

Breeding strategies and genetic variation in European roe deer *Capreolus capreolus* populations

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Based on previously published electrophoretic data on genetic variability in 31 roe deer *Capreolus capreolus* Linnaeus, 1758 populations, the proportion of loci polymorphic (P), average heterozygosity (H), and the inbreeding coefficient (F_{IS}) were examined for relationships with the social structure displayed in the various populations. Our hypothesis was that genetic variability is lower and F_{IS} -values are more positive in populations where males maintain a stable pattern of territories during the rutting season (forest dwelling roe deer) than in those characterized by pronounced fluctuations in population structure, both within and among seasons (field or mountain dwelling roe deer). P and H did not show differences among those two groups. F_{IS} was significantly more positive in the 'forest' roe deer than in the more migratory 'type', but only when populations subjected to high culling rates were excluded from the analysis. Highly negative F_{IS} -values in forest populations with high culling rates suggested that considerable perturbations of population structure may be caused by hunting. In conclusion, the 'forest' roe deer and the 'field' roe deer do not represent two distinct ecotypes with a particular genetic integrity, but rather reflect the considerable behavioural plasticity of the species.

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Introduction

Roe deer *Capreolus capreolus* (Linnaeus, 1758) live in different social organizations. In woodlands, where resources are predictable, adult males maintain territories from spring until the end of the mating period in August; females and their offspring live in family clans. With increasing density, both the home range of clans and the territories of bucks overlap, and it is always one buck and several related females which form a one-male-family. In contrast, roe deer dwelling in the agricultural landscape constitute more or less open societies. The pattern of male territories is less stable or even absent, and family bonds are hardly maintained (cf Bresinski 1982, Stüwe and Hendrichs 1984). The same principle of social organization occurs in mountaneous areas closely to the climatic forest boundary where resources are subjected to seasonal fluctuations. According to these findings the

social organization of roe deer can be predicted to a high degree by habitat structure (Kurt 1968, 1991, Strandgaard 1972, Ellenberg 1978, Dzięciołowski 1979), and differences in social organization are reflected by breeding strategies. In forest dwelling roe deer only territorial males are rutting and females usually copulate with only one and the same buck (Ellenberg 1978). Thus, depending on population density, only about 20 per cent of all males contribute to the gene pool of the next generation, which should result in a certain degree of inbreeding. The latter may be increased by the maintenance of strict mother families, where contacts with unrelated females are avoided. In contrast, the mating system in populations of field and mountain dwelling roe deer is considered promiscuous. Territorial behaviour is less pronounced, there are no mother families, and females may copulate with a number of different males (Strandgaard 1972, von Bayern 1975, Geiger 1983). Consequently, a higher degree of panmixia is to be expected.

In the present study we examine migratory and territorial roe deer as to differences in genetic variability and the inbreeding coefficient between both groups. In particular, the existence of genetic peculiarities of the so called 'field' roe deer, which has been proposed to represent a distinct ecotype by Pielowski

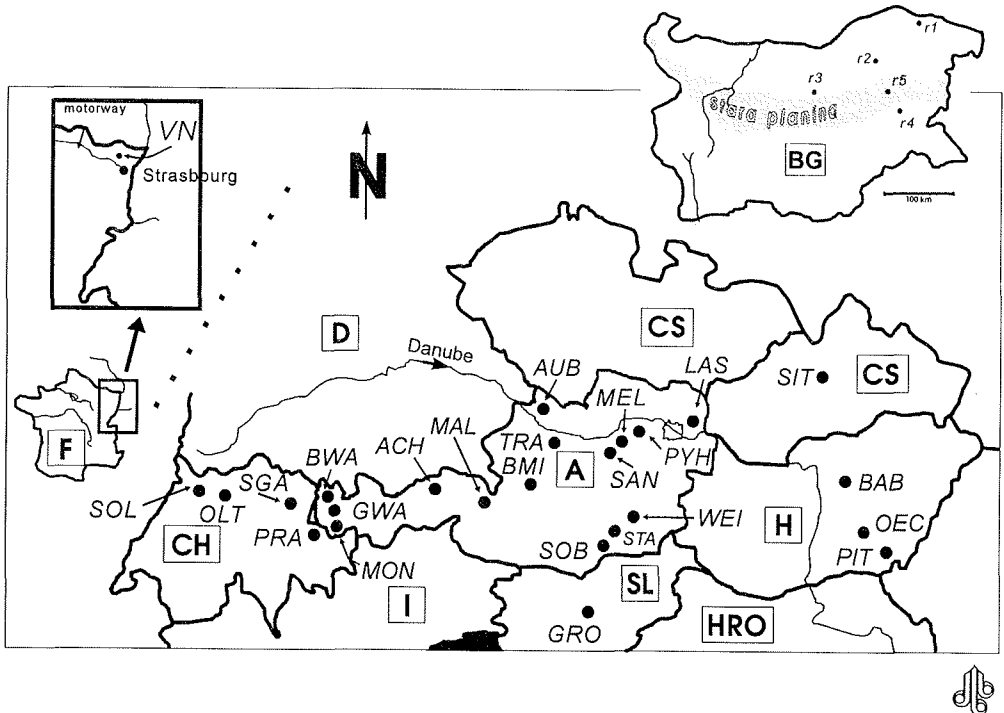


Fig. 1. Roe deer populations included in the present study. ACH - Achenkirch, AUB - Auberg, BAB - Babat, BMI - Bad Mitterndorf, BWA - Bregenzer Wald, GRO - Grosuplje, GWA - Großes Walsertal, LAS - Lasseer, MAL - Maria Alm, MEL - Melk, MON - Montafon, OEC - Öcsöd, OLT - Oltén, PIT - Pitvaros, PRA - Prättigau, PYH - Pyhra, SAN - St. Anton/J., SGA - St. Gallen, SIT - Sitno, SOB - Soboth, SOL - Solothurn, STA - Stainz, TRA - Traun, VN - Northern Vosges, WEI - Weiz, r1-r5 - Bulgarian populations.

(1977), and the genetic consequences of a high culling rate, disturbing a well established system of territories in forest dwelling roe deer are addressed.

Material and methods

Our study is based on data on allozyme variation gathered from 31 European roe deer populations by Hartl *et al.* (1991, 1993) and Gmeiner (1993) – see Fig. 1. Samples were divided into two groups (territorial and migratory roe deer, see Table 1) according to habitat structure. Roe bucks are territorial in forest habitats. These are defined as areas with more than 30 per cent of woody vegetation, which may be interspersed with meadows and groups of small fields with high crop diversity. Roe deer are expected to be migratory in sub-alpine and/or alpine habitats as well as in large, monotonous agricultural areas with less than 30 per cent of woodland.

Values of polymorphism (P , 99 per cent criterion), expected (H_e) and observed (H_o) average heterozygosity were taken from the papers cited above. The inbreeding coefficient (F_{IS}) was calculated according to Hartl (1988). In cases where a previous sample covered too large an area, we recalculated indices of genetic variation and the inbreeding coefficient for a geographically more homogeneous subsample (indicated by asterisks in Table 1). This seemed necessary to us, because estimates of F_{IS} may be influenced not only by the breeding structure of a population but also by geographic subdivision occurring within a sampling area. Differences of P , H_e , and F_{IS} between territorial and migratory roe deer were examined for statistical significance by means of the Mann-Whitney U -test.

Results

Values of P , H_e , and F_{IS} for all samples are listed in Table 1. H_e showed no difference between territorial and migratory roe deer whereas there was a tendency for P -values of being lower in the migratory group ($p = 0.058$). When all samples were considered, a difference in F_{IS} between territorial and migratory roe deer barely failed to be statistically significant ($p = 0.055$). However, when populations submitted to a high culling rate were excluded from the comparison, a difference in F_{IS} between both groups was statistically significant at $p < 0.001$. Thereby F_{IS} -values were largely positive in territorial and largely negative in migratory roe deer (see Table 1).

Discussion

The results obtained in the present study support our hypothesis that inbreeding should be more pronounced in forest than in field or mountain dwelling roe deer. However, this result became statistically significant only when samples from populations submitted to a high culling rate were excluded from the analysis. It is obvious from Table 1 that the culling rate is strongly associated with the unexpected occurrence of highly negative F_{IS} -values in some samples of the territorial group, which may be explained in the following way. Forty years ago central European hunters were interested in raising the density of roe deer populations, which had been strongly reduced by poaching during and immediately after World War II. The number of individuals killed in the course of regular

Table 1. Inbreeding coefficients (F_{IS}) in territorial and migratory roe deer. n – sample size, sources: 1 – Hartl *et al.* (1993), 2 – Hartl *et al.* (1991), 3 – Gmeiner (1993), * – subsample of GWA, ** subsamples of SGA, *** – subsample of PRA (see Hartl *et al.* 1991), **** – population with high culling rate. P and H_e are given in per cent.

Territorial (n)	F_{IS} (P, H_e)	Migratory (n)	F_{IS} (P, H_e)
Bulgaria r4 ¹ (23)	0.108 (17.5, 6.5)	Bulgaria r2 ¹ (21)	0.030 (17.5, 6.7)
Bregenzer Wald ² (16)	0.074 (15.0, 5.4)	Lasse ² (16)	0.023 (15.0, 4.3)
St. Anton/J. ² (48)	0.051 (17.5, 5.9)	Achenkirch ¹ (35)	0.0 (20.0, 4.5)
Bulgaria r5 ¹ (17)	0.048 (17.5, 6.9)	Melk ² (16)****	-0.009 (15.0, 3.4)
Grosuplje ¹ (19)	0.048 (17.5, 6.2)	Bulgaria r1 ¹ (33)	-0.016 (17.5, 6.2)
Feldkirch ² (17)*	0.047 (15.0, 4.2)	Bulgaria r3 ¹ (27)	-0.016 (17.5, 6.4)
Schaenis ² (12)**	0.030 (17.5, 3.9)	Pitvaros ² (26)	-0.023 (15.0, 4.4)
Sitno ¹ (16)	0.018 (17.5, 5.7)	Montafon ² (20)	-0.035 (17.5, 5.8)
Sonnhalb ² (10)**	0.004 (17.5, 4.8)	Bad Mitterndorf ² (19)****	-0.036 (15.0, 5.6)
Northern Vosges ¹ (36)	-0.024 (17.5, 4.1)	Babat ² (8)	-0.051 (12.5, 3.9)
Pyhra ² (23)****	-0.048 (17.5, 4.2)	Olten ³ (14)	-0.052 (15.0, 3.8)
Soboth ² (12)****	-0.049 (17.5, 8.1)	Prättigau ² (22)***	-0.066 (17.5, 6.1)
Auberg ² (9)****	-0.128 (17.5, 4.7)	Öcsöd ² (7)	-0.067 (12.5, 3.0)
Weiz ² (14)****	-0.139 (12.5, 3.6)	Traun ² (12)****	-0.087 (15.0, 4.6)
Stainz ² (30)****	-0.155 (17.5, 5.8)	Maria Alm ² (11)	-0.188 (15.0, 6.4)
		Solothurn ² (25)	-0.408 (15.0, 4.9)

hunting (until the sixties predominately bucks) increased continuously, but hardly exceeded the compensatory mortality until the seventies. During that time rather stable patterns of territories with increasing genetic differentiation among family

clans could establish in suitable habitats. Due to more and more hunters recognizing that the potential of roe deer for increasing population density had been grossly underestimated, hunting plans were further changed in favour of a high culling rate. By the end of the seventies, especially in several forest habitats the annual hunting bag was in the range of annual population increase. In the eighties, in some areas even a reduction of population density was achieved. The destruction of family clans by culling also a considerable number of fawns and high ranking old does led to alterations in the distribution of individuals among part of formerly well separated social groups. Given the establishment of one or the other allele at highly polymorphic loci in one or the other family clan, the above influence of hunting inevitably should have caused an excess of observed heterozygosity. Negative F_{IS} -values in the 'field' roe deer probably also reflect the reshuffling of temporarily separated 'sub-gene pools', but here this process is expected to occur in a natural and periodical way.

Since the electrophoretic data used in the present study had not primarily been collected for testing the hypothesis outlined in the present paper, it must also be considered that estimates of F_{IS} may be biased to some extent. Apart from considerable differences in sample sizes, several of the sampling areas represent transient habitats rather than being typical examples of a forest, field, or mountaneous habitat. Roe deer populations in such transient habitats display a transient social organization. Adult males try to maintain territories in forest patches, while females and juveniles tend to spread into the open, cultivated landscape, where groups consist of both related and unrelated members.

From a socio-ecological perspective, adult males are more conservative than females and their offspring (Strandgaard 1972, Geiger 1983, Turner 1983a). Due to differences in structure among particular transient habitats it is difficult to formulate explicit predictions as to F_{IS} -values, which are sufficiently distinct from those for territorial or migratory roe deer. Thus, in the present study samples from transient habitats have been considered either 'territorial' or 'migratory' by relaxing the criteria outlined in the material and methods section.

Concerning the question whether migratory roe deer from large agricultural areas, described as a new 'ecotype' by Pielowski (1977), are genetically different from forest dwelling roe deer, the following conclusions can be drawn from population genetic data. In spite of differences in F_{IS} between territorial and migratory roe deer, the extent of genetic diversity (H_e – see Nei 1975) within populations is the same. P -values in the migratory group are on the whole somewhat lower and more heterogeneous than in the territorial group, but this is rather the result of geographical differentiation (see Hartl *et al.* 1991, 1993) than a consequence of being migratory. Also the general presence of the same alleles and the very low genetic distances observed by Hartl *et al.* (1993) do not support the assumption of a particular genetic integrity of the 'field ecotype'. As suggested by Hofmann *et al.* (1988) and Markowski and Markowska (1988), the various morphological differences are rather due to environmental influences in conjunction with a broad

reaction norm. Turner (1979, 1983b) studied time budgeting of individually marked roe deer in a transient habitat and found that, dependent on the habitat type, each individual displayed different behavioural patterns. Thus, also the behaviour of roe deer reflects a high degree of adaptability of this species rather than a genetically well separated 'field ecotype'. Similar adaptability of behaviour and social organization has been described in several other deer species, such as the white-tailed deer *Odocoileus virginianus*, the sambar *Cervus unicolor*, the fallow deer *Dama dama* as well as in several bovids, such as the water buffalo *Bubalus bubalis* and a number of African species (Kummer and Kurt 1973, Estes 1974, Leuthold 1977, Hirth 1977, Kurt 1978, Apollonio 1989).

In view of these data it is questionable, whether the behaviour of 'field' roe deer actually reflects a very recent process of adaptation in a rapidly changing landscape as suggested by Pielowski (1977). Non-territoriality of adult males and open social groups may have been always present in certain habitats. Pronounced territoriality is a product of competition for resources and mating partners. It occurs only when the costs of marking and defending a territory are lower than the benefit obtained from living in discrete ranges, where intraspecific competition is reduced to that among closely related individuals. Such systems operate only in a habitat type where resources are abundant, permanently available and more or less equally distributed. These criteria are found in forest habitats with sufficient undergrowth, where territoriality increases the personal fitness of the owner. In habitats with seasonally changing resource availability, such as alpine areas, roe deer follow their resources according to seasons and stable patterns of territories can hardly establish. Similar organization occurs in riverine forests where resources are not predictable due to irregular inundations (Kurt 1991). In both habitats, breeding strategies are essentially the same as in 'field' roe deer with differences occurring only as to group size. The formation of large groups is an antipredator strategy in open areas with little cover (Eisenberg 1966) and not a particular breeding strategy. The ONF (outbreeding non-territorial fusion-fission system) strategy as displayed by 'field' roe deer probably occurred always in certain habitat types next to the ITO (inbreeding territorial one male family system) strategy. This assumption is supported by population genetic data.

The model of different social organizations of roe deer as discussed by Kurt (1991) clearly shows that in forest dwelling roe deer there is the tendency of an increasing population density to be accompanied by the formation of closer inbreeding groups. Thus, our results might also provide some explanation for the observation of several researchers that with an increase in population density, in the 'forest' roe deer the sex ratio of new born fawns becomes biased towards males. This phenomenon and its sociobiological significance has been discussed at length (Kurt 1968, Ellenberg 1978), but never under a genetical aspect. If inbreeding increases with density as well, the male surplus could be due to sex ratio depression as described by Senner (1980).

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