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Vespertilio murinus. By Jens Rydell and Hans J. Baagøe

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Vespertilio murinus Linnaeus, 1758 Particolored Bat

(Vespertilio) murinus Linnaeus, 1758:32. Type locality not designated but presumably near Uppsala, central Sweden.

Vespertilio discolor Natterer in Kuhl, 1819:187. Type locality "Vienna, Austria" (Wallin, 1969).

Vesperugo krascheninníkoví Eversmann, 1853:488. Type locality 'Orenburg, Russia'' (Ellerman and Morrison-Scott, 1966).

Vesperus (Marsipolaemus) albigularis Peters, 1872:260. Type locality "Mexico"? (Méhely, 1900). Vesperus siculus Daday, 1885:275. Type locality "Homorod-Almas

cave, Hungary" (Ellerman and Morrison-Scott, 1966).

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Tribe Vespertilionini, Genus Vespertilio Linnaeus (1758). The genus contains three species (Corbet and Hill, 1991). Two subspecies of V. murinus are recognized (Corbet, 1978):

V. m. murinus Linnaeus, 1758:31. See above (includes discolor, krascheninnikovi, albigularis, siculus, luteus Kastschenko, 1905, and michnoi Kastschenko, 1913).

V. m. ussuriensis Wallin, 1969:358. Type locality "southern part of Ussuri region [eastern Siberia], Soviet Union."

DIAGNOSIS. Among European bats, V. murinus is easily recognized by its dorsal fur, which has dark brown bases and silvery or grayish tips that give the back a frosty appearance, and a whitish or gray underside. Eptesicus nilssonii is smaller, and has golden tipped hairs dorsally.

The three Vespertilio species occurring in eastern Asia can be distinguished as follows (Corbet, 1978; Wallin, 1969):

1. Forearm 40-47 mm; maxillary toothrow 5.0-6.1 mm ... V. murinus Forearm 45-52 mm; maxillary toothrow 6.1-6.6 mm (2) 2. Underside, especially throat, light; maximum width of tragus is at the base ... Underside including throat, dark; maximum width of tragus is in the middle

The two latter forms may be synonymous (Yoshiyuki, 1989). The two subspecies of V. murinus can be distinguished by the shape of the tragus. It is widest in the middle in V. m. murinus, and at the base in V. m. ussuriensis (Wallin, 1969).

GENERAL CHARACTERS. V. murinus (Fig. 1) is robust and of medium size, has short, broad ears, which barely reach the tip of the snout when laid forward. The ears have 3-4 transverse folds at the outer edge and extend ventrally in a wide fold to below the corner of the mouth. The tragus is small, short, blunt and rounded. Wing membranes, ears, and face are nearly black. The wings are fairly narrow and have pointed tips. The propatagium is small. The lateral membrane (plagiopatagium) starts at the base of the outer toe. The calcar reaches more than half the distance to the tail, and a post-calcarial lobe is present. The tail extends 2.0-5.0 mm beyond the tail membrane. There are two pairs of nipples 4-5 mm apart, a feature unique among European bats (Schober et al., 1989). The penis is black, long (7-8 mm), and slender. There is a short baculum proximally and a long, cartilaginous pseudobaculum. The latter is characteristic of the genus Vespertilio (Heller and Volleth, 1984; Wallin, 1969).

The dorsal fur is dense and distinctively bicolored. The hairs at the middle of the back are ca. 7-mm long. The ventral side may be creamy white in sharp contrast to the dorsal side, or beige or grayish and less contrasting (Baagøe, in press; Miller, 1912; Spitzenberger, 1984). Measurements (in mm) are: head and body, 48-

64; tail, 37-44.5; forearm, 41.0-48.5; ear, 12-16.5. There is no significant sexual dimorphism in size (Baagøe, in press; Schober et al., 1989). Body mass (g) of V. murinus from the Sumava region of the Czech Republic are: males, 10.0-13.5 in March (n = 3), 9.8-14.5 in May (28), 13.3-15.5 in June (24), 17.6-21.2 in August/September (7); females: 10.5-13.0 in March (3), 10.2-14.5 in May (39), 13.2-16.5 in July (3) and 19.6-23.0 in October (5) (Cervený and Bürger, 1989).

The skull (Fig. 2) is short and broad and has a nearly straight dorsal profile with no sagittal crest. The lambdoidal crest is low. The rostrum is massive, flattened above, with a deep concavity on each side between the nares and the lacrymal region. The nares are large and extend backward to the interorbital constriction. The floor of the braincase has a wide and conspicuous jugular foramen between the cochlea and the basioccipital. The auditory bullae are of moderate size. The palatal emargination extends laterally such that its width is distinctly greater than its depth (in contrast to Eptesicus). The mandible is robust (Baagøe, in press; Miller, 1912; Tate, 1942).

Selected skull measurements (in mm) are: condylobasal length, 14.0-16.0; length of maxillary toothrow (C-M3), 5.0-5.7; zygomatic width, 9.5-10.2; interorbital width, 3.8-4.7 (Baagøe, in press; Spitzenberger, 1984).

The dental formula is i 2/3, c 1/1, p 1/2, m 3/3, total 32. The teeth generally resemble those of *Eptesicus* and show few peculiarities. The inner upper incisor has a well developed posterobasal cusp, which produces the distinctively trifid tooth characteristic of Vespertilio. The outer incisor has a cusp that rises to the middle of the shaft of the inner incisor, and a slightly developed secondary cusp. The transverse diameter of the upper canine is slightly greater than the longitudinal diameter. The last upper molar is not reduced (Miller, 1912; Tate, 1942).

DISTRIBUTION. This Palaearctic species occurs over an extensive area (Fig. 3), from eastern France and Switzerland northward to southern Scandinavia (60°N), eastward through central Europe, Belorussia and Ukraine, Azerbaijan, northern Iran and Afghanistan, south of 55-60°N in Russia, eastward to Manchuria and the Ussuri region of eastern Siberia (Baagøe, in press; Gromova and Baranovoj, 1981; Wallin, 1969). V. murinus is rare or absent over much of western and southern Europe. Numerous vagrants, however, have been found far outside the normal range of this species (Baagøe, in press), for instance in northernmost Sweden (Ryberg, 1947), in southern and central England (Corbet and Harris, 1991), on the Shetland and Faroe islands, and even on a North Sea oil rig (Baagøe

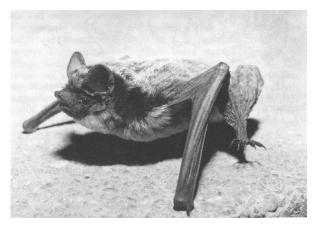
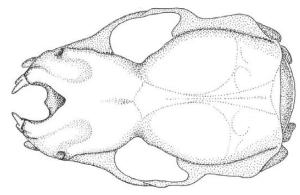
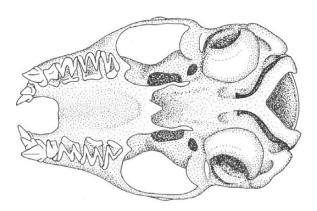
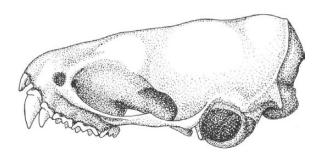


Fig. 1. Vespertilio murinus from Zealand, Denmark. Photograph by G. Brovad.

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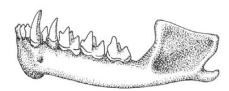


Fig. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Vespertilio murinus* from Copenhagen, Denmark (Zoological Museum of Copenhagen, ZMUC, no. CN 3081). Greatest length of cranium is 16.1 mm. Drawing by B. Rubaek.

and Bloch, pers. comm.; Stansfield, 1966). The distribution of V. murinus may be influenced by interspecific competition with Eptesicus serotinus Schreber (Baagæe, 1986), and with Nyctalus noctula Schreber (Červený and Bürger, 1989).

In central Europe, V. murinus is most common in forested upland areas around 1,000 m elevation (Červený and Bürger, 1989; Schaefer, 1974). Individuals have been found at 1,920 m in the Alps (Aellen, 1983), at 2,000 m in the Caucasus Mountains during

hibernation (Komarov and Kuchiev, 1982), and at 3,050 m in Gilgit in the western Himalaya (Ryberg, 1947).

FOSSIL RECORD. Three species of Vespertilio, of which two are now extinct, have been described from the European Pleistocene (Kormos, 1937). Cave deposits containing fossils of V. murinus are known from France and Italy and from a few places in central and eastern Europe, mostly dating from mid- and late Pleistocene 1.3 to 0.1 × 106 years ago (Kurtén, 1968). Holocene remains from Europe have been found in caves and in rock fissures (Obuch, 1989; Schaefer, 1974; Woloszyn, 1987). There are also late Pleistocene and Holocene remains of V. murinus from Crimea (Gromova and Baranovoj, 1981). The species is a relatively uncommon component of fossil bat faunas (Horáček, 1990). Its pre-Pleistocene history is unknown (Kurtén, 1968).

FORM AND FUNCTION. The wings are rather narrow and pointed and the wingspan is 270-310 mm (Schober et al., 1989). The aspect ratio is 7.0 and the wing loading 10.2 N/m² (Norberg and Rayner, 1987). The flight style is fast and straight. While foraging, *V. murinus* spends nearly all its time well away from obstacles. Its speed is about 6 m/s in straight flight in the open (Baagøe, 1987).

Masses of the locomotory muscles, measurements of the part of the skeleton associated with flight, and descriptions of the peripheral nervous system and the vascular system were given by Kovtun (1978, 1984). Skin glands around the nose and the anal region are multifunctional and serve as sources of pheromones (Černova, 1989; Sokolov and Černova, 1984). The prostate is large, and the seminal vesicles and the ampullary glands are merged into a single structure (Tiunov, 1989).

ONTOGENY AND REPRODUCTION. Characteristic of most hibernating bats, spermatogenesis in V. murinus occurs in summer, and the sperm are stored in the cauda epididymidis through the following winter. The testes are large in August. Mating presumably takes place in autumn and early winter, when the characteristic mating calls are heard. The accessory glands and the Leydig cells appear active during winter, and the latter involute only after arousal from hibernation in spring (Racey, 1982).

Births occur in late June or early July. Litter size is two, occasionally three, in central Europe, and one or two in Scandinavia and Denmark (Baagøe, in press; Ryberg, 1947; Schober et al., 1989). The young are born naked, but soon develop short, pale gray fur. They start to fly in late July or early August. Young of the year cannot be distinguished superficially from adults in October-December, suggesting a fast growth rate (Baagøe, in press).

ECOLOGY. As in most vespertilionids, there is a sexual segregation in summer when the females congregate and form maternity colonies. In Europe, such colonies usually are small, consisting of 10-100 females and their young (Baagse, in press; Červený and Bürger, 1989; Zöllick et al., 1989). Male V. murinus roost alone or in small groups, but occasionally form all male colonies of 200 or more individuals (Červený and Bürger, 1989; Collett, 1911-1912; Löhrl, 1955; Ognev, 1928; Stutz and Haffner, 1983-1984).

Three recoveries of V. murinus, banded in Belorussia and Ukraine, at distances of 850, 800 and 360 km from the place of banding, provide some evidence for long range migration in that region (Kurskov, 1961; Strelkov, 1969). There is also one long distance (130 km) recovery of a banded bat from central Europe (Aellen, 1983). On the other hand, frequent occurrence of V. murinus in winter in Scandinavia and parts of continental Europe suggest some populations are non-migratory (Baagøe, 1986; Červený and Bürger, 1989). In parts of Europe, females seem to move from summer roosts in small houses in suburban areas or in the countryside to high town and city buildings, used in autumn and winter (Baagøe, 1986, in press; Bauer, 1954, 1955).

Vespertilis murinus may be found in almost any landscape, including forested and urban areas, treeless steppes, and agricultural regions (Baagøe, 1986, in press; Červený and Bürger, 1989; Ognev, 1928). It feeds on beetles and moths, at least when foraging around street lamps in late summer and autumn (Baagøe, 1986, in press), and on insects that hatch over water (Patlyakevich, 1980). However, diet analyses from Ukraine (Petrusenko and Sologor, 1981), Poland (Bauerová and Ruprecht, 1989) and Sweden (Rydell, 1992a) all suggest that small (<10 mm body length) dipterans and other aerial food, including aphids, constitute the bulk of the food at all seasons.

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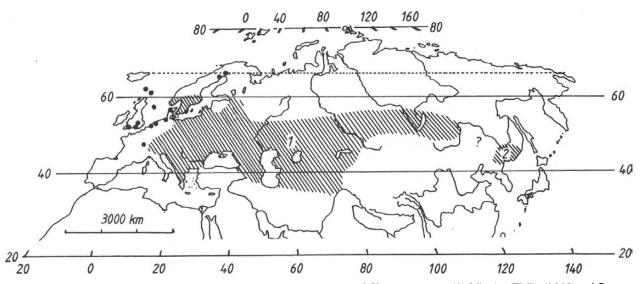


Fig. 3. Geographic distribution of Vespertilio murinus murinus (1) and V. m. ussuriensis (2) following Wallin (1969) and Baagee (in press). Boundaries in western Europe are drawn along the westernmost indications of breeding. Black dots denote outlying records.

Vespertilio murinus is considered rare or even "vulnerable" in much of central and eastern Europe (Gaisler et al., 1990; Stebbings, 1988), but there is no evidence of declining populations. In fact, the particolored bat is common in some places, and there is an increasing number of reports of nurseries (Bauerová and Ruprecht, 1989; Červený and Bürger, 1989; Moeschler and Blant, 1987; Richarz et al., 1989; Zöllick et al., 1989). The species perhaps has been overlooked in the past. It is abundant in eastern parts of Denmark and also in southern Scandinavia (north to ca. 60°N—Ahlén, 1986; Baagøe, 1986). Limited evidence from this region suggests a recent expansion of its range (Ahlén and Gerell, 1989).

One species of bat fly, Nycteribia kolenati Theodor & Moscona, (Nycteribiidae) has been recorded on V. murinus (Hutson, 1984). V. murinus is the principle host for the fleas Ischnopsyllus obscurus and I. dictaena, and an occasional host for at least six other species of fleas of the same genus (I. octaenus, I. variabilis, I. s. simplex, I. elongatus, I. intermedius and I. hexactenus), and Nycteridopsylla pentactenus and N. eusarca (Hurka, 1963a, 1963b). At least seven species of mites from three orders and families have been recorded on V. murinus from Europe and northern Asia. These species are: Argas vespertilionis (Ixodoidea, Argasidae), Ichoronyssus scutatus, Macronyssus flavus, M. diversipilis (Mesostigmata, Macronyssidae), Trombicula russica, Toritrombicula orghidani, Chiropterella muscae (Trombidiformis, Trombidiculidae-Anciaux de Faveaux, 1971). Two other genera of mites, Steatonyssus sp. (Mesostigmata) and Ixodes sp. (Ixodoidea), have been recorded on V. murinus from Kirghizia in central Asia (Rybin et al., 1989). True bugs (Cimicidae) have not been recorded from V. murinus (Usinger, 1966). There is no evidence that European V. murinus are large scale vectors of hat rabies (Anonymous, 1990; Grauballe et al., 1987); there is only one positive observation (strain unspecified), from Omsk in Russia (Anonymous, 1986).

Remains of *V. murinus* have been found in owl pellets (*Strix aluco, Tyto alba* and *Bubo bubo*—Krzanowski, 1973; Obuch, 1989; Schaefer, 1974). Since it is a house bat, *V. murinus* is occasionally deliberately killed by humans or caught by cats and dogs (Baagee, in press).

In autumn and early winter, V. murinus is often found in houses or hanging on outside walls. Presumably, these are individuals that have become exhausted by flight displays associated with mating. Later in the winter, many V. murinus, often emaciated, turn up inside tall city buildings, apparently in search of less exposed positions (Baagøe, in press).

BEHAVIOR. In central and northern Europe, females arrive at the summer roosts in May to form maternity colonies, which disperse in August (Baagøe, in press). The bats roost well hidden in crevices in the roof or walls of low, often modern and well-insulated, buildings and perhaps also in rock fissures (Baagøe, 1986; Bauer, 1954; Cervený and Bürger, 1989; Spitzenberger, 1984). In Russia, maternity colonies have been found in houses (Strelkov, 1980), in

hollow trees (Strelkov, 1969), and in nest boxes erected in tree plantations (Lichatchev, 1980). Open space in front of the shelters appears to be an important feature of all roosts (Červený and Bürger, 1989). In spring and late summer, V. murinus live singly or in small groups, occasionally residing together with other species of bats. Roosts are similar to those used in summer (Baagæe, in press; Červený and Bürger, 1989). Young individuals and single females have been found in bat boxes in late summer in Germany (Zöllick et al., 1989).

Hibernation usually occurs in crevices within walls and roofs of buildings, and probably also in rock fissures, but only rarely in caves and mines (Červený and Bürger, 1989; Khabilov, 1980; Strelkov, 1969). Houses in towns, and tall (15-30 story) buildings often are used (Ahlén, 1986; Baagøe, 1986, in press; Ryberg, 1947; Spitzenberger, 1984). The animals hibernate singly or in groups (Baagøe, in press).

While foraging, V. murinus usually flies 20-40 m above the ground (Baagøe, 1987) in open country, and sometimes over woodlands and lakes. In late summer and autumn, it also feeds in suburban areas having street lights, particularly those with bluish-white light (Baagøe, 1986, in press; Rydell, 1992a, 1992b). Insects are captured only by aerial hawking.

The echolocation calls used by *V. murinus* are variable, but those most often heard from individuals hunting at high altitudes are powerful, shallow frequency-modulated signals with maximum amplitude at 23-25 kHz and a duration of about 20 ms. Repetition rate usually is about 5 Hz, which presumably corresponds to one pulse every other wingbeat. Shorter signals (about 10 ms), which sweep from 50 to 20 kHz with maximum amplitude around 25 kHz, are used at lower altitudes (Ahlén, 1981, 1990; Baagøe, in press).

Male V. murinus are known for their characteristic display flight songs. Such songs are heard in southern Swedish and Danish towns and cities in late autumn, and during mild (above freezing) and dry winter evenings (Hemmingsen, 1922). In Denmark, the sound is heard from late September until mid-December, rarely after Christmas. The song is most frequently heard near tall (15-30 story) buildings, some known to be winter roosts (Baagøe, in press). This behavior has also been observed along vertical rock walls (Ahlén, 1981; Weid, 1988). The song is about 150 ms long and is regularly repeated ca. four times per second. The highest amplitude of the call is near 14 kHz and therefore can be heard easily by young people (Ahlén, 1981; Kullenberg and Wallin, 1963). While displaying, the bat usually flies in a regular route at least 10 m above the ground, often much higher. Interactions between individuals are heard as loud squeaks and bats are occasionally observed chasing each other (Ahlen, 1981; Baagøe, in press; Ryberg, 1947).

When disturbed, V. murinus "utters a very prolonged, loud hissing or sizzling sound reminiscent of an electric arc in the case of incomplete contact between the two conductors (Ryberg, 1947). "The mouth is held half open and the upper lip is raised" (Ryberg, 1947:132). V. murinus does not adapt well to captive conditions, and some individuals soon stop flying (Baagøe, in press).

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GENETICS. The diploid number of chromosomes of species in the genus Vespertilio is 38, and the fundamental number is 50 (Heller and Volleth, 1984). Among the autosomes, six pairs are large and metacentric, one pair is small and submetacentric, nine pairs are acrocentric, and two pairs are dot-like. The X-chromosome is metacentric, and the Y-chromosome is dot-like and acrocentric. Chromosome 15 possesses a secondary constriction immediately below the centromere (Zima, 1978). Nucleolus organizer regions occur in chromosomes 15 and 23 (Volleth, 1987).

REMARKS. Vespertilio was the first generic name proposed for bats, by Linnaeus (1758), and was applied to all bats then known. "The road to the present nomenclature," however, "ran through an unparalleled chaos in vertebrate systematics" (Wallin, 1969: 300) and subsequent changes in nomenclature "caused a . . . hopeless confusion in the literature" (Ryberg, 1947:79). The following account is based on Wallin (1969). After Linnaeus' publication of the name Vespertilio murinus in 1758, Schreber (1775) applied the same name to the species now known as Myotis myotis Borkhausen, and it was subsequently widely used for this species. Later, that same name was also used for other species of European bats. These mistakes certainly were due to Linnaeus' imprecise description, which could apply to many species of bats. In 1819, Kuhl published the name Vespertilio discolor, as suggested by Natterer. Later, Nilsson (1847) considered Kuhl's specimen to be identical to that of Vespertilio murinus Linnaeus, and hence resurrected the latter name; he also rejected the invalid name V. murinus Schreber. (It has recently been suggested that Linnaeus' description in fact referred to the same species of Myotis myotis Borkhausen-Hinkel, 1992). Later, Lilljeborg (1874) rejected Nilsson's interpretation, since he considered it impossible to assign V. murinus Linnaeus and V. discolor Natterer in Kuhl (1819) to the same species. Miller (1897), however, found no reason to reject Nilsson's (1847) interpretation, in which Linnaeus' species was made identical with V. discolor Natterer in Kuhl (1819) and he subsequently (Miller, 1907, 1912) used the Linnaean name in his important and influential work. Ryberg (1947) sharply rejected the interpretation of V. discolor Natterer in Kuhl (1819) as a synonym for V. murinus Linnaeus, hence disagreeing with Nilsson and Miller, and used the name V. discolor Natterer in Kuhl (1819) (see also Bauer, 1954, 1955). Ryberg (1947:80) asserted that the name murinus should be dropped from the nomenclature; "It would be a significant gain and a release from a heavy burden for the chiropterologist if this harmful name, which cannot be referred to a definite species, were avoided in the future." Nevertheless, the presently used nomenclature follows Nilsson and Miller (International Commission of Zoological Nomenclature, 1958).

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