did not discriminate between male and female microtines, although the sexes (particularly in lemmings) smell different during breeding, even to a human nose. Alternative mechanisms might include the aggressive behaviour of lemmings (Andersson 1976) or maybe the anti-predator strategy is effective against other species than foxes, e.g. stoats or birds of prey. There is, however, no evidence supporting this at present.

For white mouse vs chicken, the difference in preference was at the level of individuals, suggesting that food preferences may vary more between individuals than between species. In the wild, both fox species prey on available birds, but the availability in the Scandinavian mountains is seldom high (Svensson, Carlsson & Liljedahl 1984) and the amount of bird remains in scats is low (Frafjord 1995, Elmhagen 1997). Birds may thus enrich the menu, rather than being a substantial alternative to rodents.

Our experiments thus showed that arctic and red foxes have similar food preferences. The different proportions of lemmings and voles found in scats in Norway and Sweden therefore presumably reflect different habitat use for hunting (Frafjord 1995, Elmhagen 1997). In a similar case of intraguild competition in Torres del Paine National Park in Chile, Johnson & Franklin (1994) found that "home ranges of grey fox (*Dusicyon griseus*) and culpeo fox (*Dusicyon culpaeus*) were interspersed in a mosaic-like arrangement and did not overlap". The two species were separated altitudinally and exhibited differences in habitat use. Similar separations in spatial distribution have been reported for coexisting wolves *Canis lupus* and coyotes *Canis latrans* (Fuller & Keith 1981), as well as for coyotes and red foxes (Voigt & Earle 1983).

The red fox has apparently excluded the arctic fox from lower altitudes and latitudes, but until recently its fundamental niche did not extend up into the arctic fox zone (Macpherson 1964). This is probably due to its comparative sensitivity to climatic factors and low and unpredictable food resources (Hersteinsson & Macdonald 1992). In an experiment in Finnish Lapland, only supplemental feeding at arctic fox dens made it possible for the red fox to occupy areas higher up the tundra (Kaikusalo & Angerbjörn 1995). From their experiment, Kaikusalo & Angerbjörn (1995) concluded that it is impossible for red foxes to reproduce and survive on the tundra at low food abundance. Consequently, the outcome of the competition between arctic and red foxes depends on both the temporal and spatial state of the environment. In low productivity conditions, the arctic fox is limited by food and the red fox is absent. The red fox might breed at lower altitudes or latitudes and exclude the arctic fox from the more productive forest and shrubby tundra patches. Under high productivity conditions, i.e. in good lemming years, aggressive encounters (interference competition) would be more likely, because red foxes may switch food and habitat preferences, and hunting territories would overlap more. Since red foxes have larger home ranges than arctic foxes (Lindström 1989), just a small number of red foxes may be able to exclude arctic foxes locally. When red and arctic foxes were held together under penned conditions, red foxes were clearly dominant and won conflicts (Rudzinski, Graves, Sargeant, & Storm 1982, Korhonen, Alasuutari, Mäkinen & Niemelä 1997). In the wild, arctic foxes generally avoid direct physical encounters with red foxes (Schamel & Tracy 1986, Frafjord et al. 1989), but individuals may suffer reduced feeding rates, fecundity or survivorship as a result of stress and spatial and temporal restrictions (mutual competition). The red fox is also a keen predator on arctic fox cubs (Frafjord et al. 1989, and M. Tannerfeldt, pers. obs.).

From our experiment, there is no evidence of a dif-

ference in food preference that could prevent the red fox from driving the arctic fox to local extinction. In Fennoscandia, the arctic fox population is dwindling, and possibly suffering from fragmentation and inbreeding (Tannerfeldt 1997). With the loss of climatic limitations for the red fox, management programs creating a temporal competitive release are needed to allow the arctic fox population to recover (Hersteinsson et al. 1989, Löfgren & Angerbjörn 1998). A large-scale management program to that end has now started in Sweden and Finland (LIFE98NAT/S/5371).

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