

# DNA analysis on fox faeces and competition induced niche shifts

LOVE DALÉN, BODIL ELMHAGEN and ANDERS ANGERBJÖRN

Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden

## Abstract

**Interference competition can force inferior competitors to change their distribution patterns. It is, however, possible that the dominant competitor poses a higher threat during certain times of the year, for example during reproduction. In such cases, the inferior competitor is expected to change its distribution accordingly. We used a molecular species identification method on faeces to investigate how the spatial overlap between arctic and red foxes changes between seasons. The results show that arctic and red foxes are sympatric during winter, but allopatric in summer as arctic foxes retreat to higher altitudes further from the tree-line during the breeding season.**

*Keywords:* *Alopex*, ecology, PCR, species identification, *Vulpes*

Received 24 February 2004; revision received 7 May 2004; accepted 7 May 2004

## Introduction

Interference competition among predators leads to niche segregation when individuals change their use of habitat or activity patterns to avoid competition (Palomares & Caro 1999). For inferior species, the potential cost of competition may change over time, for example between seasons. The degree of niche overlap should then vary accordingly.

Arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*) both inhabit the mountain tundra in Sweden. They have similar diets and probably share the same fundamental food niche (Frafjord 2000; Elmhagen *et al.* 2002). They are therefore likely to have similar habitat preferences. However, as red foxes are larger than arctic foxes they are dominant in direct interactions, for example at dens and carcasses, and they are also predators on arctic fox cubs (e.g. Rudzinski *et al.* 1982; Frafjord *et al.* 1989; Tannerfeldt *et al.* 2002). For arctic foxes, the cost of interactions with red foxes should be higher in summer than in winter, when they are not only outcompeted for food resources and dens, but also risk losing their reproductive investment.

Arctic foxes breed in dens at higher altitudes and further from the tree-line than red foxes (Linnell *et al.* 1999; Dalerum *et al.* 2002). Assuming that the potential cost for arctic foxes changes between seasons and that red foxes, being the dominant competitor, always inhabit the optimal (preferred)

habitat, we expect a higher degree of spatial overlap in winter than during the breeding season in summer. In this study, we test this hypothesis through an analysis of the spatial distribution of red fox and arctic fox faeces, using a molecular approach for species identification.

## Materials and methods

Fox faecal samples were collected from four mountain areas throughout northern Sweden in 2000–2002 (Fig. 1). The samples were collected on dens which were surveyed systematically on foot during summer and using snow-mobiles in winter. The altitude and distance to the tree-line was noted for each sample. To control for latitudinal differences among our sampling locations, we used a relative measure of altitude by calculating the altitude above the tree-line for each sample.

Species identification followed the protocol described previously in Dalén *et al.* (2004). In brief, extracted DNA was amplified for 35 cycles in a three-primer polymerase chain reaction (PCR) with one general and two species-specific primers. Resulting PCR-products were either 100 base pairs (bp; red fox) or 332 bp (arctic fox), depending on which of the species-specific primers that annealed to the DNA template. DNA in faecal remains can be degraded and it is therefore important to be careful about contamination (Wayne *et al.* 1999). All extractions therefore took place in an isolated laboratory dedicated for DNA extractions, and each extraction was followed by at least one negative control.

Correspondence: Love Dalén. Fax: +46 8 16 7715; E-mail: Love.Dalen@zoologi.su.se

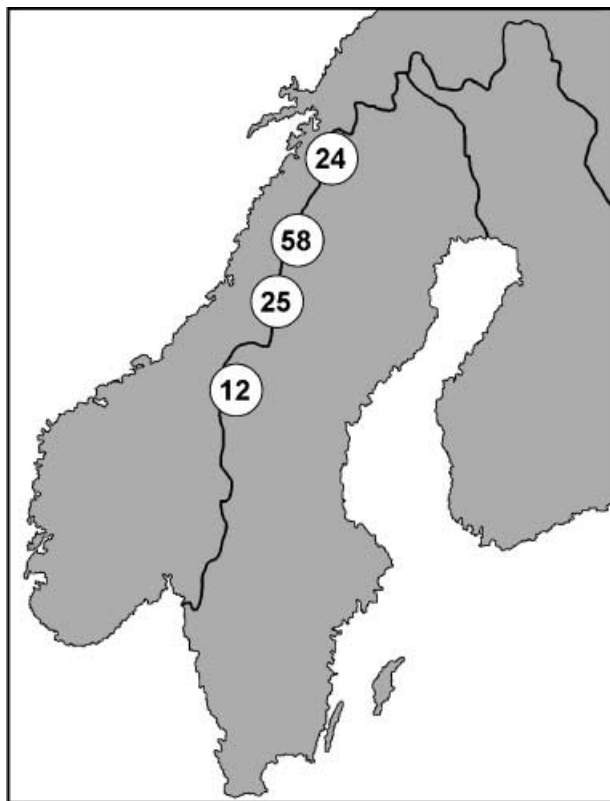


Fig. 1 Map of Scandinavia showing the sampled areas and sample sizes (within circles).

All negative controls were empty during this study. Each sample also works as a negative control for cross-species contamination, as this would result in both 100 bp and 332 bp products. This was not observed in any sample.

Of 190 successfully analysed samples, 119 were used for the statistical analyses. Seventy-one samples were excluded, as they were either collected at the same den within the same month in winter or at the same den during the breeding season. The shortest distance between two samples collected during the same period was 1.9 km.

We used a  $\chi^2$ -test to investigate if there was a seasonal difference in frequency between arctic and red fox faeces. A two-factor analysis of variance and a subsequent Tukey HSD *post-hoc* test (StatSoft Inc. 1999) were used to investigate the effect of season and species on the relative altitude and distance from the tree-line (the latter was transformed with square root to obtain homogenous variances).

## Results

Of the 119 samples analysed, 67 were from red fox and 52 were from arctic fox. There was no difference in frequency of the species over the seasons as red foxes constituted 56% of the samples in winter and 59% in summer ( $\chi^2 = 0.08$ ,  $P = 0.77$ ). There was a significant interaction over seasons

**Table 1** Significance values for the two-factor analysis of variance on relative altitude and distance from the tree-line. Degrees of freedom (d.f.) for the error term in both analyses was 115. The interactions between species and season were significant in both cases

	Effect	d.f.	F	P
Altitude	Species	1	34.4	< 0.001
	Season	1	1.95	0.17
	Interaction	1	12.0	< 0.001
Distance	Species	1	13.0	< 0.001
	Season	1	11.9	< 0.001
	Interaction	1	7.05	< 0.001

**Table 2** Results from Tukey HSD *post-hoc* test. *P*-values on relative altitude (above diagonal) and distance from tree-line (below diagonal); red ( $n = 67$ ) and arctic fox ( $n = 52$ ) are abbreviated as RF and AF, respectively

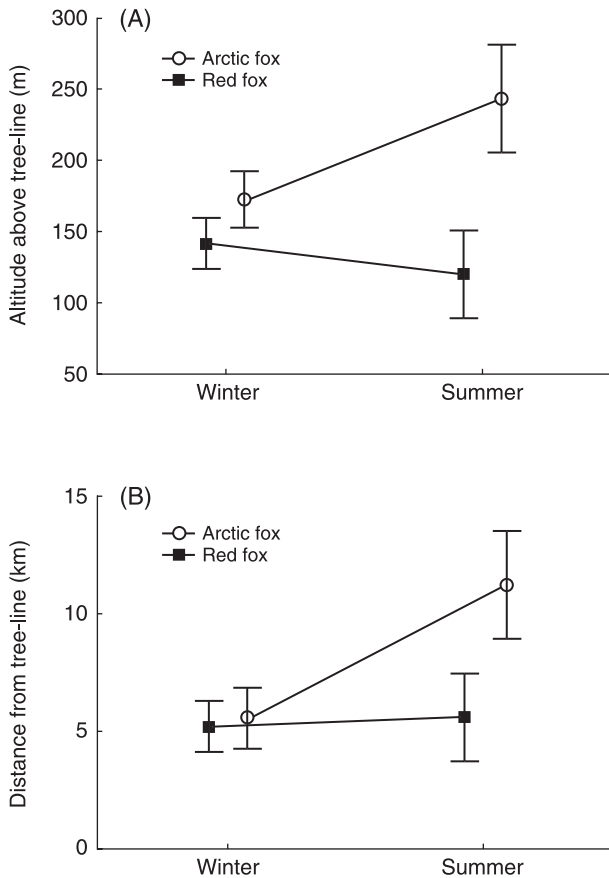
	RF winter	RF summer	AF winter	AF summer
RF winter	—	0.39	0.07	0.0002
RF summer	0.92	—	0.006	0.0001
AF winter	0.77	0.91	—	0.01
AF summer	0.0002	0.003	0.0008	—

both for relative altitude and distance from the tree-line (Table 1). In winter, both species occurred at the same relative altitude and distance from the tree-line. In summer, red foxes remained at the same altitude and distance from the tree-line as in winter, whereas arctic foxes had instead moved both further from the tree-line and higher up in the mountains (Table 2, Fig. 2).

## Discussion

Arctic and red fox reproduction in northern Sweden is food-limited in most years, as it depends on the availability of cyclic rodents (e.g. Angelstam *et al.* 1985; Angerbjörn *et al.* 1995). Both species should consequently prefer the most productive habitats during the breeding season. In mountain tundra areas, productivity and prey availability is generally higher at low altitudes close to the tree-line than at high altitudes (e.g. Svensson *et al.* 1984; Oksanen *et al.* 1999). Our results show that both species use these areas in winter, but only the dominant red fox breeds there.

Red foxes occasionally kill adult arctic foxes at carcasses (Frafjord *et al.* 1989), but systematic observations indicate that an arctic fox usually waits at a distance from the carcass until there are no red foxes around and, in the case of a hostile interaction, it runs faster and escapes unharmed (Haglund & Nilsson 1977). In summer, however, arctic foxes avoid breeding in red fox territories and when they



**Fig. 2** Mean relative altitude (A) and distance from tree-line (B) of arctic and red fox faecal samples in winter and summer. Faeces from red foxes were found at the same altitude and distance from tree-line during winter and summer, whereas arctic fox faeces were found at higher altitudes and further from the tree-line during summer than winter.

fail to do so, they risk red fox predation on their cubs (Tannerfeldt *et al.* 2002). Thus, for an arctic fox it may be worth risking interactions with red foxes in winter, for example to gain access to food, while the potential cost during reproduction forces it to retreat to relatively barren areas where red foxes are less abundant. A similar relationship may exist between red foxes and the larger and dominant coyote *Canis latrans* in North America. Voigt & Earle (1983) found an almost complete spatial segregation during summer, but a high spatial overlap in autumn as juveniles migrated through coyote territories. However, the juveniles did not establish there and segregation increased again in winter and spring.

The Swedish arctic fox population decreased dramatically in the early 1900s due to excessive hunting (Lönnerberg 1927). It was protected in 1928, but never recovered. It has been suggested that interspecific competition from red foxes limits the distribution of arctic foxes (Hersteinsson & Macdonald 1992) and that increased competition from an

expanding red fox population have contributed to the nonrecovery in Fennoscandia (Hersteinsson *et al.* 1989). A retreat of breeding arctic foxes to higher altitudes in the 20th century supports this hypothesis, but it has been pointed out that both species were trapped in the same areas for several years in the early 1900s, which could indicate coexistence (Linnell *et al.* 1999). However, trapping should have been carried out mainly in winter and we have shown that niche segregation increases during breeding. This critical period is therefore likely to determine whether or not the realized niche of the arctic fox in Fennoscandian mountain tundra areas is diminishing due to red fox expansion. At present, the arctic fox is very close to extinction and it is possible that high altitude areas are of too low quality to sustain sufficient reproduction to keep the population viable (Elmhagen 2003).

It has previously been proposed that species identification of faecal samples can be valuable for conservation biologists (Kohn & Wayne 1997), and several methods have been developed for this purpose (e.g. Hansen & Jacobsen 1999; Farrell *et al.* 2000; Palomares *et al.* 2002). This study demonstrates how such methods can be put into use, both as a tool in conservation and to investigate ecological interactions among species.

### Acknowledgements

We thank the following contributors: H. Angleby, H. Hensel, A. Götherström, M. Tannerfeldt, L. Liljemark, L. Rehnfeldt, S. Almroth, L. Strömberg, V. Esberg, S. Backe, A. Kjellström, S. Dalén, L. Axelsson and all field workers. Magnus Tannerfeldt and two anonymous referees provided valuable comments on the manuscript. This work was financed by EU-Life Nature.

### References

- Angelstam P, Lindström E, Widén P (1985) Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia – occurrence and distribution. *Holarctic Ecology*, **8**, 285–298.
- Angerbjörn A, Tannerfeldt M, Bjärvall A *et al.* (1995) Dynamics of the arctic fox population in Sweden. *Annales Zoologici Fennici*, **32**, 55–68.
- Dalén L, Götherström A, Angerbjörn A (2004) Identifying species from pieces of faeces. *Conservation Genetics*, **5**, 109–111.
- Dalerum F, Tannerfeldt M, Elmhagen B, Becker D, Angerbjörn A (2002) Distribution, morphology and use of arctic fox dens in Sweden. *Wildlife Biology*, **8**, 185–192.
- Elmhagen B (2003) *Interference competition between arctic and red foxes*. PhD Thesis, Department of Zoology, Stockholm University, Sweden.
- Elmhagen B, Tannerfeldt M, Angerbjörn A (2002) Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology*, **80**, 1274–1285.
- Farrell LE, Romant J, Sunquist ME (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology*, **9**, 1583–1590.

- Frafjord K (2000) Do arctic and red foxes compete for food? *Zeitschrift Fur Säugetierkunde*, **65**, 350–359.
- Frafjord K, Becker D, Angerbjörn A (1989) Interactions between arctic and red foxes in Scandinavia — predation and aggression. *Arctic*, **42**, 354–356.
- Haglund B, Nilsson E (1977) *Fjällräven — en hotad djurart [The Arctic Fox — A Threatened Species]*. World Wildlife Fund, Sweden [in Swedish].
- Hansen MM, Jacobsen L (1999) Identification of mustelid species: otter (*Lutra lutra*), American mink (*Mustela vison*) and polecat (*Mustela putorius*), by analysis of DNA from faecal samples. *Journal of Zoology*, **247**, 177–181.
- Hersteinsson P, Angerbjörn A, Frafjord K, Kaikusalo A (1989) The arctic fox in Fennoscandia and Iceland: management problems. *Biological Conservation*, **49**, 67–81.
- Hersteinsson P, Macdonald DW (1992) Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*, **64**, 505–515.
- Kohn MH, Wagne RK (1997) Facts from feces revisited. *Trends in Ecology and Evolution*, **12**, 223–227.
- Linnell JDC, Strand O, Landa A (1999) Use of dens by red *Vulpes vulpes* and arctic *Alopex lagopus* foxes in alpine environments: can interspecific competition explain the non-recovery of Norwegian arctic fox populations? *Wildlife Biology*, **5**, 167–176.
- Lönnerberg E (1927) *Fjällrävsstammen i Sverige 1926 [The Arctic Fox Population in Sweden 1926]*. K. Sv. Vetenskapsakad. Skr. Naturskyddsärenden No. 7. Royal Swedish Academy of Sciences, Uppsala, Sweden [in Swedish].
- Oksanen T, Schneider M, Rammul Ü, Hambäck P, Aunapuu M (1999) Population fluctuations of voles in North Fennoscandian tundra: contrasting dynamics in adjacent areas with different habitat composition. *Oikos*, **86**, 463–478.
- Palomares E, Caro TM (1999) Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492–508.
- Palomares F, Godoy JA, Piriz A, O'Brien SJ, Johnson WE (2002) Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. *Molecular Ecology*, **11**, 2171–2183.
- Rudzinski DR, Graves HB, Sargeant AB, Strom GL (1982) Behavioral interactions of penned red and arctic foxes. *Journal of Wildlife Management*, **46**, 877–844.
- StatSoft Inc. (1999) *STATISTICA for Windows* [Computer program manual]. StatSoft Inc., Tulsa, OK.
- Svensson S, Carlson UT, Liljedahl G (1984) Structure and dynamics of an alpine bird community, a 20-year study. *Annales Zoologici Fennici*, **21**, 339–350.
- Tannerfeldt M, Elmhagen B, Angerbjörn A (2002) Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, **132**, 213–220.
- Voigt DR, Earle BD (1983) Avoidance of coyotes by red fox families. *Journal of Wildlife Management*, **47**, 852–857.
- Wayne RK, Leonard JA, Cooper A (1999) Full of sound and fury: the recent history of ancient DNA. *Annual Review of Ecology and Systematics*, **30**, 457–477.

---

Love Dalén is a Phd student within the arctic fox group at the Department of Zoology, Stockholm University. His research interests are conservation and population genetics in arctic foxes and other mammals. Bodil Elmhagen recently completed her Phd thesis on interference competition between arctic and red foxes. Her main research interests are species interactions and conservation ecology. Anders Angerbjörn Phd is the project leader of the Fennoscandian arctic fox project (SEFALO +), and is a member of the IUCN / Ssc Canid Specialist Group. His major research interests are conservation aspects of arctic fauna and predator–prey relations.

---