Capreolum pygargus, 1821

Capreolum Grzv. 1775:2.
Capreoa Ogilby, 1836:135.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Family Cervidae, Subfamily Odocoileinae, Tribe Capreolini (Simpson, 1945). The genus Capreolum presently includes two extant species: Capreolus pygargus and Capreolus capreolum (Sokolov et al., 1992). A key to species follows:

Size moderate to large, coloration of head and metatarsal glands generally not different from trunk, beams of antlers set far apart, chromosome set exhibits B-chromosomes.

Size small, head and metatarsal glands darker than trunk, beams of antlers not far apart, chromosome set has no additional B-chromosomes.

Capreolus pygargus

Capreolum pygargus Pallas, 1771

Siberian Roe Deer

Cerus pygargus Pallas, 1771:453. Type locality "Right bank of river Sok, Trans-Volga area, Russia."

Capreolum tianschanicus Satunin, 1906:527. Type locality "Kuldja, Tien-Shan."

Capreolus bedfordi Thomas, 1908:645. Type locality "Mt. Chao-Cheng-Shan, 100 miles west-north-west of Taiyuanfu, Shansi, China."


Capreolus pygargus Pall. var. caucasica Dinnik, 1910:66. Type locality "Northern Caucasus."

Capreolus melanotis Miller, 1911:231. Type locality "Thirty miles east of Ching-yang-fu, Kansu, China."

Capreolus capreolum ochraceus Barclay, 1935:627. Type locality "Korea."

CONTEXT AND CONTENT. Context as in generic summary of the genus Capreolus. Two well-defined subspecies of C. pygargus are recognized (Danilkin, 1989a; Sokolov et al., 1992):


DIAGNOSIS. Capreolus pygargus is distinguished from C. capreolus by larger size of body, cranium, and antlers. Here measurements for nine C. pygargus populations (body measurements, and body mass from 282–299 individuals per population, n = 521 for skull measurements), with comparable values for eleven C. capreolus populations (body measurements and body mass for 948–2,801 individuals per population, n = 598 for skull measurements) in parentheses, are as follows: total length, 126–144 cm (107–126 cm); shoulder height, 82–94 cm (66–83 cm); body mass, 32–48 kg (22–32 kg); condylobasal length of skull, 201–233 mm (179–200 mm); maximum length of nasal bones, 69–80 mm (51–66 mm); length of lower tooth row, 71–76 mm (61–67 mm); maximum length of antlers, 276–333 mm (184–258 mm); maximum antler-to-antler distance, 168–257 mm (76–139 mm; Danilkin et al., 1992b). Auditory bullae of deer are larger and noticeably protrude from the bullar fossa.

Capreolus pygargus also differs from C. capreolus in coloration of the head and metatarsal glands. In C. pygargus, the summer coat of the head is uniformly reddish or grey-reddish, but in C. capreolus, it is gray or gray-brown (Flerov, 1952; Hemptner et al., 1961). C. capreolus has a light nose patch (lacking in C. pygargus) and brown or dark-brown metatarsal gland hair (Studhe, 1990). Metatarsal gland hair of C. pygargus is reddish (Gromov, 1986).

The karyotype of C. pygargus exhibits an extra B-chromosome (Danilkin, 1985b; Sokolov et al., 1978) that is lacking in C. capreolus (Gustavsson, 1965). GENERAL CHARACTERS. Siberian roe deer are telemetacarpalian of moderate size (Fig. 1). Their front legs are shorter than the hind ones, the neck is long, there is no mane, the ears are fairly large (15–15 cm), and the tail is rudimentary (2–4 cm), as are the preorbital glands. The winter pelage in northern populations is light gray, but grayish-brown and ochraceous in southern populations. The belly is creamy. The caudal patch is white. In summer, the coat is reddish and the white caudal patch is less pronounced or absent. Young are spotted.

Males are slightly larger than females and have three-tined antlers (Fig. 2), which are widely spaced at the base, slant upward, and are strongly tuberculated. Antlers are shed in autumn or early winter and begin to regrow immediately after shedding (Flerov, 1952; Hemptner et al., 1961; Smirnov, 1978). Mean measurements from nine different populations for females (body measurements and body mass from 124–137 individuals per population, n = 220 for skull measurements), with comparable values for males (body measurements and body mass for 158–162 individuals per population, n = 301 for skull measurements) in parentheses are as follows: total length, 126.7–144.4 cm (128.1–143.8 cm); shoulder height, 81.7–91 cm (83.1–94.1 cm); body mass, 32–46.9 kg (34.9–48.6 kg); maximum skull length, 219.3–238.8 mm (213.8–244.1 mm); maximum skull width, 92.2–99.5 mm (94.8–106.1 mm; Danilkin et al., 1992b).

The two subspecies of Siberian roe deer are morphologically and genetically distinct. Mean measurements from three different populations of C. p. pygargus (n = 102 for body measurements and body mass n = 182 for skull measurements) with comparable values for five populations of C. p. tianschanicus (body measurements and body mass for 141–173 individuals per population, n = 259 for skull measurements) in parentheses are as follows: mean total length, 140–144 cm (126–137 cm); body mass, 41–48 kg (32–40 kg); condylobasal length of skull, 223–251 mm (201–218 km). FIG. 1. Male Capreolus pygargus from Tien-Shan area. Photograph by A. Danilkin.
massifs are a considerable barrier. There is a discontinuity in the range caused by the Altai, western and eastern Sayan Ranges, Lake Baikal, Stanovoi Plateau and Stanovoi Range (Fig. 3). Ecogeographical isolation has promoted morphophysiological differentiation of northern and southern populations of deer, which are recognized as being subspecifically distinct (Danilkin, 1989b, 1992d).

**FOSSIL RECORD.** Similarities in skull, tooth, and antler morphology suggest that Pliocene species of genus Procapreolus were immediate predecessors of Capreolus (Korotkevich, 1970; Korotkevich and Danilkin, 1992). The evolutionary transformation of Procapreolus was likely promoted by gradual changes in climatic from subtropical to temperate, accompanied by steppe formation (Korotkevich, 1970).

Early Pleistocene remains of Capreolus, the most ancient in Asia, have been found in Eastern Kazakhstan (Vislobokova, 1973). However, because fossils are sparse and only tentatively aged, it is hard to determine time of appearance of roe deer in any given region of Eurasia. Since natural (glacial and aquatic) barriers existed on the boundary between Europe and Asia in Pleistocene, there are grounds for believing that European roe deer were isolated from Siberian roe for a long period, resulting in substantial genetic differences and partial reproductive isolation (Korotkevich and Danilkin, 1992).

**FORM AND FUNCTION.** Capreolus pygargus has a light slender build, with a relatively short trunk, and is adapted for life in tall, dense grass. Its galloping type of locomotion results from the hind quarters being taller than the shoulders. The hoops are narrow and short, with well-developed lateral digits, rendering these animals well-suited to travelling on soft ground (Flerov, 1952).

The skull of deer is elongated, with maximum width less than half its length. Lacrimal bones are shorter than the orbital cavity diameter. The ethmoidal aperture is variable in size. Intermaxillary bones taper anteriorly without forming blade-shaped projections on their exterior border. Anterior ends of nasal bones are forked, and touch admaxillary bones. The tooth-bearing portion of the facial region is relatively short. The dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Flerov, 1952; Korotkevich and Danilkin, 1992).

Antler processes of the frontal bone are slanted backward and upward, with height not exceeding width; they are comparatively far apart, but the distance between inner sides of pedicles is less than 1.5 times their width. Antlers of adults grow faster, attain larger size and are cleaned of velvet two or three weeks earlier than those of subadults. These differences allow adult bucks to occupy territories first (Danilkin, 1992c; Sokolov and Danilkin, 1981).

Capreolus pygargus molts twice a year, in spring and in autumn. Skin thickness on the head and neck varies seasonally in males, but remains the same throughout the year in females. In summer and in late winter, the skin of both sexes has a maximum thickness of 2.5 mm. In summer, head and neck skin of adult males is 2–5 times thicker (up to 10.5 mm behind the antlers) than on the back and sides. Skin thickening in males coincides with intensification of aggressive behavior during the breeding season and undoubtedly functions to reduce damage to the head region during territorial encounters. A consequence of the skin thickening and enlargement of muscles is that the neck circumference of males in summer is several centimeters greater than the females. The seasonally enlarged sebaceous and sudoriferous skin glands located in the thickened skin of the head and neck, together with interdigital and metatarsal skin glands, produce a secretion used for olfactory marking of territories (Danilkin, 1992c; Sokolov and Danilkin, 1981).

**ONTOGENY AND REPRODUCTION.** Rut takes place in August and September. Gonad activation in male deer occurs in February. Testis mass is highest in July (30–54 g) and lowest in winter (5–9 g; Pol, 1973; Smirnov, 1978; Sokolov and Danilkin, 1981). Spermatogenesis reaches a peak in July and August. During August, sperm production to decline and spermatogenesis is prevalent. Spermatogenesis stops by the end of September and, by late December, there are no live spermatozoa in sexual organs. Mitosis of spermatogonia begins again in April and, by May, there are sufficient numbers of spermatozoa for fertilization of eggs to occur (Tsaplyuk, 1977).

Female deer are seasonally polyestrous and have a single long mating period. In January, the ovaries contain only atretic follicles. Primary and secondary follicles begin to develop in February and
Maturation of ovulatory follicles occurs in August. In September and October, the ovaries contain developing yellow bodies, which seem to promote development of the next generation of vesicular follicles and thus support polyestrality. Fertilization of female *C. pygargus* is theoretically possible from May to December, but is much reduced in May–June because most are either in the latter stage of pregnancy or are lactating. Toward the end of the mating period (from October to December), fertilization is difficult owing to cessation of spermatogenesis in males (Tsaplyuk, 1977).

Siberian and European roe deer are the only ungulates that exhibit embryonic diapause, which is probably caused by a shortage of substances triggering and sustaining embryo development. Implantation of the embryo takes place in January (Aitken, 1974, 1981; Tsaplyuk, 1977). Gestation normally lasts 280–300 days (Gronov, 1986; Stubbe and Danilkin, 1992a).

Fawning in *Capreolus pygargus* begins in the second half of May and continues to mid-July (Stubbe and Danilkin, 1992a). About a month before fawning, an adult doe separates from its group and occupies a small fawning range that is the same each year and is protected from other females (Sokolov and Danilkin, 1981). Most fawning occurs in daylight. The female gives birth either in a lying or standing position; when several young are born, these two postures may alternate. The first fawn is delivered between 8 and 40 min after the limbs emerge. The second and third young appear at 10 to 40 min intervals. The afterbirth separates 12 to 50 min after the last is born. Normal delivery usually takes a total of 1.5 to 2 h, but can extend over 4 to 5 h (Gronov and Danilkin, 1984; Sokolov and Danilkin, 1981).

Siberian roe deer normally give birth to two young, although rarely one or three may occur (Stubbe and Danilkin, 1992a). Newborn weigh 1.5–2.5 kg, have spotted fur, and eyes are open. As soon as the young is born, it utters gentle squeaks, to which the mother responds with a hissing sound. The mother then lies beside it, removes the remains of the amnionic sac, and spends 5 to 20 min licking it. Caul and grass in the place where her young were lying are immediately eaten by the mother, as is the afterbirth. The young, still wet, noses the mother's body until it finds the udder and then sucks for 2–3 min. The fawn then may move 1–30 m from its mother on its own and lie down in high grass. Some follow their mother who evidently tries to take them from the birth place to different sites (Gromov and Danilkin, 1984; Sokolov and Danilkin, 1981; Sokolov et al., 1985). Although fawns are not weaned until approximately 4–5 months of age, they begin to eat vegetable food in 5–10 days (Sokolov et al., 1985).

During the first days of life, young are helpless and hide when alarmed; they do not attempt to run when approached and even touched, but will squeak when handled. From 3–7 days of age, fawns vocalize and flee if approached to within 1–2 m. At 1–3 weeks of age, the fawn responds this way at a distance of 10 m; thereafter, the young will flee silently if approached at 15–30 m, but will still squeak when caught. In the first 1–2 weeks of age, the female responds to this alarm signal, and to the approach of humans or other animals, with aggressive behavior. The freezing period lasts for about 2.5 to 3 months (Sokolov and Danilkin, 1981).

The development of *C. pygargus* is similar to that of *C. capreolus* (Sokolov and Danilkin, 1981), but when maintained under similar conditions, growth rate of the Siberian roe deer is considerably faster. In captivity, body mass of newborn fawns of Siberian and European roe deer averaged 1,850 g and 1,650 g, respectively. During the growth period, weight gain of Siberian roe deer averaged 6 kg, while that of European roe deer averaged 4 kg per month. By adulthood, *C. capreolus* is approximately 80% as heavy as *C. pygargus* (33 kg and 42 kg, respectively; Gronov, 1988).

Some female deer reach puberty in their first year of life, but the majority do not breed until the second year. Male *C. pygargus* reach puberty in the beginning of their second year of life, although young males rarely have a territory of their own by the rutting period. Consequently the majority of males begin breeding in the third year of life (Pole, 1973; Stubbe and Danilkin, 1992a; Tsaplyuk, 1977).

**ECOLOGY.** Siberian roe deer live in forest and steppe habitats; in forests, they prefer revegetating burns and clearings. They develop high densities (up to 4–12 individuals per 100 ha) in tall-grass meadows and floodplains. In eastern Mongolia, there are steppe populations that dwell in forestless landscape throughout the year, provided there are hills, ravines and tall grass to provide cover (Zejda and Danilkin, 1992). *C. pygargus* is adapted to severe weather

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**Fig. 3.** Modern distribution of *Capreolus* (horizontally hatched area is *C. capreolus*). 1—*Capreolus pygargus pygargus*, 2—*Capreolus pygargus tianschanicus*. 
extremes and inhabits areas where the temperatures range from <-60°C (winter in Yakutia) to >40°C (summer in central Asia; Dzhanikin, 2002).

Deer consume over 600 species of plants, the most important being herbaceous dicotyledons (58%), monocotyledons (16%) and woody species (22%; Holosiou et al., 1992). Average mass of stomach contents was 2.5 kg (1.4–7.5 kg), ranging from 2.2 kg (1.3–9.5 kg) when vegetation was actively grazed to 3.2 kg (2.1–6.7 kg) when the ground was snow-covered (Sokolov and Danilkin, 1981). Percentages of some plant species in the diet of C. pygargus vary greatly from season to season (Dorman, 1986; Smirnov, 1978). A drastic seasonal variation is usually observed in assortment and food composition, with decreasing intake of metabolic rate (Kholodova, 1986). In summer, deer visit natural salt ponds (Fetisov, 1953). Water is obtained from moisture-rich foods, allowing deer to live dozens of kilometers from natural sources, as is the situation in the Mongolian steppe (Danilkin and Dulantseren, 1981).

The sex ratio and age structure of populations of Siberian and European roe deer do not differ significantly. The life-span under natural conditions generally does not exceed 10 years. The sex ratio of young and adult of Siberian roe deer ranges from 1:1 to 1:1.3 in favor of males (in age structure; Dzhanikin, 1992b; Danilkin, 1986; Lavov, 1971; Pole, 1973; Smirnov, 1978). Immediately after the fawning period, young may constitute up to 50% of the population. By autumn, various populations were composed of 20%–48% fawns, 15–25% subadults, and >34% adults (Lavov, 1985; Dzhanikin, 1979; Lavov, 1966, 1971; Smirnov, 1978; Sokolov and Danilkin, 1981). The sex and age structure of exploited populations may vary greatly depending on relative hunting pressures on sex-age groups.

The spatial structure of populations of Siberian roe deer under natural conditions is not well defined, but is relatively stable within two long periods: summer (reproductive and territorial period), when animals are solitary and evenly dispersed; and winter (non-territorial period), when animals aggregate in feeding ranges. In spring adult males occupy and defend territories (10–170 ha) that remain unoccupied during the following season. Males of the females seasonal home ranges vary from 2–7 ha in the fawning period to 180 ha towards the end of the summer season (Smirnov, 1978; Sokolov and Danilkin, 1981). In the reproductive period, the core of spatial structure of the population is formed by home ranges of the "composite family" consisting of several closely related does and their offspring existing in the territory of a male. In winter, intrapopulation spatial structure varies from region to region. There are populations that migrate seasonally and withdraw fully from their summer range, populations that remain in one place throughout the year, and populations that include both settled animals and seasonal migrants whose numbers depend on snow depth. Winter home range of individuals and groups overlap widely (Danilkin, 1992b).

In many regions of Asia, seasonal mass migrations away from areas of insufficient food (Cervus elaphus; Danilkin, 1992b; Kolesnikov, 1984; Kolesnikov, 1992a) may be as long as 500 km (Bromlei and Kruchenko, 1983; Kruchenko, 1976; Rakov, 1965). Routes followed by individuals are the same for many years. The mean speed of animals during their autumn migration is 6.1 km per day (maximum is 26 km per day; in spring, speed averages 3.9 km per day. C. pygargus travel at any time of day, but more frequently in morning. The daily sex-age ratio of migrant animals is approximately the same as the sex-age structure of the population. As a rule, migrant group leaders are adult females. Most adult males migrate alone or in groups consisting only of males (Danilkin et al., 1992a).

The Siberian roe deer is mainly preyed upon by Canis lupus and Felis lynx. Predation by wolves increases dramatically when snow is deep and has a frozen crust, conditions which make prey movement difficult. In the Far East, approximately 3,500 Siberian roe deer are killed every year. In far eastern Siberia, where the population is destroyed (Bromlei and Kruchenko, 1983; Kruchenko, 1976, 1979; Kurchenkov and Shvetz, 1977; Kurchenko and Zubkov, 1980). In the northern Trans-Baikal Area, wolves kills 28.5 to 32.4% of the autumn stock, taking animals of any sex and age (Lavov, 1985). In eastern Siberia, they follow herds of C. pygargus during migration (Fetisov, 1953). In the Ural Mountains, remains of deer were found in 95.9% of predator's excreta (Averin, 1949; Filonov, 1974). In some regions, predation by the lynx exceeds that of the wolf in the Altai Region. Together fox and lynx are the most important predators. By autumn and early winter, young are killed by lynx yearly (Bromlei and Kurchenko, 1983; Dimin, 1975; Dimin and Yudakov, 1967; Kurchenkov and Shvetz, 1977).

Climatic factors not only determine the distribution of Siberian roe deer, but also affect numbers. Severe winters take especially heavy tolls because of combined effects of weather, increased predation, and hunting. An extremely snowy winter in 1972/1973 in the Far East provides an illustration of the impact of severe weather. Snow fell early in autumn and reached a depth of 1–1.5 m. Animals were unable to reach their wintering ranges and many were drowned crossing rivers in which thin ice was laden by a thick layer of snow. Distressed survivors were killed by poachers and predators, died of famine, or froze to death in herds of 20–30 animals. By spring, only 25–33% of the population survived (Kurchenkov and Shvetz, 1977; Shvetz, 1975; Darman, 1984; Kozhevnikov, 1975; Filonov, 1974; Ushkov, 1954), and in Kazakhstan in winters of 1945/1946, 1959/1960, 1965/1966, and 1975/1976 (Sludskii et al., 1984).

Mortality from disease is relatively rare since population densities are usually low, but is relatively high in winter, foot-and-mouth disease and anthrax. The most important parasites are as follows: Fasciola hepatica, Dicrocoelium lanceatum, Liochis scoticae, Aestinella pygargi, Taenia cerri, Taenia hydatigena, Nematodirus filicollis, Nematocteris oriatanus, Spiculopterogon altes, Trichocephalota capreoli, Trichocephalota serrata, Trichocephalota caprionis, Protrichur C. krabjasi, Prostorostrongylus Kochi, Bunostomum trigonocephalum, Setaria alata, Setaria tundra, Setaria capreola, Caprcoecus caprionis, and Dermacentor daphogenes, Dermacentor marginatus, Dermacentor silvarum, Haemaphysalis concinna, Rpibioch pals pulsula, Isodes persulcatus, Liotomus cerri, Lipoptena fortiseta, Pharangingia picta, Cephenomyia stimulator, Hypoderma capreola (Sludskii et al., 1984; Smirnov, 1978).

The most important cause of mortality of deer is hunting, Legal shooting itself has little impact, but in combination with poaching, losses from hunting may exceed those from all other causes (Danilkin and Blusma, 1992).

Major competitors of C. pygargus are domestic ungulates (Lavov, 1978; Nikolayev, 1982), moose (Alces alces) and red deer (Cervus elaphus; Danilkin, 1993). Due to lack of food, decline of Siberian roe deer populations is correlated with increased predation in red deer density, as exemplified by the change in numbers of Siberian roe deer and Altai red deer (Cervus elaphus sibiricus) in the Bogdo-Ula Preserve, Mongolia (Koval, 1924). Between the 1920s and 1950s Siberian roe deer were numerous, whereas Altai red deer were sparse. By mid-1980s, the red deer population density had increased to 55–90 animals per 1,000 ha, and Siberian roe deer had disappeared in the preserve (Danilkin and Dulantseren, 1981).

Some ungulates may have a positive effect on densities of C. pygargus. Digging snow (in the Asian portion of the area) in winter, boar (Sus scrofa) and domestic ungulates prepare feeding places for roe deer. In numerous parts of Russia where snow is deep, survival of deer in winter strongly depends on species (deer, elk, and boar) to make paths in snow, facilitating movement from one biotope to another (Danilkin and Blusma, 1992).

The total number of Siberian roe deer is about 1 million in a range of 7.4 million square km. In most regions the population density is one or two orders of magnitude lower than that of the European roe deer, mostly due to poaching, predation, and high mortality during winters with heavy snow (Danilkin, 1989a; Danilkin and Blusma, 1992; Stubbe and Danilkin, 1992b). The highest recorded population density was in the last century when up to 500,000 were taken annually in Russia alone (Turkin and Satanin, 1902).

BEHAVIOR. Siberian roe fawns display reactions to various environmental stimuli (visual inspection, sniffing, listening)
from birth. At two weeks of age, juveniles' orientative-exploratory reactions do not differ from those of adults. Newborns exhibit few comfort behaviors. The first attempts at body licking are recorded at 4–6 days of age, and at 3–4 weeks of age, young care for their own coats. However until 2–2.5 months of age, this function is performed mostly by the mother during feeding periods. Her lickings are especially long and thorough in their first fortnight when fawns have difficulty excreting on their own. Play behavior is observed in fawns from 3 days of age. Sexual play behavior in young males is recorded from 1.5–2 months of age. In this period, they also develop activities resembling marking. At 4 months of age, their play exhibits the whole range of postures peculiar to the antagonist behavior of adults. By 2.5 months of age, fawns have learned all main forms of behavior from their parents; however, juvenile terri-
itorial and sexual behavior greatly differs from adult behavior (So-
kolov et al., 1985).

In their first days, fawn active periods coincide with feeding bouts, which last about 30 min. Young fawn only rarely feeds after 30 min. Young fawn may come to them and lie down as soon as she goes away, but 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, the female feeds her offspring one at a time, alternating between them and only rarely feeding the same fawn during two sequential bouts. Later, the mother mostly feeds her young together, but the feeding periodicity remains. The number of meals of milk varies with fawn number: in the first month, it may be as high as 5–6 meals per day; in the second month, it is 2–4 meals per day; and later it decreases to 1 or 2 meals on the same meal and milk is being absorbed by joint activities increases. From 1 month of age, length of active periods is 1–1.5 h, and from two months, length is 1.5–2 h long; 30–40% of active periods is spent grazing around their beds in the mother's absence. Although the number of milk meals gradually decreases, the number of active periods (5–7 per day) remains nearly the same. Synchronization of family member activities takes place only when young are more than 2.5–3 months of age (Danilkin, 1992c; Sokolov et al., 1985).

Activity of Siberian roe deer may vary within the year, season, and time of day, depending on sex, age, degree of anxiety, climate, and other environmental factors. The daily rhythm includes alternat-
ing moving about and grazing with rest and mastication, usually from 4 to 7 times a day. The morning and evening activity periods are longest and occur with most predictable timing. Individuals and groups are most active at sunrise and sunset. Activity rhythms of group members are synchronous, apparently the result of individuals following the behavior of a leader individual (Smirnov, 1978; Sokolov and Danilkin, 1981).

Siberian roe deer are aggressive mainly during the reproductive period. Social relationships between females and their adult progeny are ended 2–4 weeks before a new generation is born. The separation is caused by increased aggressiveness of mothers toward other animals in their fawning ranges. Aggressive behavior is expressed most strongly toward individuals approaching 1–2-week-old fawns. In gen-
eral, male C. pygargus are more aggressive than females. The onset of aggressive behavior coincides with removal of velvet from antlers and marking activities. Most aggressive encounters take place during seizure of territories and before rut. Adult males are especially intolerant of aunts without territories. The emigration of young animals from their birthplace is largely caused by aggressiveness of adult males who drive them from their territories. Conflicts between neighboring territorial males are comparatively rare (Smirnov, 1978; Sokolov and Danilkin, 1981). After the reproductive period aggress-
essiveness of roe deer declines to the extent that, in winter, all group members may feed together without being noticeably antagonistic.

From spring through autumn, males provide their ranges with olfactory and visual marks. The olfactory marks are made with a secretion from the skin glands, which glandular secretion is applied by rubbing the forehead, cheeks and neck against trees, shrubs and high grasses. Visual marks are trees frayed with antlers. Other substances that may be used in signalling are urine, feces, and saliva, as well as secretions of sexual organs, metatarsal and interdigital glands, and glandular complexes in the skin on distal sections of the metatarsals and metacarpals (Sokolov and Danilkin, 1981).

In the rutting period, the territorial system is not generally violated. The rut of deer usually lasts for 2 to 5 days. The male nearly stops feeding, becomes careless and does not leave the doe even in apparent danger. In the first day of the rutting period, males, especially young ones, are quite aggressive toward females and may strike them with antlers. After a lengthy chase in large circles, the tired female begins running around trees, shrubs, high hummocks, and hillocks, where pits and holes, and the female stops as the equally tired male to mate with her. Subsequently, both lie down to rest. Running through the same place repeatedly results in characteristic paths with a circular or figure-eight configuration (Sokolov and Danilkin, 1981).

Vocal signals play an important role in the social life of roe deer. Six main types of signals can be discerned: squeaking (or whistling), rasping (panting), barking, whining, screaming, and sounds of non-vocal origin. At an early age, C. pygargus seemingly has only one type of acoustic signal—squeaking (soft and loud). All signals, except whining, are used by both males and females. Vocalizations are similar to those of European roe deer and have the same functional significance, a reflection of phylogenetic relatedness. How-

ever, C. capreolus males are not known to produce a whining sound (Sokolov and Danilkin, 1981) and paired squeaks have not been recorded in females of European roe deer. In general, sounds of European roe deer are more high-pitched and young produce squeaks with different characteristics (Sokolov et al., 1987). In Siberian roe deer, orientative-exploratory and defensive beha-

vior are a series of separate elements: orientation posture, signal be-

hips, fear reactions, moving close to other individuals, warning of
der may be gained in a different order. Twenty-

five to 50% of active periods are spent in orientative-exploratory

behavior. Although behaviors are not patterns, they are

ted threats, olfaction is the primary sensory modality for gaining precise information. In certain situations, individuals will move downwind in order to locate and indentify an odor. When danger is apparent, young lie down and press their heads to the ground; adults either stand still with their heads lowered or, in the case of dwellers of open steppe biotopes, lie down like fawns. In a group of Siberian roe

deer the flight of one member causes a similar reaction by others

(Smirnov, 1978; Sokolov and Danilkin, 1981).

GENETICS. Capreolus pygargus has a diploid number of 71–84 chromosomes; this number includes 1–14 B-chromosomes in addition to 70 chromosomes of the main set. All autosomes are acrocentric, whereas the X-chromosome is submetacentric (Danilkin, 1985b, Sokolov et al., 1978). Karyotypes are both stable and mosaic (with a different number of B-chromosomes in the same individual and in different individuals in the same population; Danilkin and Baskевич, 1987). Hybrids derived from crossing C. capreolus and C. pygargus inherit B-chromosomes (Zarnabhe, 1980).

Although interbreeding between European and Siberian roe
deer is possible, most hybrid males are sterile and many small

European roe deer females either die giving birth to large hybrid fetuses or give birth to dead young. Only about 20% of females in these experiments could normally reproduce and the equal numbers of females and males are generally identified as Pygargus of the ancestors" (Pallas, 1809).

Authorities disagree about the infraspecific taxonomy of Ca-

preolus pygargus. Different authors distinguish 2 to 5 subspecies indicate different borders of their ranges (Barantsev et al., 1981; Eitlermann and Morrison-Scott, 1951; Florov, 1952; Hepner et al., 1961; Sokolov and Gronov, 1988, 1990;Stubbe, 1990), but most do not provide diagnoses of forms accorded subspecific status. The systematic status of C. p. caucasicus is unclear (Fierov, 1952; Hepner et al., 1961). At the present time, C. p. caucasicus is not found on the northern slopes of the Caucasus, which is now included in the range of C. capreolus (Danilkin and Markov, 1985).

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