Sciurus vulgaris.   By Peter W. W. Lurz, John Gurnell, and Louise Magris

Sciurus vulgaris Linnaeus, 1758
European Red Squirrel

Sciurus vulgaris Linnaeus, 1758:63. Type locality "Habitat in Europe."

CONTENT AND CONTEXT. Order Rodentia, suborder *Sciurognathi*, family *Sciuridae*, subfamily *Sciurinae*, genus *Sciurus*. Variations in coat color and morphology led to the description of >40 subspecies (Corbet 1978; Ellerman and Morrison-Scott 1965). Taxonomic status of some of these is uncertain and the number of subspecies differs between authors (Corbet 1978; Lowe and Gardiner 1983; Sidorowicz 1971; Wiltafsky 1978). Regional differences in skull size within the subspecies *S. v. fuscoater* are larger than described differences between recognized subspecies (Wiltafsky 1976). Morphological characteristics of the different subspecies may relate to environmental conditions (Sidorowicz 1971). The following subspecies are based on Sidorowicz (1971).

S. v. altaicus Serebrennikov, 1928:422. Type locality "Kok-Su river, estuary of the Yamanuch river, Altai Mountains."

S. v. anadyrensis Ognev, 1929:83. Type locality "50–60 km im Norden von Markowo und zieht sich flußaufwärts ca. 170 km weit," Anadyr territory, forest along Anadyr River, north of Markovo.

S. v. argenteus Kerr, 1792:256. Type locality "the upper parts of the river Oby," Siberia; corrected to left bank of the lower Yenisei river, West Siberia by Matschie (1904:313); *albus* Dvigubsky, *martensi* Matschie, and *nadymensis* Serebrennikov are synonyms.

S. v. balcanicus Heinrich, 1936:41. Type locality "Lower reaches of Kamchik River, eastern Balkan Mountains, Bulgaria;" *ameliae* Cabrera, *croaticus* Wettstein, *istrandjae* Heinrich, *lilaeus* Miller, and *rhodopensis* Heinrich are synonyms.

S. v. bashkiricus Ognev, 1935:47. Type locality "Buzuluk pine forest, Shkotovskoe Forest, Samara Province, Belaya River, Russia."

S. v. exalbidus Pallas, 1778:374. Type locality "Region of isolated pine forests along the Irtysh and Ob. Siberia, Russia;" *goltzmaieri* Smirnov and *kalbinensis* Selevin are synonyms.

S. v. fuscoater Altum, 1876:75. Type locality "Harz," Harz Mountains, Germany; *alpinus* Desmarest, var. *brunnea* Altum, *carpathicus* Pietruski, *cinerea* Hermann, *fedjushini* Ognev, var. *fuscoatra* Altum, var. *gothardi* Fatio, *kessleri* Migulin, *ognevi* Migulin, *rufus* Barrett-Hamilton, *rufus* Trouessart, *russus* Miller, *rutilans* Miller, *subalpinus* Burg, and *vilnensis* Udziela are synonyms.

S. v. fusconigricans Dvigubsky, 1804:83–84. Type locality "Barguzin, Transbaikalia."

S. v. infuscatus Cabrera, 1905:227–228. Type locality "Los ejemplares que yo he estudiado proceden de las provincias de Madrid, Soria y Avil;." *baëticus* Cabrera, *numantius* Miller, and *segurae* Miller are synonyms.

S. v. italicus Bonaparte, 1838:23. Type locality "Italy."

S. v. jacutensis Ognev, 1929:81–82. Type locality "Die Verbreitung umfaßt ein breites Gebiet, welches sich von Kirensk über das Gebirgsland zwischen Witim und Aldan zieht und den mittleren Teil des Jakutiengebiets einschließt," wide area from Kirensk through the mountains between Witim and Aldan as well as the central area of Jakutsk; *arcticus* Trouessart, *borealis* Brass, *calotus* Gray, and *fuscorubens* Dvigubsky are synonyms.

S. v. jenissejensis Ognev, 1935:47. Type locality "Lower Tunguska, Turukhansk Territory, Siberia."

S. v. leucourus Kerr, 1792:256. Type locality "England."

S. v. mantchuricus Thomas, 1909:501. Type locality "Khingan,"

Manchuria; *chiliensis* Sowerby, *coreae* Sowerby, and *orientis* Thomas are synonyms.

S. v. meridionalis Lucifero, 1907:45–46. Type locality "La regione calabrese degli Appenini, e sovratutto quella parte che vien detta Sila" Sila, Calabria, Italy; *alpinus* Costa and *silanus* Hecht are synonyms.

S. v. rupestris Thomas, 1907:410. Type locality "Dariné, 25 miles N. W. of Korsakoff," Saghalien Island; *dulkeiti* Ognev is a synonym.

S. v. vulgaris Linnaeus, 1758:63. Type locality "Europe."; restricted to "Sweden (Uppsala)" by Thomas 1911:148; *albus* Billberg, *albonatus* Billberg, *europeus* Gray, *formosovi* Ognev, *niger* Billberg, *rufus* Kerr, *typicus* Barrett-Hamilton, and *varius* Gmelin are synonyms.

DIAGNOSIS. *Sciurus anomalus* is the only naturally occurring congener in the Palearctic. In contrast to *S. vulgaris* (Fig. 1), *S. anomalus* has 4 rather than 6 pads on the hind feet (Wiltafsky 1978) and fur color on underparts varies from a strong rusty color to buff yellow. *S. lis* occurs in Japan (Honshu, Shikoku, and Kyushu), but not on the island of Hokkaido, where *S. v. manchuricus*

FIG. 1.   *Sciurus vulgaris* from Valtellina, Italy. Photograph by Gianfranco Scieghi.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Sciurus vulgaris* (male from Lanzonby, near Penrith, Cumbria, United Kingdom; Tullie House Museum, Carlisle, Cumbria; specimen number 1967.24). Greatest length of cranium is 49 mm. Photographs by P. W. W. Lurz.

is present. In Italy, Ireland, and Britain, *S. vulgaris* co-occurs with the introduced, larger *S. carolinensis*, which can exhibit some chestnut color over the back and down the limbs, but the color is not uniform as in the European red squirrel. Some European red squirrels can appear quite gray, particularly in winter; however, *S. vulgaris* has ear tufts that grow in late summer and are prominent in winter and spring. Morphologically, skull (Fig. 2) of the red squirrel is smaller than that of *S. carolinensis*, cranium is deeper, and postorbital processes are longer and narrower.

France and Italy have 2 introduced species of *Callosciurus*, *C. erythraeus erythrogaster* at Cap d'Antibes in southern France and *C. finlaysonii bocourtii* at Aquiterme in Piedmont, Italy (Bertolino et al. 1999; Mitchell-Jones et al. 1999). However, the distinct appearance and color of both these 2 species makes any confusion with *S. vulgaris* unlikely. *C. e. erythrogaster* or the red-bellied tree squirrel has an olive-brown back and a reddish underside with grayish legs and feet. *C. f. bocourtii* appears dark dorsally with a striking white underside and flanks.

GENERAL CHARACTERS. *Sciurus vulgaris* shows no sexual dimorphism in size or fur color (Wiltafsky 1973). Sex can be determined by distance between genital opening and anus, which are very close in females and ca. 10 mm apart in adult males. Skull and external measurements vary across the range depending on subspecies. Condylobasal length, 44.0–49.3 mm, may increase in Eurasia from north to south (Wiltafsky 1978). However, this pattern is confused in central Europe (Wiltafsky 1973) and skull size and climate are not related (Wiltafsky 1973, 1976). Ranges of body and skull measurements (in mm) are: length of body and head, 206–250; length of tail, 150–205; length of hind foot, 51–63; length of ear, 25–36; basal length of skull, 40.2–48.4; zygomatic breadth, 29.0–35.2; length of nasals, 14.0–18.7; length of maxillary toothrow, 8.5–10.4. Subspecies descriptions are available (Miller 1912; Ognev 1940; Sidorowicz 1971; Wiltafsky 1976, 1978).

Dorsal fur is uniformly dark but variable in color from deep brown to red brown or bright chestnut to gray brown or black. Winter coat is thick, deep red to brown, gray or almost black above; thick red brown ear tufts are 2.5–3.5 cm long; tail hair is dense and dark red brown or black. Underside is pale, white, or cream. Summer coat is reddish brown or chestnut above; ear tufts are small or absent; and tail is thin, chestnut to creamy white. Color varies widely across the continental range with dorsal color ranging from dark red to black to brown to gray to blue (Corbet 1978; Ognev 1940). Winter fur of *S. v. jenissejensis* from the Turukhansk Territory in Siberia is an intense bluish ash gray with slight dark gray mottling (Ognev 1940). Tail, feet, and ear tufts may be the same color or contrast with the back.

Many populations are polymorphic and several color types may be present. However, the relative proportion of color phases (black, brown, and red) varies geographically (Andera 1985; Markov 1961; Voipio 1970; Wiltafsky 1978; Zawidzka 1958). In Denmark, European red squirrels on the island of Bornholm are smaller and tail and ears are black, similar to Scandinavian squirrels. Populations on Sealand are dominated by light-colored reddish animals, whereas the rest of Denmark (eastern Jutland) has polymorphic populations similar to *S. v. fuscoater* (Degn 1973). Populations where only 1 color type occurs are rare, such as on islands (Fünen—Wiltafsky 1973). *S. v. leucourus* Kerr, 1792, endemic to Britain and Ireland, is characterized by bleaching of the ears and tail. However, introductions of *S. v. vulgaris* from Scandinavia into Perthshire, Scotland, in 1793 (Harvie-Brown 1880–81) and *S. v. fuscoater* from western Europe to Lothians, Scotland, in 1860 (probably) and Epping Forest, England, ca. 1910 (Harvie-Brown 1880–1881; Shorten 1954) complicate the picture in the United Kingdom. Some squirrels now exhibit bleaching, whereas others do not. Black or melanistic squirrels found in continental Europe are rare in the United Kingdom, as are albino forms. In Europe, the proportion of dark color types decreases from southwest to northeast, except in mountainous areas, where dark color types may predominate. Coat color is not related to climate (Wiltafsky 1973, 1977, 1978).

DISTRIBUTION. *Sciurus vulgaris* occurs from the British Isles in the west across the Palearctic to the island of Hokkaido, Japan (Lee and Fukuda 1999), in the east (Fig. 3).

FOSSIL RECORD. The earliest record of *S. vulgaris* is from Hórvölgy Cave in Hór Valley, southern Bükk Mountains, Hungary, and is middle Pleistocene in age (Jánossy 1986). Fossils of *S. vulgaris* in Hungary are from Varbóian stage (pre-Würm) sediments in Lambrecht Cave, eastern Bükk Mountains, the Subalyukian (lower Würm) sediments on the western side of Hór Valley, and a layer at Rejtek, east of Répáshuta, which represents a transitional period between the Pleistocene and the Holocene (Jánossy 1986). *S. vulgaris* occurs in France in late Pleistocene (and Würm interglacial period) deposits bearing forest faunas (Fontéchevade, Santenay, Regurdou, and Rond du Barry—Chaline 1972).

In Britain, *S. vulgaris* appears in a few poorly stratified cave records associated with forest floras (Stuart 1982). The earliest record is from landslip debris at Binnel Point, Isle of Wight, with a radiocarbon date of 4,480 ± 100 years ago (Preece 1986). *S. vulgaris* occurs at the Ipswichian and Hoxnian interglacial stages based on pollen spectra analysis (Currant 1989). In Poland, *S. vulgaris* has been linked to warmer phases in the late Quaternary appearing in the Vistulian and then, after a long gap, in the Vistulian 3 stadial (Late Devensian) and during the Holocene (Nada-
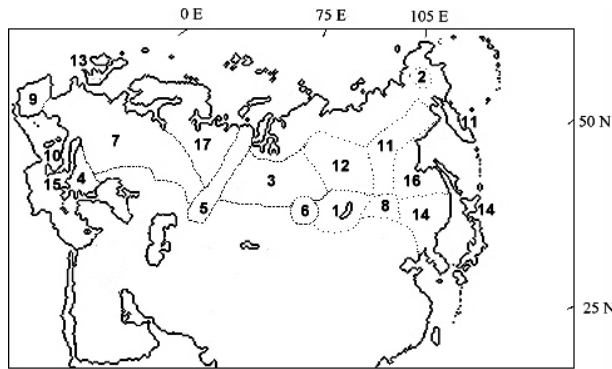
FIG. 3. Distribution of *Sciurus vulgaris* L. across Eurasia. The approximate ranges of the 17 subspecies based on Sidorowicz (1971) are indicated by dashed lines: 1, *S. v. altaicus*; 2, *S. v. anadyrensis*; 3, *S. v. argenteus*; 4, *S. v. balcanicus*; 5, *S. v. bashkiricus*; 6, *S. v. exalbidus*; 7, *S. v. fuscoater*; 8, *S. v. fusconigricans*; 9, *S. v. infuscatus*; 10, *S. v. italicus*; 11, *S. v. jacutensis*; 12, *S. v. jenissejensis*; 13, *S. v. leucourus*; 14, *S. v. mantchuricus*; 15, *S. v. meridionalis*; 16, *S. v. rupestris*; 17, *S. v. vulgaris*.

chowski 1989). *S. vulgaris* occurs from Euerwanger Bühl in Germany, dated to 8,760 ± 110 radiocarbon years ago (Königswald and Rähle 1975).

FORM AND FUNCTION. The postcranial skeleton shows adaptations for climbing and leaping; bones are relatively light and hind limbs are disproportionately long and heavy (Shorten 1962). Feet are plantigrade; long toes (except thumbs, which are reduced to tubercles) have long curved claws. Well-developed tail is used for balance, thermoregulation, and as signaling device in behavioral interactions. Epiphyseal fusion of long bones has been used to distinguish juveniles and adults (Degn 1973; Lemnell 1973).

Skull is broad, smooth, and rounded with a deep, broadly ovate braincase and a short, narrow, and deep rostrum (Barrett-Hamilton and Hilton 1910–1922; Miller 1912). Dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Upper front premolar is small and peglike (Ognev 1940). Functional cheek teeth are rooted, low crowned, quadrate with rounded marginal cusps and concave central area, and with upper teeth crossed by weak ridges (Tittensor 1977). Lower and 2nd upper premolars are deciduous and are shed at 16 weeks (Tittensor 1975). Wear of cheek teeth and growth of cementum (as well as mass of eye lens) can determine age (Degn 1973; Karpukhin and Karpukhina 1971; Kiris 1937; Lemnell 1973). The mass or length of the baculum in males is not accurate for determining age (Degn 1973).

Body fur molts twice a year; spring molt proceeds from front to back, autumn molt from back to front. Exact timing varies between individuals, particularly in relation to body condition. Ear tufts and tail hairs (from tip forward) molt once, with new hairs growing in late summer–autumn, and through to December in the case of ear tufts. Juveniles molt to appropriate summer or winter adult coat after weaning (Ognev 1940).

The European red squirrel has facial, carpal, and ventral body vibrissae (Beddard 1902; Bresslau 1912). Six sets of vibrissae are on the head: above the eyes, below the eyes, on the throat, under the chin, above the mouth, and on the nose (whiskers). Similar hairs are found on the feet, the outer sides of the forelegs, the underside of the body, and at the base of the tail (Fraefel 1995). Hyvärinen (1977) described the histology and ultrastructure of the nerve organs and Sokolov and Kulikov (1987) illustrated the vibrissal field.

Eyes are cone rich (Esteve and Jeffery 1998; Shorten 1954) with wide-angled vision and probably dichromatic color vision (Shorten 1954); the blind spot is a slender horizontal stripe above the center of the retina (Tittensor 1977). The sense of smell appears highly developed (Shorten 1954; H. Wiltafsky, pers. comm.).

Scent glands are associated with large mucous glands on side of mouth and sebaceous glands in the tissues of the upper and lower lips (Schumacher 1924). A type of apocrine gland occurs on either side of the head in the chin region (Fraefel 1995).

Daily energy expenditures of red squirrels in Scotland are available (Bryce et al. 2001). Large variations occur between in-

dividual squirrels and energy expenditure (mean ± *SE*) peaked in spring for red squirrels (389.9 ± 122.5 kJ).

ONTOGENY AND REPRODUCTION. Reproduction can last from December–January, when males and females 9–10 months old or older become sexually active, to August–early October, when the last litters are weaned. Two breeding peaks occur within a year, with mating in winter and spring leading to spring-born (February–April) and summer-born (May–August) litters, respectively. First breeding may be delayed or missed when food is limited (Gurnell 1983, 1987), resulting in a shorter breeding season. Reproductive tract regresses in autumn. When active, testes are large and scrotal; scrotum is sometimes darkly stained. Female tract has a Y-shape and embryo postattachment sites are sometimes visible. Vulva becomes pink and swollen at estrus. Mating occurs with little prior courtship other than a mating chase. Males are attracted to a female in heat by odor and follow her for 1 or more hours. The leading male in the following group tends to be heaviest and dominant and accounts for most matings (Wauters et al. 1990). Mating system is polygynous–promiscuous.

Body mass and dominance rank in females are the best predictors of fertility. Females must attain a threshold body mass before entering estrus, 300 g in Belgium (Wauters and Dhondt 1989), northern England (Lurz 1995), and Germany (Münch 1998); 325 g on Jersey, Channel Islands (Magris and Gurnell 2002). Daily changes in body mass of an autoweighed female were 2.9% in the pregestation period, 3.0% in the pregnancy period, and 6.9% in the lactation period (Lee 2000). Heavy females in high-quality home ranges live longer and produce more offspring (Wauters and Dhondt 1989). Lowered density-dependent breeding success results from a greater proportion of females living in poor habitats at high density and more nonbreeding floaters at high density (Wauters and Lens 1995). Females can reproduce the 2nd summer after their birth and lowest age of a female giving birth was 11 months (Wiltafsky 1978). Average lifetime reproductive success of a female red squirrel in Belgium was 5 offspring (range, 1–11 offspring; *n* = 46—Wauters and Dhondt 1995).

Males are fecund for most of the breeding season, with a period of inactivity in autumn and possibly into winter. In alpine habitats, males are inactive from late August to March (L. Wauters, pers. comm.). Males do not care for young. Females are polyestrus and in heat for only 1 day during each estrous cycle. Adult females can produce 2 litters of 1–6 (occasionally more) offspring each year when breeding starts early. In northern England, individual litters range from 1 to 4 (Lurz 1995; Tonkin 1983) and a supplementary-fed population at Formby, United Kingdom, had means (± *SD*) of 3.17 ± 0.47 and 2.4 ± 0.31 offspring for 1994 and 1995 (Shuttleworth 1996).

Young are blind, deaf, and naked at birth; mass is 10–15 g (Eibl-Eibesfeldt 1951; Frank 1952). Skin pigment appears on back and hairs emerge at 8–9 days. Hairs cover body by 21 days (Eibl-Eibesfeldt 1951; Shorten 1954). Lower incisors are cut at 20–23 days, uppers at 37–42 days (Eibl-Eibesfeldt 1951; Tittensor 1975). Ears open at 28–35 days; eyes open at 28–32 days (Tittensor 1975). Young begin leaving nest and start eating solid food at 40–45 days (Eibl-Eibesfeldt 1951; Ognev 1940; Tittensor 1975) and are weaned at 8–10 weeks, but suckling attempts by young and maternal protective behavior may extend beyond this (Frank 1952; Gurnell 1991; Wiltafsky 1978). In Belgian, weaning is at 10–12 weeks (Wauters et al. 1995). Molt to adult coat is at 3–4 months (Eibl-Eibesfeldt 1951).

Mass at weaning, together with being born earlier in the season, affects likelihood of local survival in the 1st few months of life (Wauters et al. 1993). No postpartum estrus occurs until young are almost weaned. Juveniles are rarely capable of breeding until 10–12 months old, and many females wean 1st litter when 2 years old (Wauters and Dhondt 1995). Some females are unsuccessful in rearing any young during a season. Intrauterine losses occur (Gurnell 1991); further losses of young can occur during suckling and at weaning (Wauters and Dhondt 1995). Young may be carried in mother's mouth to a new nest during the suckling period (Lee 2000).

Sex ratios are ca. 1:1. In Finland, sex ratios remained relatively constant over extensive areas and between years despite changes in population size. Male to female ratio varied locally between 43% and 58% males (Lampio 1965, 1967). Predation exacted a heavier toll on males during the breeding season (Lampio

1967). Based on capture–mark–recapture data, operational sex ratio is locally male biased in spruce plantations in northern England during the breeding period (Lurz 1995).

ECOLOGY. Across much of the Palearctic, *S. vulgaris* occurs in boreal coniferous forests consisting mainly of larch (*Larix*), pine (*Pinus*), and spruce (*Picea*—Gurnell and Anderson 1996). In central and southern Europe, *S. vulgaris* also occurs in broad-leaved and mixed woodlands. Mixtures of tree species provide a more reliable year-to-year seed food supply than do single-species forests because of differences in mast intervals, seed size, and timing of seed dispersal (Lurz et al. 1995). Observed densities are highest in mixed deciduous and conifer mixtures dominated by pine and lowest in those dominated by Sitka spruce (*Picea sitchensis*) and in forests just reaching cone-bearing age (Gurnell 1983, 1991; Lurz et al. 1995, 1998; Tonkin 1983a; Wauters and Lens 1995). European red squirrels readily use suburban parks and gardens (Magris and Gurnell 2002) as well as small woods and copses. Long-term densities average between 0.5 and 1.5 individuals/ha in both conifer and broad-leaved forests, but year-to-year fluctuations can be large and vary with weather and the availability of tree seeds, particularly in monoculture plantation forest (Wauters and Lens 1995). Very low densities of 0.02–0.2 squirrels/ha occur in boreal forests in Scandinavia and large conifer forests in northern England and Scotland (Andrén and Lemnell 1992; Halliwell 1997a; Lurz et al. 1995). Populations can recover from very low densities in 2–3 years. Annual cycles of numbers occur, with lows in spring before breeding and peaks in autumn after breeding.

Habitat fragmentation as a result of road building and urbanization with loss of habitat can decrease population size, because of reduced immigration rates with a concomitant decrease in genetic diversity relative to nonisolated populations (Wauters 1997; Wauters et al. 1994a). Small, isolated populations have higher chances of extinction, although viable populations persist in small, highly fragmented woodlands on the island of Jersey, Channel Islands (Magris and Gurnell 2002). Woodland size, distance between woodlands, and habitat composition affect European red squirrel presence (Andrén and Delin 1994; Celada et al. 1994; Rodriguez and Andrén 1999; Rushton et al. 1999; Verboom and van Apeldoorn 1990; Wauters et al. 1994a).

In the wild, mean expectation of life at 6 months of age is ca. 3 years; some individuals may live to 7 years of age and in captivity for up to 10 years (Tittensor 1975). Causes of death include predation, starvation, very cold weather, and possibly parasitic disease in undernourished animals. Year-to-year survival is positively related to availability of autumn–winter tree seeds (Gurnell 1983). On average, 75–85% of juveniles disappear during their 1st winter; average year-to-year survival improves thereafter to ca. 50%. Annual predation rate is 16% for adults, with a population turnover of up to 54% in spruce plantations in northern England (Lurz 1995; Petty et al. 2003). In the seminatural forests of Bavarian National Park, predation rates were 61% (Münch 1998). Predators include pine marten (*Martes martes*), wild cat (*Felis silvestris*), some owls, and raptors such as goshawk (*Accipiter gentilis*) and buzzard (*Buteo buteo*—Halliwell 1997b; Kenward et al. 1981; Marquiss and Newton 1982; Pulliainen 1984; Pulliainen and Ollimaki 1996). Stoats (*Mustela erminea*) may take nestlings, and foxes (*Vulpes vulpes*), cats (*Felis catus*), and dogs (*Canis familiaris*) could take European red squirrels when they are on the ground. Domestic cats are important predators in suburban areas (Magris and Gurnell 2002). *S. carolinensis* is not a direct cause of mortality. Humans influence mortality by destroying or altering habitats, causing road casualties, or controlling populations under license.

One flea, *Monopsyllus sciurorum*, is specific to European red squirrels. Another flea, *Orchopeas howardii*, came with *S. carolinensis* from North America and is sometimes found on European red squirrels in Britain (Blackmore and Owen 1968; Shorten 1954). *Taropsylla octodecimdentata* present in continental Europe is found locally in Scotland and England (Coles and Jessop 1993). The most common tick is the sheep tick (*Ixodes ricinus*). The spirochaetes *Borrelia afzelii*, *B. burgdorferi* sensu lato, and *B. b.* sensu stricto were transmitted to *S. vulgaris* by feeding ticks (Humair and Gern 1998). Sucking lice include *Enderleinellus nitzchi* and *Neohaematipinus sciuri*. Mange mites have been found, but signs may be mistaken for sick, undernourished squirrels suffering from alopecia and heavy infestations of fleas and lice. Helminths are uncommon but *Enterobius* nematodes have been found in the

gut. The intestinal protozoan *Eimeria* is common and causes coccidiosis (Keymer 1983; Sainsbury and Gurnell 1995). Coccidiosis may be the proximate cause of death in undernourished or stressed animals and deaths on a large scale have been ascribed to coccidiosis in Scandinavia (Lampio 1967), but not elsewhere. *Eimeria sciurorum* is pathogenic in Britain. Other protozoa include *Hepatozoon* and *Toxoplasma*. Ringworm fungal infections (*Microsporum cookie* and *Trichophyton*) are known, and bacterial infections are rare, although pasteurellosis (*Pasteurella multicoda*) has been detected (Keymer 1983). Viruses isolated include parainfluenza (Vizoso et al. 1966), members of the encephalomyocarditis group (Vizoso et al. 1964; Vizoso 1968), adenovirus (Sainsbury et al. 2001), and parapoxvirus (Sainsbury and Gurnell 1995; Sainsbury and Ward 1996; Scott et al. 1981). Individuals infected with parapoxvirus have been found only in Britain and the disease resembles contagious pustular dermatitis in sheep. The virus is highly pathogenic and the resulting mortality is very high. *S. carolinensis* is unaffected by the virus, acts as a reservoir host (Sainsbury et al. 2000; Rushton et al. 2000), and thus may contribute to the decline of the European red squirrel in Britain (Tompkins et al. 2001). Reports of myxomatosis, diptheria, distemper, and "consumption" are unfounded. Malignant melanoma on upper and lower eyelids with metastasis to the lung was observed in European red squirrels (Fukui et al. 2002). Nutritional diseases due to a lack of selenium and an imbalance of calcium and phosphorus have been reported in both wild and captive European red squirrels (J. Gurnell, pers. comm.; Gurnell et al. 1990; Keymer and Hime 1977).

Primary foods are berries, fruits, fungi, and tree seeds but other foods are eaten when seeds are not available. These include the buds and bark of trees, flowers, shoots, and other green plant material as well as bird eggs, nestlings, invertebrates, and lichens (Moller 1983; Nour et al. 1993; Ognev 1940; Rajala and Lampio 1963; Wauters and Dhondt 1987). Tree seeds are scatterhoarded in the autumn and fungi are cached on branches in trees (Gaukler 1963; Lurz and South 1998; Sulkava and Nyholm 1987). Hoarding appears more intense in broad-leaved than in conifer forests (Tonkin 1983a; Wauters and Casale 1996). European red squirrels that spend more time recovering hoards are more likely to survive, and in the case of females, tending to wean more young in their lifetime (Wauters et al. 1995). Their spatial memory for the location of stored food does not appear to last as long as that of *S. carolinensis* (MacDonald 1997).

Between 60% and 80% of active period may be spent foraging and feeding, with more time spent in coniferous than in deciduous woodland (Moller 1983, 1986; Tonkin 1983b; Wauters et al. 1992). Winter activity patterns are influenced by the need to forage for food and to conserve energy in the nest (Reynolds 1985a). European red squirrels are active all year (they do not hibernate) but may remain in nest for several days during severe winter weather (Tonkin 1983b; Wauters and Dhondt 1987). The European red squirrel is diurnal; onset of daily activity is related to sunrise, but termination is not related to sunset. Considerable individual variation exists but generally, a single main active phase occurs during winter, peaking in late morning. During summer, 2 phases peak 2–4 hours after sunrise and 2–4 hours before sunset. Spring and autumn activity patterns are intermediate between winter and summer. High winds, very hot or cold conditions, and heavy rain reduce activity. *S. vulgaris* may lie outstretched on a branch to keep cool during very hot weather. Standing water may be sought in hot weather. Food availability also influences activity; activity patterns and nest use are described by Tonkin (1983b) and Wauters and Dhondt (1987).

Nests or dreys are spherical, ca. 30 cm in diameter but sometimes larger, and situated close to the trunk of a tree or in a fork in the branches, usually from 6 m upward, but they can be lower. In northern Germany, 15% of 110 surveyed dreys in predominantly deciduous woodland were <8 m, 64% were 8–16 m, and 22% were >16 m high (Borkenhagen 2000). Nests are often hidden by climbing plants (Magris 1998; Tonkin 1983a). Outer layers consist of twigs, sometimes with needles or leaves attached; inner cavity (12–16 cm in diameter) is lined with soft material such as moss, leaves, needles, clipped dry grass, and bark. Inner lining consists of 57% grass, 19% moss, 16% needles, and 8% of other materials ($n = 50$—Tittensor 1970). Individuals use 2, 3, or more dreys at a time, frequently alternating dreys on consecutive nights. Up to 8 dreys were used within 2 weeks (Halliwell 1997a; Lurz 1995). Nests are of 2 types: day nests used for resting and night nests used for

sleeping, although the latter also may be used for diurnal resting (Wauters and Dhondt 1990). Drey counts are a crude, relative index of population size or habitat use (Cagnin et al. 2000; Gurnell et al. 2001; Wauters and Dhondt 1988; Yalden 1980). Hollow trees may be used as dens, especially in broad-leaved woods. Denser spruce trees rather than pines are preferred for drey location in conifer plantations (Halliwell 1997a; Lurz and Garson 1998).

Occasionally, European red squirrels have caused economic bark-stripping damage to conifer plantation forest between May and July in Britain, especially when densities of *S. vulgaris* approach 2 individuals/ha (Kenward 1983; Shorten 1962). Ringbarking, which results in dieback and wind-snap, and crown damage also occur. Locally, these squirrels may be a nuisance to seed orchards and horticultural crops.

The effects of supplementary food on red squirrel populations are equivocal. A heavily supplementary-fed conifer site had higher densities compared to a conifer control site (Shuttleworth 1996). However, supplemental feeding did not allow all females to enter breeding condition or to produce young and some degree of reproductive suppression occurred at the fed site as a result of high population densities. Also, heavy parasite burdens and evidence of preweaning mortality were found in the supplementary-fed site (Shuttleworth 1996). Adding supplementary feed to a previously "unfed" conifer ecosystem increased breeding activity and turnover rates but did not significantly raise densities in fed areas to above those in the control site (Lurz 1995). Broad-leaved woods with supplemental forage held higher densities of European red squirrels but turnover and immigration were higher than in woods without added forage (Magris and Gurnell 2002).

European red squirrels can be captured with wire cage traps (single catch) commonly fitted with a box at the back for the animals to shelter in. Wooden box traps also can be used (Magris and Gurnell 2002; Münch 1998). A mixture of sunflower seeds, peanuts, and hazelnuts and pieces of apple are successful bait. Traps must be checked midmorning and last thing before night. Wild adult European red squirrels can suffer heavy mortality shortly after capture when confined to cages; this is probably related to stress or "shock disease," which is associated with a reduction in body temperature and hypoglycemia (Merson et al. 1978). Ear tags, ear tattoos, colored collars, tail topiary, fur dying (Rice-Oxley 1993), and radiocollars are successful marking methods. Census methods include cone lines, drey counting, visual counts, nest boxes (Shuttleworth 1996), hair tubes, focal feeding points, and snow tracking. Most of these methods will not give very accurate estimates of population density but will indicate population trends over time (Gurnell et al. 2001, 2004).

In captivity, nestlings can be raised on a low-lactose milk substitute followed by soft fruits and shelled nuts as they are weaned (Dickinson 1995). Milk should be offered at body heat every 2 h during the day and every 3 h during the night. Young animals need a constant heat source of ca. 25°C (a heating pad covered with a towel is considered suitable). Defecation and urination should be encouraged after each feed by gentle stimulation of the anogenital area with warm, damp cotton wool. The young should be carefully dabbed clean of milk after each feed. Care must be taken to offer a balanced diet to avoid metabolic bone disease (Gurnell et al. 1990; Sainsbury and Gurnell 1995). Coccidiosis can occur in captive animals, particularly if animals are stressed. Toxoplasmosis, which can be fatal to European red squirrels, can be contracted from domestic cats.

BEHAVIOR. European red squirrels are solitary for much of the time but communal nesting may occur, particularly in the winter and spring; animals that share dreys tend to be familiar with each other (Holm 1991; Wauters and Dhondt 1990). Social organization is based on dominance hierarchies among and between sexes, although males are not necessarily dominant to females (Wauters and Dhondt 1989). Dominant animals tend to be larger and older than subordinate animals and dominant males tend to have larger home ranges than subordinate males or females, but much variation in range size is related to habitat quality, season, and sexual activity as well as changes in food availability (Andrén and Delin 1994; Lurz and Garson 1998; Lurz et al. 1997, 2000; Wauters and Dhondt 1985, 1992). Average home-range area for both sexes varies with location and habitat, but males tend to have larger home ranges than females. Observed average sizes (ha, ± *SD*, females then males, respectively) include 2.4 ± 1.61, 6.2 ± 4.94 on the island

of Jersey, Channel Islands ($n = 11, 22$); 6.22 ± 1.62, 20.44 ± 5.2 and 19.7 ± 6.06, 31.4 ± 8.76 in conifer-dominated habitats in northern England ($n = 56, 4$) and Scotland ($n = 5, 7$—Halliwell 1997a; Lurz 1995; Magris 1998; Wauters et al. 2000); and very large ranges (up to 47 ha) in mixed high-altitude forest in Bavarian National Park (Münch 1998). Home ranges overlap, particularly in areas of abundant food, but extent of overlap can be small, notably in breeding females, which reduce their range when suckling young (Lurz et al. 2000; Wauters and Dhondt 1985, 1992).

European red squirrels run across the ground in a series of leaps with the tail held out behind. They frequently stop and sit upright on their hind legs in an alert posture; the head is held high with ears erect and nose sniffing the air. They are agile climbers and can move rapidly, leaping from branch to branch and between trees up to 4 m apart. They climb down tree trunks headfirst with frequent pauses. When disturbed, they move up on the opposite side of a tree to the observer or predator, or "freeze" motionless on a branch or against the tree trunk. They are able to swim.

Food is held and rotated by forefeet. Cone bracts are gnawed off to expose seed and the wings are discarded.

Dispersal is not sex-biased and strict philopatry is rare; local competition determines dispersal distance (Wauters et al. 1994c). Dispersal in spring probably involves animals moving away from marginal, overwintering habitats; summer dispersal involves early-born young; and dispersal in autumn can involve adults as well as juveniles. A seasonal sex bias in dispersal occurs, with more males dispersing in spring and more females in autumn (Lurz et al. 1997; Wauters and Dhondt 1993). Postbreeding dispersal of adult females occurred after seasonal changes in seed availability (Lurz et al. 1997). Dispersal of females is affected by food availability; dispersal of males is affected by distribution of females (Lurz et al. 1997). Mass movements have been reported from the former United Soviet Socialist Republic in autumns with poor food supplies (Ognev 1940).

Urine is an important form of olfactory signal; vaginal secretions in estrous females may complement urine as a sign of reproductive condition, drawing males from >1 km away (Lurz 1995). Scent marking occurs at specific places within home range (on branches or tree trunks) by using urine and secretions from glands on the chin by face-wiping behavior (Fraefel 1995; Holm 1991). Scent marks denote occupation of home range, social status, and reproductive condition. Countermarking was observed at point sources of food such as feeding stations (Magris 1998). Vocal communication is associated with typical body postures and includes loud and soft chucking calls, an explosive "wrruhh" sound, and various moans and teeth chattering. Young make shrill piping calls. Aggressive acts include loud chucks, foot stamping, and tail flagging. Aggressive encounters may result in high-speed chasing, tail biting, and screaming (Eibl-Eibesfeldt 1951). They can occur when males group together in mating chases as they follow a female in heat. The dominant male is at the front of the group and is the one most likely to mate with the female (Wauters et al. 1990).

GENETICS. Diploid chromosomes number is 40; FN = 70 and 72 (Zima and Kral 1984). Phylogenetic relationships and genetic distance between *S. vulgaris* and squirrels from North America have been described by Oshida and Masuda (2000). Comparisons of karyotypes and ribosomal RNA genes between *S. vulgaris* and *S. lis* suggest that they may be conspecific rather than distinct species (Oshida et al. 1996; Oshida and Yoshida 1997). In Belgium, although small populations have high levels of band sharing, population processes rather than genetic factors are the real threats to small isolated populations (Wauters et al. 1994b). High band-sharing rates and low levels of immigration also were reported from fragmented forests in Germany (Wiegand and Schröpfer 1997). Mitochondrial DNA from European red squirrels from 12 locations in the United Kingdom and 3 from mainland Europe indicated no obvious geographical pattern across the United Kingdom, thus the use of larger geographically distinct populations within the United Kingdom for augmentation of small isolated populations is unlikely to pose genetic problems (Barratt et al. 1997, 1999). However, the United Kingdom has been subject to introductions from continental Europe (Harvie-Brown 1880–1881) and the genetic structure of the European red squirrel populations in the 3 most northern regions of England (Cumbria, Northumberland, and Durham) was very different with highly significant genetic subdivision between Cumbria and northeastern England (Hale et al. 2001a, 2001b). Defragmen-

tation of the landscape as a result of large-scale forestation has resulted in significant genetic and morphological changes in local squirrel populations over the last 40 years (Hale and Lurz 2003; Hale et al. 2001b, 2004; Lurz 2002).

CONSERVATION STATUS. The European red squirrel is widespread and common over much of its range. It is a game animal in northern conifer forests of the Palearctic and is hunted for its fur (Gurnell 1987). Local range expansions have occurred as a result of translocations (onto Dutch or German islands in the North Sea—Degn 1973, 1974; Wiltafsky 1978). However, in Britain and Ireland, interspecific competition from alien *S. carolinensis* has caused the loss of European red squirrels over large areas (Bryce 1997; Gurnell 1987, 1996a, 1996b; Gurnell and Pepper 1993; Lloyd 1983; Lurz et al. 2001; Reynolds 1985b; Skelcher 1997; Staines 1986; Teangana et al. 2000; Usher et al. 1992; Wauters et al. 1997). Population declines also have been observed in Piedmont, Italy, where the gray squirrel was introduced in 1948 (Currado 1998; Currado et al. 1987; Lurz et al. 2001; Wauters et al. 1997). *S. carolinensis* has a competitive advantage in broad-leaved woodlands, its native habitat, where it reaches higher densities than European red squirrels (Kenward et al. 1998). *S. carolinensis* is more efficient at digesting acorns than are European red squirrels (Kenward and Holm 1993). However, competition for food and interference competition among adult *S. vulgaris* and *S. carolinensis* is not solely responsible for the replacement of *S. vulgaris* by *S. carolinensis* (Wauters and Gurnell 1999; Wauters et al. 2001). Differences between the 2 species in fat accumulation in the autumn may contribute to the replacement process in deciduous habitats (Kenward and Tonkin 1986), but are not significant in conifer habitats where autumn and winter food supplies are more predictable and maneuverability to feed on cones in the canopy is important (Lurz and Lloyd 2000). The presence of *S. carolinensis* decreases summer breeding in European red squirrels and decreases juvenile recruitment in the autumn (Wauters and Gurnell 1999; Wauters et al. 2000, 2001). *S. carolinensis* also steals the seed caches of red squirrels in areas of overlap, which results in a reduced energy intake in European red squirrels and a reduced body mass in spring (Wauters et al. 2002). Parapoxvirus disease mediates interspecific competition in Britain (Rushton et al. 2000; Tompkins et al. 2001) but no evidence exists that this occurs in continental Europe (L. Wauters, pers. comm.).

Short-term conservation tactics in Britain include short-term supplementary feeding, European red squirrel reintroductions, and control of *S. carolinensis*. In the long term, management of forest habitats to favor European red squirrels and deter *S. carolinensis* is the only option (Gurnell and Pepper 1988, 1993; Pepper and Patterson 1998). Large conifer forests (2,000–5,000 ha) are ideal but smaller forests (>100 ha) can support viable European red squirrel populations. Clear-cutting should be kept to small areas, and good seed and nest trees left behind where possible (Gurnell et al. 1997a, 2002; Lurz et al. 2003; Rushton et al. 1997). Reviews of management exist for European red squirrels in captivity (Dickinson 1995) and in the wild (Gurnell and Lurz 1997; Gurnell and Pepper 1988, 1993; Gurnell et al. 1997b; Lurz and Garson 1997; Lurz et al. 1998; Pepper and Patterson 1998; Rowe 1983). Translocation to reinforce dwindling populations or replace lost populations is feasible but has potential problems of disease (Sainsbury and Gurnell 1995; Sainsbury et al. 1997, 2000, 2001; Venning et al. 1997). A captive-breeding program was established in Britain in 1995.

REMARKS. *Sciurus* is from the ancient Greek, *skia* meaning shadow or shade, and *oura* for tail; *vulgaris* is Latin for common. European common names are scoiattolo comune in Italian, Eichhörnchen in German, ecureuil roux in French, ekorre in Swedish, egern in Danish, and ardilla roja in Spanish.

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