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Eptesicus nilssonii.

By Jens Rydell

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Eptesicus nilssonii (Keyserling and Blasius, 1839)

Northern Bat

Vespertilio kuhlii Nilsson, 1836:pl. 34, upper fig. Type locality Torpe, Hallingdalen (Norway—Ryberg, 1947). A misidentification. Not *V. kuhlii* Natterer in Kuhl.

V[esperugo]. nilssonii Keyserling and Blasius, 1839:315. Based on Nilsson's description and possibly also on specimens from Harz in Germany (Knolle, 1981).

Amblyotus atratus Kolenati, 1858:252. Type locality "Altwater [probably = Bruntal], Austrian Silesia [now in Czechoslovakia], 800-1500 m" (Miller, 1912).

Vesperus propinquus Peters, 1872:262. Type locality "Ysabel de Guatemala" (in error, see Davis, 1965).

E[ptesicus]. nilssoni: Miller, 1907:209. First use of current name combination.

Eptesicus japonensis Imaizumi, 1953:91. Type locality "Hokujo Mura (Shinden), 720 m altitude, Kita-Azumi Gun, Nagano Pref., Central Honsyu, Japan".

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Tribe Vespertilionini, Genus *Eptesicus*. The genus contains 21 species (Corbet and Hill, 1991).

The following two subspecies of *E. nilssonii* are currently recognized (Hanák and Horáček, 1986):

E. n. nilssonii Keyserling and Blasius, 1839:315. See above.
E. n. japonensis Imaizumi, 1953:91. See above.

A third named form *parvus* Kishida, 1932 from North Korea may be a misidentification of *Pipistrellus savii* (Hanák and Horáček, 1986). However, Yoshiyuki (1989) assigns *E. nilssonii* from Sachalin and Hokkaido to *E. n. parvus.*

DIAGNOSIS. Among European vespertilionids, *Eptesicus nilssonii* can be recognized by its long, dark brown dorsal fur with distinct golden tips on the hairs of the head and the back. Its only European congener is *E. serotinus* Schreber, which is much larger (forearm 48-55 mm). *Pipistrellus savii* Bonaparte and *Vespertilio murinus* Linnaeus overlap slightly in size with *E. nilssonii. P. savii* also is dark brown and may have golden tipped hairs dorsally, but it usually is smaller (forearm 31-37 mm), the tragus broadens rather than narrows toward the tip, and the baculum is I-shaped rather than Y-shaped (Hanák and Horáček, 1986). *V. murinus* also is dark but has grayish or silvery, not golden, tips on the dorsal fur and usually is larger (forearm 39-49 mm). *E. nilssonii* differs from *V. murinus* in its very narrow post-calcarial lobe (usually distinct in *V. murinus*); the calcar, which is shorter than the tibia (longer than the tibia in *V. murinus*), and the short and bulbous penis (long and slender in *V. murinus*—Greenaway and Hill, 1988).

In central Asia, the situation is more complex, because several species of *Eptesicus* occur there. A key, following Corbet (1978), Hanák and Gaisler (1971), Hanák and Horáček (1986) and Strelkov (1986, 1989), is provided. Additional characters and illustrations are available in Hanák and Horáček (1986), Heller and Volleth (1984), and Strelkov (1986, 1989). Diagnostic characters of *Pipistrellus savii* are provided by Hanák and Horáček (1986).

1. Outer upper incisors more than half the length of the inner incisors which are clearly bicuspid .... (2)
   Outer upper incisors about half the length of the inner incisors which are unicuspid or bicuspid .... (3)
2. Greatest width across upper canines exceeding interorbital width by at least 0.4 mm; forearm 37-44 mm; ears rounded, upper third of the outer edge of the ears curved; baculum 1.27-1.50 mm long .... *E. nilssonii*
   Canine width equal to interorbital width or up to 0.2 mm greater; forearm 34-37.5 mm; ears pointed, outer edge of ears almost straight; baculum 0.62-0.72 mm long; Kazakhstan .... *E. bobrinskoi*
3. Inner incisors clearly bicuspid. Northern Iran to Mongolia and Tibet .... *E. gobiensis*
   Inner incisors unicuspid or very slightly bicuspid .... (4)
4. Condylobasal length < 15.0 mm; C-M3 < 5 mm; forearm 34-42 mm; hairs < 5 mm; tail extends only slightly beyond the tail membrane. S. Arabia to Pakistan .... *E. nasutus*
   Condylobasal length > 15.5 mm; C-M3 > 5 mm; forearm 37-56 mm; hairs > 5 mm long. At least one tail vertebra extends beyond the tail membrane .... (5)
5. Condylobasal length 14.5-17.0 mm; C-M3 5.6-6.3 mm; forearm 37-51 mm; baculum 0.80-1.00 mm long. NE Egypt to Turkestan .... *E. bottae*
   Condylobasal length 18.5-22.0 mm; C-M3 6.5-8.2 mm; forearm 48-56 mm; baculum 1.02-1.40 mm long. England to Korea .... *E. serotinus*

Eptesicus n. nilssonii and *E. n. japonensis* may be distinguished as follows: The tail is relatively shorter in *japonensis* (35.5-38.5 mm) than in *nilssonii* (38-50 mm). The hair on the dorsal side of the uropatagium extends up to one quarter of the tail length in *japonensis*, but at least to the middle in *nilssonii*. The basic fur color is darker (very dark brown) in *nilssonii* than in *japonensis* (chocolate brown), and the golden hair tips therefore contrast with brown more in the former (Imaizumi, 1953; Wallin, 1969).

By means of a bat detector, foraging *E. nilssonii* can be identified, at least among the European bats, by characteristics of its echolocation pulses. The pulses most often heard consist of shallow sweeps about 10-13 ms long with maximum intensity approximately at 30 kHz. They are emitted at a rate of about 5/s but longer (300 ms) pulse intervals are included occasionally. The species is most easily located by means of a bat detector while the observer drives slowly along rows of street-lights (Ahlén, 1981; Rydell, 1991; Skiba, 1990).

GENERAL CHARACTERS. *Eptesicus nilssonii* (Fig. 1) is medium sized with short, rounded, fleshy ears, which are broadest near the base. The edge of the ear has five transverse folds. The tragus is short, rounded on top, and bends slightly toward the inside. The dorsal fur is long and dark brown or blackish (chocolate brown in *E. n. japonensis*) with golden tipped hairs in the head and back regions. The contrast with the yellow-brown ventral side is sharp. The nose, ears, and the tail and wing membranes are black or blackish-brown. Juveniles lack the golden sheen of the fur; instead the hair tips on the back are silvery (similar to young *V. murinus*), and their underparts are light gray (Miller, 1912; Schober et al., 1989).

The wings are moderately long and broad and have short, rounded tips (Norberg and Rayner, 1987). The calcar extends about half the length of the tail membrane, and the post-calcarial lobe is narrow. The last tail vertebra (3-4 mm) extends beyond the interfemoral membrane. The lateral membrane (the plagiopatagium) starts at the base of the toe (Miller, 1912; Schober et al., 1989).

Measurements of *E. n. nilssonii* from Europe are: head and body length, 54-64 mm; tail, 35-50 mm; forearm, 37-44 mm; ear, 13.0-17.5 mm; wingspan, 240-280 mm (Schober et al., 1989), and of *E. n. japonensis* from Honshu, Japan: head and body length, 58-68 mm; tail, 35-43 mm; forearm, 38-42 mm; ear, 13.0-16.5 mm (Yoshiyuki, 1989). The mass of adults normally is 8-12 g

FIG. 1. *Eptesicus nilssonii* leaving its hibernation site in April (a), and nursing young while clinging to a chimney wall in a typical fashion (b). South Sweden. Photographs by J. Rydell.

(Ryberg, 1947), but during the last weeks of pregnancy females may weight 16 g (Rydell, 1990*b*); heavier individuals (17–18 g) have been found before hibernation in autumn (Mosansky and Gaisler, 1965).

In comparison with other *Eptesicus* species, the skull (Fig. 2) is relatively delicate and tapered and the braincase is low. The dorsal profile shows evident convexity at the middle. The lambdoidal crests curve slightly toward the point of contact at the middle, the rounded posterior outline of the occiput is plainly visible behind them when the skull is viewed from above. There is little or no sagittal crest. The braincase is subspherical or broadly ovate in outline when viewed from above, its depth slightly more than half the mastoid breadth. The interorbital region has an hour-glass shape, and a lacrimal swelling is present. The rostrum is laterally rounded, with only a trace of lateral concavities (Miller, 1912).

Skull measurements (in mm) of *E. n. nilssonii* from central Europe (Czechoslovakia and Austria) are: greatest length of skull, 14.7–16.0; condylobasal length, 14.2–15.6; zygomatic breadth, 9.5–10.5; interorbital width, 3.8–4.5; length of maxillary tooth row (C-M3), 5.0–5.8 (Mosansky and Gaisler, 1965; Spitzenberger, 1986), and of *E. n. japonensis* from Honshu, Japan: greatest length of skull, 15.4–16.3; condylobasal length, 14.9–15.9; zygomatic breadth, 9.1–10.5; length of maxillary tooth row (C-M3), 5.3–5.8 (Yoshiyuki, 1989). In *Eptesicus* including *nilssonii*, the teeth are normal throughout and show no peculiarities, but are large and robust relative to the size of the skull. The dental formula is i 2/3, c 1/1, p 1/2, m 3/3, total 32 (Miller, 1912).

DISTRIBUTION. *E. n. nilssonii* is found (Fig. 3) from eastern France and Switzerland to northern Scandinavia and Finland, through the northern half of eastern Europe, northern Ukraine and through Russia to Kamchatka, Sachalin, and Hokkaido. There is also an isolated population in the Caucasus area (Hanák and Horáček, 1986; Rakhmatulina, 1989; Ryberg, 1947). Specimens, that may be either *nilssonii* or *gobiensis*, have been obtained from Iraq, Kashmir, and Nepal (Hanák and Horáček, 1986). *E. n. japonensis* is endemic to Honshu, Japan (Wallin, 1969; Yoshiyuki, 1989).

In Scandinavia and Finland, including the larger Baltic islands, and in Estonia and Latvia, *E. nilssonii* is one of the most common bats (Ahlén, 1983; Ahlén and Gerell, 1989; Stebbings, 1988). It commonly is found and breeds regularly near the Arctic Circle (65–66°N) in Sweden and well above it (69°05′N) in Norway (Rydell, 1992*a*; Rydell et al., in press). In Siberia, it occurs to about 60°N (Ognev, 1928). In the Scandinavian mountains (southern Norway), it may be found up to 1,000 m altitude (Collett, 1911–1912).

Eptesicus nilssonii is absent from much of the lowlands of western Europe. There is, however, an old record from Denmark (Baagøe, 1981) and a recent one (a male) from England (Greenaway and Hill, 1988). In central and eastern Europe it is common in some regions, but has a patchy distribution and occurs mostly in forested uplands (about 200–2,000 m—Hanák and Horáček, 1986; Hůrka, 1967; Moeschler et al., 1986; Mosansky and Gaisler, 1965; Ohlendorf, 1989; Skiba, 1989; Spitzenberger, 1986; Zukal and Gaisler, 1989). In southern Europe, there are outlying records from Italy, former Yugoslavia, Romania and Bulgaria. In Asia the southern limit of the distribution is obscure, because records are few and isolated (Hanák and Horáček, 1986).

FOSSIL RECORD. Fossils of *Eptesicus* forms have been found in cave deposits from early Pliocene and later in Poland, and the oldest *E. nilssonii* dates from early Pleistocene (Woloszyn, 1987). Fossil or subfossil *E. nilssonii* are known from at least 17 localities in central Europe, mostly from cave deposits. From the former Soviet Union, late Pleistocene and Holocene remains are known from Crimea, Siberia and the Russian far eat (Gromova and Baranovoj, 1981).

Eptesicus nilssonii is relatively rare among central European bat fossil localities. It is more common, however, in deposits from the late Pleistocene (0.6–0.1 million years ago) and the Holocene, occurring at 40% of these sites (Horáček, 1990). This reflects a trend toward a more boreal bat fauna at this time. Several remains from Karlukovo in northern Bulgaria indicate that the distribution during the late Pleistocene was continuous in parts of southern Europe and not confined to upland areas (Horáček, 1982). Measurements of *E. nilssonii* fossils from Pleistocene deposits in central Europe do not differ substantially from those of extant populations (Spitzenberger, 1986; Woloszyn, 1987).

FORM AND FUNCTION. The wing form of *E. nilssonii* is unspecialized; the wing area is about 112 cm^2, aspect ratio about 6.6, and wing loading about 8.1 N/m^2. These values are near the average for northern European bats (Baagøe, 1987; Norberg and Rayner, 1987). From the wing form, a generalized flight pattern may be predicted, with moderately fast and maneuverable flight and aerial pursuit of insects in open surroundings. Field observations support these predictions (Baagøe, 1987; Rydell, 1990*a*).

The number of vertebrae is common for all *Eptesicus* including *E. nilssonii* (cervical, 7; thoracic, 11; lumbar, 5; sacral, 4; and caudal, 10). However, the relative lengths of the vertebral sections of the vertebral column (in relation to thoracic-lumber length) in *E. nilssonii* differ from those of other *Eptesicus*; the cervical and lumbar sections are shorter, and the thoracic and caudal sections are longer. The humerus is relatively longer in *E. nilssonii* than in other *Eptesicus* species (Kovtun, 1984, 1990*a*; pers. comm.).

The anatomy, topography and relative development of muscles in *E. nilssonii* are typical for the genus, and are generally similar in all vespertilionids. However, m. abductor pollicis longus is more developed in *E. nilssonii* than in other *Eptesicus* species; m. extensor digitorum brevis is composed of six heads, more than in other species of the genus. The peripheral nervous system is typical for vespertilionids. In the vascular system, arcus aortae in *E. nilssonii* bifurcates into two symmetrical columns. The blood supply to the muscles and flight membranes is similar to that of other vespertilionids (Kovtun, 1984, 1990b; pers. comm.).

The morphology of the accessory glands of the male genitalia is characteristic for the subgenus *Amblyotus* Kolenati. The ampullary glands enlarge during the mating season (Tiunov, 1989).

ONTOGENY AND REPRODUCTION. Births usually occur in mid-June in Germany (Braun and Häussler, 1990), in late June or early July in southern Scandinavia, and in mid-July farther north (Collett, 1911–1912; Rydell, 1989*a*, 1992*a*). A strong negative correlation exists between mean air temperature during early pregnancy and date of parturition. This suggests pregnant females regularly enter torpor during periods of cool weather, presumably because foraging is not energetically profitable (Rydell, 1989*c*), thereby lengthening the gestation period.

A birth takes a few minutes, during which the mother hangs head downward with the tail bent inward against the body. Within a few minutes after birth, the mother cuts the umbilical cord and licks the young clean and dry (Collett, 1911–1912).

Litter size usually is one in Scandinavia, but twins are more common farther south (Collett, 1911–1912; Ryberg, 1947; Hůrka, 1967). Young are born with their eyes closed and they are pink and almost hairless. Their body length at birth is 45–48 mm, and forearm length is 12.5–14 mm (Collett, 1911–1912). The young start to fly and feed by themselves during maximal insect abundance at the height of the summer. Their first training flights outside the roost occur when about two (Sweden) or three (Germany) weeks old (Rydell, 1989*a*; Tress et al., 1989).

ECOLOGY. The sexes segregate during summer when females congregate and form maternity colonies, as in most vespertilionids. Seventy percent or more of the adult females return to the same roost each summer (Rydell, 1989*a*; Tress et al., 1989). The maternity colonies include parous and non-parous females but no adult males, and consist of matrilines; female young are recruited to their native breeding group. There are stable, age-related, dominance relationships among individuals. Females aged 1–3 years frequently do not breed. Among breeding females, older individuals maintain higher body masses than do younger ones. There is little or no exchange of individuals between adjacent maternity colonies. Young males disperse during their first year (Rydell, 1989*a*, in press; Tress et al., 1989). The maximum age recorded is 15.5 years (Masing, 1990).

FIG. 2. Dorsal, ventral and lateral views of the skull and lateral view of the mandible of *Eptesicus nilssonii nilssonii* from Silvåkra, southernmost Sweden (Lund University). Greatest length of the skull is 15.7 mm. Photographs by J. Rydell.

The densest populations of *E. nilssonii* occur where the foraging habitat is most diverse, in small farmland areas with deciduous woodlands, and near lakes (De Jong and Ahlén, 1991; Putintsev

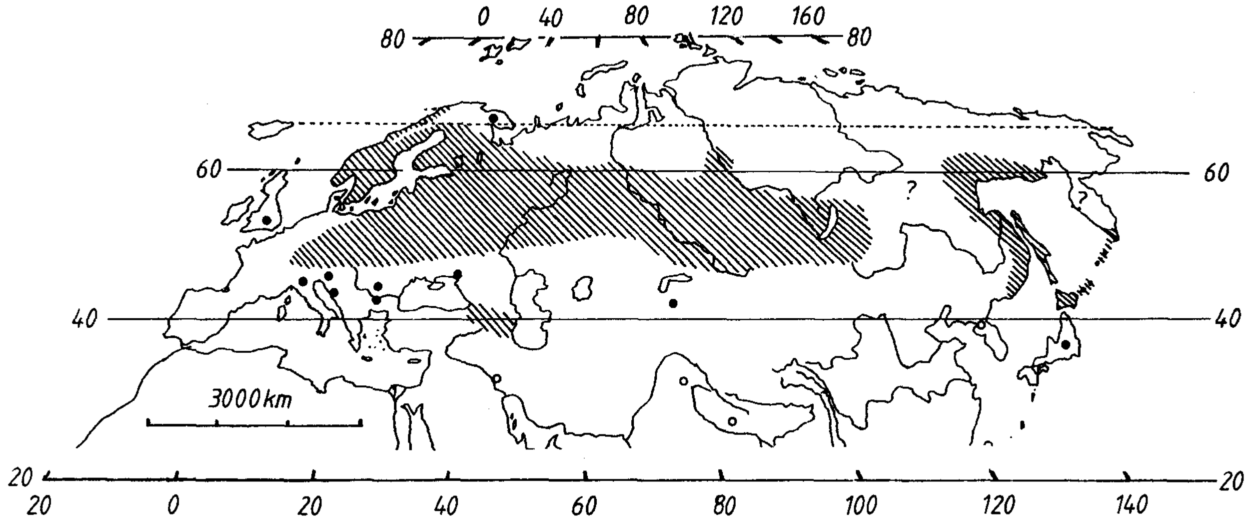

FIG. 3. Geographic distribution of *Eptesicus nilssonii* modified after Hanák and Horáček (1986) and Strelkov (1986). Black dots denote some outlying records. The record from Honshu, Japan, is the type of *E. n. japonensis* Imaizumi. Circles represent records from Iraq, Nepal, Kashmir and Korea which need confirmation with respect to species identity.

and Arakchaa, 1980; Rydell, 1986*b*). In Scandinavia, the density of *E. nilssonii* declines with increasing latitude and is about five times higher at 57°N than in a similar landscape at 65°N (Rydell, 1992*a*). *E. nilssonii* is the only species of bat throughout much of the extensive coniferous forests of northern Scandinavia (Ahlén and Gerell, 1989) and Russia (Ognev, 1928).

Eptesicus nilssonii is non-migratory (Aellen, 1983; Strelkov, 1969). The longest movement known from banding is 115 km (Kraus and Gauckler, 1966). Early (nineteenth century) suggestions of long-distance migration in Europe are wrong (Ryberg, 1947).

The diet consists of nocturnal insects captured in flight. Analysis of feces suggests that small (3–10 mm) dipterans constitute 30–80% (by volume) of the diet, but moths, small beetles and various insects that fly over water also are frequently eaten (Patlyakevich, 1980; Rydell, 1986*b*, 1989*b*). In Sweden, foraging flights are energetically profitable only at ambient temperatures above 6–9°C, when the aerial insect density exceeds 0.1 m^{-3}. The time spent foraging by reproducing females is therefore positively correlated with the ambient temperature (Rydell, 1989*c*).

European *E. nilssonii* populations do not appear to be threatened or declining (Stebbings, 1988). The species is abundant, and limited evidence indicates that it has become more common and widely distributed in recent years (Ahlén and Gerell, 1989; Zukal and Gaisler, 1989). Difficulty in finding this species while it is roosting may have caused it to be overlooked in the past (Skiba, 1990).

Since *E. nilssonii* is common and normally resides in human dwellings, accumulations of droppings often cause concern to house-owners. However, serious conflicts are relatively uncommon and there seldom is reason to control the number of bats. Maternity colonies are small, relatively quiet, and usually well concealed (Rydell, 1989*d*).

There are no records of bat flies (Nycteribiidae) or true bugs (Cimicidae) from *E. nilssonii* (Hutson, 1984; Usinger, 1966), but the species serves as an occasional host for at least six species of fleas of the genus *Ischnopsyllus* (*I. octanenus*, *I. variabilis*, *I. simplex*, *I. intermedius*, *I. obscurus*, *I. hexactenus*) (Hůrka, 1963*a*, 1963*b*). Four species of parasitic mites have been found on *E. nilssonii*: *Spinturnix kolenatii*, *Macronyssus flavus*, *Neomyobia chiropteralis* and *Ichoronyssus biarcuatus* (Anciaux de Faveaux, 1971). The species of parasitic nematodes found in central European *E. nilssonii* are the same as in other sympatric bat species and there is no evidence for host-specificity (nematode species found in *E. nilssonii* were not specified—Hosek and Horáček, 1989). Rabies has not been found in *E. nilssonii* (Anonymous, 1989; Hagner et al., 1990).

Predators of *E. nilssonii* include tawny owls (*Strix aluco*), eagle owls (*Bubo bubo*), house cats (*Felis catus*) and European sparrow hawks (*Accipiter nisus*—Obuch, 1989; Rydell, 1992*a*; Schaefer, 1974).

BEHAVIOR. *E. nilssonii* enters hibernation sites in early winter (November–December), and leaves again in March or April (Liiva and Masing, 1987). Individuals are found alone or in groups of 2–4, and both sexes often occur in the same place. Hibernation takes place in houses, cellars, and sometimes in caves and mines. Each individual may use several hibernation sites each winter. Cool sites, frequently 0–2°C and occasionally −5°C, are selected (Knolle, 1973; Masing, 1987; Ohlendorf, 1987; Ryberg, 1947; Rydell, 1989*d*; Spitzenberger, 1986; Strelkov, 1969).

In summer, males roost alone (Lehmann, 1983), whereas females form maternity colonies consisting of 10–80 adults. Colonies form in early summer (May in continental Europe, early June in southern Sweden, still later in the far north) and disband again soon after the young start to fly in August. They are nearly always located in houses and often near artificial heat sources. The bats roost in crevices or on vertical surfaces (Braun and Häussler, 1990; Hůrka, 1967; Lehmann, 1983; Ohlendorf, 1989; Ryberg, 1947; Rydell, 1989*b*; Tress et al., 1989). Colonies may shift roosts several times each summer and each maternity colony may use several adjacent buildings, and several sites within each (Henkel et al., 1989; Rydell, 1989*a*).

The northern bat hunts insects in the air by echolocation using a variety of pulses. Those used in the search phase in the typical foraging habitat, open situations, usually consist of 10–13 ms, occasionally up to 18 ms, long, loud, shallow sweeps sometimes preceded by steeply frequency-modulated (FM) components (about 40–30 kHz). Pulses are emitted about every 200 ms, but longer (300 ms) intervals are included on occasion. When the bat hunts close to vegetation or near (<5 m) the ground, pulse repetition rate ranges from 5/s to 8–9/s, usually without lengthened pulse intervals. Maximum intensity is near 30 kHz in all search phase signals. Steep FM signals without a shallow sweep component are used in the immediate vicinity of obstacles or targets, and also during flight indoors. Such signals are 0.4–8.4 ms long (Ahlén, 1981, 1990; Patlyakevich, 1980; Rydell, 1990*a*; Skiba, 1990). In a high quality bat detector with a heterodyne system (see Sales and Pye, 1974), search phase echolocation signals can be detected 50–70 m from the bat (Rydell, 1990*a*).

The northern bat flies in open spaces while hunting, usually 8 m or more from surrounding obstacles. The flight is straight or slightly curved and the altitude usually is 5 to 10 m, but ranges from 2 to 50 m. Flight speed in straight flight outdoors is 5–6 m/s (extremes 4–8 m/s—Baagøe, 1987; Rydell, 1990*a*).

Habitats where foraging occurs are diverse and vary seasonally. In summer, these bats hunt for flying insects in farmland and forest and over water, and during spring and autumn also near artificial lights like street-lights (De Jong and Ahlén, 1991; Rydell, 1986*b*, 1991, 1992*b*).

Female northern bats usually are nocturnal, but at the highest latitudes, nights are short or absent in summer, and the bats must fly in daylight. During pregnancy, foraging activity is uni- or bimodal with peaks after dusk and sometimes before dawn, but after parturition the females forage intermittently throughout the night. At 57°N, reproducing females leave the roost on average 47 min after sunset. The females spend on average 3 h outside the maternity roost each night, but during pregnancy, about 20% of this is spent roosting in trees. Hence, pregnant females forage for 150 min each night on average. In lactating females, the foraging time reflects increasing energetic demands of milk production, and averages 120–130 min per night just after parturition, 220–260 min at mid lactation, and 320 min at peak lactation (Rydell 1990*b*, 1992*a*, in press).

Female *E. nilssonii* often establish small (about 100 m^2) feeding territories in places where insects are abundant, for example along forest edges or around isolated trees in open farmland. Such territories are used by the same individuals night after night and sometimes also in subsequent years (Rydell, 1986*a*, 1989*a*). From a characteristic level flight path following an established route within the territory, a hunting northern bat typically makes capture attempts by short (usually 1–2 m) or sometimes much longer (almost to the ground) vertical dives, after which the former flight path is quickly resumed. When large (presumably indefensible) concentrations of insects appear, like hatching water insects or moths concentrated around street-lights, the bats may leave individual territories and forage in groups (Rydell, 1986*b*).

Feeding territories are vigorously defended against intruders by aerial chases and/or audible vocalizations with maximum amplitude at 14 kHz (Rydell, 1986*a*). Aerial chases and "social" vocalizations also occur outside hibernation sites in autumn. "Social calls" consist of long sweeps with powerful second and third harmonics (Ahlén, 1981).

GENETICS. The diploid number is 50 and the fundamental number is 48 as in other species of *Eptesicus* (Heller and Volleth, 1984; Zima, 1982). The X chromosome is metacentric, and all autosomes and the small Y chromosome are acrocentric. There may be polymorphism in the length of the secondary constriction of chromosome 15. The chromosome complement of *E. nilssonii* from Finland is similar to that of individuals from continental Europe (Hongell et al., 1989).

REMARKS. The species epithet *nilssonii* honors Professor Sven Nilsson of Lund, for his efforts in describing this species. The type specimen was collected by Nilsson in southern Norway (Ryberg, 1947), although Miller (1907) and many others assumed it was collected in Sweden, where Nilsson resided.

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Editors of this account were J. Alden Lackey and Karl F. Koopman. Managing editor was Craig S. Hood.

Jens Rydell, Department of Ecology, University of Lund, Helgonavägen 5, S-223 62 Lund, Sweden.