

Glis glis (Rodentia: Gliridae)

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Abstract: *Glis glis* (Linnaeus, 1766) is a glirid commonly called the fat or edible dormouse. It is the largest dormouse and the only species in the genus *Glis*. Range mainly overlaps with a deciduous and mixed forest zone in Europe and southwestern Asia. Principal habitat is deciduous and mixed woodland and the species is strictly nocturnal. *G. glis* is unusual among small rodents in its long life expectancy (mean is about 9 years), prolonged hibernation (up to 7 months), and periodic reproductive failure. It is a species of conservation concern along the northern part of its range, and a game animal in Slovenia and Croatia. DOI: 10.1644/865.1.

Key words: beech mast, edible dormouse, fat dormouse, glirid, hibernation, reproduction skipping, western Palearctic

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Glis Brisson, 1762

Glis Brisson, 1762:113. Type species *Sciurus glis* Linnaeus, 1766:87, by designation under the plenary powers of the International Commission on Zoological Nomenclature (1998) in Opinion 1894.

Myoxus Zimmermann, 1780:351. Type species *Sciurus glis* Linnaeus, 1766, by original designation.

Myorus Reichenbach, 1835:7. Incorrect subsequent spelling of *Myoxus* Zimmerman, 1780.

Elius Schulze, 1900:200. No type species selected; name initially used as a subgenus of *Myoxus*, containing 2 species *glis* (*Sciurus glis*) and *dryas* (*Myoxus dryas*, now in *Dryomys*).

CONTEXT AND CONTENT. Order Rodentia, suborder Sciuromorpha, family Gliridae, subfamily Glirinae. *Glis* is monotypic (Holden 2005).

Glis glis (Linnaeus, 1766) Fat Dormouse

Sciurus glis Linnaeus, 1766:87. Type locality “Habitat in Europa australi,” restricted to Southern Carniola (= southern Slovenia), by Violani and Zava (1995:111).

Sciurus persicus Erxleben, 1777:417. Type locality “Habitat in Persiae prouincia Gilan,” restricted to Rasht, Province of Ghilan, Iran, by Lay (1967:193).

Glis esculentus Blumenbach, 1779:79. Type locality “südlichen Europa,” restricted to Central Europe, by Miller (1912:577).

Glis vulgaris Oken, 1816:868. Type locality “Europa, Mittelasien, an Wolga, mehr südlich, in Deutschland, nicht selten, besonders ums Fichtelgebirg, in Krain,” restricted to Germany, by Miller (1912:577). Oken (1816) has been rejected for nomenclatural purposes (International Commission on Zoological Nomenclature 1956). Nomen nudum.

Myoxus giglis Cuvier, 1832:444. Nomen nudum (Miller 1912).

Myoxus avellanus Owen, 1840:25, pl. 105, fig. 6. Nomen nudum (Miller 1912).

Glis italicus Barrett-Hamilton, 1898:424. Type locality “Siena,” Italy.



Fig. 1.—Adult *Glis glis* from Mt. Kočevski Rog, Slovenia. Photograph courtesy of A. Kryštufek.

- Glis insularis* Barrett-Hamilton, 1899:228. Type locality “Monte Aspro, near Palermo,” Sicily, Italy.
- Myoxus glis orientalis* Nehring, 1903:533. Type locality “Gebirge Alem-Dagh, nordöstlich von Scutari, Kleinasien” (= Üsküdar, Alem Dağı, İstanbul—Kryštufek and Vohralík 2005).
- Myoxus glis caspius* Satunin, 1905:55. Type locality unknown; stated as “Chuli Canyon, some 40 km from Ashkhabad (Turkmenistan)” by Ognev (1947:467).
- Myoxus glis caspicus* Satunin, 1905–1906:54. Type locality “Kupferbergwerk Katar, Kreis Zangezour, Gov. Elisabethpol Chuliysk Gorge, 40 versts from Ashkhabad, Transcaspia.” Unjustified emendation of *Myoxus glis caspius* Satunin, 1905.
- Glis glis spoliatus*: Thomas, 1906:220. Type locality “Khotz, near Trebizond” (= Çosandere, Trabzon, Turkey—Kryštufek and Vohralík 2005); first use of current name combination.
- Glis melonii* Thomas, 1907:445. Type locality “Marcurighè, Urzulei, Ogliastra, Sardinia,” Italy.
- Glis glis pyrenaicus* Cabrera, 1908:193. Type locality “neighborhood of Allo, province of Navara,” Spain.
- Glis italicus intermedius* Altobello, 1920:22. No type locality specified.
- Glis glis subalpinus* Burg, 1920:419. Type locality “Münstertal” Val Müstair, Kanton Graubünden, Switzerland.
- Glis glis tshetshenicus* Satunin, 1920:150. Type locality “Chechn’ na r. Shara-Argun” (= Shara Argun’ River, tributary of the Terek—Ognev 1963).
- Glis glis postus* Montagu, 1923:866. Type locality “Veliki Dergonel [= Veliki Drgomalj—Petrov 1992], the Gorski Kotar, Croatia.”
- Glis glis abrucci* Altobello, 1924:35. Type locality “Abruzzi e Molise,” Italy.
- Glis glis minutus* Martino, 1930:60. Type locality “Predejane, 30 km. S. from Leskovac. Serbia.”
- Glis glis petrucii* Goodwin, 1939:1. Type locality “Gouladah foothills of the Kurkhud Mountains, district Bujnurd, northeastern Iran, alt. about 3,000 ft.
- Glis glis vagneri* Martino and Martino, 1941:9. Type locality “Vrhpolje, Kamnik, Kamniške Alpe (= Steiner Alps), Slovenia.”
- Glis glis intermedius* Martino and Martino, 1941:9. Type locality “Presača [= Pesača—Petrov 1992], Donji Milanovac, N. E. Serbia.”
- Glis glis argenteus* Zimmermann, 1953:28. Type locality “Wäldern der Weissen Berge, Kreta” (= White Mts, near Samaria, Crete, 1,000 m—Corbet 1978).
- Glis glis martinoi* Mirić, 1960:36. Replacement name for *Glis glis intermedius* Martino and Martino, 1941, preoccupied by *Glis italicus intermedius*, Altobello, 1920.
- Glis glis pindicus* Ondrias, 1966:25. Type locality “Moni Stomiou, near Konitsa, Epirus, Greece, 1600 m.”

Glis glis germanicus Violani and Zava, 1995:112. Type locality “Marxheim, Bavaria, Germany.”

CONTEXT AND CONTENT. Context as for genus. Subspecific variation was not assessed across the entire range; 10 subspecies of unresolved geographical boundaries are tentatively recognized (Corbet 1978).

NOMENCLATURE NOTES. Until recently there was continuous uncertainty over the validity of the generic names *Myoxus* and *Glis*. Many argue that Brisson’s (1762) names are invalid because they are not Linnean or binomial and the name *Myoxus* is the oldest valid generic name (Holden 2005; Hopwood 1947; Wahlert et al. 1993). However, *Glis* was conserved, based on the argument that this name has had historical common usage, by a ruling of the International Commission on Zoological Nomenclature (Opinion 1894 [International Commission on Zoological Nomenclature 1998]; includes comments and original literature associated with the opinion).

The generic and specific name *glis* (genitive *gliris*) means a dormouse (Gotch 1995). *Glis* (or *glir*, *gliris*, or *glirus*) was quoted by many early authors starting with T. M. Plautus in 3rd to 2nd century BC and is either derived from the Sanskrit *girich* or from the verb *gliscere*, which means to grow (Carpaneto and Cristaldi 1995).

DIAGNOSIS

Glis is distinguished from other dormice (Gliridae) as follows (Storch 1995; Wahlert et al. 1993): glans penis without spines on lateral pads, sphenofrontal and stapedial foramina lost, lateral pterygoid process short and fossa pterygoidea reduced, coronoid process of lower jaw arises in an anterior position and conceals m3 in lateral view, angular process of lower jaw not perforated, molars only slightly concave and main cusps weak, and protoloph separated from metaloph.

Glis glis is externally recognizable by a combination of large size (head and body length > 123 mm; usually 160–190 mm), long tail (length up to 168 mm), small ears (extending barely to eye when laid forward), grayish dorsum and white belly, absence of black pattern on face, bushy tail uniformly haired throughout and conspicuously distichous, and 4–6 pairs of nipples (Miller 1912; Storch 1978).

GENERAL CHARACTERS

Glis glis (Fig. 1), the largest dormouse, is squirrel-like in general form and appearance. Both sexes are about the same size (Kryštufek 2001). Means (*SD*, *n*) of adult body measurements (mm) of specimens from Austria were: length of head and body 152.60 (9.41, 55), length of tail 124.50

(9.64, 52), length of hind foot 26.79 (2.32, 48), length of ear 18.52 (1.90, 46—Spitzenberger 2001).

Pelage consists of soft underfur interspersed on the back with long, coarse guard hairs. Tail is bushy and flattened dorsoventrally. Upper parts range from a grayish brown (“yellowish broccoli-brown”—Miller 1912:577) to bluish smoke-gray, darkest along the spine and lighter on flanks. A narrow dusky ring occurs around eyes. Underparts and inner surface of legs are white to pale buff and the line of demarcation is rather well defined. Tail is like back but usually darker. Young are dull plumbeous gray above, white below (Miller 1912). Albino and melanistic animals are rare (frequency $< 10^{-3}$) and albinos do not survive more than 2 years (Kryštufek 2007).

Ears are relatively short and rounded. Legs are short and feet are more robust than in other European dormice. Front feet and hind feet have 4 and 5 digits, respectively. Palm and sole are naked (Miller 1912).

Skull is rather deep and broad, with widely expanded zygomatic arches (Fig. 2). Interorbital region is moderately broad and inconspicuously ridged. Braincase is squarish and smooth; deep rostrum tapers toward point. Incisive foramina are short but broad; diastema is longer than maxillary toothrow. Auditory bullae are moderately enlarged and only slightly pneumatized. Mandible is robust and all 3 processes are well developed; the angular process is not perforated (Miller 1912; Potapova 2001). Means (*SD*, *n*) of adult cranial measurements (mm) of specimens from Austria were: condylobasal length 36.02 (1.33, 64), length of maxillary toothrow 6.66 (0.22, 76), length of diastema 9.31 (0.51, 81), zygomatic width 22.46 (0.89, 68), width of interorbital constriction 4.95 (0.15, 80), length of mandible 22.36 (0.93, 81—Spitzenberger 2001). Overall body size varies geographically (Storch 1978).

Upper cheek teeth are squarish, M1 and M2 are the largest and subequal, and premolars are the smallest. Crowns are low and nearly flat but lateral borders are slightly raised. The crown of each tooth is crossed by low and finely spaced ridges (Miller 1912). Upper molars have 3 roots each, lower molars and P4 are double rooted, and p4 has a single root (Storch 1978).

DISTRIBUTION

The range mainly coincides with the deciduous forest zone in the western Palearctic (Fig. 3). *Glis glis* is widespread in western, central, and southeastern Europe except Denmark, the Atlantic coasts of the Low Countries, and France; it is also absent from the majority of the Iberian Peninsula (Storch 1978). The range is mosaic in deforested regions of central Europe and in the forest-steppe zone in Moldova, Ukraine, and Russia. Range in Russia is in 2 main parts, the western and the eastern, with additional scattered isolates (Likhachev 1972). The northern border follows the line of Gauja National Park (Latvia—Valdis 2003)—Pskovk—River

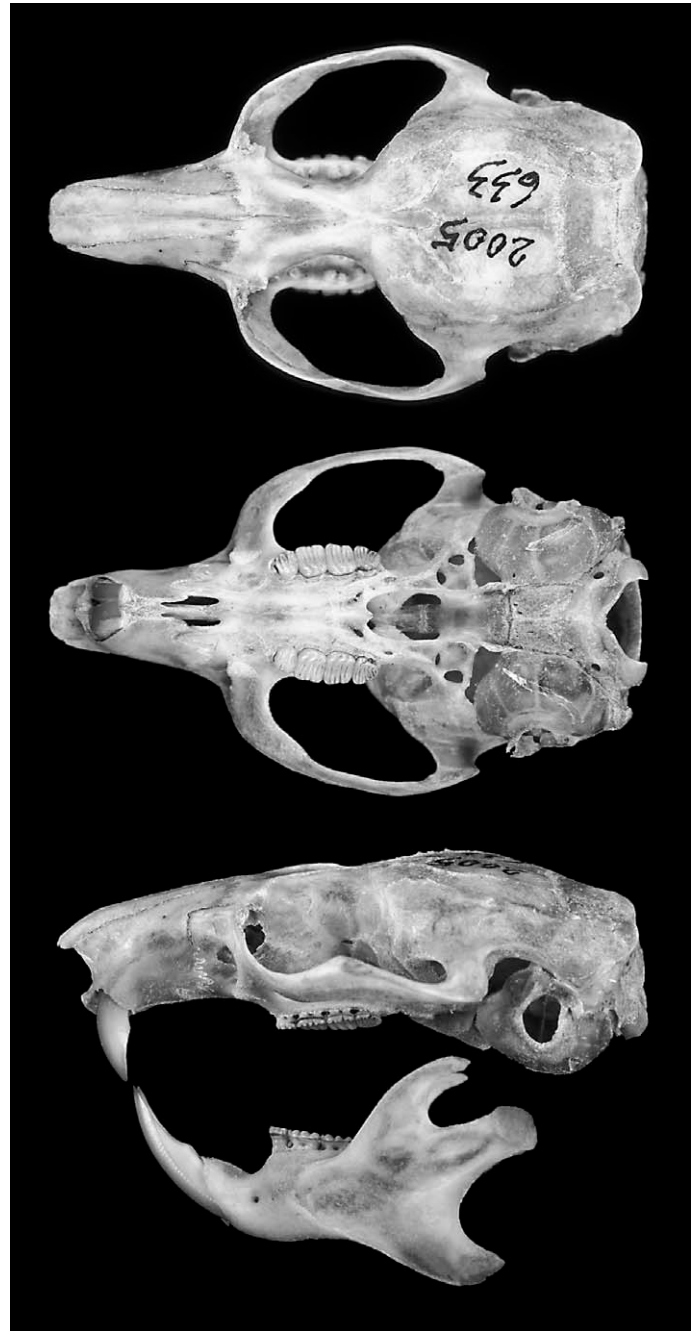


Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Glis glis* (adult female from Donje Bare, Mt. Zelengora, Bosnia and Herzegovina; Slovenian Museum of Natural History 2005/633). Greatest length of skull is 43.0 mm. Photographs by C. Mlinar used with permission.

Oka—Upper Volga. The River Volga is also the eastern boundary of distribution and the only occurrences on its east bank are at Makaryev and Samarskaa Luka (Rossolimo et al. 2001). Range in Anatolia is presumably disjunct (Kryštufek and Vohralík 2005). In the Caucasus, *G. glis* extends as far north as Krasnodarsk and the River Kuban

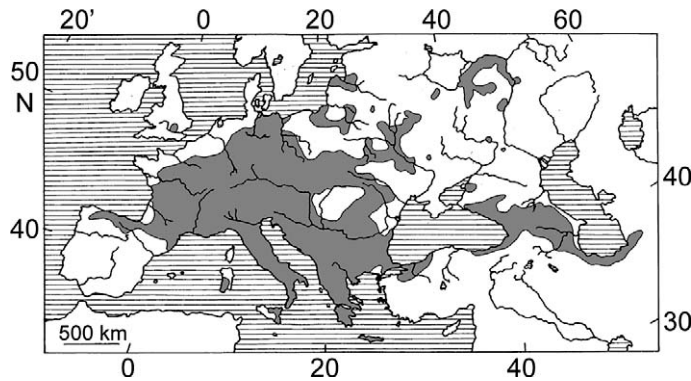


Fig. 3.—Distribution of *Glis glis*. Based on Castién (2002), Kryštufek (1999), Kryštufek and Vohralík (2005), Lay (1967), Likhachev (1972), and Shidlovskiy (1962).

and reaches across Armenia and Azerbaijan (Rossolimo et al. 2001) on the southern coast of the Caspian Sea in Iran as far east as Gouladah, Khorassan (Lay 1967). A report from Turkmenistan is dubious (Ognev 1963; Rossolimo et al. 2001). *G. glis* was reported from 19 islands in the Mediterranean (Elba, Salina, Corsica, Sardinia, Sicily, Krk, Cres, Brač, Hvar, Korčula, Mljet, Lastovo, Corfu, Keffalinia, Ándros, and Crete—Carpaneto and Cristaldi 1995; Dimaki 1999; Storch 1978; Tvrtković et al. 1995) and Baltic (Rügen, Usedom, and Wolin—Bitz 1990) seas. In 1902 *G. glis* was introduced, possibly from Hungary, to Tring Park about 100 km northwest of London, England. The population spread very little after 90 years and remained within about 35 km of its point of introduction (Jackson 1994; Morris 1997).

Elevational range is from sea level to the upper margin of deciduous and mixed forests: up to 1,545 m in the Alps (Spitzenberger 2001), and 2,000 m in the Pyrenees (Storch 1978) and the Caucasus (Rossolimo et al. 2001).

FOSSIL RECORD

Ten fossil species of *Glis* have been tentatively recognized since the middle Oligocene. In Miocene faunas the genus is rare but becomes common in central Europe from the Pliocene onward (Daams and de Bruijn 1995). In the Pliocene and Pleistocene only 1 well-established lineage possibly remained in which *G. sackdillingensis* (early Pleistocene) links *G. minor* (Pliocene) with the recent *G. glis*. The recent species probably emerged in the early-middle Pleistocene deposits and was afterward widespread across Europe west of Russia (Kowalski 2001); reports from the lower Pleistocene are dubious (Maul 1990). Eastward expansion was evidently postponed given that the earliest evidence from the Russian Plain is from early-late Pleistocene (Markova 2000). After the Last Glacial Maximum (about 19,000 years ago), central Europe was recolonized at the beginning of the Holocene (Horáček 1986).

FORM AND FUNCTION

Form.—The glans penis (length 9.6–11.3 mm, width 3.5–4.0 mm) is club-shaped, with a small, sharp protrusion. The ventral side is creased by longitudinal folds and covered with small spines. Baculum (length 8.5–9.5 mm, width 2.4–2.6 mm) is of simple triangular shape with pointed apex that usually bends laterally (Kratochvíl 1973).

Females have 8–12 nipples (Koenig 1960; Miller 1912; Storch 1978). Ten nipples are the most common count in specimens from Slovenia (82% of specimens, $n = 51$), followed by 11 (13.7%) and 12 (3.9%—Kryštufek 2004). Mean nipple count in specimens from northern Italy is 11.25 ± 0.85 SD (range = 10–12, $n = 20$ —Marin and Pilastro 1994).

Dental formula is $i\ 1/1, c\ 0/0, p\ 1/1, m\ 3/3$, total 20 (Miller 1912). Enamel is 36 μm thick on upper incisors and 39 μm on lower incisors, which is less than in other dormice (Hillson 1990).

In young, sexually inactive individuals the paired tubulo-alveolar circumanal glands produce secretions, but the glandular activity is most intense during the peak of sexual activity (Hrabě 1971). Active secretion of the bulbourethral gland also peaks in reproductively active males (Hrabě 1968).

Glis glis changes pelage slowly, molting and replacing hairs over a full year (Morris 2004). Guard hairs are oval in cross section with a diameter of about 55 μm ; medulla is relatively small and indistinct (Teerink 1991). Skin on tail breaks readily when grasped and easily slides off from tail vertebrae. The animal amputates the exposed vertebrae and the stump partly regenerates and puts forth a dense brush of long hairs (Jones-Walters and Corbet 1991). In comparison to other rodents, *G. glis* has relatively long vibrissae organized on the head in 7 groups (Sokolov and Kulikov 1987).

Function.—At an ambient temperature (T_a) of 28°C, body temperature (T_b) = $36.7^\circ\text{C} \pm 0.79^\circ\text{C}$ SD and is at an optimum point, and oxygen consumption is $0.552\ \text{ml}\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1} \pm 0.051\ \text{SD}$, heart rate is maintained at 170–200 beats/min, and the resting ventilation frequency is about 40 breaths/min (mean oxygen pulse of 54 $\mu\text{l}\ \text{O}_2$ per breath—Wilz and Heldmaier 2000). The daily energy budget of active *Glis glis* ($23.61\ \text{kcal}\ \text{animal}^{-1}\ \text{day}^{-1}$ at $T_a = 20^\circ\text{C}$) is identical with that of nonhibernating rodents. The resting metabolic rate ($\text{ml}\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}\ ^\circ\text{C}^{-1}$) is significantly higher in spring (1.14) than in autumn (0.81; both at $T_a = 20^\circ\text{C}$ —Gębczyński et al. 1972). Mean body temperature, heart rate, and oxygen consumption are higher during the night compared to daytime (Elvert and Heldmaier 2000; Gębczyński et al. 1972). Captive individuals of *G. glis* at normal body temperature are nocturnal (Elvert and Heldmaier 2000) and monophasic (Koenig 1960; Rodolfi 1994).

Glis glis is capable of all 3 distinct forms of dormancy that are based on the same physiological mechanism of thermal and metabolic regulation, but differ in bout length. In captive *G. glis*, bouts are shortest in daily torpor (3–21 h), intermediate in aestivation (69–106 h), and longest in

hibernation (39–768 h). The average minimum metabolic rate (in ml O₂ g⁻¹ h⁻¹) correlates with ambient temperature and is the lowest during hibernation (about 0.017), intermediate during aestivation (0.031), and the highest during daily torpor (0.053—Wilz and Heldmaier 2000). Limiting food availability results in an increase in frequency of daily torpor until the animals enter hibernation (Elvert and Heldmaier 2000).

Glis glis hibernates over the winter period, normally for 7–8 months, from October to May. It does not store food before hibernation and relies instead on body fat reserves that accumulate in autumn (Vietinghoff-Riesch 1960). Body mass roughly doubles prior to hibernation, from the normal 120–150 g to more than 250 g in individuals from England (Morris 2004). During the prehibernation fattening period, *G. glis* eats lipid-rich food with a high content of linoleic acid (Fietz et al. 2005). Entry into torpor occurs in the same coordinated manner for hibernation, aestivation, or daily torpor (Elvert and Heldmaier 2005). Minimum body temperature (0.7°C at T_a = 0°C—Wilz and Heldmaier 2000) is reached about 6 h after metabolic functions have reached their minimum (Elvert and Heldmaier 2005). In steady-state torpor the metabolic rate remains unchanged (0.0382 ml O₂ g⁻¹ h⁻¹ ± 0.0037 SD) and shows no relation with ambient temperature. Heart rate is 8.2 beats/min at T_b = 7°C (Elvert and Heldmaier 2005). The duration of apnea is up to 60 min at T_b = 4.5°C (Wilz et al. 2000). Blood glucose is low during dormancy, whereas plasma insulin remains at the same level as in normothermic animals (Castex et al. 1984).

The duration of arousal from dormancy is temperature dependent: 1.2 h at T_a = 22°C and up to 9 h at T_a = 2°C (Wilz and Heldmaier 2000). Reduction in body mass (up to one-third) during hibernation correlates negatively with the prehibernation linoleic acid content in the white adipose tissue (Fietz et al. 2004).

In captive *G. glis*, cycles with a period of about 2 months occur in body mass, food and water intake, maturation of spermatozoa, body temperature, wheel-running activity, and weight of the liver, adrenal and salivary glands, and testes (Mrosovsky et al. 1980). Infradian body-mass cycles are programmed independently from changes in gonadal activity (Joy 1981). The testis cycle is induced by the thyroid cycle which, in turn, is synchronized with annual temperature and not with photoperiod (Jallageas et al. 1991).

ONTOGENY AND REPRODUCTION

Ontogeny.—Young *Glis glis* are helpless at birth, with ears and eyes closed. By 16 days the pelage is well developed, eyes open at 21–23 days, and by 30 days they can leave the nest (Jones-Walters and Corbet 1991). Total birth mass (g) varies between 4.5 (1 juvenile in a litter) and 26 (9 juveniles—Bieber and Ruf 2004). Body mass at birth is 2 g in European

Turkey (Özkan 2006), 3.4 g in Anatolia (Çolak et al. 1997), and 3.7 g ± 0.6 SD (*n* = 21) in Austria (Bieber and Ruf 2004). The seasonal onset of reproduction is extremely late in *G. glis* (Bieber and Ruf 2004) and juveniles need to reach viable size within less than 12 weeks to survive winter (Morris 2004). Mean daily mass gain (g) within about 1st month is 0.93 in European Turkey (*n* = 25—Özkan 2006) and 1.9 in England (*n* = 47—Burgess et al. 2003). Within 30 days juveniles reach a body mass of 39.2 g ± 5.9 SD (*n* = 48—Bieber and Ruf 2004). Daily growth rate in young that are 30 days of age is negatively correlated with litter size: 1.651 g (*n* = 3) versus 0.839 g (*n* = 7—Pilastro 1992). Lactation lasts 25–30 days (Ognev 1963).

Thermoregulatory mechanisms of *G. glis* develop more slowly in comparison to nonhibernating rodents. Metabolic rate (ml O₂ g⁻¹ h⁻¹) is low until the age of 15 days (1.51 at age 7 days; T_a = 20°C) but rises afterward to 17.9 ± 1.3 SD (age 15 days) and 34.4 ± 1.0 SD (26 days). Metabolism stabilizes after young attain 3 weeks of age (Gębczyński 1981). Mean survivorship rate over the hibernation period is low in juveniles (0.21—Burgess et al. 2003) and varies in adults from 0.27 (England—Burgess et al. 2003) to 0.86 (northern Italy—Pilastro et al. 2003). Adult life expectancy is up to about 9 years in nature (range 6–12 years—Pilastro et al. 2003) and maximum age recorded in captivity is 9 years (Vietinghoff-Riesch 1960).

Reproduction.—The testes descend into the scrotum after *Glis glis* has terminated hibernation. Mean mass (mg; *n*) of 1 testis is high in May (780, 4), June (712, 17), and 1st half of July (816, 11), and low in 2nd half of July (377, 8) and August (355, 5—Kryštufek 2001). Paired testes mass > 550 mg indicates spermatogenesis (Joy et al. 1980). In males reduced body temperature and gonadal development are mutually exclusive and T_b = 30°C is the critical lower limit enabling the start of the testosterone cycle (Jallageas and Assenmacher 1984). Reproductive condition in males does not depend on their body mass (Fietz et al. 2005; Kryštufek et al. 2003).

Females reach sexual maturity when 351–380 days old (Özkan 2006). Although they occasionally reproduce after their 1st hibernation in Continental Europe (Özkan 2006; Pilastro 1992), they sometimes do not breed until 3rd calendar year in England (Morris 2004).

Glis glis produces a single litter per year, although reproductive failure may occur in some years with poor food supply (Gaisler et al. 1977; Ivashkina 2006; Morris 2004; Ognev 1963; Pilastro 1992). Mating season is between the end of June and the beginning of July (central Germany—Bieber and Ruf 2004) and 15 June and 18 August (European Turkey—Özkan 2006). Gestation lasts 20–25 days (Caucasus—Ognev 1963), 28 days (Slovenia—Kryštufek 2007), and 30–31 days (Germany—Koenig 1960). Young are born between 26 July and 19 August in Germany (Schlund and Scharfe 1997). In England 93% of births occur in August (Burgess et al. 2003).

Mean litter size (range, n), based on embryos and placental scar counts, was 5.0 in northern Moravia (3–8, 12—Gaisler et al. 1977) and 5.8 in Slovenia (4–9, 9—Kryštufek 2001). Embryonic mortality was 14.3–21% in the Caucasus (Ognev 1963). Mean number of suckling juveniles per female (range, n) was 4.75 (2–7, 44) in northern Italy (Pilastro 1992), 4.9 (1–10, 24) in Slovenia (Kryštufek 2007), 5.5 (2–8, 8) in Sicily (Milazzo et al. 2003), 6.05 (1–12, 100) in European Turkey (Özkan 2006), and 6.8 (1–11, 49) in England (Burgess et al. 2003). Mean litter size is higher in adult females compared to yearlings (Ruf et al. 2006), and does not differ among years (Pilastro et al. 2003) but depends on habitat (Ruf et al. 2006; Schlund and Scharfe 1997).

During a 9-year study period in Germany, 75.0% of females had 1 litter, 21.4% had 2 litters, 2.9% had 3 litters, and 0.7% had 5 litters ($n = 140$ —Ruf et al. 2006).

ECOLOGY

Principal habitat is deciduous and mixed woodland with a high proportion of mast seeders (Jones-Walters and Corbet 1991; Rossolimo et al. 2001). Preferred habitats are forest edge with sparse trees but dense herb and shrub stratum (Gaisler et al. 1977), structured forest with high trees and dense understory (Milazzo et al. 2003), and denser forest stands with well-connected tree canopies (Juškaitis and Šiožinytė 2008). Geomorphologically diverse areas with cliffs, caves, and sinkholes are preferred over lowland forests (Anděra 1986). Beech (*Fagus*) woodland mixed with *Castanea sativa*, *Ostrya*, *Abies*, and *Picea* is inhabited throughout the range (Kryštufek and Vohralík 2005; Ognev 1963; Storch 1978). Deciduous oak (*Quercus*) forests are the principal habitat along the northern range (Juškaitis 1995) and in Russia (Ivashkina 2006). Under the Mediterranean climate *Glis glis* occurs in evergreen woodland and tall maquis vegetation (Tvrtković et al. 1995). Deciduous shrubs, orchards (Jones-Walters and Corbet 1991), and parks are also inhabited, but coniferous forests and pine plantations are avoided (Anděra 1986). *G. glis* readily enters beehives (Juškaitis 1995) and houses (Morris 1997). In central Europe, *G. glis* frequently occurs on the outskirts of towns and it has entered cities as large as Prague (Anděra 1986).

Caves are inhabited wherever present (Hrabě 1971; Rossolimo et al. 2001). Animals were detected up to 2,500 m inside the cave and up to 400 m deep. Shafts are more frequently utilized than horizontal caves and the majority of dormice shelters are inaccessible for the beech marten (*Martes foina*—Polak 1997).

Key trees in the majority of deciduous forests (*Quercus* and *Fagus*) are mast seeders, producing large seed crops every 2–6 years, whereas production in the intervening years is low or even fails. Although the major physiological event in the annual cycle of *G. glis* is hibernation (see “Function”), the animal responds to strong year-to-year fluctuations in

food availability by skipping reproduction. In years with a lack of masting trees *G. glis* typically remains sexually inactive (Pilastro et al. 2003). Proportion of breeding females varies from 0 in years of reproductive failure, to 19.8–91.2% in breeding years (Pilastro et al. 2003). Parturition is postponed about 3 months after the start of the vegetation period, which gives juveniles and lactating females access to beech mast of higher fat content (43.1% on 9 August as compared to 15.8% on 19 July—Bieber and Ruf 2004). Females in good condition breed 1st, lose body mass during lactation, and wean litters when food availability is optimal, which allows young to gain maximal prehibernation body mass. Females in poor condition postpone parturition and do not lose weight during lactation because it coincides with the peak of food supply, but young run short of time and do not reach maximal weight prior to hibernation. Males are heavier in nonreproductive years than during reproductive years (Pilastro et al. 2003). Variability in reproductive effort among years leads to differences in yearly survival rates in both sexes. Survival rates are significantly lower in dormice that are 2 years or older after reproductive years (0.32 ± 0.04 SD , $n = 5$) compared to years with absent or below average reproduction (0.58 ± 0.07 SD , $n = 4$ —Ruf et al. 2006).

With the absence of new recruits in some years there is considerable interannual variability in population density, for example 0.6–4.1 individuals/ha over 6 years in England (Burgess et al. 2003). The periodicity of peak densities is 1–3 years in Slovenia ($\bar{X} = 1.55$, $n = 33$ —Kryštufek and Zavodnik 2003).

Adult densities (individuals/ha) are 0.6–1.8 in England (Hoodless and Morris 1993), about 6 in Slovenia (Kryštufek et al. 2003), and 2.3–22 in Germany (Bieber 1995). In central Europe densities have doubled over the last 2–3 decades (Adamík and Král 2008; Koppmann-Rumpf et al. 2003). In the adult category, 49% of *G. glis* are >2 years old and 11% are >4 years old ($n = 81$). Females attain higher mean age (3.3 years) than males (2.2 years—Kryštufek et al. 2005).

Glis glis travels only as far as necessary to find suitable food. The areas used each night (ha) are small (0.05 in a female and 0.56 in a male) and the mean distance traveled was 523 m per night for a male and 111 m for a female (Morris and Hoodless 1992). Distances covered each night by males are larger in a low-density population than in a high-density population (Jurczyszyn and Zgrabczyńska 2007). *G. glis* disperses over at least 46 m of treeless agricultural land. Adult males disperse during peak reproductive periods and juveniles when about 2 months of age (Bieber 1995). Habitat fidelity is high and shifts between woodlands 1 km apart are rare (Ruf et al. 2006).

Males have significantly larger home ranges and use more nest sites than females (Ściński and Borowski 2008). Home ranges (ha) in continental Europe are 0.15–0.76 (females) and 0.82–7.0 (males—Jurczyszyn 2006; Ściński and Borowski 2008). Home-range size is density dependent

(Jurczyszyn and Zgrabczyńska 2007) and also relates to energetic value of mast but does not depend on reproductive activity (Ściński and Borowski 2008). Mean overlap in home ranges (in %) is higher among males (from 57.2 ± 30.3 SD to 74.9 ± 23.4 SD) than in females (from 0 to 25.7 ± 20.5 SD—Ściński and Borowski 2008).

Glis glis is predominantly a vegetarian. An excellent source of food, particularly for young and lactating females, is beech mast, which is rich in energy and protein content (27%—Bieber and Ruf 2004). In a predominantly oak forest in the Pyrenees, fleshy fruits (blackberry, apple, bilberry, and rowan-berry) form the bulk of the diet (frequency = 46.5%) and are eaten regardless of the degree of ripeness. Next in importance are nuts (acorns and hazelnuts; 37.0%), followed by leaves and flowers (8.0%), arthropods (6.9%), fungi (1.1%), and mosses (0.5%). Nuts are most prevalent in the diet in September and October, and arthropods in July (Gigirey and Rey 1999). In a deciduous forest in Slovakia, the basic diet in early summer is composed of buds and bark of *Euonymus verrucosus*, whereas fruits of the hazelnut, *Cornus mas*, *Carpinus betulus*, and *Acer campestre* become important in full summer (Holišová 1968). In the Caucasus region, the 1st diet in late May and early June consists of bark and in June of unripe fruits. In late summer and in autumn acorns and beech nuts form the staple diet (Ognev 1963). In England free-living *G. glis* fed mainly on fruits of yew and berries of elder in addition to hazelnuts, acorns, blackberries, apples, and pears (Morris and Hoodless 1992).

Feeding on preferred diet continues until the supply runs out; for example, total intake of hazelnuts corresponded to 84.5% (1988) and 91.2% (1989) of the crop in Italy (Rodolfi 1994). Invertebrates (slugs, caterpillars, aphids, myriapods, and beetles) are only a supplementary diet and predation on vertebrates is unusual (Holišová 1968; Ognev 1963). *G. glis* becomes carnivorous in some populations and may consume eggs of hole-nesting birds and kill and eat both nestlings and incubating parents (Adamík and Král 2008; Juškaitis 2006).

In some areas *G. glis* competes for nest boxes with hole-nesting birds. In the past, the dormouse and birds had a distinct temporal pattern of cavity use that has been disturbed in the last decades by a changing climate in central Europe due to unequal shifts in phenology. Although the phenology for *G. glis* advanced (days/decade) by about 8, this is at most only 3.5 in birds. The growth of numbers of *G. glis* is positively correlated with the number of predated nests of European pied flycatcher (*Ficedula hypoleuca*), collared flycatcher (*F. albicollis*), blue tit (*Parus caeruleus*), great tit (*P. major*), and Eurasian nuthatch (*Sitta europaea*—Adamík and Král 2008; Juškaitis 2006; Koppmann-Rumpf et al. 2003). *G. glis* also outcompetes smaller dormice (forest dormouse [*Dryomys nitedula*] and hazel dormouse [*Muscardinus avellanarius*]) from nest boxes (Bakó and Hecker 2006).

At least 14 species of vertebrates prey on *G. glis*: 1 snake (common European adder [*Vipera berus*]), 5 birds (barn owl

[*Tyto alba*], Eurasian tawny owl [*Strix aluco*], long-eared owl [*Asio otus*], little owl [*Athene noctua*], and golden eagle [*Aquila chrysaetos*]) and 8 mammals (roof rat [*Rattus rattus*], wolf [*Canis lupus*], red fox [*Vulpes vulpes*], brown bear [*Ursus arctos*], European pine marten [*Martes martes*], *M. foina*, wildcat [*Felis silvestris*], and wild boar [*Sus scrofa*]); the majority of predation is occasional (Scaravelli and Aloise 1995). Locally *G. glis* is important prey of owls and medium-sized carnivores. For example, *G. glis* comprised 47% of total biomass preyed upon by the Eurasian tawny owl in Sicily (Sara and Casamento 1995) and 50% of predated animals in the middle Volga region (Ivashkina 2006).

Sixty-three species parasitize *G. glis*: 1 Sporozoa, 2 Trematoda, 6 Nematoda, 16 Acari, 1 Heteroptera, 2 Anoplura, and 35 Siphonaptera (Kryštufek 2007). The proportion of *G. glis* infected by the flea *Ceratopsyllus sciurorum* is 75–100% in the Caucasus (Rossolimo et al. 2001). Infection by ectoparasites is higher in adults than in juveniles and higher in males as compared to females (Kirillova et al. 2006). Two encephalocarditis viral strains were isolated from *G. glis* in Tuscany, Italy (Carpaneto and Cristaldi 1995). *G. glis* is a host of Hantaan virus in Slovenia (prevalence of 13.3%, $n = 98$ —Prosenc et al. 1997) and of *Borrelia* spirochetes in Croatia (prevalence of <10%, $n = 45$ —Turk et al. 2008).

Glis glis sporadically causes damage in silvicultural practice by bark-stripping of Norway spruce, European larch, Scots pine, cypress, and birch. Damage mainly occurs in June and July (Morris 2004). The average loss of discounted revenue was 25% in England (Jackson 1994). Damage also occurs in orchards on various fruit trees, including apples, pears, peach, grape, hazel, Persian walnut, figs, and almond (Carpaneto and Cristaldi 1995; Morris 2004; Ognev 1963; Yiğit et al. 2001). Loss to crops can be considerable; for example, 12.5–41.7% to grape in the Caucasus (Ognev 1963) and 50–60% to hazelnut in Italy (Santini 1993). In the past, when *G. glis* becomes a real economic problem control measures were implemented (Jackson 1994).

During the Roman age, *G. glis* was prized as a culinary delicacy and was bred in walled gardens of oak (*gliraria*) and fattened up on currants and chestnuts in large earthenware pots (*dolia*) for the table (Jackson 1994; Morris 2004). In Mediterranean Europe (Spain, France, Italy, Slovenia, and Croatia) and in Russia, dormice were hunted for food, fur, and medical utilization (Carpaneto and Cristaldi 1995; Ivashkina 2006; Kryštufek and Haberl 2001). Various hunting techniques were practiced in different countries but mainly trapping and shooting. In Italy hunting was still widespread in the 20th century (Carpaneto and Cristaldi 1995). *G. glis* is a game species in Slovenia (hunting season 1 October–15 November) and in Croatia (16 September–30 November—Kryštufek 2007). Impact of hunting is little known but might be considerable; for example, an estimated

>3 dormice/ha may be taken during peak years in Slovenia. Hunting of *G. glis* occurred as early as 1240 in Slovenia and is still practiced today (Kryštufek and Haberl 2001).

BEHAVIOR

Duration of nocturnal activity depends on the length of the day and is longest in September (11 h) and shortest in August (4 h—Rodolfi 1994). During the day, *Glis glis* tends to lie up in nests, built like squirrel dreys or taken over from birds, and it also uses hollow trees, especially mature beeches (Morris 2004). Nests in nest boxes are rudimentary; the box is simply filled with fresh leaves (Milazzo et al. 2003), or has no nest material at all. *G. glis* sleeps and hibernates tightly curled up, its tail wrapped over its head and back (Morris 2004).

Glis glis normally hibernates underground in the soft soil (Jurczyszyn 2007; Morris and Hoodless 1992) or in caves (Polak 1997), occasionally in cellars (Valdis 2003; Vogel 1997), but not in nest boxes (Milazzo et al. 2003). Hibernation cavities of free-living *G. glis* have an oval shape (volume 429–1,174 cm³, $n = 27$) and are located 18–70 cm underground, frequently found close to roots of old trees (Jurczyszyn 2007). *G. glis* digs cavities on its own (Jurczyszyn 2007) or uses rabbit holes, fox earths, and badger setts (Morris 2004). No nesting material is used in hibernacula (Jurczyszyn 2007). In Poland communally hibernating *G. glis* were observed only under captive conditions (up to 2 dormice) but not in nature (Jurczyszyn 2007). Contrary to this, 2 hibernacula in England contained 3 dormice of both sexes each (Morris and Hoodless 1992) and in Switzerland 11 were found hibernating in a wooden container (Vogel 1997).

Glis glis is an agile climber capable of moving down tree trunks headfirst and clinging from branches by its hind feet. During climbing on smooth surfaces grip is assisted by sticky secretions of plantar glands (Koenig 1960). As an arboreal animal it is reluctant to descend to the ground and 63% of position fixes were 3–5 m above the ground (Morris and Hoodless 1992). Dormice are poor jumpers (maximum 1 m) and are able to swim (Koenig 1960).

Glis glis explores its environment by forwardly oriented mystacial vibrissae, relying on tactile information and ignoring optic boundaries (Sokolov and Kulikov 1987). Hearing sensitivity is fairly uniform without significant maxima and minima in the frequency range from <1 kHz to >35 kHz (Hutterer and Peters 2001). Acoustic communication is through a variety of squeaks, snuffling noises, and churring (Jones-Walters and Corbet 1991). *G. glis* leaves scent trails from scent glands on feet and circumanal glands around the base of tail (Morris 2004). The animal rubs its anal region on the substrate thus leaving traces of the secretion. Scent-trailing behavior has been observed in animals as young as 21 days of age but the activity of these

glands increases during sexual activity (Hrabě 1971; Koenig 1960). *G. glis* also deposits piles of droppings in latrines and on top of its nest boxes (Morris 2004).

Glis glis is reported to be a nonsocial species (Marin and Pilastro 1994) or social and living in loose groups (Koenig 1960; Morris 2004). Mating system is polygamous (Vietinghoff-Riesch 1960) and presumably promiscuous (Ściński and Borowski 2008). Females are territorial and the nonterritorial males directly compete for access to receptive females (Ściński and Borowski 2008). Males become aggressive during the mating period and may exhibit a variety of threatening postures (Jones-Walters and Corbet 1991). During courtship a squeaking male closely follows the female, mounts after a circular dance, bites the female's shoulders, and copulates. Close-kin breeding females occasionally share the same nest and communally nurse their young. In northern Italy 109 nests were single and 19 were communal (Marin and Pilastro 1994).

Young animals lick the mother's mouth and ingest saliva before and after they leave the nest (Jones-Walters and Corbet 1991). The mother also provides young with chewed pulp of food from her own mouth (Morris 2004) and grooms them (Koenig 1960).

Livetrapping was successful in population studies in Poland (Ściński and Borowski 2008) and Russia (Ivashkina 2006) but not in England (Hoodless and Morris 1993). Nest boxes (e.g., 30 by 10 by 15 cm with a diameter of the entrance hole of 50–55 mm—Burgess et al. 2003) are used in population monitoring in various parts of the range (Milazzo et al. 2003). “Nest tubes” are an inexpensive modification of nest boxes (Morris 2004); however, dormice prefer wooden boxes over tubes (Bakó and Hecker 2006). The entire population is not active simultaneously over the entire active period and July is proposed as the most suitable period for undertaking adult population density estimates (Kryštufek et al. 2003; Schlund and Scharfe 1997). Distance sampling of vocal dormice along a linear transect (about 550 m in length) was adopted in population density assessment (Hoodless and Morris 1993). Estimates are 2.5- to 3.3-fold higher than those obtained from surveying nest boxes (Jurczyszyn 1995).

GENETICS

The diploid number for *Glis glis* is 62. All the autosomes are metacentric and submetacentric ($FNa = 120$). The X chromosome is a medium-sized submetacentric or metacentric. The dot-like Y chromosome is acrocentric or biarmed. The chromosome bearing the nuclear organizing region is a medium-sized metacentric pair (chromosome 16—Civitelli et al. 1995).

The mitochondrial DNA of *G. glis* conforms to that of other mammalian species: it is 16,602 base pairs and encodes for 13 protein-coding genes, 2 ribosomal rRNAs, and 22

tRNAs. The control region is 1,157 nucleotides and does not contain repetitive motifs (Reyes et al. 1998).

Differentiation in gene markers such as protein allozymes occurs among populations of *G. glis*. Nei's unbiased genetic distances at 42 loci range between $D = 0.011$ and 0.090 . Levels of intrapopulation genetic variation are within the range generally reported for other rodents: proportion of monomorphic loci = 59% ($n = 42$), mean observed heterozygosity per locus $H_O = 0.040$, and average number of alleles per locus $A = 1.154$ (Filippucci and Kotsakis 1995). Variability in 12 nonmetric cranial traits suggests low phenotypic diversity among 6 Bulgarian populations (Markov 2001).

Sequence data consisting of 831 base pairs of the cytochrome-*b* gene revealed the presence of 3 main haplogroups (Sicilian, Southern Italian, and European), which are presumed to be a legacy of an earlier fragmentation of the range during the Quaternary glacial-interglacial dynamics and survival of glacial peaks in classical Mediterranean refugia in southern Europe. The widespread European lineage bears a strong footprint of a recent population expansion from a single unidentified refugium and dated at about 2,000 years ago (Hürner et al. 2010).

CONSERVATION

Glis glis is a species of conservation concern along its northern range where populations are fragmented and densities low; for example, in Lithuania (Juškaitis 1995), Latvia (Pilāts 1995), and Poland (Jurczyszyn 2001). A reintroduction program was initiated in Poland in 1997 (Jurczyszyn 2001). All European Community countries are contracting parties to the Bern Convention, which lists *G. glis* in Appendix III (Kryštufek 1999). The *International Union for Conservation of Nature and Natural Resources Red List* ranks *G. glis* as "Lower Risk—Near Threatened" (International Union for Conservation of Nature and Natural Resources 2008).

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