MAMMALIAN SPECIES 46(913):71–87

Spermophilus citellus (Rodentia: Sciuridae)

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Abstract: *Spermophilus citellus* (Linnaeus, 1766) is a medium-sized sciurid commonly called the European ground squirrel. The species inhabits grasslands in central and southeastern Europe on a range from short-grass steppes to meadow orchards, and from sea level to an elevation of 2,500 m. These squirrels live in colonies and construct burrows used for hibernation, reproduction, refuge, and resting. Due to serious declines in many portions of its range, the species is listed as "Vulnerable" by the International Union for Conservation of Nature and Natural Resources. It is also protected by the Bern Convention (Appendix II), and the European Union Habitats and Species Directive (Annexes II and IV).

Key words: *Citellus citellus*, endemic species, Europe, European ground squirrel, European souslik, suslik

Synonymy completed 25 September 2012
DOI: 10.1644/913.1
www.mammalogy.org

Spermophilus citellus (Linnaeus, 1766)
European Ground Squirrel

Mus citellus Linnaeus, 1766:80. Type locality "Austria, Bohemia, Polonia," restricted to Austria by Miller (1912:924); restricted to Wagram, Austria, by Martino and Martino (1940:496).

Mus citillus Pallas, 1779:119. Incorrect subsequent spelling of *Mus citellus* Linnaeus, 1766.

Spermophilus citellus: Cuvier, 1825:255. First use of current name combination.

Citellus citellus gradojevici Martino and Martino, 1929:76. Type locality "Djerdjelija [= Gevgelija], Macedonia."

Citellus citellus istricus Calinescu, 1934:106. Type locality "Ebene Munteniens [= lowlands of Muntenia]," southeastern Romania.

Citellus citellus karamani Martino and Martino, 1940:495. Type locality "Karadjica [= Mt. Karadžica] Mountains, above Patiška, 30 km south of Skoplje [= Skopje], southern Serbia," Macedonia.

Citellus citellus laskarevi Martino and Martino, 1940:498. Type locality "Dolovo, southeastern Banat, Yugoslavia," Serbia.

Citellus citellus martinoi Peshev, 1955:290. Type locality "Rodopite, okolnostite na v. Kolarov (Belmeken)," (= Rhodopen Mts., neighborhoods of the peak Kolarov [Belmeken]), Bulgaria.

Citellus citellus balcanicus Markov, 1957:465. Type locality "Okolnostite na s. Lokorsko, Sofijsko, na ûg ot Balkana, Blgariâ," (= neighborhoods of the village Lokorsko, region of Sofia, southern Balkan Mts., Bulgaria).

Citellus citellus thracius Mursaloğlu, 1964:260. Type locality "A valley-meadow in front of the south-east slope of Murattepe, near Yenibedir, Lüleburgaz, Kirklareli, Turkey in Europe."

Fig. 1.—An adult *Spermophilus citellus* from Mladá Boleslav, Czech Republic. Photograph courtesy of A. Kryštufek.

Citellus citellus macedonicus Fraguedakis-Tsolis, 1977:65. Type locality "Kozani;" restricted to Pontokomi, Kozani, West Macedonia, Greece, by Fraguedakis-Tsolis and Ondrias (1985:196).

Context and Content. Order Rodentia, suborder Sciuromorpha, family Sciuridae, subfamily Xerinae, tribe Marmotini, genus *Spermophilus* (Helgen et al. 2009). Designation of subspecies for *S. citellus* has been contentious. Eight subspecies have been described since 1929 based on slight differences in color, size, and body proportions (Ružić 1978), but with no proof of discontinuity (Corbet 1978). Ružić (1978) tentatively recognized 7 subspecies (all, except *balcanicus*, which she synonymized with *martinoi*), whereas other authors have recognized only 4 subspecies (Thorington and Hoffmann 2005; Thorington et al. 2012): *citellus*, *gradojevici* (*karamani* is a synonym), *istricus* (*laskarevi* is a synonym), and *martinoi* (*balcanicus* and *thracius* are synonyms). Skull characters, ratios, and coloration are of low diagnostic value in *S. citellus* and the above subspecies were not consistent with the interlocality variation observed in an analysis of 13 cranial measurements of ground squirrels from throughout the range (Kryštufek 1996), suggesting that further revision of the subspecies is needed.

Nomenclatural Notes. The name *Citellus* (Oken, 1816) was in routine use for the genus until Hershkovitz (1949) argued that Oken's work was invalid, and that *Spermophilus* (Cuvier, 1825) was the oldest available name for the genus. The opinion was supported by the International Commission on Zoological Nomenclature (1956; Opinion 417), and has been adopted by American authors. However, some European and Russian authors continued to use *Citellus* as recently as 1995, although others adopted *Spermophilus* (Harrison et al. 2003). Until recently, *Spermophilus* contained all Holarctic ground squirrels, except those in the genera *Marmota*, *Cynomys*, and *Ammospermophilus* and was further divided into 6 subgenera. Presently, *Spermophilus* contains 14 species (sensu lato), all restricted to Eurasia (Helgen et al. 2009). *Spermophilus* is derived from the Greek *spermatos* for seed and *phileo* for love (Helgen et al. 2009), whereas *citellus* is from the Latin *ziesel* (German for ground squirrel or souslik—Palmer 1904). *S. citellus* also has been referred to as the European souslik (Coroiu et al. 2008).

DIAGNOSIS

Spermophilus citellus together with *S. xanthoprymnus* (Asia Minor ground squirrel), *S. dauricus* (Daurian ground squirrel), *S. suslicus* (speckled ground squirrel), *S. alashanicus* (Alashan ground squirrel), and *S. taurensis* (Taurus ground squirrel) form a group of closely related species, so that single specimens are sometimes indistinguishable; however, their distributions are different (Vinogradov and Argiropulo 1941; Herron et al. 2004; Gündüz et al. 2007; Helgen et al. 2009). Compared to *S. taurensis*, diagnostic characters for *S. citellus* are as follows: less reddish dorsal pelage, underside more yellow, smaller body size (*S. taurensis*, range: 194–201 mm; *S. citellus*, range: 174–228 mm), tail slightly longer (*S. taurensis*, range: 62–65 mm; *S. citellus*, range: 31–90 mm) with a dark stripe along its dorsal side, and hind-foot length shorter (*S. taurensis*, range: 39–44 mm; *S. citellus*, range: 30–43 mm—Kryštufek and Vohralík 2005, 2012; Gündüz et al. 2007; Özkurt et al. 2007). Compared to *S. xanthoprymnus* (see Gür and Gür 2010), diagnostic characters for *S. citellus* are as follows: the skull is less angular, back indistinctly spotted, and tail longer (*S. xanthoprymnus*, range: 30–72 mm; *S. citellus*, range: 31–90 mm) with black hairs dorsally (Kryštufek and Vohralík 2005, 2012). *S. citellus*, *S. taurensis*, and *S. xanthoprymnus* can be clearly distinguished on the basis of their alarm calls (Schneiderová and Policht 2011a, 2011b).

GENERAL CHARACTERS

Spermophilus citellus is a medium-sized ground squirrel, with a round body, short tail (20–40% of length of head and body), and reduced outer ears (Fig. 1). Head is convex in profile with large eyes (about 8 mm in diameter) and short vibrissae (25–30 mm—Ružić 1978; Kryštufek and Vohralík 2005). The eyes, situated wide apart on the upper side of head, present an ill-defined eye-ring, whitish or yellowish according to general coloring of body (Miller 1912; Ružić 1978). The tail is cylindrical at the base and inconspicuously flattened beyond the middle, where hairs are about 15 mm long. The tail lacks a definite color pattern, with the upper surface grizzled, essentially like the back, somewhat darker at tip, and the pencil with light margin; the undersurface is a nearly clear dull buff. The ears are low, obscurely pointed above, and densely covered with fine, short hairs on both surfaces but without tufts (Miller 1912; Kryštufek and Vohralík 2005). The back and sides of the body are usually cream-buff but occasionally more yellowish, with sides inconspicuously lined with black, the entire dorsal surface from nape to rump vermiculated with black, and the dark and light areas along the middle of the back usually well enough defined to produce an effect of obscure light mottling, with spots about 5 mm in diameter. The belly is washed with a buff usually somewhat more yellow than that of sides. The crown and upper half of cheeks are grizzled, with the light element paler than on the body and the dark relatively more evident, the muzzle sometimes with a rusty tinge, and the sides of muzzle and lower half of cheeks clear whitish or buffy, continuous with the similarly colored pale area covering throat and forepart of chest and inner side of foreleg (Miller 1912). Feet are yellowish, with longest claws up to 8 mm in length, and 4 fairly large and naked pads on palms and soles; rudimentary thumbs still bear a nail (Kryštufek and Vohralík 2005). Soles are covered with short silvery hairs from heel to pads (Calinescu 1934; Kryštufek and Vohralík 2012). In 2012, a light-colored morph was detected in Vienna, Austria, with white tail and belly, and interspersed white blotches on head and dorsum ($n > 5$—I. E. Hoffmann, in litt.).

Size and body mass of *S. citellus* vary with age, sex, and activity cycle, but also with locality and environmental conditions (Ružić 1978; Hoffmann et al. 2008; Millesi and Hoffmann 2008). Male-biased sexual dimorphism develops during the juvenile summer (Millesi et al. 1999b) and increases with age (Ružić 1978: table 15; Spitzenberger and Bauer 2001). Mean body mass of Pannonian juveniles at 30 days of age was 61.4 g (Ružić 1965). Data from an Austrian population ranged between < 50 g (juveniles at emergence from their natal burrow) and > 450 g (≥ 1-year-old males prior to hibernation). At vernal emergence, males were heavier than females in the same age class, and adult animals were heavier than yearlings. Adult males attained a minimum annual mass during the mating phase (Millesi et al. 1999b), whereas yearling males and females weighed least at emergence from hibernation (Millesi et al. 1998; Millesi and Hoffmann 2008). Growth of hind feet may terminate in juveniles, whereas head length still increases during the 2nd year (Ružić 1978; Millesi et al. 1999a).

Ranges of external measurements (mm) for adult (≥ 1 year old) *S. citellus* were: length of head and body, males: 176–228, females: 174–217; length of tail, males: 31–90, females: 38–75; length of hind foot, males: 32–43, females: 30–41; length of ear, males: 6.0–15.4, females: 6.7–12.2; and body mass, males: 125–380 g, females: 131–353 g (Miller 1912; Ružić 1978; Spitzenberger and Bauer 2001; Kryštufek and Vohralík 2005). In spite of geographic heterogeneity observed in 13 cranial measurements (Kryštufek 1996), sexual dimorphism in cranial size is apparently fairly constant across the species' range (Kryštufek and Vohralík 2012). Mean (mm ± *SE*) cranial measurements from Austria and Hungary ($n = 27$), Romania ($n = 8$), Bulgaria ($n = 3$), and Turkey ($n = 1$) were: condylobasal length, 43.11 ± 1.15; zygomatic breadth, 28.84 ± 0.59; breadth of rostrum at front of nasals, 7.62 ± 0.29; interorbital breadth, 9.60 ± 0.30; postorbital breadth, 11.78 ± 0.54; mastoid breadth, 20.24 ± 0.60; occipital depth, 12.96 ± 0.48; length of nasals, 14.60 ± 4.89; length of diastema, 11.82 ± 0.33; length of mandible, 29.95 ± 0.63; length of maxillary toothrow, 9.73 ± 0.37; and length of mandibular toothrow, 9.49 ± 0.33 (Fig. 2; Miller 1912).

Baculum varies geographically, with its spoonlike expanded distal spatula triangular, and with toothlike projections along its ventral margin (Kryštufek and Vohralík 2005). The baculum is asymmetrical, most clearly in the shape of the spatula. Mean measurements (mm) of 35 bacula from the Czech Republic ($n = 2$), Serbia ($n = 18$), and

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Spermophilus citellus* (Slovenian Museum of Natural History 7082) from Samoš, Deliblato Sands, Voivodina, Serbia. Greatest length of skull is 42.7 mm. Photographs by C. Mlinar used with permission.

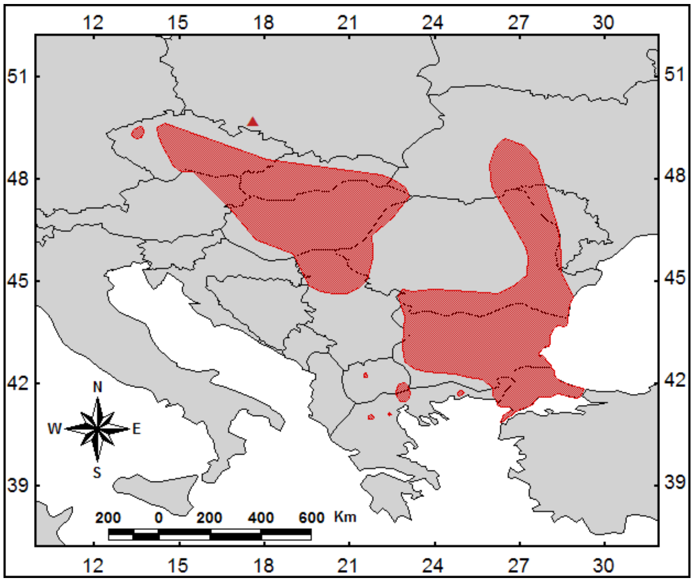

Fig. 3.—Geographic distribution of *Spermophilus citellus*. The red triangle shows the area where the species has been successfully reintroduced in Poland. Map created by N. Ramos-Lara based on Coroiu et al. (2008).

Macedonia ($n = 15$) were: length of baculum, 2.5–3.2; basal breadth, 0.9–1.2; spatula breadth, 1.1–1.6; and number of denticles, 8.7–13.0 (Kryštufek and Hrabě 1996).

DISTRIBUTION

Endemic to central and southeastern Europe, between 40°20′N and 51°00′N and 12°40′E and 29°00′E (Fig. 3; Ružić 1978), the range of *Spermophilus citellus* is disjunct, the Carpathians and the Djerdap Canyon of the Danube divide the range into 2 portions. The northwestern portion extends through the lowlands of the Czech Republic, Austria, Hungary, Slovakia, Serbia (to the north of Danube and Sava), and eastern Romania. The southeastern portion extends from eastern Serbia, Macedonia, and northern Greece through Bulgaria to Turkish Thrace, southern and eastern Romania, Moldova, and Ukraine (Kryštufek 1999; Kryštufek and Vohralík 2005; Coroiu et al. 2008). Extinct in Germany, Poland, and Croatia, the western margin of its distribution is in the Czech Republic (Coroiu et al. 2008; Hulová and Sedláček 2008). Nonetheless, the species was successfully reintroduced in Poland (Fig. 3; Coroiu et al. 2008; Matějů et al. 2010b). Evidence suggests that *S. citellus* started to spread across its recent distribution 5,000 years ago, after Neolithic deforestation (Spitzenberger and Bauer 2001). Knowledge of the distribution in the southern portion of its range remains incomplete (Koshev 2008).

FOSSIL RECORD

The genus *Spermophilus* (sensu lato) is known in Europe from the late Miocene and *Spermophilus citellus* appears in the middle Pleistocene when known in Bulgaria, Greece, Hungary, and Romania (Kowalski 2001). Examination of paleontological data suggests that ground squirrels manifest morphological variability from the early Pleistocene through the present and the evolution of *S. citellus* apparently occurred mainly in the Balkans (Peshev et al. 2004). The species apparently has been confined to its current range since its earliest appearance in the fossil record (Kryštufek et al. 2009). No fossils of *S. citellus* are known from Austria (Spitzenberger and Bauer 2001).

FORM AND FUNCTION

Form.—The skull of *Spermophilus citellus* is similar to that of *Sciurus* but smaller (Kryštufek and Vohralík 2005). The braincase is broadly ovate when viewed from above, with greatest width equal to length, and its posterior width exceeding that at the postorbital constriction (Miller 1912). Dental formula is: i 1/1, c 0/0, p 2/1, m 3/3, total 22. P1 has 1 root; P2, M1, M2, and M3 have 3 roots; p1 has 2 roots; and m1, m2, and m3 have 4 roots (Özkurt et al. 2007). Age of individuals can be assessed through enamel abrasion of dental material (Ružić 1966) and on the basis of layers of appositional bone in the mandible (Hrabě and Zejda 1981). Kryštufek (1998) found differences in 15 pelvic measurements between localities and sexes. The characters most affected by interlocality variation were those describing general length and pelvis breadth, whereas males attained higher average sample means in all characters except breadth at pubic symphysis and pubis width at symphysis. The number of mammae is: 1-1 p, 2-2 a, 2-2 i, total 10 (Miller 1912).

Spermophilus citellus has internal cheek pouches. The paired retractor muscles attach dorsally to scapular metacromion and ventrally to sternum. These muscles are presumably derived only from the facial musculature (*platysma myoides* p. *branchialis* and *musculus sphincter colli profundus* p. *intermedia ventralis*), rather than from *musculus trapezius* p. *auricularis*, as is the case in other rodents (Zherebtsova 2005).

The eye lens is yellow and does not transmit ultraviolet radiation (50% cutoff around 493 nm—Hut et al. 2000). The retinal photoreceptor mosaic is composed mainly of cones and < 3% of the visual cells show rod-like characteristics (Szél and Röhlich 1988). Half of the rod-like cells are recognized solely by a rhodopsin antibody, whereas the other half also are recognized by a blue opsin antibody (Schantz et al. 1994). The species is dichromat having only blue (440 nm) and green (520–525 nm) photopic spectral sensitivities, together with 1 scotopic component with an absorption peak at about 500 nm (Szél and Röhlich 1988).

Similar to other burrowing mammals (Kley and Kearney 2007), the forelimb of *S. citellus* is characterized by well-developed scapular retractors, arm retractors with distal insertions upon a robust humerus, elbow extensors and flexors, forearm pronators with distal insertions, and carpal and digital flexors with extensive origins from a prominent medial humeral epicondyle (Lagaria and Youlatos 2006). Three anal glands secrete an odorous scent that is perceivable near burrow entrances, especially during the mating season. Subcutaneous fat layer ranges from 2 to 5 mm in width (Ružić 1978).

Function.—During hibernation, *Spermophilus citellus* exhibits a regular pattern of torpor interrupted by euthermic arousal phases (Strijkstra 1999). Evidence suggests that animals interrupt torpor states regularly during hibernation to protect the brain against the effects of prolonged hypothermia (Ruediger et al. 2007). Memory retention in captive *S. citellus* was negatively affected by hibernation. The resulting memory loss is apparently related to the physiological processes occurring during torpor and the short euthermic phases (Millesi et al. 2001). Protein and RNA contents in liver were higher during arousals than during torpor. However, adrenal ascorbic acid concentration was less in aroused squirrels than in hibernating or euthermic controls (Petrović et al. 1985).

Average euthermic body temperatures are highest after hibernation and lowest during hibernation. Lowest body temperatures during torpor may reach $< 0°C$ (Hut et al. 2002a). *S. citellus* shows reduction or absence of circadian rhythmicity in body temperature for several days posthibernation, which may be due to the effects of prolonged periods of extreme low body temperatures on the suprachiasmatic nuclei (Hut et al. 2002b). Blood glucose concentrations in captive *S. citellus* decreased substantially during hibernation, as in other hibernators, but hemoglobin levels remained the same. Despite decreased liver metabolic activity in captive hibernating animals, antioxidant defense was maintained at a level comparable to that of animals in the spring, or actually increased (Buzadžić et al. 1990).

Levels of the glucocorticoid hormone cortisol in captive individuals varied seasonally in euthermic animals, being higher from July to August than from April to May, and most elevated from late October to December. In torpid animals, blood cortisol levels also were low from October to December and higher from January to March (Shivatcheva et al. 1988). The levels of 17-hydroxycorticosteroids and free amino acids in the plasma of aroused animals were higher than those in hibernation and euthermic controls in captive individuals (Petrović et al. 1985). Estradiol levels in free-living *S. citellus* increase from proestrus to estrus among females (Millesi et al. 2000). During late lactation, estradiol levels also are considerably elevated, indicating initiation of follicular maturation processes during that period (Huber et al. 1999). After the termination of lactation, both estradiol and progesterone secretion peak and decrease before hibernation (Millesi et al. 2008). Females with high estrogen titers produce larger litters the following year (Huber et al. 1999). Testosterone levels in mature males are high at the beginning of aboveground activity and during mating, and decrease thereafter. In nonreproductive yearling males, androgen levels remain baseline throughout the active season (Millesi et al. 1998; Strauss et al. 2007b).

ONTOGENY AND REPRODUCTION

Ontogeny.—Gestation period for *Spermophilus citellus* was 25–26 days in captivity (Ružić 1978) and on average 29 days in the field (Millesi et al. 1999a; Aschauer et al. 2006), with a positive correlation between gestation length and litter size (Huber et al. 2001). In embryos of 10 mm in length, the extraocular muscles were already developed as independent bundles. At this stage, the attachment of the musculature to the ocular wall was already distinctly defined, with muscles fixed on the connective tissue surrounding the eye. However, the final arrangement of the musculature can be observed only after the embryo has exceeded 2 cm in length, and the facial region of the head has developed (Lešer 1925). External characters for 7 newborn specimens from European Turkey were: mean total length, 57.18 mm; mean tail length, 7.75 mm; mean hind-foot length, 7.50 mm; mean ear length, 1.00 mm; and mean body mass, 5.25 g (Özkurt et al. 2005). The abdomens of newborns were light pink, the backs of their bodies gray, eyes and ears closed, and bodies hairless. Newborns became hairy at 15–17 days, and eyes opened between 22 and 25 days. Between 25 and 27 days after birth upper and lower incisors erupted, and ears opened on day 30 (Özkurt et al. 2005). Structural growth ceases at about 57 days of age, which is probably related to gain of fat reserves for hibernation (Millesi et al. 1999b). Sexes display similar patterns of ontogenetic allometry and the majority of cranial shape changes during growth probably are due to the shift from liquid to solid diet (Klenovšek and Kryštufek 2013). Juveniles 1st emerged from their burrows at 25 days of age (Ružić 1965, 1978). Juveniles remain in their natal burrow for about 1 month, and weaning begins in mid-June depending on litter size and maternal condition (Millesi et al. 1999a). Weaning occurs on average between 49.4 and 56.1 days, depending on litter size. Juvenile weaning body mass is unaffected by litter size, although a trade-off exists between litter size and juvenile body mass at natal emergence (Huber et al. 2001). In Turkey, individuals born between late April and early May reached adult size by August and became reproductively active after 1 hibernation period (Özkurt et al. 2005).

Reproduction.—Reproduction in *Spermophilus citellus* is constrained by hibernation, limiting the timing of mating and gonadal development (Huber et al. 1999). Females deliver only 1 litter annually (Ružić 1978; Kryštufek and Vohralík 2005), with litter sizes at emergence from natal burrows ranging from 2 to 11 young/litter (Peshev 1955; Pakizh 1958; Straka 1961; Ružić 1978; Millesi et al. 1999a; Huber et al. 2001; Aschauer et al. 2006; Strauss et al. 2007a). Litter size varies with latitude (Kryštufek and Vohralík 2005) and population density (Hoffmann et al. 2003a), with southern and sparse populations having larger litters. Consistency of litter size at natal emergence and in utero (2–9 young/litter—Ružić 1978) suggests that the number of offspring is determined prenatally, but whether the decision is made preimplantation or later during pregnancy remains unknown (Millesi et al. 1999a). In northern Serbia, the proportion of nonreproductive females was very low (1.3%); 35.3% of pregnant females resorbed 1 or 2 embryos (Ružić-Petrov 1950). Large litters typically emerge early in the season whereas small litters emerge later (Huber et al. 2001). Although most females are sexually mature after their 1st hibernation, the timing of puberty in males is facultative (Millesi et al. 1998), becoming sexually active either as yearlings or as 2 year olds (Millesi et al. 1999b). Testicular condition is apparently predetermined before male emergence, as adult males emerge with maximal testes size (8.5–10 mm—Millesi et al. 1998) and elevated plasma testosterone levels (Millesi et al. 2002). Early yearlings with emergence masses > 220 g also present developed testes, and display a pattern of testicular regression similar to that of adults (Millesi et al. 1998). Male mating opportunities are limited by availability of receptive females, and gonadal regression starts at the end of the mating period (Millesi et al. 2000, 2002), after the majority of females have been impregnated. Females mate within 3 weeks after vernal emergence to give their offspring time to grow and fatten before hibernation (Millesi et al. 1999a, 2000). In a free-ranging population in Austria, vaginal estrus occurred 2–13 days after emergence from hibernation (Millesi et al. 2000), with estrous dates ranging between 20 March and 19 April (Millesi at al. 1999a). Females with low emergence mass show delayed estrus, resulting in smaller and female-biased litters (Aschauer et al. 2006); early litters, in contrast, are larger and male-biased (Millesi et al. 1999a). Presence of males seems to have no effect on the latency to go into vaginal estrus. However, in absence of males, duration of vaginal estrus is lengthened by females (Millesi et al. 2000). It is unknown whether *S. citellus* is a spontaneous or induced ovulator (Millesi et al. 1998). Mating can be a relatively long-lasting and costly event for males. The average duration (mean ± *SD*, $n = 12$) of the mating event is 0.7 ± 0.3 h (Millesi et al. 1998). Copulation occurs exclusively underground, but examination of behavioral data suggests that each female mates only with a single male (Millesi et al. 1998). Copulatory plugs were not detected in free-living adult females from Austria (Huber et al. 2001).

Female *S. citellus* are monestrous; but there is growing evidence for a 2nd nonreproductive estrous cycle in summer (Millesi et al. 2008; Strauss et al. 2009). Follicular development apparently is initiated during summer prior to the hibernation period (Huber at al. 1999; Millesi et al. 2008; Strauss et al. 2009). The end of the follicular phase and pregnancy are accompanied by luteal development (Millesi et al. 2000). The ovaries of 36 captive squirrels were enlarged in March, with vesicular follicles on the surface surrounded by blood vessels. In April, the ovaries were further enlarged due to the presence of corpus luteum, whereas in July their sizes were greatly reduced (Tsvetkov and Takeva 1991).

Females usually breed as yearlings, with 1st-time breeders often producing smaller litters than older females. In Austria, yearling females weaned smaller litters (mean ± *SD*; 5.36 ± 1.86 young/litter) than older mothers (6.8 ± 1.72 young/litter—Huber et al. 1999). However, early-breeding females also produced larger litters than later-breeding females (Huber et al. 2001). Large litters are nursed longer than smaller ones, with lactation in one season affecting estrous delay in the next (Huber et al. 1999). Duration of lactation varied from 22 to 52 days (Millesi et al. 1999a; Aschauer et al. 2006) and 45 to 61 days (Huber et al. 2001; Özkurt et al. 2005). According to Ružić (1978), lactation typically continues after natal emergence, and lasts up to 6 weeks (Ružić-Petrov 1950). In Austria, onset of lactation varied from late April to mid-May in accordance with ovulation dates (Millesi et al. 1999a). Nonetheless, late-reproductive females may nurse their offspring for a shorter period to have ample time to prepare for hibernation (Millesi et al. 2000).

ECOLOGY

Population characteristics.—*Spermophilus citellus* occurs in loosely structured populations or colonies (Millesi et al. 1999b). In Austria, colonies occur mainly in isolated habitat fragments, characteristic of relict populations (Hoffmann et al. 2003b). Population densities may be quite variable, and in low-density populations with few males, a female may wait several days before being detected by a male (Millesi et al. 2000). In 2 steppe areas of Hungary, population densities varied from 15 to 55 and 50 to 90 individuals/ha over the same active season (Váczi et al. 2006). Densities between 18 and 48 individuals/ha for optimal and 5 and 14 individuals/ha for mountainous habitats in Serbia (Ružić 1978), as well as 41–68 reproductive individuals/ha in Austria (Millesi et al. 1998), have been reported. In the Pannonian plain, densities of about 30 individuals/ha are considered high (Ružić-Petrov 1950). Reduced immigration and increasing mortality caused a drastic decline from 61 to 6.3 individuals/

ha within a few years in a suburban area north of Vienna, Austria (Hoffmann et al. 2003a).

Spermophilus citellus exhibits a remarkable plasticity in life-history adaptations (Hoffmann 2002). Individuals can live for up to 5 reproductive seasons (Millesi et al. 2000). Maximum life span is 4 years for males and 6 years for females (Hoffmann et al. 2003a), but may be $>$ 9 years in captivity (Andjus et al. 2000). Disappearance rates during the active season are severalfold higher than overwinter mortality, and may lead to the complete loss of a sex and age class (Millesi et al. 1999b). Sex ratios in natural populations from Austria were male-biased (1.6:1.0) with 26 juvenile males and 12 juvenile females (Strauss et al. 2007a), and on average 30.75 adult males and 19.25 adult females over a 4-year period (2.1:1.0—Millesi et al. 1998). Annual percentages of surviving juveniles from Austria were lower than those of nonjuveniles. Age-specific survival of males also was lower than that of females in each cohort (Hoffmann et al. 2003a), with late-born juveniles experiencing reduced survival to the next season (Millesi et al. 2000). Litter emergence date and offspring weaning body mass do not affect juvenile survival to yearling age (Huber et al. 2001), but do influence juvenile reproductive output in the following season (Huber et al. 1999). However, offspring body mass at natal emergence is positively related to overwinter survival in young. Preweaning mortality is lower in heavier young, whereas postweaning mortality is unaffected by juvenile body mass (Huber et al. 2001). Body condition at onset of hibernation has a strong influence on overwinter survival, and is related to maternal effort (Aschauer et al. 2006). A mother's probability of surviving to subsequent breeding period is not influenced by either litter size or mean body mass of young at emergence (Huber et al. 1999).

Space use.—*Spermophilus citellus* characteristically inhabits short-grass steppe, pastures, and meadows (natural or anthropogenic), with sporadic shrubs and trees, from sea level up to 2,500 m (Fig. 4; Kryštufek 1999; Hoffmann et al. 2003b; Kryštufek and Vohralík 2005). It occurs in arid lowlands with sandy loam-loess humus and alluvial-meadow soil types (Brinkmann 1951; Ružić 1978; Koshev and Kocheva 2007). The species is absent from annually plowed arable land as well as tall-grass meadows (Kryštufek and Vohralík 2005). However, it may dwell in field margins, farm tracks, edges of sand or gravel pits, embankments, and other anthropogenic environments (Gloger 1833; Straschil 1972; Hoffmann et al. 2008). The species has developed a tolerance toward tall vegetation, shrubs, and trees in the past decades (Ružić 1978; Spitzenberger and Bauer 2001). In Bulgaria, it may be found in localities with average annual temperatures between 10°C and 13°C (Koshev and Kocheva 2007). In Macedonia, it is associated with dry, warm, open places with deep soil that are regularly grazed by domestic animals, whereas it is absent from stony, eroded slopes, and lowlands with a high groundwater level (Kryštufek 1993). In the Czech Republic, the species does not depend on a specific plant or vegetation assemblage (Matějů et al. 2011) nor does it require a particular soil type (Janderková et al. 2011). Dominant plants occurring in the habitat of *S. citellus* in the Black Sea coast of Bulgaria are *Andropogon ischaemum*, *Artemisia absinthium*, *Bromus arvense*, *Convolvus arvensis*, *Cynodon dactylon*, *Eragrostis pilosa*, *Erodium cicutarium*, *Euphorbia rupestris*, *Festuca pseudovina*, *Filipendula hexapetala*, *Galium verrum*, *Marrubium peregrinum*, *Medicago orbicularis*, *M. lipulina*, *Papaver rhoes*, *Plantago lanceolata*, *Poa angustifolia*, *Polygonum aviculare*, *Salvia nemorosa*, and *Thymus marschallianus* (Paspalev and Peshev 1957).

Individual squirrels usually move within 60–80 m from their own burrows, but when searching for nutritious food, may travel $>$ 100 m (Ružić 1978). One of us (IEH) observed home ranges exceeding 1 ha in adult males throughout the active season, but typically home ranges cover between 0.1 and 0.4 ha, depending on reproductive condition, sex, age, population density, and habitat attributes (Huber 1996; Matějů 2008; Turrini et al. 2008). After emergence from hibernation, adult males show little aggression or locomotion and have small home ranges ($\bar{X} = 0.05$ ha, interquartile range = 0.30––0.07 ha). This changes with mating when aggression, locomotion, and home ranges increase considerably ($\bar{X}$ = 0.17 ha, interquartile range = 0.15–0.27 ha—Millesi et al. 1998), although after the mating period, range sizes decrease again (Millesi et al. 2002), and do not differ from female home ranges (Turrini et al. 2008). In a nearly natural habitat, mean ($\pm$ *SD*) adult home ranges were 0.435 ha ($\pm$ 0.387 ha) for males and 0.330 ha ($\pm$ 0.300 ha) for females. Minimum home-range span in juveniles was 71 m and in nonjuveniles 39 m, whereas maximum home-range span in juveniles was 338 m and in nonjuveniles 203 m (Turrini et al. 2008).

Dispersal starts about 30–40 days after natal emergence. Juveniles begin to depart from their natal sites at 9 weeks of age, and both sexes cover similar linear distances (up to 350 m—Hoffmann et al. 2004). Juvenile males move faster and incur in a higher risk of predation than females when leaving their natal home range (Hoffmann et al. 2004). According to Sutherland et al. (2000), allometric relationships between body mass and dispersal distance predict distances of $<$ 1 km. Hence, dispersal is possible if the population is growing and environments are suitable (Hulová and Sedláček 2008). In a nearly natural habitat in Austria, a yearling male traveled at least 750 m (Turrini et al. 2008).

Spermophilus citellus constructs and maintains simple and elaborate burrows by scratch-digging (Lagaria and Youlatos 2006). Burrows may be permanent (with a nest) or temporary; the former are deeper. Burrows are located mainly in open areas to allow good visibility, but depending

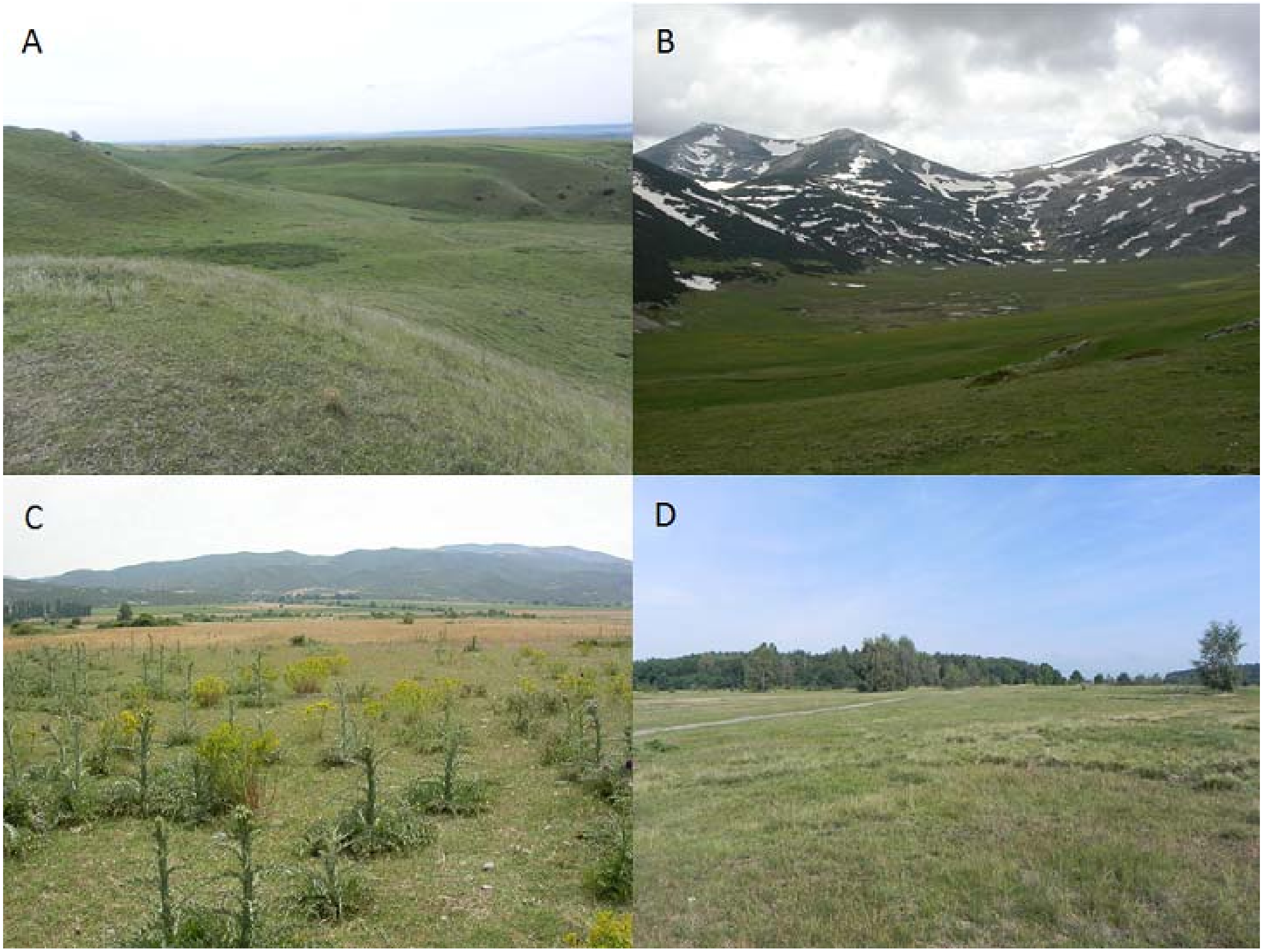

Fig. 4.—Habitats commonly occupied by *Spermophilus citellus* in portions of its range: A, Romania, Iaşi County, Osoi, elevation 140 m; B, Macedonia, Mt. Jakupica, Gorno Begovo, elevation 2,000 m; C, Macedonia, Valandovo, elevation 150 m; D, Czech Republic, Mladá Boleslav, elevation 205 m. Photographs courtesy of B. Kryštufek (A) and A. Kryštufek (B–D).

on habitat attributes and soil quality, burrows also occur under shrubs (Kryštufek and Vohralík 2005), grapevines (Hoffmann et al. 2008), or rocks (Calinescu 1934; Brinkmann 1951). When scratch-digging new or excavating collapsed tunnels, *S. citellus* loosens the soil with forefeet and incisors, scratches backwards, and uses the hind feet to remove the material that accumulates under it during digging (Ružić 1978; Lagaria and Youlatos 2006; Kley and Kearney 2007). Individuals inhabit permanent burrow systems with typically 1 chamber used for hibernation, lactation, sleep, copulation, protection of food, and short-term retreat (Ružić 1978; Lagaria and Youlatos 2006). Most shelter burrows consist of blind-ending tubes without a nest, but may be converted into permanent burrows, with number and length of branches increasing with use of the burrow (Ružić 1978). Each burrow system possesses 1–5 entrances (5–10 cm wide) with up to 6 tunnels that vary in length from 0.5 to 4.5 m, reaching a maximal depth of 2 m (Brinkmann 1951; Ružić 1978). Trodden trails in the vegetation cover connect burrow entrances on the surface (Brinkmann 1951). Prior to hibernation, the inhabitant plugs the entrance with soil and digs a blind-ending side branch (Ružić 1978). When emerging in spring, the squirrel either opens the original entrance or digs through a side branch (Ružić 1978), both resulting in soil mounds at the entrance (Brinkmann 1951).

The 16- to 25-cm-wide nesting chamber is either the deepest part of the burrow system (Ružić 1978) or is situated higher than the entry tunnel to protect against floods (Brinkmann 1951). If present, a 2nd chamber is used as a latrine (Ružić 1978) and plugged with soil when filled (Brinkmann 1951). Nesting material consists primarily of grasses (Brinkmann 1951; Ružić 1978; Gedeon et al. 2010).

Fig. 5.—An adult *Spermophilus citellus* from calcareous grassland in Perchtoldsdorf, Lower Austria, elevation 300 m, feeding on sage flowers (*Salvia*) on 30 June 2007. Used with permission of the photographer C. J. Böswarth.

In Hungary, *S. citellus* preferred *F. pseudovina* versus *Bothriochloa ischaemum* under laboratory conditions, with fresh *F. pseudovina* providing flexible material that allowed squirrels to construct nests with better insulation (Gedeon et al. 2010). Common plants in nesting material in northern Serbia were *A. ischaemum*, *C. dactylon*, *Festuca valesiaca*, and *Poa bulbosa* (Ružić-Petrov 1950).

Diets.—*Spermophilus citellus* is predominantly herbivorous, consuming green leaves, flowers, seeds, roots, and shoots, but also may include arthropods in its diet (Fig. 5). Specimens from Moldavia (419 stomachs) and Romania (650 pouches) contained 194 plant species from 45 families (Dănilă 1984). Poaceae, Fabaceae, and Asteraceae together constituted 33–100% of the plant diet (Dănilă 1984). Squirrels in a recreation area in Austria foraged up to 75% on dandelion (*Taraxacum officinale*) and switched to 50% clover (*Trifolium*) as it became abundant. Dandelion and clover species contain higher amounts of water, calcium, and magnesium than the less-preferred ryegrass (*Lolium perenne*—Pieta 1997). Thirty-one plants were identified in northern Serbia (Ružić-Petrov 1950) and 38 in southeastern Romania as part of its diet (Popescu 1972). In northern Serbia, *S. citellus* consumed green parts (23 species of plants), flowers (9 species), seeds (17 species), and underground parts (5 species—Ružić-Petrov 1950) of plants. When available, the species also feeds on agricultural crops (seedlings, grains, fruits, and storage organs—Ružić 1978; Dănilă 1984; Turrini et al. 2008). In northern Serbia insects occurred in 13.4% of the stomachs of *S. citellus* (Ružić-Petrov 1950; Ružić 1978), whereas in the Czech Republic insects occurred in 33–66% of the stomachs of pregnant females and 20% of adult males (Grulich 1960). Vertebrates (i.e., young northern white-breasted hedgehogs [*Erinaceus roumanicus*], common voles [*Microtus arvalis*], house mice [*Mus musculus*], common shrews [*Sorex araneus*], European mole [*Talpa europaea*], and eggs of ground-nesting birds) are occasionally consumed by *S. citellus* (Matějů et al. 2010a). The species has not been observed caching food prior to hibernation, apparently relying completely on stored body fat (Millesi et al. 1999b). Young squirrels begin to feed on grasses and forbs soon after emergence from their natal burrows (Huber et al. 2001). Nutritional manipulation in captive squirrels resulted in rapid gain in body mass in juvenile males, but the specific nutritional factors did not affect total body mass during the study period (Strauss et al. 2007a).

Diseases and parasites.—Studies of coccidian parasites in *Spermophilus citellus* are scanty. Three species of *Eimeria* were observed in 14 specimens of *S. citellus* from Bulgaria (prevalence in parentheses): *E. citelli* (80%), *E. callospermophili* (70%), and *E. cynomysis* (35%—Wilber et al. 1998; Golemansky and Koshev 2007). *E. citelli* produces catharal enteritis in the small and large intestines of infected *S. citellus* (Golemansky and Koshev 2007). Six specimens from different localities in Bulgaria also contained *Klossia* (Golemansky and Koshev 2009). A cytomegalovirus strain was recovered from the submaxillary glands of healthy full-grown *S. citellus* in Romania (Diosi et al. 1967). A new herpesvirus recovered from the kidneys of mature *S. citellus* produced an effect in tissue culture cells resembling that of herpesviruses (Diosi et al. 1975). Hall (1916) described the following 3 nematode species as parasites of *S. citellus*: *Oxyuris obvelata*, *Physaloptera citilli*, and *Trichuris leporis*. Other internal parasites may include *Hymenolepis fraternal* and *Moniliformis moniliformis* (Matějů et al. 2010a). The following ectoparasites were detected in nests of *S. citellus*: ticks (*Ixodes laguri*), mites (*Haemogamassus citelli* and *Hirstionyssus criceti*), and fleas (*Neopsylla setosa*, *Citellophilus simplex*, *C. orientalis*, *C. assimilis*, and *C. agyrtes*—Matějů et al. 2010a).

Interspecific interactions.—Predators of *Spermophilus citellus* include black kite (*Milvus migrans*), falcons (saker falcon [*Falco cherrug*], common kestrel [*F. tinnunculus*], and peregrine falcon [*F. peregrinus*]), eagles (greater spotted eagle [*Aquila clanga*], eastern imperial eagle [*A. heliaca*], tawny eagle [*A. rapax*], booted eagle [*Hieraaetus pennatus*]), hawks (northern goshawk [*Accipiter gentilis*] and Eurasian sparrowhawk [*A. nisus*]), harriers (western marsh harrier [*Circus aeruginosus*], hen harrier [*C. cyaneus*], and Montagu's harrier [*C. pygargus*]), common buzzards (*Buteo buteo*), great bustards (*Otis tarda*), weasels (ermine [*Mustela erminea*], steppe polecat [*M. eversmanii*], least weasel [*M. nivalis*], and European polecat [*M. putorius*]), marbled polecats (*Vormela peregusna*), red foxes (*Vulpes vulpes*), beech martens (*Martes foina*), Eurasian magpies (*Pica pica*), carrion crows (*Corvus corone*), and feral domestic cats (*Felis catus*—Grulich 1960; Ružić 1978; Millesi et al. 1999b; Hoffmann et al. 2004; Biró et al. 2005;

Lanszki 2005; Adamec et al. 2006; Hapl et al. 2006; Hulová and Sedláček 2008; Matějů et al. 2010a). Low abundance of *S. citellus* apparently caused a decline of imperial and tawny eagles, saker falcons, and steppe polecats in Bulgaria, Romania, Ukraine, and Slovakia (Adamec et al. 2006; Matějů et al. 2010a). *S. citellus* is believed to avoid predation by blocking its burrow tunnels with sand when entering and leaving (Hut and Scharff 1998). Koshev (2010) reports 3 types of interspecific aggressive behavior of *S. citellus* toward different vertebrate species: Balkan green lizard (*Lacerta trilineata*), rook (*Corvus frugilegus*), and least weasel. In Serbia, burrows of *S. citellus* are used by beetles of the families Tenebrionidae, Copridae, and Carabidae, and by European toads (*Bufo bufo*—Ružić-Petrov 1950). The coprophagous beetles *Ontophagus vitulus* and *Aphodius citellorum* use excrement of *S. citellus* as food (Matějů et al. 2010a).

***Miscellaneous*.**—Temperature data loggers implanted in the abdominal cavity of *Spermophilus citellus* proved a reliable technique in hibernation research (Hut et al. 2002a). Light-sensitive radiocollar transmitters have been used to measure daily patterns of light perceived by *S. citellus* in natural conditions (Hut et al. 1999). In an assessment of population density using distance sampling, the effective strip width along a linear transect was estimated at about 60 m (Kryštufek et al. 2012).

BEHAVIOR

***Grouping behavior*.**—Although *Spermophilus citellus* lives in colonies, with individual home ranges overlapping (Turrini et al. 2008), each individual beyond maternal care inhabits its own burrow system, and consequently the species cannot be regarded as truly social (Váczi et al. 2006). Nonagonistic interactions between males and females precede mating events, increasing from proestrus until mating and decreasing again through the postmating period. During mating, male aggression is primarily composed of chases and fights, resulting in frequent injuries. Aggression is intense and directed particularly toward other adult males (80.4%), and less intense toward females (8.2%) and nonreproductive yearlings (11.4%). After mating, aggression is noninjurious, composed of chases and displacements directed equally among ages and sexes (Millesi et al. 1998). Similar results were reported by Strauss et al. (2007b), with adult males directing most attacks toward mature competitors and only a few against nonreproductive yearlings. The communal use of focal areas indicates that there are no distinct mating territories (Millesi et al. 1998). Despite endogenous components, environmental releasers are important for the expression of male mating behavior; however, the physiological basis is unclear (Millesi et al. 2002). Infanticide has not been observed in *S. citellus* (Millesi et al. 1999a).

***Reproductive behavior*.**—*Spermophilus citellus* is a polygynous species (Huber at al. 2002). Mating occurs after a courtship period of a few days when a male interacts regularly with a female (Millesi et al. 1998). Receptivity begins before mating, with females tolerating genital inspection and grooming by males (Millesi et al. 2000). During the premating and mating periods, adult males begin aboveground activities earlier than yearling males. However, during the mating season adult males spend less time foraging than yearling males (Everts et al. 2004). Females rear offspring in litter burrows that are normally separate from hibernacula. After weaning, each offspring takes over a separate burrow (Huber et al. 2002). During the postmating period, considerable digging behavior in both reproductive and nonreproductive males is commonly observed. Whereas digging behavior in nonreproductive males is restricted to their own burrows, reproductive males dig at both their nest burrows and litter burrows of their former mates. Saving the female time and energy to invest more in gestation and lactation has been considered as paternal effort (Huber et al. 2002).

***Communication*.**—Eight call types have been described in *Spermophilus citellus*: 3 tonal (alarm call, scream, and chatter) and 5 wideband (grunt, rapid grunt, snarl, chirr, and pant) calls; alarm calls are the loudest and most common (Koshev and Pandourski 2008; Matrosova et al. 2012). Alarm calls may last 65–152 ms and are tonal sounds usually consisting of 2 different elements that can be joined together or separated by an interval (mean $\pm$ *SD*) of 6 $\pm$ 3 ms. The 1st element, which may last 45–112 ms with a peak frequency of 7,230–9,210 Hz, lacks modulation in frequency, whereas the 2nd element, which may last 13–62 ms with a peak frequency of 9,300–14,550 Hz, is highly frequency modulated (Schneiderová and Policht 2011a). In Hungary, emission of alarm calls peaked in June when litters emerged from natal burrows (Katona et al. 2002). Scent marking is restricted to the mating season (Millesi et al. 1998).

***Miscellaneous behavior*.**—*Spermophilus citellus* is a diurnal species with a pronounced annual cycle of aboveground activity (Everts et al. 2004). The onset of daily activity apparently does not track either dawn or dusk. On average, squirrels emerge from their burrows 3.9 h after civil twilight at dawn, and retreat 3.2 h before civil twilight at dusk (Hut et al. 1999; Everts et al. 2004). *S. citellus* is more active during the morning hours (0900–1100 h) than at midday (1200–1400 h) on sunny days, but not on cloudy days (Váczi et al. 2006). Daily activity is centered around 1200 h and has an average length of 8.8 h. Within this daily activity phase animals are on average 4.7 h (53%) aboveground and 3.5 h (74%) of that time is spent foraging (Everts et al. 2004). In arid parts of southern Macedonia, individuals become lethargic during the summer peak, when water content in plants falls from 70% to 22.5% (Kryštufek and Vohralík

Fig. 6.—A lactating female *Spermophilus citellus* from calcareous grassland in Perchtoldsdorf, Lower Austria, elevation 300 m, in bipedal vigilance on 19 June 2004. Used with permission of the photographer C. J. Böswarth.

2005). During aboveground activity, vigilance and foraging are the dominant behaviors in all periods for males and females (Youlatos et al. 2007). Scanning the surroundings for potential threat in a bipedal posture is a conspicuous and typical behavior (Fig. 6). Time spent in bipedal vigilance peaks subsequent to juvenile emergence, coinciding with peaks in population density, numbers of predators and alarm calls, and elevated stress load (Hoffmann 1995; Brenner 2011).

Spermophilus citellus is an obligate hibernator. Adult and yearling females commonly enter hibernation in August, hence the time for molt and fattening is limited (Millesi et al. 2000). Duration of hibernation in an enclosed population was on average shorter in males (127.8 days) than in females (171.3 days—Hut et al. 2002a). The same was observed in a natural population in Austria where females (median = 228 days) hibernated longer than males (median = 185 days), yearling males (median = 178 days), and juveniles (median = 191 days—Millesi et al. 1999b). During hibernation, squirrels seem to lack the need for a functional circadian system (Hut et al. 2002b). Hibernation terminates in early spring, when temperatures constantly range above 0°C (Straschil 1972), and hence depends on altitude and latitude. On the Black Sea coast of Bulgaria, the 1st active individuals are reported on 18 March and mass emergence starts on 1 April (Peshev 1955). Emergence dates range from 15 February to 28 April in Austria (Millesi et al. 1999a; Millesi and Hoffmann 2008), 2 to 12 March in the lowlands of northern Serbia, and 6 to 24 April in the mountains of eastern Serbia (Ružić-Petrov 1950). Timing patterns of emergence resemble those of other *Spermophilus*, in which adult males emerge first from hibernation, but contrarily, immerge into hibernation later than adult females, followed by yearlings and juveniles (Millesi et al. 1999a, 1999b; Strauss et al. 2007b; Youlatos et al. 2007; Millesi and Hoffmann 2008). Nonreproductive yearling males are able to dedicate 1 complete active season to growth and preparation for hibernation, which may result in improved body condition at spring emergence and higher survival rates (Strauss et al. 2007b). However, late-born juveniles may have less time to grow and fatten for hibernation (Millesi et al. 2000). Juveniles terminate aboveground activity between 3 September and 22 October, with a distinct drop in temperature preceding immergence of the last squirrels (Straschil 1972; Millesi et al. 1999b; Millesi and Hoffmann 2008).

GENETICS

Cytogenetics.—The diploid chromosome number (2n) in *Spermophilus citellus* is 40. Traditionally, the autosomal set has been reported to include 2 pairs of metacentric, 12 pairs of submetacentric, and 5 pairs of acrocentric chromosomes, therefore a fundamental number (FN) of 69 and a fundamental number of autosomes (FNa) of 66 (Belcheva and Peshev 1979; Zima and Král 1984; Özkurt et al. 2002, 2007; Mitsainas et al. 2008). There may be inconsistencies involved in the interpretation of autosomes with tiny short arms. Therefore, Özkurt et al. (2007) reported for European Turkey a cytotype with FN = 78, FNa = 74. Mitsainas et al. (2008) claimed that all autosomal pairs are biarmed. The X chromosome can be biarmed or acrocentric, whereas the Y chromosome is the smallest element, either biarmed (Zima and Král 1984) or acrocentric (Özkurt et al. 2002). The biarmed Y chromosome was reported only from Turkey (Özkurt et al. 2007). Soldatović et al. (1984) suggested that the acrocentric Y chromosome was derived from a biarmed condition by deletion. One Bulgarian population is unique in that members have a pericentric inversion involving the X chromosome (Belcheva and Peshev 1979). The C-band staining technique indicated that all autosomes, as well as the X chromosome, possessed prominently stained centromeres. Some pairs demonstrated additional heterochromatic bands at different positions on the short or long arms (6, 8, 9, and 15). The Y chromosome appeared fully heterochromatic (Mitsainas et al. 2008).

Molecular genetics.—Kruckenhauser et al. (1999) used DNA sequences of the mitochondrial cytochrome-*b* (*Cytb*) and mitochondrial cytochrome-b (Cytb) and NADH-dehydrogenase subunit 4 (*ND4*) genes from *Spermophilus citellus* to revisit the phylogeny of the genus *Marmota*. Harrison et al. (2003) used complete mitochondrial *Cytb* sequences from *Spermophilus* and *Cynomys* to reconstruct the phylogeny and evolutionary history of ground squirrels. Divergence based on *Cytb* sequences suggests that *S. taurensis* separated from *S. citellus* 2.5 million years ago and that the ancestor of these 2 species diverged from *S. xanthoprymnus* about 5 million years ago (Gündüz et al. 2007). Using *Cytb* gene sequences, Herron et al. (2004) suggested that the name *Spermophilus* is appropriate for the species included in the Old World clade of the genus *Spermophilus* (*S. citellus*, *S. dauricus*, *S. erythrogenys* [red-cheeked ground squirrel], *S. fulvus* [yellow ground squirrel], *S. major* [russet ground squirrel], *S. musicus* [Caucasian Mountain ground squirrel], *S. pallidicauda* [pallid ground squirrel], *S. pygmaeus* [little ground squirrel], *S. relictus* [relict ground squirrel], *S. suslicus*, and *S. xanthoprymnus*). Based on parameters of DNA reassociation kinetics, the genome size calculated for *S. citellus* was 3.07 pg (Ginatulina et al. 1982). Three highly divergent phylogenetic lineages (southern, northern, and Jakupica) were recognized using 31 *Cytb* haplotypes from different locations ranging from the Czech Republic to European Turkey and beyond (Kryštufek et al. 2009). These lineages presumably originated from independent Quaternary refugia for steppic biota in southeastern Europe. Haplotypes of the northern lineage were found on both sides of the Danube River, and in both of the 2 main geographical fragments of the species. The Jakupica lineage is an isolate on a high plateau in central Macedonia. The southern lineage diverged at about 0.58 million years ago, whereas the northern and the Jakupica lineages separated at about 0.3 million years ago (Kryštufek et al. 2009). Variability in 25 nonmetric cranial traits retrieved 3 main groups of populations (Kryštufek 1990) that concur with phylogeographic groups.

Population genetics.—The first 6 microsatellite markers for *Spermophilus citellus* (loci ST7, ST10, SB10, SC2, SC4, and SX) were extracted from ethanol-stored tissue samples from the tail to establish a partial genomic library (Hanslik and Kruckenhauser 2000). Gondek et al. (2006) cross-tested primer pairs from *S. suslicus* with 10 individuals of *S. citellus* from Austria, obtaining positive amplification for 6 of 9 loci (Ssu1, Ssu3, Ssu5, Ssu13, Ssu15, and Ssu16); significant deficit of heterozygotes occurred for loci Ssu1 and Ssu16, although no deviation from Hardy–Weinberg equilibrium was detected when analyzing larger numbers of individuals. A total of 382 specimens of *S. citellus* from central Europe were genotyped using microsatellite loci designed originally for the alpine marmot (*Marmota marmota*; MS41, MS45, and MS56), Idaho ground squirrel (*Urocitellus brunneus*; IGS-1 and IGS-110b), and *S. suslicus* (Ssu1, Ssu5, Ssu7, Ssu8, Ssu13, Ssu15, and Ssu16). Populations of *S. citellus* were strongly differentiated, with high levels of inbreeding. Coefficients of inbreeding were higher in populations from the western range (Czech Republic and western Slovakia; F_{IS} = 0.27–0.79) than those from the east (Hungary and eastern Slovakia; F_{IS} = –0.060–0.119), whereas interpopulation differentiation was similarly high in both groups: $F_{ST} = 0.23$ (west) and $F_{ST} = 0.25$ (east). No evidence was found for contemporary selection on major histocompatibility genes (Říčanová et al. 2011). Another assessment of 117 individuals from Austria, Hungary, and Romania for 11 microsatellite loci revealed a high (23.4%) proportion of private alleles, presumably the result of disintegration of local populations that might have been historically connected genetically (Ben Slimen et al. 2012).

CONSERVATION

Spermophilus citellus was considered an agricultural pest during centuries when rural communities paid rewards for killed specimens (Brinkmann 1951; Spitzenberger and Bauer 2001), and large-scale pest-control measures were implemented, for instance in northern Serbia (Ružić-Petrov 1950) and Macedonia (Gradojević 1928). The species is "Critically Endangered" in the northwestern portion of the range (Koshev 2008). Serious declines have been reported from many portions of the range, particularly in the Pannonian Plain, with some marginal isolates becoming extinct during the past century (e.g., Germany, Poland, and Croatia). The 1st decline was reported in the 1930s from the northwestern portion of the range (Matějů et al. 2010a). In habitats of northern Serbia, high densities of *S. citellus* declined from $>$ 30 individuals/ha in the late 1940s to approximately $\leq$ 5 individuals/ha in the late 1960s. The decline was less conspicuous in high mountain pastures in eastern Serbia, where densities dropped from $<$ 22 individuals/ha in the 1940s to $<$ 5 individuals/ha in the 1960s. In colonies with low densities, individuals do not expose themselves any longer and avoid vocal communication (Ružić 1979). Although large, stable populations still exist in many parts of the species' range, fragmentation already seems to be critical. Nonetheless, Ćosić et al. (2013) found that populations in Vojvodina are highly fragmented, but their genetic variation is still higher than in peripheral populations in Central Europe. In the cultural landscape that dominates the distribution range, *S. citellus* relies on heterogeneous, extensively cultivated farmland (Hoffmann 2002); hence, numbers have declined with increased intensification of agriculture (Spitzenberger 2005). Abandonment of tripartite crop rotation, afforestation, and cultivation of fallows led to population declines in Saxonia and Silesia (then Germany) as early as in the 1930s (Brinkmann 1951). Presently, the main threats are habitat loss due to urban sprawl and other construction activities (Hoffmann et al. 2003b), the transformation of steppe into arable land, and the abandonment of grazing, resulting in tall-grass meadows where *S. citellus* cannot survive (Kryštufek 1999; Coroiu et al. 2008). In 2007, the majority (74%) of *S. citellus* in the Czech Republic lived in airfields (Matějů et al. 2010a). Persistence in Austria largely depends on dispersal and recolonization among colonies (Hoffmann et al. 2003b).

Spermophilus citellus is currently listed as "Endangered" under the Bern Convention, Appendix II (Kryštufek 1999) and is listed in the European program NATURA 2000 (Hulová and Sedláček 2008). The species is included in the *Red List of Threatened Species* by the International Union for Conservation of Nature and Natural Resources as "Vulnerable" (Coroiu et al. 2008). It also is protected by the European Union Habitats and Species Directive, Annexes II and IV (Kryštufek 1999). In the Czech Republic, where *S. citellus* was still widespread in the early 1950s (Grulich 1960), 34 colonies remained by 2007, but only 5 colonies included > 200 individuals each (Matějů et al. 2008, 2010a). As a result, the species is included in the list of endangered species (category: "Critically Endangered"), and is thus under strict legal protection (Zima and Anděra 1996). In addition, an action plan for *S. citellus* has been developed in the Czech Republic (Matějů et al. 2010a). Several conservation programs have attempted to reintroduce or translocate the species into suitable habitats without great success (Hulová and Sedláček 2008; Matějů et al. 2010b), except in Poland, where it is considered as successful (Coroiu et al. 2008; Matějů et al. 2010b, 2012). In Moldova, *S. citellus* is rare in the steppe and meadow ecosystems and has been included in the country's Red Book (Teleuta et al. 2004). In Slovakia, *S. citellus* uses areas managed by humans (e.g., airfields, golf courses, sport areas, and horse race courses) when degradation of its original habitat occurs (Hapl et al. 2006). The State Nature Conservancy of the Slovak Republic has conducted several transfers and reestablishments of *S. citellus* (Adamec et al. 2006). The species is included in the Slovak National Red List as "Endangered" (Hapl et al. 2006). Turkey has not declared the species protected, although the population size in Thrace is decreasing to a very low level because of intensive land use (Özkurt et al. 2005). In Bulgaria, the species is covered by the Biological Diversity Act, as a species "requiring priority conservation of its habitat" (Annex 3 to Art. 37—Stefanov and Markova 2009).

Kryštufek et al. (2009) recommended that 3 phylogeographical lineages (southern, northern, and Jakupica) of *S. citellus* should be regarded as independent units for conservation. The Jakupica lineage is the smallest, being restricted to mountain pastures (1,500–2,250 m altitude) in the Jakupica–Karadjica mountain system of central Macedonia. The total area (884 ha) is fragmented and 94% of *S. citellus* occur in 4 colonies. Densities (0.8–5.5 adults/ha) are lower than elsewhere and the total population is estimated at < 2,000 adult individuals (Kryštufek et al. 2012). In a field experiment, Gedeon et al. (2012) found that squirrels preferred angled artificial burrows (about 30°), which facilitated digging, and medium-height grass ($\bar{X} = 18 \pm SE$ 1.5 cm) with overhead protection by grasses as an important component after a translocation of animals. Matějů et al. (2012) found that a soft method of releasing (i.e., use of artificial burrows or fences or both) is an essential component of a successful reintroduction.

ACKNOWLEDGMENTS

We thank Ö. Özkurt, Y. Koshev, J. Matějů, and S. Shilova for providing information on *Spermophilus citellus*. C. Mlinar took the photographs of the skull. A. Kryštufek and C. J. Böswarth generously provided photographs of live animals and habitats occupied by the species. Two anonymous reviewers provided valuable comments that improved the manuscript.

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Associate Editors of this account were Pamela Owen and Eric Rickart. Editor was Meredith J. Hamilton.