



Review

Evidence for separate specific status of European (*Capreolus capreolus*) and Siberian (*C. pygargus*) roe deer

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Receipt of Ms. 14. 06. 2000

Acceptance of Ms. 13. 09. 2000

Abstract

Two forms of roe deer, the European (*Capreolus capreolus*) and the Siberian (*Capreolus pygargus*), are widely recognised. Some authors consider these two forms as separate species, while others classify them as merely subspecies or races which are closely related. In this study, we compare the geographic distribution, morphological characteristics, karyotypes, biochemical variability, and potential for hybridisation of European and Siberian roe deer, addressing the question of their phylogenetic status. For most of historical times, the ranges of these two forms have been independent due to physical barriers such as glaciers or flooding. Overlap occurred for a time in the Middle Ages and again more recently, for the last few decades, but even then, the potential hybrid zone was small and hybrids are not thought to have persisted. The Siberian roe deer is substantially larger than its European counterpart in all body measurements, with only the very smallest Siberian individuals and the very largest European deer of approximately equivalent size. Furthermore, the two forms can be reliably distinguished on the basis of cranial shape, due to differential rates of growth of the skull, illustrating the hiatus in morphology between the two forms. All European roe have a karyotype of $2n = 70$, while Siberian roe possess between 1 and 14 additional accessory B-chromosomes, increasing clinally from west to east. Changes in karyotype seem to occur at physical boundaries, suggesting the differences are due to partial or total absence of gene flow. On the basis of polymorphism of several enzymes as well as blood and muscle proteins, the genetic distance between the two forms is characteristic of fairly reliable species.

A series of hybridisation experiments have illustrated that, although successful crosses can be achieved, they more often result in stillbirths or birth complications leading to the death of both mother and kid, and reduced or complete infertility among F1 hybrid bucks. It is likely therefore that hybridisation in the wild would be rare or absent, and that hybrids would not persist in the face of immigration of either pure form. We conclude that by all the criteria of classical systematics, the European and Siberian roe deer are separate, good, species, albeit phylogenetically closely related.

Key words: *Capreolus capreolus*, *Capreolus pygargus*, species status, systematics

Introduction

Although roe deer (*Capreolus* sp.) were once classified as belonging to the Cervinae subfamily, it now seems clear that they are in fact part of the Odocoileinae (GROVES and GRUBB 1987; GRUBB 1993). However, taxonomic relationships within this group are far less evident, in particular the status of the various geographical forms of the genus *Capreolus*. Roe deer cover an enormous geographical distribution, ranging from Great Britain and Spain to the Far East and from Kazakhstan and central Asia to northern Scandinavia and Siberia, and a large amount of data has now accumulated which reveals great variation of form over this range. This has led certain authors to suggest that the genus contains more than one species and perhaps several subspecific forms (CORBET 1978; DANILKIN 1986a; LEHMANN and SÄGESSER 1986). Here, we review published data on geographic distribution, morphometry, and genetics of *Capreolus* to conclude whether this genus is monospecific or not.

Geographic range

Fossil records suggest that both the European and Siberian roe deer forms have existed since the Pleistocene period (DANILKIN and HEWISON 1996). However, it seems that their geographical ranges remained independent due to the glaciation of the Russian plains and the Caspian Sea floods which extended far northward along the Volga. Once these barriers receded, the Siberian roe deer moved west, colonising the plains up to the Dneiper and possibly reaching the northern Caucasus in the Middle Ages (FLEROV 1952). Thus, more recently, prior to the twentieth century, the ranges of European and Siberian roe deer overlapped in a small part of their overall distribution, in the northern Caucasus and possibly also in the Dnepropetrovsk, Kirovograd and Orel regions (Fig. 1). Hybridisation may well have occurred here, but due to reproductive barriers (see below) and the predominance of the European form, they almost certainly did not persist. In

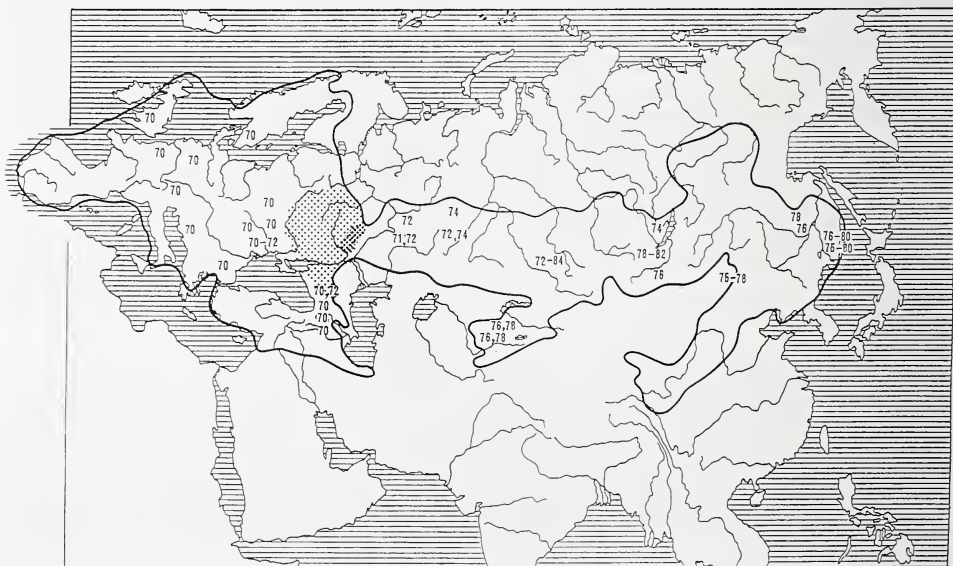


Fig. 1. The distribution of *Capreolus*, showing variation in chromosome number (70–84) across its present geographical range (black line), the extent of historical maximal overlap in range between the European and Siberian forms (▨) and of present day overlap (▧). The range of the European roe is to the left of this overlap zone and the range of the Siberian roe is to the right. Adapted from DANILKIN and HEWISON (1996).

modern times, reduction in range and numbers of the Siberian roe due to excessive hunting and the abundance of predators resulted in discontinuities in geographical range and isolation of the European and Siberian populations (DANILKIN and HEWISON 1996). However, numbers started to recover from the 1930s due to moderation of hunting and a warmer climate and the overall range increased once again. As recently as the 1960s, the advance westward of Siberian roe deer reached the Volga and subsequently the Koper and Don rivers in the Volgograd region, bringing European and Siberian deer into contact once more during the last couple of decades (Fig. 1).

Thus, the geographic ranges of the European and the Siberian roe deer have been largely independent for much of history, overlapping only in a restricted area during certain periods. The complete isolation of the ranges of these two forms has only very recently been bridged again and the potential hybrid zone remains very small with respect to the total geographic range. Furthermore, there is little evidence that hybrids have persisted in any area, probably due to reproductive isolation between the two forms. Despite the fact that a large number of Siberian deer have been used for introduction programmes within the European roe deer's range, only those introductions that took place where the European form was present in very low numbers or entirely absent have proved successful (DANILKIN and HEWISON 1996).

Morphology

Despite the fact that there is clearly substantial environmental influence on overall body size and weight of roe deer (e.g. GAILLARD et al. 1996; HEWISON et al. 1996 a, b), the European form is markedly smaller than the Siberian form in all body dimensions (Fig. 2), including size of antlers (European: length 17–26 cm, span 7–14 cm, Siberian: length >27 cm, span 17–20 cm) and skulls (condylobasal length: European 180–200 mm, Siberian 201–231 mm). Some over-

lap in size may occur between the very largest individuals of the European form and the very smallest Siberian roe deer, but more generally there is discontinuity in average size between adjacent populations at the range limits between these two forms. This discontinuity is due to differential rates of early growth and development: kids averaged 4 kg weight gain per month for European roe and 6 kg per month for Siberian roe when the two were kept together under identical environmental conditions (DANILKIN and HEWISON 1996). The difference persisted through to adulthood, when the Siberian roe weighed about 20% more in all seasons.

In addition to simple size variation, European and Siberian roe deer can be distinguished on the basis of cranial shape. Multivariate analyses of 905 skulls from populations over the entire geographical range have identified two well-differentiated morphs, the Siberian and the European (SOKOLOV et al. 1985 a). Again, this discontinuity appears early in life due to differential growth rates of the skull (SOKOLOV et al. 1985 b). There are also some indications from this type of analysis that further discrimination within each main group may be possible, particularly for the Siberian morph (northern Siberia and the Far East), perhaps supporting the designation of two or more subgroups (MARKOV et al. 1985 a; SOKOLOV et al. 1986 a; see also HEWISON 1997). An analogous analysis of antler characteristics was unable to distinguish clearly between European and Siberian forms, presumably because of the pronounced influence of age, condition and environmental factors on these structures which are regrown annually (DANILKIN and HEWISON 1996).

Genetic and biochemical variability

The karyotypes (chromosomal morphology) of European and Siberian roe deer differ dramatically. All populations of the European form are characterised by an identical karyotype of $2n = 70$, while all Si-

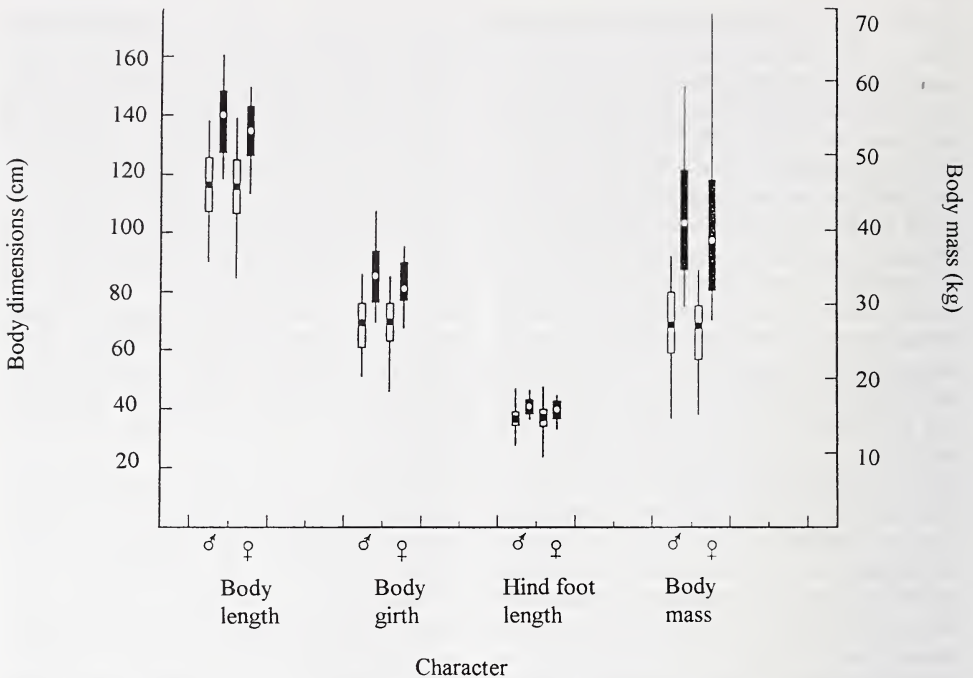


Fig. 2. Variation in total body length, body girth, hind foot length and body mass of European (white bars) and Siberian (black bars) male and female roe deer (adapted from DANILKIN and HEWISON, 1996). The central dot denotes the average value for each group, the bar gives the limits for population averages and the vertical line shows the range of extreme values of single individuals.

berian populations have karyotypes which contain 1 to 14 additional accessory B-chromosomes, $2n = 70 + (1-14)$ (DANILKIN 1985; SOKOLOV et al. 1986 b). Furthermore, the Siberian roe deer exhibits mosaicism, particularly in the Far East, where different numbers of B-chromosomes occur within different tissues of the same animal, as well as among individuals of the same population. In addition, all 35 pairs of the main set of chromosomes differ in length between the European and Siberian groups. The number of B-chromosomes present shows clear clinal variation, increasing steadily from west to east (Fig. 1). However, changes in karyotype across the geographic distribution of roe deer are abrupt and seem to occur at physical barriers such as mountain ranges. Hybridisation (see below) leads to inheritance of some B-chromosomes among offspring, but the number inherited is usually less than half the number

of the Siberian parent, probably due to unequal segregation during meiosis. At the notional boundary between the two forms in the Ukraine and the northern Caucasus, individuals both with and without B-chromosomes have been identified (DANILKIN and HEWISON 1996).

At the biochemical level, electrophoresis of certain enzymes has revealed differences in protein polymorphism between European and Siberian roe. Of 14 systems tested, 3 were polymorphic in the European sample, while only two were polymorphic in the Siberian sample and frequency differences between the two forms were found at one particular enzyme locus (SOKOLOV et al. 1986 c). Isoelectric focusing of blood plasma proteins has identified differences in the pre-albumin zone of the spectrum which are fixed, i.e. all Siberian individuals are different from all European roe. Similarly, differences are also present in the IEF spec-

tra of soluble proteins of the muscle tissue. These different protein fractions probably represent the products of alternative alleles for particular loci. Additionally, immunochemical investigations have indicated that the blood serum of European roe deer contains certain antigens which are characteristic of this group only and may also include two accessory antigens with very different molecular weights (MARKOV et al. 1985 b).

Hybridisation

A large number of introductions of Siberian deer into areas inhabited by European roe have been carried out with the aim of increasing body weights and improving trophy quality (DANILKIN and HEWISON 1996). Indeed, those hybrids that are able to survive are heavier and have larger antlers than the pure European form. However, it seems probable that such operations have proved unsuccessful (see above), with even the introduction of a substantial number (several dozen) of Siberian animals resulting in gradual but complete loss of the Siberian form.

Hybrid populations have not developed in the wild due to rather high level of reproductive isolation between the European and Siberian groups, illustrated by a series of experiments on captive deer. In the first experiments (STUBBE and BRUCHHOLZ 1979, 1980), two Siberian bucks were mated with a group of European does a total of 32 times. Of these matings, 13 did not result in pregnancy while 19 births were recorded. Caesarean delivery was necessary in 9 cases and another 3 required manual assistance due to the large size of the kid. The level of reproductive isolation between the Siberian and the European roe deer is clearly demonstrated by the fact that 10 subsequent matings between two F1 hybrid bucks and a group of hybrid does did not produce a single offspring. Indeed, it seems that many hybrid bucks are sterile, however, back-crosses between hybrid does and pure bucks of either form did produce viable offspring. Similarly, SOKOLOV and GROMOV (1985) found

Table 1. Some outcomes of experimental hybridization of Siberian and European roe deer (adapted from DANILKIN and HEWISON 1996)

Cross ¹	n	Result	
		Successful Mating ²	Normal Delivery ³
Sib. × Eur.	19	7	4
Eur. × Sib.	38	22	8
F1 × Eur.	4	3	2
F1 × Sib.	3	3	3
Eur. × F1	11	1	1
Sib. × F1	2	1	1
F1 × F1	10	0	–
BC1Sib. × Sib.	2	2	1
BC1Eur. × Eur.	2	2	–

¹Designations for crosses are: Sib. – Siberian roe; Eur. – European roe; F1 – first generation hybrid; BC1Sib. – progeny of F1 doe × Siberian buck cross; BC1Eur. – progeny of F1 doe × European buck cross; ²successful mating indicates embryos were produced; ³normal delivery indicates unassisted birth of live kids

that European roe does were unable to bare hybrid offspring, often dying in the process of giving birth, while all attempts to cross European bucks with Siberian does were unsuccessful. In yet another set of experiments, DANILKIN (1986 b) did succeed in crossing European bucks with Siberian does, however, this resulted in a high proportion of stillbirths. Overall, crosses between the two roe deer forms seems to be possible, but with a much lower level of success than that observed from normal reproduction, with about 20% resulting in the birth of live offspring without the need of some form of assistance (Tab. 1).

Discussion

Species are generally distinguished according to the independence of their geographical distribution, discontinuity in character variation and reproductive isolation. We have highlighted clearly here that the Siberian and the European roe deer have occupied geographically independent ranges during the vast majority of historical times.

The ranges of these two forms have come to overlap again since the 1970s, but this potential hybrid zone is very small with respect to the overall geographic distribution and is unlikely to have had substantial impact due to its recent occurrence. Introductions of the Siberian roe to sites within the range of the European form have generally proved unsuccessful and are of local importance only.

There is discontinuity in a wide variety of morphological or physiological characters between the European and Siberian forms, notably in body size, craniometry (SOKOLOV et al. 1985 a), including non-metric characteristics (ZIMA 1989), and basal metabolic rates (GRAYEVSKAYA et al. 1980), even between geographically adjacent populations. This discontinuity is also found at the tissue level as cytogenetic, immunochemical and biochemical differences (SOKOLOV et al. 1986 b, 1986 c) and may include a certain degree of histoincompatibility. Combining the results of studies of biochemical variation suggests that the genetic distance between the European and the Siberian groups is characteristic of fairly reliable species and indicates a rather high degree of reproductive isolation (see HARTL et al. 1998 for comparison of within species gene flow for European roe deer).

The roe deer phenotype seems to vary according to the number of B-chromosomes present, indicating a pivotal role for these accessory structures in roe deer taxonomy and providing a defining character for species designation. Indeed, patterns of B-chromosome distribution may indicate that roe deer originated in central Asia, perhaps in the Altai mountains, and therefore that the Siberian form is the more ancient. It seems likely that the modern European karyotype may have been greatly influenced by the glaciation of the Russian plains which curtailed gene flow, leading to accumulation of genetic differences between the European and Siberian forms and eventually to allopatric speciation and reproductive isolation, although the possibility that this simply represents clinal variation without speciation should be considered.

When crosses produce sterile offspring sub-genus status is generally accorded, while when offspring are fertile but have a reduced probability of survival and/or reproduction parental forms are considered good species. Hybrids of several other cervid species have been reported (WISHART 1980; BARTOS et al. 1981) and these are often fertile, forming hybrid populations in the wild (HARRINGTON 1985). However, the data summarised above clearly show that European and Siberian roe deer crosses are associated with a high proportion of stillbirths, the frequent death of both mother and young due to the inability of European roe does to give birth to large hybrid kids and a high level of sterility among hybrid bucks. Thus, in a potential hybrid zone in the wild, we might expect a low rate of successful mixed-pair reproduction and generally low productivity of the hybrid population.

Thus, there is overwhelming evidence for all the criteria of classical systematics that the European and the Siberian roe deer are two distinct species, albeit very closely related. The ecological similarities between the European and Siberian forms in feeding (differences in diet composition are essentially due to contrasting plant availabilities in Asia and Europe), behaviour (communication, sexual and maternal behaviour, ontogeny), social and spatial organisation (group size, family group structure, male territoriality) and dynamics underlines their extremely close phylogenetic relationship. Siberian roe deer are more adapted to living under extreme climatic conditions, particularly deep snow and prolonged periods of low temperatures (DANILKIN and HEWISON 1996). This may be a result, in part, of physiological differences in energy metabolism, including the presence and activity of regulating hormones such as the catecholamines and enzymes involved in metabolic functions such as glucose-6-phosphatase (GRAYEVSKAYA et al. 1980). The further division of this taxonomic group into the northern Siberian form (*C. p. pygargus*) and the southern Tien Shan form (*C. p. tianshanicus*) representing either separate species or subspecies is far less researched and can be

considered rather speculative in view of the current state of knowledge (DANILKIN and HEWISON 1996). Further research could usefully concentrate on the relationships between European and Siberian roe deer in

the zone of overlap (e. g. extent and consequences of hybridisation) in order to advance our understanding of their distinctiveness.

Zusammenfassung

Beweise für den Artstatus von Europäischem (*Capreolus capreolus*) und Sibirischem (*C. pygargus*) Rehwild

Beim Rehwild wird im allgemeinen die Existenz zweier verschiedener Formen, des Europäischen (*Capreolus capreolus*) und des Sibirischen (*Capreolus pygargus*) Rehs angenommen. Einige Autoren betrachten diese beiden Formen als eigenständige Arten, andere betrachten sie lediglich als nahe verwandte Unterarten oder Rassen. Im Hinblick auf eine Überprüfung des Artstatus werden in der vorliegenden Arbeit Ergebnisse über geographische Verbreitung, morphologische Merkmale, Karyotypen, biochemisch-generische Variabilität und die Fähigkeit zur Bildung von Hybriden zwischen dem Europäischen und dem Sibirischen Reh zusammenfassend gelistet und verglichen.

Über den Großteil ihrer Geschichte hinweg war das jeweilige Verbreitungsgebiet der beiden Formen durch Barrieren wie etwa Gletscher oder überflutete Landstriche separiert. Im Mittelalter und in den letzten Jahrzehnten gab es Überlappungen, aber auch dann war eine potentielle Hybridzone klein und es wird nicht angenommen, daß etwaige Hybriden längeren Bestand gehabt haben. Das Sibirische Reh ist in allen Körpermaßen deutlich größer als das Europäische Reh, wobei lediglich die kleinsten Sibirischen Rehe den größten Europäischen Rehen annähernd gleichkommen. Außerdem sind die beiden Formen als Resultat unterschiedlicher Wachstumsraten und aufgrund ihrer Schädelform verlässlich zu unterscheiden. Alle Europäischen Rehe haben einen Karyotyp von $2n = 70$, während die Sibirischen Rehe zwischen 1 und 14 akzessorische B-Chromosomen besitzen, in Anzahl klynal von West nach Ost ansteigend. Der Wechsel im Karyotyp scheint an geomorphologischen Barrieren aufzutreten, was auf ein partielles oder totales Fehlen von Genfluß zurückzuführen sein dürfte. Auf der Grundlage von Enzympolymorphismen und von genetischer Variation in Blut- und Muskeleiweißen liegt der genetische Abstand in einem Bereich, wie er üblicherweise zwischen validen Arten gefunden wird. Eine Serie von Kreuzungsversuchen zeigte, daß trotz des Vorkommens erfolgreicher Bastardierung, meist Totgeburten auftreten oder Komplikationen bei der Geburt zum Tod von Mutter und Kind führen. Außerdem gab es eine reduzierte oder vollständige Unfruchtbarkeit bei F1-Böcken. Das Vorkommen von Hybriden in freier Wildbahn dürfte daher selten oder überhaupt nicht möglich sein, und ein Überdauern von Hybriden wäre angesichts der Überzahl von Individuen der jeweiligen reinen Formen auch nicht wahrscheinlich. Wir schließen, daß nach allen Kriterien der klassischen Systematik das Europäische und das Sibirische Reh valide, wenngleich stammesgeschichtlich nahe verwandte Arten sind.

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

Jahr/Year: 2001

Band/Volume: [66](#)

Autor(en)/Author(s): Hewison A. J. M., Danilkin A.

Artikel/Article: [Evidence for separate specific Status of European \(*Capreolus capreolus*\) and Siberian \(*C pygargus*\) roe deer 13-21](#)