



Does protection from hunting favour genetic uniformity in the red fox?

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Receipt of Ms. 27. 05. 1999

Acceptance of Ms. 27. 08. 1999

Abstract

Allozymes and mtDNA sequences were used to assess genetic variability in six hunted and three non-hunted populations of red foxes *Vulpes vulpes* in Central Europe and the Mediterranean area. Allozyme variability was very low ($P = 0.0\text{--}4.4$; $He = 0.0\text{--}0.006$) and significantly smaller in protected populations than in hunted ones ($P = 8.9\text{--}15.6$; $He = 0.010\text{--}0.044$). As a trend, this result was confirmed by the distribution of mtDNA variation. Differences of genetic variability were independent from sample size. Most likely, foxes evolved under predation by larger carnivores, which probably have primed the turnover of territorial reproducers. In absence of predation, hunting could superficially mimic such an effect and favour a greater genetic variability and, thus, a better viability in the red fox. This may suggest an explanation to the failure of intensive hunting campaigns as a measure to reduce strongly the population size of red foxes.

Key words: *Vulpes vulpes*, genetic variability, hunting, predation

Introduction

The social organisation of the red fox *Vulpes vulpes* (L., 1758) includes territorial individuals, who are resident and thus responsible for reproduction, as well as itinerant individuals, who are subordinate and often subadult, who may reproduce only when they replace a territorial fox (MACDONALD 1980 a, 1987). In a fox population genetic variability is most likely dependent on effective population size (N_e), on frequency of replacement events in territories by itinerant individuals, and on the relatedness of the replacing individual to the group. Replacement rate should increase in populations with a high mortality rate in the adult age class, induced by predation or hunting. Several proximate evolutionary determinants may also have an effect on reproduction of red fox populations, thus presumably on their genetic structure. These include effects of mortality rate on the proportion of reproducing vixens and on litter size, as well as dispersal “sinks” (e.g. HARRIS and SMITH 1987; ZIMEN 1984; ARTOIS 1989, for a review).

Allozymes and DNA sequences are useful markers to study population genetics in mammals. Statistical indices inferred from allele frequencies at protein loci and the distribution of different mitochondrial DNA haplotypes can be used to quantify the extent of genetic variability and differentiation of natural populations. Estimates of genetic diver-

sity can be correlated with several parameters (ecology, climate, vegetation, population density, life cycle and style), which may influence the level of variability (NEVO et al. 1984), thus providing useful suggestions for management (MORITZ 1994). The organisation of mating systems (APOLLONIO and HARTL 1993) and other factors, e. g., replacement rate of territorial individuals where they are the only reproducers, may also influence genetic variation. In this study we examine the relationships between hunting and protection from hunting with genetic variability in red fox populations.

Material and methods

Standard allozyme and DNA analyses have been carried out on samples of liver tissue removed from foxes freshly killed by hunters in the course of occasional sampling/targeted control operations (i. e. rabies monitoring and livestock protection) and regular hunting (Tab. 1) from selected sites in Central Europe and the Mediterranean range (Fig. 1). Sampling in protected areas was limited because of ethical and legal constraints on the collection of specimens, although all sampled populations of red foxes were abundant. All samples came from adult (>1 year old) individuals to decrease the probability of close relatedness between them. To our knowledge, no bottleneck has occurred in these populations in the last few centuries. Liver samples were preserved at -80°C prior to analyses and used to perform an electrophoretic screening of 45 presumptive loci (GRILLITSCH et al. 1992; HARTL and HÖGER 1986). A subset of the same samples was used to extract DNA. The 5'-end of the mitochondrial Cytochrome *b* gene (Cyt *b*: 375 bp) was PCR-amplified and sequenced according to the procedure outlined in SIMON et al. (1991). A detailed analysis of several statistical parameters derived from allele frequencies and from DNA sequences was obtained with the computer programs BIOSYS-1 (SWOFFORD and SELANDER 1989), REAP (MCELROY et al. 1992) and MEGA (KUMAR et al. 1993) and was presented in FRATI et al. (1998).

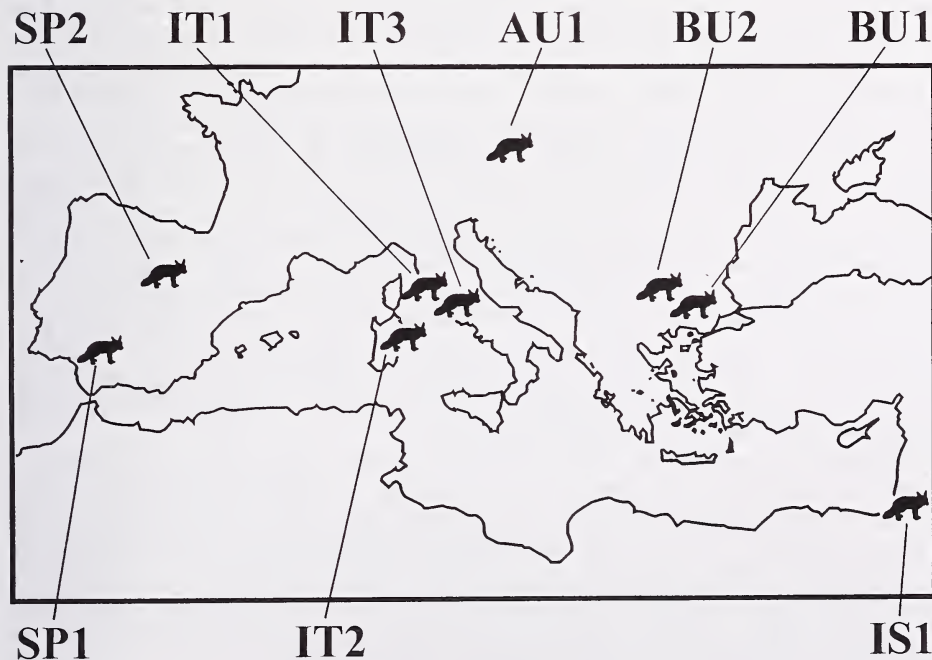


Fig. 1. Map of collecting sites for the nine fox populations: Spain (SP1, SP2), Italy (IT1, IT2, IT3), Austria (AU1), Bulgaria (BU1, BU2), Israel (IS1).

The nucleotide sequences reported in this study have been deposited in the EMBL, GenBank and DDBJ Nucleotide Sequence Databases under accession numbers Z80957-Z80984 and Z80987-Z80997 (cf. FRATI et al. 1998).

Results and discussion

Several indices of genetic variability, inferred from both allozymes and mtDNA, are shown in table 1. Red foxes in non-hunted populations showed a significantly lower level of allozyme variability than those in hunted populations (Mann-Whitney U-test, two-tailed: $U = 0.0$; $n_1 = 3$; $n_2 = 6$; $p < 0.05$, in both the proportion of polymorphic loci and heterozygosity; Tab. 1). Our results might also be a consequence of sample sizes, e.g., only a small number of family groups may have been sampled in the unhunted sites. In fact, there was a significant correlation between sample size and allozyme variability ($r = 0.68$, $df = 7$, $p < 0.05$). We reduced all sample sizes to three specimens, i.e., the smallest sample (IT3), randomly chosen within each population, to avoid partly such a correlation. In spite of this reduction (repeated three times, independently), hunted populations remained much more variable than non-hunted ones at the same level of significance and parameters as above (Tab. 1).

A relationship between hunting and the increase of genetic variability appeared to be confirmed by the two indices inferred from Cyt *b* sequence data (Tab. 1), except for the IT3 population, which showed a higher level of variability than that observed with allozymes. Sequence divergence between haplotypes ranged from 0 to 2.67% and it was maximum among specimens of the AU1 population.

Our data suggest that genetic variability in unhunted fox populations is almost absent, independently from sample size, and it is significantly lower than that in hunted populations where heterozygosity and proportion of polymorphic loci are within the range of those found amongst other wild canids (HAMILTON and KENNEDY 1986; KENNEDY et al. 1991; LORENZINI and FICO 1995). Differences in polymorphism are found not only at the population level, but also at the individual level (Tab. 1, Ho). This should rule out the possibility that a lower variability in non-hunted populations is due to sampling of related individuals.

Variability of fox behaviour and ecology is influenced by habitat structure and richness (e.g. ARTOIS 1989; LUCHERINI and LOVARI 1996; MACDONALD 1980 a). This includes aspects of the reproductive system and of spatial organisation (territory size, dispersal patterns), which in turn may influence genetic structure. The most likely factor underlying an unusually low genetic variability in a population is the local scarcity of assortative mating (CROW and KIMURA 1970). Non-territorial foxes occur in non-hunted populations (e.g. CAVALLINI and LOVARI 1994; LOVARI et al. 1994; LUCHERINI et al. 1995), but apparently they fail to reproduce. Therefore, the nomadic fraction of a fox population may not contribute to reproduction, unless territories become vacant. This effect of protection is perplexing as natural, unhunted populations should be able to maintain enough genetic variability through ecological and behavioural mechanisms.

Polygynous mating systems decrease genetic variability among ungulates, because only a few males contribute to reproduction (APOLLONIO and HARTL 1993). If foxes were polygynous, i.e. one male would reproduce with several females, this could favour the loss of genetic variability. Up to six vixens are known to share their territory with one dog fox, especially at the comparatively high density found in protected areas, with no predators, but normally only the alpha female has cubs (MACDONALD 1979; SCHANTZ 1981; ZABEL and TAGGART 1989). Therefore, little or no difference in allozyme variability can be expected between polygynous and monogamous fox populations.

There may be another explanation to the low level of genetic variability in protected fox populations. The general rule amongst canids is that "larger species dominate – or

Table 1. Estimates of genetic variability in nine populations of red foxes. Abbreviations as in fig. 1. (Compiled from FRANI et al. 1998). ss: sample size, P: Percentage of polymorphic loci (99% criterion); He: Expected heterozygosity according to the Hardy-Weinberg equilibrium, Ho: Observed heterozygosity.

Sampling areas	Allozymes										mtDNA			
	complete data set					resamplings with 3 specimens					ss	haplotype diversity	nucleotide diversity	
	Hunted	ss	P	He	Ho	P	He	P	He	P				He
Doñana Natl. Park, Sevilla	NO	10	4.4	0.006	0.007	2.2	0.007	0	0.000	0	0.000	5	0.000	0.000
prov. (SP1)														
Maremma Reg. Park, Grosseto prov. (IT3)	NO	3	0	0.000	0.000	0	0.000	0	0.000	0	0.000	3	0.667 ± 0.314	0.733
Grofit (IS1)	NO	4	0	0.000	0.000	0	0.000	0	0.000	0	0.000	3	0.000	0.000
Valladolid province (SP2)	YES	9	8.9	0.010	0.010	6.7	0.022	4.4	0.015	2.2	0.007	3	0.667 ± 0.314	0.533
Siena province (IT1)	YES	42	15.6	0.025	0.025	4.4	0.021	4.4	0.019	13.3	0.055	9	0.694 ± 0.147	0.236
Sardinia region (IT2)	YES	19	11.1	0.044	0.026	4.4	0.024	8.9	0.043	8.9	0.039	5	0.800 ± 0.164	0.380
Tullner Feld, Lower Austria (AU1)	YES	8	11.1	0.033	0.025	6.7	0.027	4.4	0.024	2.2	0.016	6	0.933 ± 0.122	1.427
Vitocha (BU1)	YES	17	13.3	0.036	0.021	8.9	0.030	8.9	0.039	4.4	0.019	2	1.000 ± 0.500	0.800
Rila (BU2)	YES	6	8.9	0.031	0.028	8.9	0.043	8.9	0.038	8.9	0.039	3	0.667 ± 0.314	0.733

even kill – smaller ones” (MACDONALD 1992: 90). This has been reported for, e.g., wolves and coyotes (CARBYN 1982; FULLER and KEITH 1981), coyotes and red foxes (DEKKER 1983; MAJOR and SHERBURNE 1987; VOIGT and EARLE 1983; but see also GESE et al. 1996), red and arctic foxes (BAILEY 1992; FRAFJORD et al. 1989; HERSTEINSSON and MACDONALD 1992; RUDZINSKI et al. 1982), coyotes and kit foxes (RALLS and WHITE 1995; WHITE et al. 1994). Most likely, if the red fox evolved under the pressure of a community of larger predators such as other canids as well as felids, e.g., cougar and leopard (CAVALLINI 1996), this may have strongly influenced the development of its great biological flexibility and resilience (NOWAK 1991). The only larger canid in southern Europe is the wolf, which is known to feed on foxes on occasion (MATTEUCCI 1992; MERIGGI et al. 1991). Presently, predation pressure by the wolf on foxes is likely to be small in most of Europe, as the wolf is an endangered species while the red fox is one of the most successful mammals in terms of numbers and range width. The Iberian lynx *Lynx pardinus* occurs in one (SP1) of the protected areas of our sample, but it is rare and unlikely to prey on red foxes because of its small size (RAU et al. 1985). No wolves – or any other larger predator – have occurred in our other protected sampling areas for at least a few decades. The lack of natural predators may result in relatively stagnant fox populations, where the same individual could successfully defend a territory for several years. This may prevent a frequent turnover of reproducers over several years, eventually leading to a decrease of genetic variability. In polygynous groups of red foxes, vixens are closely related, often mothers (the alpha female) and daughters (MACDONALD 1979; SCHANTZ 1981). If the alpha female dies, one of the “helpers” will replace her as reproducer (MACDONALD 1987). Thus, some inbreeding can be expected. The occurrence of protected areas, devoid of larger predators, is a very recent event in fox evolution. No equally effective, alternative process to predation may have yet been developed in red foxes to favour genetic variability.

Hunting may increase genetic variability in fox populations by partly mimicking the effects of natural predation with which foxes have probably evolved. A high genetic variability in a population is believed to enhance its viability (ALLENDORF and LEARY 1986; LACY 1997, for a review). If our hypothesis is correct, this may suggest one important reason why persecution campaigns or intensive hunting have never succeeded to eradicate foxes from large areas, e.g., for rabies control in Europe (MACDONALD 1980 b, for a review). In this connection, the ecological adaptability of a generalist species, such as the red fox, should also not be underestimated.

On the other hand, hunting alone is unlikely to be a valid replacement for natural predation. Long-lasting hunting practices can alter the genetic structure of mammalian populations, often acting in an anti-Darwinian sense (HARTL et al. 1991; HARTL et al. 1995; RYMAN et al. 1981; SCRIBNER et al. 1985), thus being poor substitutes of natural predation. We wish to stress that our results need confirmation from larger samples and from observational data of territory turnover in areas where a community of predators of foxes does and does not occur. If hunting is in principle an acceptable activity, there is no reason not to admit it for red foxes. Conversely, our data must not be used to justify intensive hunting or persecution campaigns, which are quite a different, controversial issue on biological and ethical grounds, beyond the scope of this paper.

Acknowledgements

We are grateful to F. CASSOLA, M. FESTA-BIANCHET, H. and LOESKE KRUUK, RITA LORENZINI and F. MORIMANDO for improving earlier drafts of this paper with their comments. GIORGINA ROMEO kindly gave technical help. We are also indebted to M. DELIBES, LIDIA FLEBA, G. MARKOV, R. MAZZONI DELLA STELLA and Y. YOM-TOV for providing fox samples. FF and SL were supported by a grant from the Amministrazione Provinciale di Siena and by the Ministero per l'Università e la Ricerca Scientifica e Tecnologica (40 % and 60 %).

Zusammenfassung

Trägt die jagdliche Schonung zur genetischen Einförmigkeit beim Rotfuchs bei?

Mittels Allozymelektrophorese und mtDNA-Sequenzierungen wurde die genetische Variabilität von sechs bejagten und drei nicht bejagten Populationen des Rotfuchses *Vulpes vulpes* in Mitteleuropa und in mediterranen Gebieten untersucht. Die genetische Variabilität war deutlich geringer in den nicht bejagten ($P = 0,0\text{--}4,4$; $H_e = 0,0\text{--}0,006$) als in den bejagten ($P = 8,9\text{--}15,6$; $H_e = 0,010\text{--}0,044$) Populationen. Die mtDNA (Cyt *b*)-Sequenzen zeigten denselben Trend. Diese Ergebnisse werden wie folgt interpretiert: Wahrscheinlich entwickelte sich der Fuchs im Laufe seiner Stammesgeschichte unter dem Druck von größeren Predatoren, die im territorialen Fortpflanzungsgefüge einer Fuchspopulation eine gewisse Durchmischung bewirkten. In Abwesenheit dieser Räuber wurde derselbe Effekt möglicherweise durch die Jagd hervorgerufen und so eine größere genetische Variation und damit Überlebensfähigkeit bewahrt. Dies mag eine Ursache dafür sein, daß intensiver Jagddruck bisher nicht zu einer bedeutenden Reduktion von Fuchsbeständen geführt hat.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 2000

Band/Volume: [65](#)

Autor(en)/Author(s): Lovari Sandro, Hartl Günther B., Frati Francesco

Artikel/Article: [Does protection from hunting favour genetic uniformity in the red fox? 76-83](#)