Vespetilio murinus Linnaeus, 1758
Particolored Bat

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


Vesperugo krascheninikovi Eversmann, 1853:488. Type locality “Orenburg, Russia” (Ellerman and Morrison-Scott, 1966).

Vesperus (Marisonpalaeus) albigeratus Peters, 1872:260. Type locality “Mexico”? (Méhely, 1900).


V. m. murinus Linnaeus, 1758:31. See above (includes discolor, krascheninikovi, albigerus, siculus, latus Kastschenko, 1905, and michini Kastschenko, 1913).

V. m. usuriensis Wallin, 1969:358. Type locality “southern part of Usuri 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 Vespetilio 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 ............................... V. supranus
   Underside including throat, dark; maximum width of tragus is in the middle ............................... V. orientalis

The two latter forms may be synonymous (Yoshinuki, 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. usuriensis (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 (plagiotapagium) 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 Vespetilio (Heller and Völlath, 1984; Wallin, 1969).

The dorsal fur is dense and distinctively bicolor. 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 (Baagoe, 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 (Baagoe, 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 (n = 3), 9.8–14.5 in May (n = 3); females: 10.5–13.0 in March (n = 3), 10.2–14.5 in May (n = 3), 13.2–16.5 in July (n = 3) and 19.6–23.0 in October (n = 5) (Cervený and Birger, 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 coeclea 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 (Baagoe, 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; symphatic width, 9.5–10.2; interorbital width, 3.8–4.7 (Baagoe, in press; Spitzenberger, 1984).

The dental formula is 2/2, 1/1, 0/1, 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 postero- bacular cusps, which produces the distinctively trifid tooth characteristic of Vespetilio. 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, Belorusia and Ukraine, Azerbaijian, northern Iran and Afghanistan, south of 55–60°N in Russia, eastward to Manchuria and the Usuri region of eastern Siberia (Baagoe, in press; Gromova and Barazovich, 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 (Baagoe, 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 (Baagoe, in press).
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 (Oubsch, 1989; Schaefer, 1974; Woloszyń, 1987). There are also late Pleistocene and Holocene remains of *V. murinus* from Crimea (Konovalov and Baranova, 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 (Schroer 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. When 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 (Baagoe, 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 Koval (1978, 1984). Skin glands around the nose and the anal region are multifunctional and serve as sources of pheromones (Ceranova, 1989; Sokolov and Ceranova, 1984). The prostate is large, and the seminal vesicles and the ampullary glands are merged into a single structure (Tunov, 1989).

**ONTOGENY AND REPRODUCTION.** Characteristic of most hibernating bats, spermatogenesis in *V. murinus* occurs in summer, and the sperm are stored in the cauda epididymis 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 (Baagoe, in press; Ryberg, 1947; Schroer 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 (Baagoe, 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 (Baagoe, in press; Ceréveny 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 (Ceréveny and Bürger, 1989; Collett, 1981–1982; Löhr, 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-distance migration in that region (Kuskov, 1961; Strélkov, 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 (Baagoe, 1986; Ceréveny 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 (Baagoe, 1986, in press; Bauer, 1954, 1955).

*Vespertilio murinus* may be found in almost any landscape, including forests and urban areas, treeless steppes, and agricultural regions (Baagoe, 1986, in press; Ceréveny and Bürger, 1989; Ognev, 1928). It feeds on beetles and moths, at least when foraging around street lamps in late summer and autumn (Baagoe, 1986, in press), and on insects that hatch over water (Patylyakovich, 1980). However, diet analyses from Ukraine (Petrusenko and Sokolov, 1981) and 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. 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. Rubæk and Bloch, pers. comm.; Stansfeld, 1966). The distribution of *V. murinus* may be influenced by interspecific competition with *Eptesicus serotinus* Schreiber (Baagoe, 1986), and with *Nyctalus noctula* Schreiber (Ceréveny and Bürger, 1989).

In central Europe, *V. murinus* is most common in forested upland areas around 1,000 m elevation (Ceréveny 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...
Vesperilio marinus is considered rare or even “vulnerable” in much of central and eastern Europe (Gaiser et al., 1990; Stebbins, 1988), but there is no evidence of declining populations. In fact, the particular bat is common in some places, and there is an increasing number of reports of nurseries (Bauerova and Ruprecht, 1989; Cervený and Bürger, 1989; Mooschler and Blant, 1987; Richarz et al., 1989; Zöllck et al., 1989). The species has sometimes 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 by, Nycteris kolenati Theodor & Moscona, (Nycteribiidae) has been recorded on V. marinus (Hilton, 1984). V. marinus is the principle host for the fleas Ichnospyllus obscurus and I. dictaena, and an occasional host for at least six other species of fleas of the same genus (L. octonius, L. variabilis, L. s. simplex, L. elongatus, L. intermedius and L. hexactenius), and Nycteridopsetylla pentactenius and N. casvica (Härka, 1963a, 1963b). At least seven species of mice from three orders and families have been recorded on V. marinus from Europe and northern Asia. These species are: Arga vespertilionis (Ixoidea, Argasiidae), Ichnospyllus flavus, Macropus flavus, M. davispalii (Mesogameta, Macrorynchidae), Trembitchia ruscica, T. trembitchica orbighani, Chirotterula muscae (Trombiculiformes, Trombiculidae—Aniaux de Faveaux, 1971). Two other genera of mice, Steatomys sp. (Mesogameta) and Iodes sp. (Ixoidea), have been recorded on V. marinus from Kirghizia in central Asia (Rybin et al., 1989). True bugs (Cimicidae) have not been recorded from V. marinus (Usinger, 1966). There is no evidence that European V. marinus are large scale vectors of bat rabies (Anonymous, 1990; Grauballe et al., 1987); there is only one positive observation (strain unspecified), from Orobok in Russia (Anonymous, 1986).

Remains of V. marinus 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. marinus is occasionally deliberately killed by humans or caught by cats and dogs (Baagøe, in press). In autumn and early winter, V. marinus 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. marinus, often emaciated, turn up in bird houses, 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 (Lichachev, 1980). Open space in front of the shelters appears to be an important feature of all roosts (Cervený and Bürger, 1989). In spring and late summer, V. marinus live singly or in small groups, occasionally roosting together with other species of bats. Roosts are similar to those used in summer (Baagøe, in press; Cervený and Bürger, 1989). Young individuals and single females have been found in nest boxes in late summer in Germany (Zöllck 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 (Cervený and Bürger, 1989; Khahlov, 1980; Strelkov, 1969). Roosts 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. marinus 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. marinus 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. marinus 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 (Ahlén, 1981; Baagøe, in press; Ryberg, 1947).

When disturbed, V. marinus "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. marinus does not adapt well to captive conditions, and some individuals soon stop flying (Baagøe, in press).
GENETICS. The diploid number of chromosomes of species in the genus *Vesperitillo* is 38, and the fundamental number is 50 (Heller and Volleth, 1984). Among the autosomes, six pairs are large and medium, one pair is small, and one pair is 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). Nuclear organizer regions occur in chromosomes 15 and 23 (Volleth, 1987).

REMARKS. *Vesperitillo* 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) and Linnaeus' publication of the name *Vesperitillo marinus* 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 are certain due to Linnaeus' imprecise description, which applied to many species of bats. In 1819, Kuhl published the name *Vesperitillo discolor*, as suggested by Natterer. Later, Nilsson (1847) considered Kuhl's specimen to be identical to that of *Vesperitillo marinus* Linnaeus, and hence resurrected the latter name. He also stated the invalid name *V. marinus Schreber* and has recently been suggested that Linnaeus' description in fact referred to the same species of *Myotis myotis* Borkhausen—Hinkel, 1992). Later, Lillieborg (1874) rejected Nilsson's interpretation, since he considered it impossible to assign *V. marinae Linnaeus and V. discolor Natterer* 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. marinae Linnaeus*, hereby 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 *marinae* 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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LITERATURE CITED


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JENS RYDELL, DEPARTMENT OF ECOLOGY, UNIVERSITY OF LUND, HELGONAVÄGEN 5, S-223 62 LUND SWEDEN. HANS J. BAAGØE, ZOOLOGISK MUSEUM, UNIVERSITETSPARKEN 15, DK-2100 KØBENHAVN O DENMARK.