

Capreolus capreolus.

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Capreolus capreolus Linnaeus, 1758

European Roe Deer

- Cervus capreolus* Linnaeus, 1758:68. Type locality "Sweden."
Cervus capreolus albus Kerr, 1792:302. Type locality "Franche Comté, France."
Capreolus vulgaris Fitzinger, 1832:317. Type locality "Austria."
Capreolus caprea Gray, 1843:176. Renaming of *Cervus capreolus* Linnaeus, 1758.
Cervus capreolus plumbeus Reichenbach, 1845:3 Type locality "Germany."
Cervus europaeus Sundevall, 1846:184. Renaming of *Cervus capreolus* Linnaeus, 1758.
Capreolus vulgaris niger Fitzinger, 1874:247. Type locality "Germany."
Capreolus vulgaris varius Fitzinger, 1874:247. Type locality "Germany."
Capreolus transylvanicus Matschie, 1907:224. Type locality "Bana, Rumania."
Capreolus capreolus balticus Matschie, 1910:263. Type locality "Wichertshof, East Prussia."
Capreolus capreolus albicus Matschie, 1910:263. Type locality "Jesziorki, near Lissa, Poland."
Capreolus capreolus rhenanus Matschie, 1910:263. Type locality "Rouffach, Haut-Rhin, France."
Capreolus capreolus thotti Lonnberg, 1910:297. Type locality "Aberfeldy, Scotland."
Capreolus capreolus canus Miller, 1910:460. Type locality "Quintanar de la Sierra, Burgos, Spain."
Capreolus capreolus warthae Matschie, 1912:301. Type locality "Dombrowo, east of Beuthen, Poland."
Cervus (Capreolus) capreolus cistaunicus Matschie, 1913:139. Type locality "Dunnwald, north of Cologne, Germany."
Cervus (Capreolus) capreolus transvosagicus Matschie, 1913:139. Type locality "Staufen, in the Vosges, Eastern France."
Capreolus capreolus decorus Cabrera, 1916:175. Type locality "El Vierzo, Province of Leon, Spain."
Capreolus capreolus armenius Blackler, 1916:78. Type locality "Sumela, 30 miles south of Trebizon, N. E. Asia Minor."
Capreolus capreolus joffrei Blackler, 1916:79. Type locality "Ferrieres, near Paris, France."
Capreolus zedlitzii Matschie, 1916:272. Type locality "Slonim, Poland."
Capreolus coxi Cheesman and Hinton, 1923:608. Type locality "Zakho, Kurdistan, N. W. Persia." This locality is in what is now northern Iraq.
Capreolus capreolus italicus Festa, 1925:1. Type locality "R. Tentate di Castelporziano, Central Italy."
Capreolus capreolus grandis Bolckay, 1925:14. Type locality "Neighbourhood of Sarajevo, Yugoslavia."
Capreolus capreolus whittali Barclay, 1936:405. Type locality "near Alemdagh, 15 miles from Moda, Istanbul."
Capreolus capreolus garganta Meunier, 1983:147. Type locality "La Garganta, 60 km north of Cordoba, South Spain."

CONTEXT AND CONTENT. Context as in generic summary above. *Capreolus capreolus* is monotypic (Sokolov et al., 1992).

DIAGNOSIS. *Capreolus capreolus* is distinguished from *C. pygargus* (Siberian roe deer) by smaller size of body, cranium and antlers, by coloration of head and metatarsal glands, and by lack of B-chromosomes in chromosome set. Measurements for 11 different populations of *C. capreolus* ($n = 948$ – $2,801$ for body measurements and mass, $n = 598$ for skull measurements) compared

with nine different populations of *C. pygargus* (in parentheses; $n = 262$ – 299 for body measurements and mass, $n = 521$ for skull measurements) are as follows: total length, 107–126 cm (126–144 cm); shoulder height, 66–83 cm (82–94 cm); mass, 22–32 kg (32–48 kg); condylobasal length of skull, 179–200 mm (201–231 mm); maximum length of nasal bones, 51–66 mm (69–80 mm); length of lower tooth row, 61–67 mm (71–76 mm); maximum length of antlers, 184–258 mm (276–333 mm); and maximum antler-to-antler distance, 76–139 mm (168–257 mm—Danilkin et al., 1992).

Auditory bullae of *C. capreolus* are small, not protruding from bullar fossae; auditory bullae of *C. pygargus* are larger and noticeably protrude from the bullar fossae. In *C. capreolus*, when in summer coat, the superior aspect of the head is gray or brown, in sharp contrast with the reddish of the back and sides. Hair bases are gray-brown or dark-brown and the epidermis is light and unpigmented. In *C. pygargus*, the summer coat of the head, back and sides are monotonously reddish. Hair bases are light and the epidermis is brownish gray and pigmented (Flerov, 1952; Heptner et al., 1961). *C. capreolus* has a markedly lighter nose patch and the metatarsal glands are brown or dark brown (Meyer, 1968; Stubbe, 1990). Coloration of metatarsal glands of *C. pygargus* are reddish, similar to the trunk (Gromov, 1986).

C. capreolus has a diploid number of 70 chromosomes (Gustavsson, 1965); the karyotype of *C. pygargus* is $2n = 70 + (1\text{--}14)$ due to extra B-chromosomes (Danilkin, 1985; Sokolov et al., 1978). In contrast to *C. pygargus*, *C. capreolus* has two additional blood serum antigens (Markov et al., 1985). Unlike *C. capreolus*, *C. pygargus* occurs in Siberia (Heptner et al., 1961).

GENERAL CHARACTERS. *Capreolus capreolus* is a telemetacarpalian deer of small size (Fig. 1). Its front legs are shorter than the hind ones, the neck is long, there is no mane, the ears are fairly large (12–14 cm), the tail is rudimentary (2–3 cm), and there are no preorbital glands. Coloration in winter is grayish-brown to dark-brown, with a large white caudal patch. In summer, coloration is reddish to red-brown, the superior aspect of the head is gray or brown, metatarsal glands are brown or dark brown and the caudal patch is less pronounced than in winter or is absent. In Germany, there is a melanic European roe deer population. The fawns are spotted. Antlers are present only in males and are short (15–30 cm long) and close together at the base. There is no preorbital tine and basal rosettes or burrs are well-defined (Fig. 2). Antlers are shed annually in October and November (Flerov, 1952; Hell, 1979; Heptner et al., 1961; Stubbe, 1990). Mean measurements for 11 different populations for females ($n = 340$ – $1,270$ for body measurements and mass, $n = 322$ for skull measurements), with comparable values for males in parentheses ($n = 608$ – $1,531$ for body measurements and mass, $n = 276$ for skull measurements), are as follows: mean total length, 107–125.7 cm (108–126.5

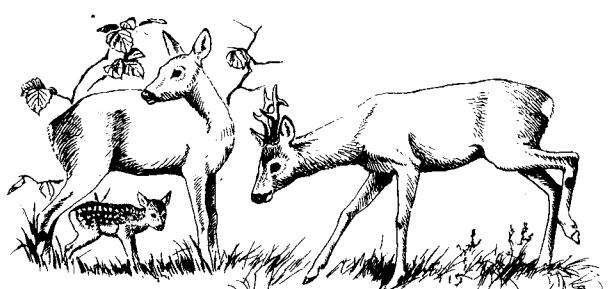


FIG. 1. *Capreolus capreolus* (right, adult male; left, adult female and fawn). Drawing by V. M. Gudkov.

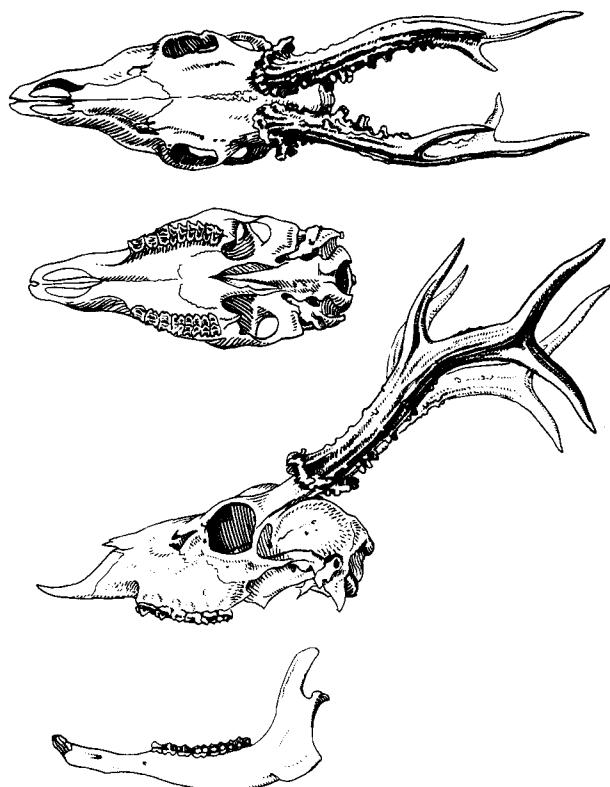


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Capreolus capreolus* from Mogilev district, Byelorussia (male, Museum of Moscow University, S-150060). Greatest length of cranium is 208 mm. Drawing by V. M. Gudkov.

cm); shoulder height, 66–83.3 cm (66–80.7 cm); body mass, 22.6–30 kg (23.7–32 kg); maximum skull length, 191–212.2 mm (193.3–212.6 mm); and maximum skull width, 84.3–91.5 mm (87.2–95.7 mm—Danilkin et al., 1992).

DISTRIBUTION. *Capreolus capreolus* ranges virtually throughout the whole of Europe (except the islands of Corsica and Sardinia, Ireland and the eastern margin of eastern Europe) and Asia Minor (Fig. 3). Between the late 19th and early 20th centuries, the distribution was greatly reduced due to human impacts (Heptner et al., 1961). In the 1960–1980s, conservation measures and more rational game management resulted in an increase in European roe deer. Its range was completely restored and extended northward, in particular in the Scandinavian Peninsula (Gill, 1990) and eastwards. In the interfluve of the Don, Khoper and Volga Rivers, its range overlaps (Fig. 3) with that of *C. pygargus* (Danilkin, 1992a).

FOSSIL RECORD. Based on skull and antler morphology, the genus *Capreolus* is likely to be descended from Pliocene species of the genus *Procapreolus* (Korotkevich, 1970, 1974). Forms of *Capreolus* similar to recent species were recorded in the late Pliocene–middle Pleistocene. Most of the fossil records are from the late Pleistocene and Holocene (Kahlke, 1956, 1958, 1960; Korotkevich and Danilkin, 1992). However, the scarcity of fossil remains and their inaccurate dating do not allow precise estimates of when *Capreolus* appeared in specific geographic areas. Perhaps *Capreolus*, as well as some other Pleistocene mammals, migrated to Europe from Asia (Kurtén, 1986). Pleistocene specimens from Europe are as large as *C. pygargus* (Kurtén, 1968). Nevertheless skeletal remains of a “big” *Capreolus* found in Europe (Boessneck, 1956) are within the range of characters peculiar to the European roe deer (Paaver, 1965), but they differ significantly from those of fossil *C. pygargus* (Kosintsev, 1981). Genetic differences between European and Siberian roe deer, which are accompanied by partial reproductive isolation (Danilkin, 1985; Gromov, 1986; Stubbe and Bruchholz, 1980), suggest a long period of divergent evolution that

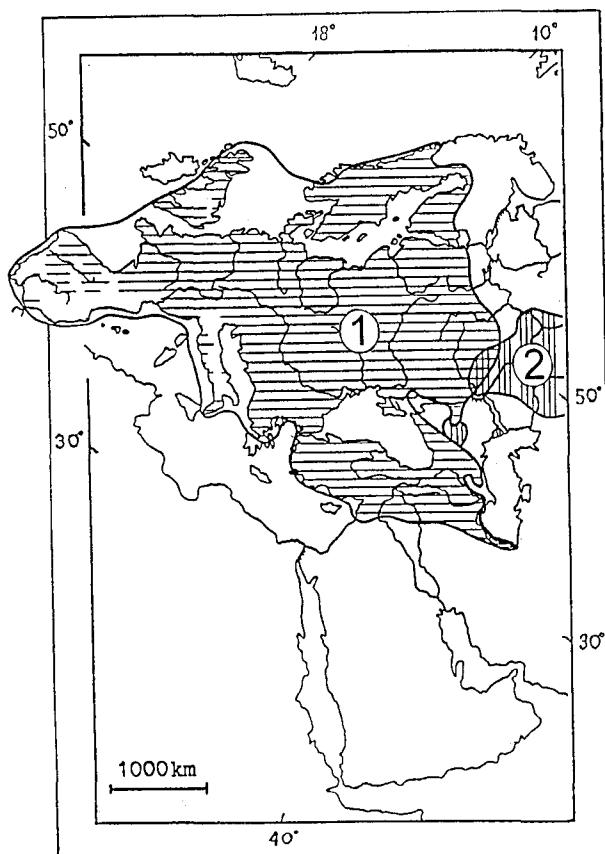


FIG. 3. Modern distribution of *Capreolus capreolus* (1), showing relationship to distribution of *Capreolus pygargus* (2).

perhaps reflects the occurrence of natural barriers between Europe and Asia during Quaternary glaciations.

Based on morphological and genetic characters (Baccus et al., 1983; Flerov, 1952), *Capreolus* are closer to Alcini and Odocoileini than they are to *Cervus* (Groves and Grubb, 1987). Telemetacarpalian Capreolidae are older than the plesiometacarpalian Pliocervinae (Bubenik, 1990).

FORM AND FUNCTION. *Capreolus capreolus* are small deer of light and slender build, with a relatively short trunk. The posterior part of the body is taller than the anterior. In terms of their size and body shape, European roe deer are most adjusted to life in tall dense grass and in low shrubs. Their hooves are narrow and fairly short, and the lateral digits are well developed. These characteristics make them well-adapted for travelling on soft ground. Molt occurs in spring and autumn. The skull is relatively broad, with a reduced facial portion. The lachrymal fossa is small, and the preorbital glands are rudimentary. The tympanic bullae are small (Fig. 2). The dental formula is: i 0/3, c 0/1, p 3/3, m 3/3, total 32. There are no incisors in the maxilla in most individuals (Flerov, 1952; Stubbe, 1990). The antlers normally have three tines and are used in fighting (Bubenik, 1990). In summer, males develop a thickened skin on the head, neck, and anterior portion of the trunk. The forehead has sudoriferous glands, the secretions of which serve for marking the territory. These glands are extremely reduced in winter and enlarged during the summer breeding season (Schumacher, 1936). Males react aggressively to the odor of these secretions in summer, but show no response in late winter (Broom and Johnson, 1980). Interdigital and metatarsal skin glands are well-developed (Meyer, 1968; Raesfeld, 1956). Interdigital glands are present in both sexes in the front and the back legs, but do not vary in size throughout the year (Johnson and Leask, 1977). The function of sebaceous glands is not well-defined, but Broom and Johnson (1980) suggest that odors from the metatarsal glands of European roe deer would be similar in function to the tarsal gland of black-tailed deer (*Odocoileus hemionus*; Muller-Schwarze, 1971). The olfactory organ is the most important of European roe

deer sensory organs. The olfactory surface of the nostrils measures up to 90 cm² (compared to 2.5 cm² in man) and olfactory cells number 300 million (compared to approximately 30 million in man; Kolb, 1979).

Although European roe deer clearly belong to the group of antlered telemetacarpalian deer (Groves and Grubb, 1987; Harrington, 1985), they exhibit some divergent characteristics. For example, *C. capreolus* does not have well-developed eye canthus glands. Also, adult males shed their antlers in autumn or early winter. The antlers may begin to regrow within a week (Sempéré, 1982) or after a delay of more than one month (von Barth et al., 1976; Schams and von Barth, 1982). However, in other telemetacarpalian species (*Odocoileus hemionus*—Markwald et al., 1971; *Rangifer tarandus*—Meschaks and Nordkvist, 1962; *Odocoileus virginianus*—Wislocki et al., 1947), antlers are usually shed from January to April and begin to regrow only in spring. In this respect they also differ from the plesiometacarpalian deer, whose antlers are shed in spring and always begin to regrow immediately (*Dama dama*—Chapman, 1975; *Cervus nippon*—Goss, 1983; *Cervus elaphus*—Lincoln, 1985). In *C. capreolus*, activation of gonads occurs in late winter (Sempéré and Boissin, 1981) or early spring (Schams and von Barth, 1982), whereas in other cervids it takes place in early summer (Bubenik, 1986). The mating period of European roe deer begins in late July and lasts less than one month (Bramley, 1970; Sempéré et al., 1989, 1992a, 1992b; Short and Mann, 1966; Strandgaard, 1972), whereas breeding in other deer occurs in early or late autumn (Lincoln, 1985).

ONTOGENY AND REPRODUCTION. Breeding activity in female *C. capreolus* occurs when the females are 14 months old. Males become sexually mature by the end of their first year of life. They begin to secrete LH and FSH within a few months after birth. This is followed by a testosterone increase and the occurrence of spermatogenesis when fawns are 7 months old (Sempéré et al., 1983). Males that weigh >16 kg by early winter (78%) exhibit two antler cycles. In the first cycle, 1-cm pedicles develop by early winter and are shed in January. A second set of antlers begins to grow immediately, attaining a length of 15 cm. Males that weigh 12 kg by early winter present only one antler cycle, with 3–5 cm antlers growing in spring (Sempéré, 1982). Despite attaining sexual maturity by one year of age, males are not likely to begin breeding until the third year of life (Borg, 1970; Ellenberg, 1978; Sempéré, 1982; Wandeler, 1975).

Mass and volume of testes of adult males vary seasonally; in winter, they average 5 to 10 times smaller than in the summer breeding season (Bramley, 1970; Sempéré and Lacroix, 1982; Short and Mann, 1966; Stieve, 1950). Although spermatogenesis ceases after the rut, fertilization is possible until the end of October (Short and Mann, 1966). An increase in gonadotropic hormones in January is followed by a rise in testosterone one month later (Sempéré and Lacroix, 1982; Sempéré et al., 1992a, 1992b). By March (in France), mature spermatozoa are present (Sempéré, 1982). Thus, European roebucks are physiologically capable of reproduction from March to October. However, the rutting season is largely restricted to June–August, and occurs earlier or later only in few individuals (Aitken, 1974; Bramley, 1970; Kurt, 1970; Short and Mann, 1966; Stieve, 1950).

Female European roe deer are monestrous, with duration of estrus typically being 36 h (Strandgaard, 1972). In female *C. capreolus* held in captivity during the breeding season in the absence of a male, the corpus luteum secretes progesterone continuously from July to March (Hoffmann et al., 1978; Schams et al., 1980). If the corpus luteum is destroyed during this period, a new corpus luteum can be induced spontaneously, demonstrating that the estrous season could potentially extend until early spring (Sempéré et al., 1992b).

The reproductive cycle and breeding period differ significantly from those of closely related ungulate species in that gestation proceeds in European roe deer only after a unique embryonic diapause. The fertilized ovum at the morula stage penetrates into the uterus where it quickly divides, reaching a blastocyst stage 0.1 mm in diameter. This is followed by 4–5 month period with minimal mitotic activity and slow development, resulting in a blastula 5 mm in diameter (Aitken, 1974). Delayed implantation in European roe deer, in contrast to Mustelidae, is not a function of photoperiod (Lincoln and Guinness, 1972). It is controlled by the development of the blastocyst itself, and not by the formation of an anatomical

link between the blastocyst and the uterus. Implantation of the embryo normally occurs in January. Late pregnancy is characterized by rapid growth of the embryo (Aitken, 1974, 1981; Aitken et al., 1973; Sempéré, 1982; Sempéré et al., 1989; Short and Hay, 1966; Wandeler, 1975).

The gestation period is between 264 and 318 days and fawns are born between April and July. The new-born fawns (normally two, occasionally three or one) weigh 1–1.7 kg, are furred, and have vision (Ellenberg, 1978; Kurt, 1970; Prior, 1968; Rieck, 1955; Sagesser, 1968; Sagesser and Kurt, 1966; Wandeler, 1975). During the first days of life the fawns are virtually helpless and hide continuously even without danger, but fall easy prey to predators. The female nurses the fawns during the early months of life, usually in turn. She feeds them 5–9 times a day during the first month, 2–4 times during the second month, and subsequently 1–2 times (Espmark, 1969). Lactation usually declines in August and ceases in early autumn, but occasionally occurs through December (Sempéré et al., 1988). At weaning, the fawns feed completely on vegetation, which they had begun to eat as early as the first 5–10 days of life (Bubenik, 1965; Kossak, 1981). Growth is rapid, with fawns doubling their birth mass by 2 weeks of age. By autumn, 60–70% of the body mass of adult individuals is attained (Gromov, 1988; Stubbe, 1990).

ECOLOGY. *Capreolus capreolus* prefers forest-steppe and small insular forests among croplands, as well as high-grass meadows with some shrubs. In forestlands revegetating burns and cutovers are especially preferred, as are croplands (Hell, 1979; Piełowski, 1970; Raesfeld, 1956; Zejda, 1978). Historically, human modification (felling of trees, formation of meadows and croplands, planting forest belts in the steppe) and intensive methods of agriculture have been beneficial to these ungulates in regions with little snow. Compared with other species, European roe deer are the best adapted to modern agroecosystems (Zejda and Danilkin, 1992).

Within their range, *C. capreolus* consume approximately 1,000 plant species; of these, woody plants constitute about 25%, herbaceous dicotyledons 54%, and monocotyledons 16% (Holíšová et al., 1992). European roe deer are very selective feeders, preferring soft, energy-rich foods containing much water. The small volume of the stomach and relatively rapid process of digestion require frequent food intake (Eßer, 1958; Kurt, 1970; Něcas, 1975). The proportions of plant types and of individual species in the European roe deer diet vary with habitat and seasonality. In winter, forage reserves sharply decline and the diet becomes less diversified. Concurrently, metabolic rate and food consumption also decline. In spring (with the onset of plant growth), the process of digestion accelerates, metabolic rate increases, and energy requirements increase, reaching a sustained peak during the rutting season, at the end of gestation, and during lactation. In autumn, European roe deer prefer concentrated foods, such as seeds and fruits. However, recent studies have shown that adult European roe deer do not exhibit significant seasonal variations in body weight. Kidney fat and bone marrow fat constitute the main fat reserves in animals living in northern (Holland, 1992a, 1992b; Holland and Staaland, 1991) or in temperate oceanic climates (Boutin, 1994). Fat reserves are minimal in summer during rut, whereas all reserves (kidney and bone marrow) are restablished in late autumn. This stored energy promotes survival during potentially critical late winter and early spring periods (Drozd, 1979; Ellenberg, 1978; Holíšová et al., 1992; Něcas, 1975; Weiner, 1975, 1977).

During summer, animals are either solitary or live in family groups (females with offspring), but in winter almost all are found in family groups. The family group forms the basis for population social organization (Kurt, 1968; Raesfeld, 1956) with members usually staying together throughout the winter (Bideau et al., 1983a; Danilkin and Minayev, 1988). The composition of large groups changes continually (Strandgaard, 1972). Group size may be as large as 40–90 in open biotopes, whereas groups in forest biotopes are smaller and only occasionally include 10–15 members. The average group size increases with increasing population density, falling temperature and deepening snow cover, as well as with decreasing feeding grounds. Hence the social organization of the European roe deer population depends largely on abundance and distribution of food resources and cover (Bramley, 1972; Bresinski, 1982; Reichholt, 1980; Zejda, 1978).

Spatial structure of populations varies seasonally. During summer, animals are dispersed throughout the territory, but during winter,

ter European roe deer concentrate in foraging ranges and their distribution is aggregated (Danilkin and Minayev, 1988). *Capreolus capreolus* is essentially sedentary (Stubbe, 1990). Every spring, adult males (>2–3 years of age) hold the same territories, which they mark with olfactory-optical cues on vegetation and soil until the end of the breeding season (Sempéré et al., 1980). Vegetation structure influences the intensity of scent marking, which is more frequent in fields or forests than in dense brushy vegetation where visibility is limited (Sempéré, 1982). The right to hold territory is asserted in fights with competitors every year. However, the establishment and control of neighboring territories involves little direct contact with the adult male that held the same territory during the previous year. However, fights are frequent between an adult in one territory and a young male that wants the neighboring territory (Sempéré, 1982). Moreover, the territory occupied by a new dominant male may coincide with that of the displaced male or this territory could be separated in two parts by two young males, which strongly confirms the rigidity of the territorial system in European roe deer (Bramley, 1970; Sempéré, 1982). The size of male territories varies from 2 to 200 ha, depending on habitat quality and population density. The majority of yearlings and some two-year-old males have no constant territories, are ousted by adult males, and provide a reserve of potential breeders (Bideau et al., 1983b; Bobek, 1977; Bramley, 1970, 1972; Cederlund, 1983; Danilkin, 1992b; Kurt, 1968; Strandgaard, 1972). The territorial system in place from March to late August allows dominant males total control of included resources, including access to adult females. The success of this social structure is reflected in the extremely high fertility rate observed in a natural populations (98%—Gaillard et al., 1992).

About a month before parturition, adult females occupy family ranges that are several hectares in size and in the same location as the previous year. At the time of parturition, a female will separate from the group and may defend a portion of the range against other females. The choice of the family range is determined by protective and foraging conditions and also by the vicinity of water. The majority of females remain near their familiar ranges to the end of the breeding season, and usually mate with the male holding the territory where their ranges are situated. Female home ranges and male territories may coincide or the female home range may extend over territories of two or more males (Cibien and Sempéré, 1989). In the latter situation, the female chooses her mate. Thus, the basis of spatial structure of the European roe deer population during the breeding season is “complex family” ranges, consisting of several, normally closely related females and their offspring, attached to the territories of specific males (Bramley, 1970, 1972; Cederlund, 1983; Kurt, 1968, 1970; Strandgaard, 1972). In winter, individual and group home ranges overlap widely and normally exceed 300–500 hectares (Cederlund, 1982, 1983; Danilkin, 1992b; Ellenberg, 1978; Maublanc et al., 1987; Vincent et al., 1983; Zejda and Bauerova, 1985; Zejda and Homolka, 1980).

The life-span of an individual in a natural population is about 10 years (Andersen, 1953; Pielowski and Bresinski, 1982; Pikula et al., 1985), but some individuals may reach 15–17 years (Strandgaard, 1972; Stubbe and Passarge, 1979). Females continue to breed until near the end of their life-span (Gaillard et al., 1992; Sempéré et al., 1989). The sex and age structure of the population varies with season. The sex ratio in fawns is close to 1:1 (Borg, 1970; Kurt, 1970), adult sex ratios approximate 1 male:2 females. This shift is caused by social autoregulatory processes and increased mortality of males (Ellenberg, 1978; Strandgaard, 1972). The proportion of juveniles in the population immediately after fawning can reach 50%, but by the next spring juveniles constitute 15–35%. The sex and age composition of exploited populations are essentially a function of the level of hunting pressure on particular age and sex classes (Bluzma, 1975; Fruzinski and Labudzki, 1982; Pielowski and Bresinski, 1982; Strandgaard, 1972).

C. capreolus is mainly preyed upon by wolf (*Canis lupus*; Bluzma, 1975; Gaross, 1979), lynx (*Lynx lynx*; Brietenmoser and Haller, 1987; Bubenik, 1966; Hell, 1979; Randweer, 1985), and to a lesser extent by fox (*Vulpes vulpes*), which mostly kill fawns (Borg, 1962; Raesfeld, 1956; Stubbe and Passarge, 1979). The main competitors are domestic ungulates and the red deer (Skriba, 1975; Smoktunovich, 1980, 1983; Vladishevskii, 1968).

The European roe deer is susceptible to infections and parasitic diseases, most of which are common in many species of wild and domestic ungulates (Necas, 1975). The main infectious dis-

eases are rabies, foot-and-mouth diseases, lymphatosis, Aueski disease, anthrax, pasteurellosis, tuberculosis, brucellosis, necrobacillosis, actinomycosis, and aspergillosis. Of parasites, the most important are as follows: *Fasciola hepatica*, *Dicrocoelium dendriticum*, *Paramphistomum cervi*, *Monoczia expansa*, *Cysticercus tenuicolleis*, *Cysticercus cervi*, *Echinococcus milocularis*, *Echinococcus cystis*, *Haemonchus contortus*, and worms of the genera *Ostertagia*, *Trichostrongylus*, *Nematodirus*, *Bunostomum*, *Dityocaulus*, and *Capreocaulus* (Borg, 1970; Raesfeld, 1956; Stubbe and Passarge, 1979).

Capreolus capreolus is the most abundant wild ungulate species in Europe (Gill, 1990). During the second half of the 1980s, an area of 6 million km² supported about 7–7.5 million. The European roe deer population in some countries is excessive, leading to declines in size and body mass and deterioration of antler quality, while in Russia and Ukraine the populations are almost an order of magnitude lower than optimum (Danilkin and Blusma, 1992). In the western part of the range, where game management is practiced, population density is mainly determined by anthropogenic factors (Turner et al., 1987), with hunting and loss from motor vehicles (8–27%; Eiberle, 1972) and farm machines in the agroecosystems (<5 individuals/100 ha) being the most important (Beklova et al., 1982; Engl, 1982; Stubbe and Passarge, 1979). Among natural mortality factors, parasitic diseases have greatest impact where population density is high. Mortality from predation is less important, although foxes prey extensively on European roe deer fawns in some areas. Comparatively rare severe winters bring about increased mortality of weakened animals (predominantly young and old individuals and those infected by parasites or disease), somewhat compensating for the absence of selection otherwise exerted by predators (Stubbe and Passarge, 1979). In the northern portions of the range, natural mortality from exhaustion increases. The incidence of disease is low, but the role of predators increases, in particular during the years with much snow. In the eastern part of the range, the major factors influencing European roe deer numbers are large predators and poachers. Mortality from disease and parasites in populations with low density is negligible. Since it is mainly juvenile and old individuals that die during the winter, game management recommendations include the autumn harvest of these age classes, with maximal retention of highly productive middle-aged animals (Danilkin and Blusma, 1992).

BEHAVIOR. The activity of *C. capreolus* is conditioned by numerous factors and varies during the year, season, hour of day and with sex, age, extent of stress, availability of forage, weather conditions and other factors. Nevertheless, during the day European roe deer display some definite periodic behavioral patterns: grazing and displacement alternate with rest and rumination, normally from 6 to 12 times a day. Morning and evening periods of activity are practically always manifested and they are of greatest duration (Berg, 1978; Cederlund, 1981; Sempéré, 1982; Turner, 1979, 1980; Vincent et al., 1979).

In their first days, European roe fawns' active periods coincide with feedings that last for about half an hour. Fawns stand up only when their mother comes up to them and lie down as soon as she goes away; as early as their second week, they walk several minutes before and after suckling without their mother beside them. In the first two or three weeks, a doe with more than one fawn feeds them one at a time in rotation. Later, the mother mostly feeds her fawns together, but the feeding periodicity remains. In the first month, it may be as high as five to nine meals per day; in the second month, it is 2–4 meals per day; later it decreases to one to two meals, but the time of family members' joint activities increases. The length of active periods increases from 1–1.5 h (1–2 months of age) to 1.5–2 h (>2 months of age). About half of this activity occurs in their mother's absence, with fawns grazing near the breeding site. Although the number of milk meals gradually decreases, the number of active periods remains nearly the same (5–7 periods per day). The synchronization of family (mother and fawns) activities takes place only when fawns are >2.5–3 months old (Bubenik, 1965; Danilkin, 1992c; Dathe, 1966; Espmark, 1969; Kurt, 1968, 1970).

European roe deer females are aggressive toward other individuals that approach their offspring during the first 1–2 weeks after parturition. Social relationships between does and their adult progeny are severed 2–4 weeks before a new generation is born. This estrangement results from increased aggressiveness of mothers

toward all adults that occupy the portion of the range in which fawning occurs (Esmark, 1969; Kurt, 1968).

Aggressive behavior of bucks coincides with cleaning of velvet from antlers and with marking activities. Most aggressive encounters take place during seizure of territories and before rut (Sempéré et al., 1980; Sempéré, 1982). Adult bucks are especially intolerant of aterritorial animals. The emigration of young animals from places where they were born is largely caused by the aggressiveness of adult bucks who drive them from their territories (Sempéré, 1982; Strandgaard, 1972). Conflicts between neighboring territorial bucks are comparatively rare (Sempéré, 1982). The conflict behavior of European roe deer is largely ritualistic (Ellenberg, 1978; Kurt, 1966, 1968; Meyer, 1968). After the reproductive period, *C. capreolus* aggressiveness markedly declines and may disappear. In winter, all free-ranging group members may feed together without being noticeably antagonistic to each other. Nevertheless, antagonism is observed in places where animals congregate, such as at feeding racks and in supplementary feeding grounds (Esmark, 1974).

From spring through autumn European roebucks identify their ranges with olfactory and optical marks (Kurt, 1966, 1968; Raesfeld, 1956; Sempéré et al., 1980). During this time, daily movements are determined by the necessity for patrolling and marking territory (Sempéré, 1982). Olfactory marks are made with a secretion of skin glands, which swell in summer. The secretion is applied by rubbing the forehead, cheeks and neck against trees, shrubs and high grasses. Optical marks consist of trees that are frayed with antlers. Other substances informing of European roe deer's presence, age, sex, and physiological status are urine, feces, and saliva, as well as scented secretions of sexual organs, metatarsal and interdigital glands. These substances are deposited on the ground and vegetation during feeding and licking (Meyer, 1968).

In the rutting period, the territorial system is not generally violated. The European roe deer's rut usually lasts for 2 to 5 days (Kurt, 1968, 1970; Sempéré, 1982; Stubbe, 1990). The buck stops feeding (Lochman et al., 1961), becomes careless and does not leave the doe even when danger is apparent. In the first day of the rutting period, males, especially young ones, are quite aggressive toward does, even to the extent of beating them with antlers. After a continuous and long chase in large circles, the tired doe begins running around trees, shrubs, high hummocks, pits and, exhausted, she stops and allows the equally tired male to mate, whereupon both lie down to rest. Following the same path repeatedly results in runs with a circular or figure-eight configuration (Danilkin, 1992c; Raesfeld, 1956; Stubbe, 1990).

Vocal signals play an important role in the social life of *Capreolus capreolus*. Five main types of signals can be discerned: squeaking (or whistling), rasping (panting), barking, screaming, and sounds of non vocal origin. At an early age, European roe deer seemingly have only one type of acoustic signal—squeaking (Meyer, 1968; Stubbe and Passarge, 1979). These sounds are similar to those of Siberian roe deer and also function to maintain contact between fawns and their mothers, suggesting that *C. pygargus* and *C. capreolus* are closely related. However, European roebucks are not known to produce the whining sound made by some Siberian roebucks (Sokolov and Danilkin, 1981). Squeaks produced by European roe deer fawns are higher in pitch than those of Siberian roe deer fawns (Sokolov et al., 1987).

Exploratory and defensive behaviors are composed of individual elements such as orientation posture, signal jumps, flight reaction, approaching other individuals, search for and identification of the stimulus, escape, and hiding. In particular situations, some of these elements may be absent or their sequence can vary (Kurt, 1968, 1970; Raesfeld, 1956). The olfactory organ is the most important sensory organ. Of 42 elements of social behavior, 26 are triggered by olfactory perception, 13 are provoked by acoustic perception, and only three are caused by optical perception, which confirms the supposition that these animals have a fine sense of smell and relatively poor vision (Kurt, 1968). When danger threatens, group members follow a leader (mostly an adult female) in flight (Bresinski, 1982).

GENETICS. All populations of *Capreolus capreolus* studied display an identical chromosome set: $2n = 70$, NF = 72. Sex chromosomes of females are XX, those of males XY. All autosomes are acrocentric, whereas both sex chromosomes are submetacentric. Karyotypes are stable with an identical number of chromosomes in

all animals (Amrud and Nes, 1966; Danilkin, 1985; Gustavsson, 1965; Gustavsson and Sundt, 1968; Sysa and Kaluzinski, 1984; Wurster and Benirschke, 1967; Zima and Harvankova, 1987).

With 30% polymorphic loci and 4.9% average heterozygosity, *C. capreolus* is one of the genetically most variable deer species studied (Hartl et al., 1991).

REMARKS. Taxonomy of the genus *Capreolus* needs revision. A century ago, different authors distinguished up to four species in the genus; at present the European roe deer is considered to be either a monotypic species, or a species containing numerous subspecies (Ellerman and Morrison-Scott, 1951; Flerov, 1952; Heptner et al., 1961; Lydekker, 1915; Miller, 1912; Stubbe, 1990). We favor the monotypic concept. Nevertheless, we call attention to *C. c. garganta* Meunier, 1983 from the south of Spain. This subspecies differs from typical European roe deer in having gray summer coloration and a large white patch, as well as in some body proportions. Systematic study is needed to determine the placement of this population.

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