Northern Bat Eptesicus nilssonii (Keyserling and Blasius, 1839)

Suominen, Kati Marie

2022-12-08

Suominen, K M, Kotila, M, Blomberg, A S, Pihlström, H, Ilyukha, V & Lilley, T M 2022, Northern Bat Eptesicus nilssonii (Keyserling and Blasius, 1839). in K Hackländer & F E Zachos (eds), Handbook of the mammals of Europe. Springer, pp. 1-27. https://doi.org/10.1007/978-3-319-65038-8_

http://hdl.handle.net/10138/568146
10.1007/978-3-319-65038-8_45-1

unspecified
acceptedVersion

Klaus Hackländer
and
Frank E. Zachos
Handbook of the Mammals of Europe
Handbook of the Mammals of Europe
10.1007/978-3-319-65038-8_45-1

Northern Bat *Eptesicus nilssonii* (Keyserling and Blasius, 1839)

Kati M. Suominen[1] , Miika Kotila[2] , Anna S. Blomberg[3] , Henry Pihlström[4] , Viktor Ilyukha[5] and Thomas M. Lilley[1]

(1)BatLab Finland, Finnish Museum of Natural History Luomus, University of Helsinki, Helsinki, Finland

(2)Biodiversity Unit, University of Turku, Turku, Finland

(3)Department of Biology, University of Turku, Turku, Finland

(4)Molecular and Integrative Biosciences Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

(5)Institute of Biology, Karelian Research Centre, Russian Academy of Sciences, Petrozavodsk, Russia

Kati M. Suominen (Corresponding author)
Email: kati.suominen@helsinki.fi

Miika Kotila
Email: miika.h.kotila@utu.fi

Anna S. Blomberg
Email: asblom@utu.fi

Henry Pihlström
Email: henry.pihlstrom@helsinki.fi

Viktor Ilyukha
Email: ilyukha.62@mail.ru

Thomas M. Lilley (Corresponding author)
Email: thomas.lilley@helsinki.fi

Abstract

This comprehensive species-specific chapter covers all aspects of the mammalian biology, including paleontology, physiology, genetics, reproduction and development, ecology, habitat, diet, mortality, and behavior. The economic significance and management of mammals and future challenges for research and conservation are addressed as well. The chapter includes a distribution map, a photograph of the animal, and a list of key literature.

440376_0_En_45-1_Fig1_Print.tif

Fig. 1

A northern bat in southeastern Finland. (Photo: Katarina Meramo)

Common Names

English	Northern bat
German	Nordfledermaus
French	Sérotine de Nilsson
Spanish	El murciélago hortelano norteño
Italian	Serotino di Nilsson
Russian	Северный кожанок

Taxonomy, Systematics and Paleontology

The northern bat belongs to the global and speciose genus of serotine bats, *Eptesicus* (family Vespertilionidae, subfamily Vespertilioninae). The members of this genus are very similar to each other, which has made it difficult to resolve their relationships (Hoofer et al. *2006*).

Nilsson (*1836*) misidentified a northern bat from its type location Torpe, Norway, as *Vespertilio kuhlii* (Rydell *1993a*). Keyserling and Blasius (*1839*) then described *Vesperugo nilssonii* after Nilsson's description and possibly specimens collected in Germany (Knolle *1981*). The species was also named *Amblyotus atratus* by Kolenati (*1858*) based on a specimen collected in Austrian Silesia (modern Czech Republic) (Miller *1912*). The current combination of names was first used by Miller

(1907). A synonym, *Amblyotus nilssonii*, is sometimes used in respect to a suggested division of the genus *Eptesicus* (Horáček et al. 2000).

Seven subspecies have been named (Horáček et al. 2000), of which two are presently widely recognized: *E. n. nilssonii* Keyserling and Blasius, 1839 and *E. n. parvus* Kishida, 1932. The latter is present in Hokkaido, Sakhalin, Korea, and the Siberian Far East (Yoshiyuki 1989, according to Horáček et al. 2000). However, genetic data do not support this distinction, as only low levels of genetic variability have been measured between the two taxa (Dolch et al. 2007).

Previously considered as a subspecies of the northern bat (Rydell 1993a), the Japanese short-tailed bat *Eptesicus japonensis* Imaizumi, 1953 from Honshu, Japan, and the Gobi big brown bat, *Eptesicus gobiensis* Bobrinski, 1926 from Central Asia, are now recognized as distinct species, and two other suggested subspecies, *E. n. centralasiaticus* and *E. n. kachinensis*, have been included in the Gobi big brown bat (Artyushin et al. 2018). Another taxon, the sombre bat *Eptesicus tatei* Ellerman and Morrison-Scott, 1951 from northeastern Bengal, India, has been suggested to be a synonym of the northern bat, but confirmation is required because of the disjunct location (López-Baucells and Burgin 2019).

During the mid-Pleistocene glacial periods, the northern bat was found further south than today (Kurtén 1968). Fossils have been found in Kozi Grzbiet in central Poland (Woloszyn 1987), in Hungary (Jánossy 1986), Bulgaria (Horáček 1982) (Popov and Pandurska 2000), and Italy (Salari and Kotsakis 2011, 2017). Other records from this period are known from Crimea, Siberia, and the Far East of Russia (former USSR) (Baranovoj and Gromova 1981). In southeastern Russia, the northern bat is the second or third most common species in fossil deposits from the last glacial maximum.

In Europe, all bats were likely absent in areas north of the Alps during the last glacial maximum. However, in the Mediterranean region, boreal species such as the northern bat found refugia outside of their contemporary range (Kurtén 1968; Benda et al. 2003). Cave subfossil deposits in central Italy show that the northern bat inhabited areas lower in latitude than any modern location during the last glacial maximum. Grotto del Fosselone in Latium, Italy, at 41°13′ is the southernmost-recorded European site for the species (Salari and Kotsakis 2011, 2017) .

Current Distribution

The northern bat has a wide trans-continental distribution across Eurasia, which is demonstrated by the records discussed below. Despite the large gaps between the available records, the trans-continental distribution is probably rather continuous as there are no obvious barriers. In Asia, the northern bat occupies a latitudinal band with suitable boreal, temperate, and alpine environments and climate via Kazakhstan, southern Siberia, and Mongolia (Botvinkin et al. 2003; Dolch et al. 2007; Datzmann et al. 2012; Orlova et al. 2015). There is an isolated patch of occurrence in the Caucasus (Bukhnikashvili et al. 2009), which is accompanied by a few records from northern Iran, marking the southern extreme for the species (Benda et al. 2012).
On the Pacific coast, the continental distribution ranges from the Korean Peninsula (Jo et al. 2018; Yoon 2010) and southeastern Russia to the Okhotsk Sea (Tiunov et al. 1992). The northern bat occurs on the island of Hokkaido (Fukui et al. 2004), the Kuril Islands (Kawai et al. 2014), Sakhalin (Artyushin et al. 2018), and the Kamchatka peninsula (Hanák and Horáček 1984). The northern bat

is the most common bat species in northeastern Russia, but rare in the Russian south-east (Tiunov et al. 1992) (Fig. 2).

440376_0_En_45-1_Fig2_Print.eps

Fig. 2

Current uniform distribution limits for the northern bat in Europe. (Data from IUCN, references cited in text. Map template: ©Copyright Getty Images/iStockphoto)

In Europe, the continuous range of the northern bat covers the Scandinavian Peninsula (Ahlén 2011), Finland (Nyholm 1983; Tidenberg et al. 2019), Russian Karelia (Belkin et al. 2015), and the Baltic countries (Masing 1983; Vintulis and Pētersons 2013). There are much fewer hibernation and summertime observations from Lithuania compared to Latvia, where the northern bat is common (Pauza and Pauziene 1998). The northern bat is rare but present at least in the northern and central part of Belarus (Shpak 2018), observed in Ukraine (Miroposlki 2001), and, according to the number of hibernating individuals, common in Samara, Russia (Smirnov et al. 2008). Similarly, the species is patchily present in Poland (Sachanowicz et al. 2006; Lesiński et al. 2008), and in southern and eastern Germany (Hutterer et al. 2005). Distribution is most uniform adjacent to the Carpathian, Sudeten, and Alp mountain ranges. Other Central European locations where the northern bat is a common species are the Białowieża forest in eastern Poland (Sachanowicz et al. 2006) and the Hartz Mountains in central Germany (Haupt and Schmidt 2007).

In the Czech Republic, the species is relatively common throughout the country, except for the few lowland regions (Anděra and Hanák 2007). In the Alps, the species is abundant in southern Germany (Hutterer et al. 2005), eastern France and Switzerland (Arthur and Lemaire 2015), Austria (Hutterer et al. 2005; Widerin and Reiter 2017), and northern Italy (Lapini et al. 2015; Toffoli et al. 2016). The northern bat is one of the most common if not the dominant species in high alpine habitats (Widerin and Reiter 2017, 2018). It has also been observed in the French Pyrenees (Dietz and Kiefer 2016). The northern bat occurs in the Carpathians in Slovakia and Romania but becomes more infrequent toward the southern parts of the mountain range (Jére et al. 2018; Kaňuch et al. 2008; Naďo et al. 2019; Uhrin and Hapl 2004; Lučan 2007; Uhrin et al. 2014). Another isolated population has been observed in the Velebit Mountains in Croatia (Pavlinić and Tvrtković 2003). A specimen from Rila Mountains in Bulgaria represents the southernmost contemporary observation from Europe (Benda et al. 2003; Horáček et al. 2000).

Above the Arctic Circle, the northern bat becomes gradually less common with increasing latitude, but it has been observed foraging and breeding at latitudes of up to 69° N in Troms, Norway (Rydell et al. 1994; Speakman et al. 2000). There are records from the Kola Peninsula (Hanák and Horáček 1984). A single individual has also been found in Vorkuta, Komi Republic, in the arctic tundra (Bykhovets and Petrov 2019).

Vagrant individuals have sometimes been observed far from their current area of distribution. An individual was found in a hibernaculum in Betchworth, southeastern England (Greenaway and Hill 1987). Northern bats have also been recorded in the Netherlands (Bruijn 2004), at oil rigs in the Dutch sector of the North Sea (Boshamer and Bekker 2008), and on the Faroe Islands (Baagøe and Bloch 1993).

In Fennoscandia, the northern bat exploits all areas below and, in some cases, above the treeline (Siivonen and Wermundsen 2008; Michaelsen et al. 2013; Tidenberg et al. 2019). In lowland areas of southern Sweden, Finland, Estonia, and Latvia, the northern bat is one of the most abundant species, even though high altitude environments are not available (Masing 1983; Ahlén 2011; Tidenberg et al. 2019). This trend roughly correlates throughout the continent with the climate and conditions suitable for the growth of boreal or hemiboreal forests. Despite the abundance in Skania, southern Sweden, they are curiously absent from Denmark apart from a few observations (Ahlén et al. 2009; Degerbøl 1935; Baagøe 2007). In Central Europe, the presence of the northern bat becomes increasingly connected to mountainous areas, and the species exploits higher altitudes more than other sympatric bat species. Higher altitude areas, such as mountain ranges, often sustain relatively isolated populations where the climate in the lowlands is too warm for the northern bat (Benda et al. 2012; Hanák and Horáček 1984; Pavlinić and Tvrtković 2003). These patches are probably refugia, where the species survived after the warming climate become unfavorable after the last glacial maxima (Kurtén 1968; Benda et al. 2003).

In the Czech Republic, observations range between 250 and 1320 m above sea level with an average of 657 m (Anděra and Hanák 2007). The Carpathian population exhibits a similar relationship with altitude. The occurrence in Slovakia is linked to coniferous trees, especially spruce, which grows at higher altitudes compared to beech and other deciduous tree species. Moreover, the occurrence of the species is biased toward higher altitudes compared to other species of bats (Kaňuch et al. 2008). Records from Romania show an even higher altitudinal preference, with most observations of hibernating individuals occurring above 1000 m above sea level (Jére et al. 2018). Summer ecology of the northern bat in the area is unknown due to scarce records. However, summertime observations exist from northeastern Italy from alpine environments down to 113 m above sea level (Lapini et al. 2015).

The northern bat most likely exploits European montane habitats up to the edge of permafrost. For example, Widerin and Reiter (2017) were able to record over 18,000 call sequences at a single Austrian observation site at 2315 m above sea level during two consecutive summers. Moreover, they demonstrated that the species is active at seven other sites between 2250 and 3106 m above sea level. Apart from the records from the European Alps, there is a single observation from an Iranian site at 2920 m above sea level (Benda et al. 2012) .

Description

Body

The northern bat is a medium-sized bat (Krzanowski 1977), which is distinguishable from other bats by its long, dark fur with golden tips on the dorsal side, whereas the ventral side is lighter. The contrast of the fur color on the dorsal and ventral is sharp. Juveniles do not have golden, but rather silvery tips to their hairs (Rydell 1993a).

The northern bat has rounded, dark ears that are at their widest close to the base and have five transverse folds at the edge. The tragus is short, rounded at the top and bends slightly toward the inner parts of the ear (Rydell 1993a). The inner edge of the ear typically has a golden or yellowish hair tuft (Dietz and Kiefer 2016).

The wing and tail membrane, face, nose and ears are dark, either black or blackish brown (Rydell *1993a*). The hair on the dorsal side of the uropatagium extends to at least half of its length (Rydell *1993a*). The plagiopatagium extends to the base of the toes (Miller *1912*) and has a narrow post-calcarial lobe. The calcar extends to roughly half the length of the tail membrane and is shorter than the tibia. Up to 4 mm of the northern bat’s last caudal vertebra extends beyond the tail membrane. The baculum is Y-shaped, and the penis is short and rounded (Greenaway and Hill *1987*) (Table 1).

Table 1

Average measurements of the northern bat from Europe. All measurements are in millimeters (mm)

	Sex	Range	Mean	SD	N	Reference
Head and body length	F	50.00 – 66.00	55.31	4.41	16	Mosansky and Gaisler (*1965*) and FMNH (2020)
	M	48.40 – 59.20	53.32	3.36	17	Mosansky and Gaisler (*1965*) and FMNH (2020)
	All	54.00 – 64.00				Schober et al. (*1989*)
Tail length	F	41.00 – 46.00	44.07	2.69	3	Mosansky and Gaisler (*1965*)
	M	38.00 – 48.00	42.24	3.7	7	Mosansky and Gaisler (*1965*)
	All	35.00 – 50.00				Schober et al. (*1989*)

Forearm length	F	37.10 – 43.60	40.01	1.33	91	Mosansky and Gaisler (*1965*) and FMNH (2020)
	M	36.30 – 43.20	39.29	1.55	103	Mosansky and Gaisler (*1965*) and FMNH (2020)
	All	37.00 – 44.20				Schober et al. (*1989*) and Dietz and Kiefer (*2016*)
Ear length	F	13.80 – 14.60	14.47	0.61	3	Mosansky and Gaisler (*1965*)
	M	12.80 – 15.50	13.49	3.52	8	Mosansky and Gaisler (*1965*)
	All	13.00 – 17.50				Schober et al. (*1989*)

FMNH (2020) = Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329

Typical weight varies from about 8 to 13 g (Dietz and Kiefer *2016*; Ryberg *1947*), but may increase during pregnancy or late in the autumn (Table 2) before hibernation to up to 16–18 g (Rydell *1989*; data from the collection of Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329).**Table 2**

Weight (in grams) varies between sexes and increases from the beginning of the season toward the end (Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329)

Weight																
	May				June				July				August			

FMNH 2020 = Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329

The wings are broad, or medium broad, and have short rounded tips (Norberg and Rayner *1987*; Rydell *1993a*). The northern bat has average aspect ratio, wingspan, and wing loading (Table 3) (Norberg and Rayner *1987*).**Table 3**

Wing measurements in mm

Wingspan (mm)	Wing area	Aspect ratio	Wing loading	Wing tip len	Wing tips	Relative wing load	Reference

	(mm^2)			**gth index**	**hape index**	**ing**	
277	11,500	6.7	8.4	1.21	1.54	39	Thollesson and Norberg (1991)
277	11,200	6.6	8.1				Gaisler (1959)
240–280							Schober et al. (1989)

Skull

The average length of the skull of the northern bat (Table 4) varies from 14 mm (Strelkov *1986*) to 16.5 mm (Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329). The braincase is low, with an obvious convexity in the middle. The outline of the skull is subspherical or roughly ovate and its depth is slightly greater than half the mastoid breadth. The crest of lambdoid curves toward the contact point at the middle and occiput posterior, and rounded outlines of the skull can be seen behind them. The sagittal crest is minimal or absent. The interorbital region is hourglass-shaped and has a lacrimal swelling.

Table 4

Skull measurements; ranges, means, and standard deviations

Measuremen	**Rang**	**Mea**	**SD**	**N**	**Source**

t	**e**	**n**			
GSL	14.80–15.70	15.32	0.26	11	Mošanský and Gaisler (1965)
	14.80–15.80	15.28	N/A	25	Hanák and Horáček (1984)
	14.70–16.00	15.26	0.3	33	Spitzenberger (1986)
	14.00–15.40	15	N/A	21	Strelkov (1986)
	14.25–16.52	15.42	0.55	15	FMNH (2020)
CBL	14.50–15.40	14.91	0.3	11	Mošanský and Gaisler (1965)
	14.43–15.33	14.93	N/A	25	Hanák and Horáček (1984)
	14.20–15.60	14.9	0.31	33	Spitzenberger (1986)
	14.10–15.40	14.8	N/A	21	Strelkov (1986)
	13.75–15.87	14.76	0.57	20	FMNH (2020)
ZW	9.40–10.40	10	0.3	9	Mošanský and Gaisler (1965)
	9.45–10.45	9.95	N/A	20	Hanák and Horáček

					(1984)
	9.50–10.50	9.95	0.26	26	Spitzenberger (1986)
	8.70–9.70	9.4	N/A	14	Strelkov (1986)
	8.92–10.35	9.71	0.32	22	FMNH (2020)
IOW	4.00–4.60	4.28	0.16	11	Mošanský and Gaisler (1965)
	3.90–4.30	4.09	N/A	25	Hanák and Horáček (1984)
	3.80–4.50	4.18	0.17	42	Spitzenberger (1986)
	3.85–4.75	4.27	0.19	43	FMNH (2020)
UTR	5.30–5.70	5.54	0.11	11	Mošanský and Gaisler (1965)
	5.35–5.82	5.53	N/A	10	Hanák and Horáček (1984)
	5.00–5.80	5.42	0.22	40	Spitzenberger (1986)
	5.10–5.60	5.3	N/A	27	Strelkov (1986)
	5,07-5,63	5.31	0.14	38	FMNH (2020)

LTR	5.70–6.20	6.04	0.16	11	Mošanský and Gaisler (1965)
	5.80–6.40	6.03	N/A	10	Hanák and Horáček (*1984*)
	5.60–6.10	5.8	N/A	26	Strelkov (*1986*)
	5.36–6.35	5.89	0.21	38	FMNH (2020)
ML	10.70–11.30	11.07	0.23	11	Mošanský and Gaisler (1965)
	10.05–11.40	10.97	N/A	25	Hanák and Horáček (*1984*)
	10.50–11.50	11.01	0.3	13	Spitzenberger (*1986*)
	10.50–11.10	10.7	N/A	24	Strelkov (*1986*)
	10.22–11.76	10.98	0.36	43	FMNH (2020)

All measurements are in millimeters (m)

GSL greatest skull length, *CBL* condylobasal length, *ZW* zygomatic width, *IOW* interorbital width, *UTR* upper tooth row length (C–M^3), *LTR* lower tooth row length (C–M^3), *ML* mandible length, *FMNH* Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329

Physiology

Studies on the hibernation physiology of the northern bat exist mostly from the Republic of Karelia and Sakhan Republic in Russia. It is known that the species expresses longer average bouts of torpor compared to the brown long-eared bat (*Plecotus auritus*), or Daubenton's bat (*Myotis daubentonii*) (Solomonov et al. 2010), which in itself suggests adaptation to longer total periods of hibernation.

Ilyukha et al. (2015) compared physiological parameters in three species of bats hibernating in Karelia: brown long-eared bat, Brandt's bat (*Myotis brandtii*), and northern bat. They concluded that the northern bat was different from the other species, standing out for a number of parameters (peripheral leukocyte and lymphocyte counts, LDH isoenzyme profile in some organs). They suggested that the relatively high peripheral lymphocyte count in hibernating northern bats must be a species-specific trait reflecting their physiological–biochemical characteristics.

The hibernating northern bat also has a higher content of vitamin E in the liver than the brown long-eared bat or the Brandt's bat. Vitamin E is one of the most important natural antioxidants. Sufficient uptake of vitamin E before the winter period is paramount, especially in northern regions, in connection with significant metabolic changes. The uptake, transport, and tissue delivery of α-tocopherol, a form of vitamin E, involves molecular, biochemical, and cellular processes closely related to overall lipid and lipoprotein homeostasis (Rigotti 2007). In addition, vitamin E accumulation in animal tissues in the autumn induces hibernation behavior (Kalabukhov 1985), and adequate levels of tocopherol during hibernation are essential for reproduction in spring. Kalabukhov (1985) showed that northern bats living in colder climates with a shorter photoperiod, and a longer period of hibernation, had in general higher values of low-molecular natural antioxidants, such as vitamin E, than bats from warmer climates with less variability in the annual photoperiod.

Anufriev and Revin (2006) were able to measure the rate of oxygen consumption in the northern bat hibernating at an ambient temperature of 1–3 °C. The value they obtained, 0.056 ml g^{-1} h^{-1}, is roughly 0.2–0.4% of the oxygen consumption in the active state. Information about the metabolic rate reduction during hibernation in other northern chiropteran species is rather scarce, but these have been measured at least for Daubenton's bat (0.070 ml g^{-1} h^{-1}) and Natterer's bat (*Myotis nattereri*, 0.031 ml g^{-1} h^{-1}, Kulzer et al. 1970; Speakman et al. 1991). These measurements indicate there are differences between bat species, but how they correlate with hibernation success or micro-climate selection needs to be investigated in more detail.

The hibernation period is associated with a dramatic decrease in numbers of circulating leukocytes and thrombocytes in hibernating mammals, which is an adaptation to the torpid phase (Lechler and Penick 1963; Lyman and Chatfield 1955; Reddick et al. 1973; Reznik et al. 1975; Spurrier and Dawe 1973). The cells do not undergo apoptosis, but rather, as shown for hibernating ground squirrels and Syrian hamsters during torpor bouts, leukocytes are separated from the circulation and stored in other body compartments, such as the lung, liver, or secondary lymphoid organs (Bouma et al. 2010). These are then released back into circulation after restoration of body functions at arousal. Indeed, Uzenbaeva et al. (2015) showed that the northern bat, the brown long-eared bat, and Brandt's bat exhibit low mean WBC values during hibernation. Kizhina et al. (2018) took a closer look at changes in hematological parameters during the hibernation period, demonstrating that the leukocyte profiles are dependent on the temporal stage of hibernation. For instance, the number of leukocytes rises during late hibernation period, when the frequency of spontaneous arousals is increased. These changes suggest dynamic leukopoiesis during the hibernation period. However, no significant changes in red blood cells were observed.

Previous studies have demonstrated that of the leukocytes, the numbers of lymphocytes in European and tropical bats exceeded the numbers of neutrophils (Davis et al. 1967; Paksuz et al. 2009; Schneeberger et al. 2013; Wolk and Bogdanowicz 1987), and that neutrophils and lymphocytes appear in equal quantities in torpor (Kovalchuk et al. 2017). However, a majority of leukocytes in the northern bat in the study by Kizhina et al. (*2018*) were neutrophils; these data are consistent with reports on other hibernating mammals that the leukocytes remaining in blood during torpor are mainly neutrophils (Bouma et al. *2010*; Szilagyi and Senturia *1974*). The number of lymphocytes was significantly higher in the spring, compared to the winter. Kizhina et al. (*2018*) suggested that lymphopenia is unlikely to be caused by decreased lymphocyte production because the half-life of the cell is several months (Bouma et al. *2010*); however, it could be caused by the inhibition of lymphocyte proliferation by 5-AMP released from brown adipose tissue (Atanassov et al. *1995*).

Kizhina et al. (*2018*) suggested that the rise in band neutrophils, lymphocytes, and basophils by the end of the hibernation period is indicative of the activation of leukopoesis, which, along with favorable environmental conditions, apparently provides for a high survival of the northern bat. On a related note, for instance in the edible dormouse (*Glis glis*) the amount of energy available for investing in the immune system after the hibernation period is limited, and therefore the depleted stocks of monocytes and neutrophils were found to be slow to recover and immune defense was delayed (Havenstein et al. *2016*), which may contribute to their high mortality directly after emergence from hibernation (Lebl et al. *2011*) .

Genetics

Chromosomes

As in other species in the genus *Eptesicus*, the diploid chromosome number of the northern bat is 50, and there are 48 fundamental chromosomes (Gorobeyko and Kartavtseva *2018*; Heller and Volleth *1984*).

Phylogeography

Artyushin et al. (*2009*) proposed that the northern bat comprised two distinct mitochondrial lineages that the authors named by the geographical locations from which the lineages were found. The European lineage occurs only in Europe, to the west of the Russian border, whereas the Siberian lineage is detected only in Russia. However, a later study showed that the Siberian lineage extends into eastern Finland (Lempiäinen *2014*). Later studies (Juste et al. *2013*; Kruskop et al. *2012*) have confirmed the intraspecific geographical division. So far, no information exists on the mitochondrial lineages present in the Far East: Mongolia, Kamchatka, Korea, and Japan.

The existence of different mitochondrial lineages suggests that population bottle-necks have occurred, and these have been followed by events of rapid population growth. The population bottlenecks most likely took place when the European lineage and Siberian lineage populations were forced into reproductive isolation in multiple and single refugial subpopulations during glacials. Using two mitochondrial markers (cytochrome b and HVII), Lempiäinen (*2014*) estimated that the population divergence occurred between the middle Pleistocene and the Holocene epochs (ca. 0.85–1.1 Mya).

Kruskop et al. (2012) suggested that the unique phylogeographic pattern in the Siberian lineage is consistent with the possible existence of a glacial refugium in the Ural Mountains (e.g., see Markova et al. 2008), where the northern bat was common at least in the late Pleistocene–early Holocene (Fadeeva and Kruskop 2008). From the Ural Mountains, the species could have recolonized Siberia and easternmost Europe. The European lineage most likely resided in one or more of the major European glacial refugia: the Iberian Peninsula, the Apennine Peninsula, and the Balkans (Lempiäinen 2014). The Apennine Peninsula was likely occupied by the northern bat during glacials, because the contemporary range of the species reaches northern Italy, to the south of the Alps (López-Baucells and Burgin 2019). The contemporary presence of the northern bat in the Balkans has also been confirmed (Pavlinić and Tvrtković 2003). Furthermore, Bennett et al. (1991) identified the western Balkan Peninsula as the most important refugium for forests, supporting the suggestion that northern bats may have occupied the peninsula during the Pleistocene glacial periods. However, no fossil findings confirm their presence The third major refugium in Europe could have existed in Iberia, but data on the contemporary existence of the species in, for instance, the Pyrenees are lacking.

Hybridization with Related Species

Mayer and Helversen (2001) suggested hybridization between the northern bat and the serotine bat based on a mitochondrial sequence, ND1. This was also reported by Artyushin et al. (2009) using the cytb mtDNA-marker, and further reaffirmed by Juste et al. (2013) with a more comprehensive set of mtDNA-markers. Artuyshin et al. (2009) further described differences between the European and Russian mtDNA sequences of the serotine bat, and suggested that serotine bats from Russia preserved the original, specific mitochondrial lineage, which was lost in the western European population most probably due to complete introgression of mtDNA of the northern bat and a subsequent fixation of the alleles. This introgression was consequently validated by Juste et al. (2013) with a more comprehensive set of mtDNA and nuDNA markers. Their results showed introgression of the mtDNA, but a nuDNA-based molecular phylogeny distinguished the northern bat and the serotine bat as different species (Juste et al. 2013).

Fixation of mtDNA from other species is a rather common phenomenon under a number of realistic evolutionary scenarios (Currat et al. 2008). The karyotypes of the serotine bat and the northern bat are nearly identical (Volleth et al. 2001), and thus cytogenetic barriers to interspecific hybridization are expected to be inefficient. Therefore, the hybridization could have occurred asymmetrically, when post-glacial populations of the west- and northwards- expanding serotine bat came in contact with resident, or earlier arrived, populations of the northern bat. Juste et al. (2013) suggest that the captured northern bat mtDNA has been transmitted to all present western populations of the serotine bat, whereas the nuclear imprint of this hybridization event has most likely been diluted due to demographic factors. Indeed, analysis of nuclearDNA shows that the northern bat and the serotine bat possess unique species-specific pools of alleles (Artyushin et al. 2018). Artyushin et al. (2009) allocate the hybridization event to the last or penultimate glacial cycle based on relatively low level of divergence (~1.8%; ML based distance) in cytb between serotine bat and northern bat.

Life History

Reproduction

Birth takes place in summer, but the exact date varies in different parts of the distribution range. In Central Europe, the young are born in June (Hůrka *1967*; Tress et al. *1989*), whereas in Scandinavia birth takes place in July (Rydell *1989*, *1993a*) or even early August (Frafjord *2013*).

The northern bat gives birth to one or two young (Ryberg *1947*; Taake *1985*). Taake (*1985*) suggested that, among European vesper bats, species that are the subjects of relatively high predation pressure more frequently give birth to twins than species that suffer less from predators. Quantitative data on actual predation pressure still appear to be lacking for the northern bat. The energy intake of females increases significantly during the lactation period, which forces them to spend more time foraging and makes them more vulnerable to predation (Duvergé et al. *2000*). This increase in the females' foraging time expenditure may be more than 100% compared to the time before parturition (Rydell *1993b*; de Jong *1994*). Northern bats do not necessarily breed every year; thus, when they do reproduce, females may be able to invest more resources in their pups (Rydell *1989*).

At birth, the young are large relative to the weight of the female, being circa 37% of the mother's body mass (Haarsma and Siepel *2013*). The young grow rapidly, and are weaned as soon as they are able to fly at the age of two to three weeks (Rydell *1992a*, *1993a*). The short interval between birth and weaning is likely an advantage to the relatively short summers at the northern latitudes where northern bats live (Haarsma and Siepel *2013*). After weaning of the pups, maternity colonies may move to a new locations (Kosonen *2013*).

Other bat species have been recorded from localities north of the Arctic Circle (Siivonen and Wermundsen *2008*). However, the northern bat is the only bat species with records of breeding in the far North (Rydell et al. *1994*).

Longevity

Most bats are unusually long-lived by small mammal standards, and the northern bat is no exception. Although it is not known to reach the longevity of some other European bat species, northern bat individuals are known to have survived for longer than a decade in the wild (e.g., Martinoli et al. *2007*). The longest recorded lifespan is circa 15.5 years (Masing et al. *1999*) .

Habitat and Diet

The northern bat is typically found bat in boreal and mountain forest areas, where it prefers semi-open and edge habitats. In northern Europe, it also lives in the lowlands, but in Central and South-East Europe, it is mainly distributed in mountain areas up to 2000 m above sea level e.g., (Benda et al. *2003*; Piksa and Nowak *2002*; Pocora et al. *2008*; Rydell *1986a*).

Foraging Habitat

The northern bat utilizes different habitats opportunistically and may shift from one habitat to another during the season. De Jong and Ahlén (*1991*) discovered in Sweden that early in the season, in May and June, bats favored deciduous and mixed forests, which often were located near rich water bodies. Results from southern Germany, where northern bats were observed to forage in forests before females gave birth, support these findings (Haupt et al. *2006*). In Finland, the northern bat utilizes mature but low-productivity forest patches in early summer, and are seldom detected over open water (Ijäs et al. *2017*; Vasko et al. *2020*). This might be due to the high insect abundance in boreal forests. Water bodies, such as lakes, are key habitats of the northern bat in Sweden (Rydell *1989*; de Jong *1994*) and Russian Karelia (Belkin et al. *2019*). In Finland, the northern bat favors more humid forests in July. Above-average humidity might promote insect emergence and food abundance during a drier period of the year (Vasko et al. *2020*).

Open canopy forests are important foraging habitats throughout the season in northern Europe (de Jong *1994*; de Jong and Ahlén *1991*; Haupt et al. *2006*; Rydell *1986a*; Vasko et al. *2020*), where the northern bat usually flies relatively high, circa 8 to 15 m above the ground, sometimes even around 50 m (Rydell *1990*). The species also forages in other kinds of habitats, such as open meadows, pastures, and clear-cuts (de Jong *1994*; de Jong and Ahlén *1991*). In addition, edge habitats, shorelines (Kosonen *2013*) parks, and urban areas (de Jong *1994*; Haupt et al. *2006*; Haupt and Schmidt *2007*; Kosonen *2013*; Rydell *1986a*) provide suitable foraging patches for the species.

Although it typically forages in open and edge spaces, the northern bat can sometimes successfully capture insects in clutter overlap zones where background echoes mask prey echoes. This was reported by Jensen et al. (*2001*), who observed northern bats feeding on large ghost moths (Hepialidae) over a meadow in Sweden.

The northern bat utilizes illuminated areas early in the spring and again in late summer and early autumn (Rydell *1992b*). Haupt et al. (*2006*) observed that the northern bat uses urban areas after parturition, taking advantage of the insect abundance around artificial light. Urban areas are considered to be key habitats for the species in Germany (Haupt et al. *2006*). However, the shift to LED and white halogen lights has decreased the occurrence of the northern bat in illuminated areas, because these lights attract fewer insects (Rydell et al. *2020*).

In southwestern Finland, radio-tracked females began their nightly foraging from a city center, in which the most frequently utilized foraging area was less developed (Kosonen *2013*). However, some individuals were also observed to forage over paved areas, such as parking lots overlaid with tarmac. In this case, the city center was close to the roost, and thus a good location to begin nightly foraging (Kosonen *2013*). Rydell (*1992b*) divided a town into four different areas, “urban”, “residential”, “industrial”, and “rural”, where the residential and rural areas were most used by bats. However, the use was associated with tree occurrence and the presence of short wave-length street lamps, but not with density of buildings or distance from the city center.

The short northern summer nights in the middle of the active season bring challenges to the northern bat. Frafjord (*2013*) showed that the species forages only in the darkest hours and as close to the roosts as possible in the middle of the summer, and increases its foraging time and home range with the night length in the northern parts of its distribution. These are supported by results of de Jong (*1994*) from southern Sweden, who found the home range size increasing from the beginning of the season toward autumn.

Roosts

Northern bats, especially female colonies, often roost in heated buildings taking advantage of the warmth (Rydell *1993a*), but occasionally they choose abandoned buildings as nursery roost, and occupy roofs that are heated by the sun (Rydell *1993a*; Frafjord *2013*; Kosonen *2013*).

Occasionally a solitary northern bat can accept a bat box or a tree crevice for shelter (Dietz and Kiefer *2016*; Rydell *1993a*). Individuals preferring other shelters are often male, non-breeding females or females that have weaned their pups (Kosonen *2013*). The roost sites are located near abundant foraging areas, and females return to the same roost year after year (Rydell *1989*).

Hibernation Habitat

The northern bat utilizes a plethora of man-made over-wintering sites, such as mines (Rydell et al. *2019*), cellars, and bunkers (Siivonen and Wermundsen *2008*; Wermundsen and Siivonen *2010*; Vintulis and Pētersons *2013*; Rydell *1989*), as well as natural formations such as caves (Lučan *2007*), glacial erratics, bedrock crevices (Blomberg et al. *2021*), rock scree (Michaelsen et al. *2013*), and even ancient shores (photo 2), which are post-glacial formations consisting of rocks and pebbles left behind by retreating sea shore as a consequence of land rising, where observations have been made in early spring and late autumn in Finland (Fritzén and Hägg *2020*) (Fig. 3).

440376_0_En_45-1_Fig3_Print.tif

Fig. 3

Northern bats have been detected in this ancient shore in Finland early in the spring and late in the autumn. (Photo Niclas Fritzén)

Diet

The northern bat is an insectivorous species, which utilizes short-term food resources (Dolch et al. *2007*). It has been considered a generalist (Haupt et al. *2006*; Smirnov *2018*), even though the majority of its diet consists of nematoceran flies (Rydell *1986a*; Rydell et al. *2016*; Vesterinen et al. *2018*). Vesterinen et al. (*2018*) found that up to 77% of the insect DNA in the feces belong to the order Diptera (flies), among which Pediciidae (hairy-eyed craneflies) (21.3%), Trichoceridae (winter craneflies) (18.4%), Tipulidae (craneflies) (13.0%), and Chironomidae (chironomids) (10.7%) were the most abundant families. Occasional gleaning of stationary prey items is suggested by a small portion of terrestrial arthropods in the diet (Gajdošík and Gaisler *2004*; Vesterinen et al. *2018*). At more southerly latitudes, the northern bat's diet consists mostly of species belonging to the dipteran suborder Nematocera, followed by the orders Lepidoptera and Heteroptera, genus *Phyllomorpha* belonging to the order Hemiptera, suborder Brachycera belonging to the order Diptera, Aphidomorpha (an infraorder of the order Hemiptera), and Coleoptera (beetles). The remains of Brachycera often found in pellets suggests an additional foliage gleaning strategy (Gajdošík and Gaisler *2004*). In the north, the species also complements its diet with Lepidoptera, Coleoptera, and

Trichoptera (Rydell *1986a*; Vesterinen et al. *2018*). In the Samarskya Luka area in Russia, lepidopterans were the predominant order in the feces of the northern bat (Smirnov *2018*).

Behavior

Acoustic Behavior

The northern bat utilizes ultrasonic echolocation to locate and catch insects in flight. In foraging habitats, relatively long, low and loud calls are beneficial because they maximize detection distance (Schnitzler and Kalko *2001*). Typically, the northern bat uses quasi-constant frequency (QCF) calls in an open environment (photo 3). These calls are characterized by a linear descent in frequency and a bandwidth of only 1 to 5 kHz (Fig. 4).

440376_0_En_45-1_Fig4_Print.eps

Fig. 4

(**a**) Northern bat foraging or commuting high above the ground using QCF calls. (**b**) Northern bat foraging in a narrow forest clearing with FM calls. (Both recordings by Harry J. Lehto with Petterson M500 full spectrum detector)

In contrast, northern bats emit flat-ended frequency modulated (FM) calls while flying in the vicinity of obstacles or the ground (photo 4), or upon approaching a prey item. These calls start with a rapidly descending frequency modulated part of up to 40 kHz in bandwidth, which breaks into a horizontal terminal part, resulting in an L- or “banana”-shaped spectrogram. The border between these call types is fluid, however, and forms that do not clearly represent one or another type may exist (Ahlén *1981*; Rydell *1993c*; Barataud *2015*). Peak frequencies of 26 to 29 kHz are common in open environments, where bats use QCF-calls (Barataud *2015*). On the other hand, when northern bats are close to obstacles or during an approach, peak frequencies usually range from 27 to 33 kHz.

Distance to the obstacles also affects the duration of the calls. QCF-calls in an open environment are up to 22 milliseconds long, but shorter calls and a higher repetition rate to increase temporal resolution are utilized in a cluttered environment or while engaged in a chase (Barataud *2015*). The attack usually ends with a terminal buzz typical for all aerial hawking bats (Schnitzler and Kalko *2001*). During the buzz, the northern bat utilizes an extremely short call duration and a repetition rate of up to 200 calls per second (recordings made by the authors, 2019). Other acoustic descriptions from Sweden (Ahlén *1981*, Rydell *1990*, *1993c*) and Hokkaido, Japan (Fukui et al. *2004*), present values fitting within the ranges mentioned above. While there may be geographical variation across Eurasia and latitudinal gradient, it is not apparent in these studies, because a difference in average values alone might be caused by the recording situation and surroundings (Rydell *1993c*).

An experimental study by Eklöf et al. (*2002*) revealed that vision was involved during the initial detection of stationary prey items located in the clutter overlap zone 0–1.5 m above the grass tips. However, the typical echolocation sequence from search to terminal phase was still present.

Moreover, the frequency of attempted attacks on rapidly moving targets within the clutter was not affected by visual conspicuousness of the target, hence the detection was probably based on echoes in these situations. However, this behavior appears rare because the species is most often avoiding dense vegetation and staying 1–2 m away from background clutter (Rydell *1986a*, *1992b*).

As the prey insects consumed by northern bats differ in size, they are handled by the bat in a different manner. Rydell (*1992b*) measured times elapsed between one terminal buzz and the subsequent return into the normal echolocation routine. The processing time for smaller dipteran prey was almost non-existent, but after catching a larger moth, handling time increased drastically and could be as long as 40 s. During this time, the bat usually flew in circles while remaining within the feeding site and avoiding nearby obstacles .

Social Behavior

Northern bats are mainly solitary foragers. They establish temporary individual feeding territories and aggressively chase intruding bats away. The territories or repetitive flight paths can last at least up to 90 min before the bats move to a new spot (Rydell *1986a*, *b*, *1989*, *1992b*; Kosonen *2013*). In times of high insect abundance, they sometimes tolerate conspecifics sharing the area (Rydell *1986a*, *b*, *1992b*; Kosonen *2013*). Rydell (*1986a*) observed northern bats foraging in a group of ten or more individuals with overlapping flight paths. This kind of behavior most likely occurs only in situations with especially high and concentrated insect abundance, but nevertheless demonstrates a degree of behavioral flexibility.

Roughly 20–30% of the foraging cases involve more than one individual at the same site (Rydell *1986b*, *1992b*), which usually leads to conflict. Established feeding territories are defended but replacement of the original occupant by an intruder is not unusual (Rydell *1986b*; Kosonen *2013*). Sometimes a conflict is not apparent after intrusion, but both bats rarely remain at the same site for more than one minute (Rydell *1986b*). Aggressive behavior is also typical in cases where territories are not clearly defined, and bats forage together for a prolonged period (Rydell *1992b*).

Maternity colonies have a linear hierarchical structure and disputes tend to get resolved quicker if the bats are from the same colony (Rydell *1986b*). The disputes settle in favor of the dominant individual in about 90% of the cases. Normally, a single agonistic call, a chase, or both initiated by the dominant individual suffice (Rydell *1986b*).

Social vocalizations are often involved in the disputes between bat individuals (Rydell *1986a*, *b*, *1992b*; Kosonen *2013*; Middleton et al. *2014*). These calls often consist of steep, descending FM calls extending into the audible range, with energy peaks around 14 kHz and up to 3 harmonics present. They are usually emitted simultaneously with the normal echolocation routine (photo 5). Another common social call type consists of repetitive feeding buzz-like trills mixed with variable shorter elements. These can be long, songlike sequences with great complexity lasting for over a second (Middleton et al. *2014*).

During foraging, it is typical for northern bats to rest in trees for short periods of time before continuing. Sometimes multiple individuals rest in the same tree, but the possible social function of this is unknown (de Jong *1994*; Kosonen *2013*).

The distance to the feeding grounds is dependent on the abundance of insect prey. When prey is scarce, bats spend more time feeding and fly further from the roost. On the other hand, at times when prey is plentiful, all individuals of a colony can be found foraging less than 200 m away from the day roost. High insect abundance also decreases the total time spent outside the roost, because the energy demand is satisfied in a shorter time (de Jong *1994*). According to Rydell (*1986b*), bats often begin their daily foraging close to the roost but move further away to other feeding grounds after 20–40 min. Kosonen (*2013*) also reported a pattern of beginning in one feeding area before moving to another.

Frafjord (*2013*) observed a clear increase in foraging range sizes from July to October in Troms, North-West Norway. The increase in range was accompanied with increased foraging hours and decreased ambient light. However, bats have been observed feeding under the midnight sun too (Speakman et al. *2000*). In southern Scandinavia, the emergence time in relation to sunset was postponed during late pregnancy and early lactation, possibly to control predation risk (Duvergé et al. *2000*).

The seasonal dynamics could be determined by spatiotemporal variation in insect abundance, which depends heavily on the studied area. In addition, there is seasonal variation in the use of different feeding areas. For example, de Jong and Ahlén (*1991*) observed a shift from a productive lakeshore habitat to a less productive coniferous woodland, where insect abundance peaks in the middle of the summer (Haupt et al. *2006*). Haupt et al. (*2006*) observed a switch from a generalist habitat use into more selective behavior around the birth of the young. During the latter part, high interindividual variation indicated variable feeding strategies.

During late summer and autumn, bats may fly considerable distances to reach preferred foraging sites. The selection of these sites is probably driven by insect availability (de Jong and Ahlén *1991*; Rydell *1992b*; de Jong *1994*; Haupt et al. *2006*). Key habitats, where insect abundance is relatively high at particular times, are probably essential in satisfying energy demand both early and late in the summer (de Jong *1994*; Haupt et al. *2006*).

In studies conducted in southern Sweden, female northern bats started foraging in the beginning of May, when night temperatures reached 7–10 °C (Rydell *1989*; de Jong *1994*). The foraging activity is linked with temperature, which also predicts insect abundance. Bats often stay in the roost during colder nights (Rydell *1989*).

The northern bat could be sensitive to competition from other open space-foraging bat species. Haupt and Schmidt (*2007*) suggested avoidance of other species as a key determinant of the current distribution and habitat selection in Central Europe. They observed that the northern bat rarely utilizes the same areas as the serotine bat, the noctule bat (*Nyctalus noctula*), the parti-colored bat (*Vespertilio murinus*), and Leisler's noctule (*Nyctalus leisleri*). However, they could not verify the observation statistically. In the same study, northern bat was often observed foraging together with the common pipistrelle (*Pipistrellus pipistrellus*). The two species have also been observed exploiting the same deciduous lakeside habitats, indicating succesful resource partitioning (de Jong and Ahlén *1991*). It has also been suggested the northern-most populations of the northern bat could be in competition for resources with swifts (*Apus apus*) and barn swallows (*Hirundo rustica*) during the light summer nights of the Arctic region (Speakman et al. *2000*).

Even though northern bats are able to cover distances of up to 40 km during a single night between their roosts and foraging grounds (de Jong *1994*), they are considered to be mostly sedentary (Rydell *1993a*). The northern bat has been detected to forage at the same location over multiple years, suggesting a high degree of foraging site fidelity (Kosonen *2013*; Martinoli et al. *2007*; Rydell *1989*). Some ringed individuals have however covered distances of over 100 km. The longest recorded transect is 450 km from Germany to Austria (Hutterer et al. *2005*). Further evidence of long movements is provided by the numerous offshore observations in western Europe (Petersen et al. 2014). Dispersal is usually considered the primary purpose for such flights (Hutterer et al. 2005) .

Hibernating Behavior

The northern bat lives in cold conditions of the north and at times even below freezing temperatures (Masing 1981; Masing and Lutsar 2007; Siivonen and Wermundsen 2008; Wermundsen and Siivonen 2010). In Yakutia, northern bats enter torpor in October–November and leave their hibernation sites in April–May, totaling to 7.5–8 months of torpor (Anufriev and Revin 2006). Similarly, Kizhina et al. (2018) reported that the hibernation period in Karelia lasts from October to May.

Northern bats spend 97% of their hibernation period in torpor (Anufriyev 2008) . They also express longer bouts of torpor (428 h on average) compared to brown long-eared bats and Daubenton's bats. The microclimate in which the northern bat has been observed to hibernate is relatively dry and cold, and the species can tolerate temperatures below freezing and relative humidity as low as 70% (Kizhina et al. 2018; Siivonen and Wermundsen 2008; Smirnov et al. 2008). The ambient hibernation temperature of species in southeastern Finland has been reported at 2.0 ± 0.1 °C, with a preferred relative humidity of 78.0 ± 0.6%, but they regularly hibernated in temperatures below 0 °C (Siivonen and Wermundsen 2008). Masing (1981) concluded that the lower critical temperature at which northern bats arouse from torpor was −3.13 °C. However, hibernation temperatures as low as −5.3 °C have been recorded (Masing 1983; Masing and Lutsar 2007).

Most studies have found northern bats typically hibernating openly on walls (Ilyukha et al. 2015; Kizhina et al. 2018, Belkin et al. 2019). Siivonen and Wermundsen (2008) reported that 54% of northern bats observed in their study selected crevices for hibernation. While clusters as large as eight individuals have been recorded in southeastern Finland (Siivonen and Wermundsen 2008), the northern bat usually hibernates solitarily or in small groups consisting of 2–4 individuals (Ilyukha et al. 2015; Kizhina et al. 2018; Rydell 1993a). Northern bats have been found clustering with Daubenton's bat, brown long-eared bats, and whiskered/Brandt's bats (*Myotis mystacinus/brandtii*) (Siivonen and Wermundsen 2008).

Winter mortality of northern bats has not been extensively studied, but an annual mortality rate of 5.1% for northern bats in Karelia has been reported, whereas the mortality rates of Daubenton's bat and Brandt's bat were 5.3% and 10.0% respectively (Kizhina et al. 2018) .

Reproductive Behavior

Male sperm availability fluctuates during the mating period. Pfeiffer and Mayer (2013) studied swarming flight activity of males and females in southern Germany, and measured the epipididymal volume. Swarming was strongly male-biased, and the female activity peak was timed with the maximum volumes of male epididymi. The males' testis volumes increased from week 24 to week 28, and epididymal filling increased from the beginning of July to mid-August. After that, the volumes started to decrease rapidly, and by mid-September, when they were no longer measurable, the mating season was over. Thus, at least in the southern parts of the northern bats' distribution, it appears that the sperm production of males is timed to coincide with the reproductive cycle of females (Pfeiffer and Mayer 2013).

In late May or early June females gather into maternity colonies consisting of up to several dozens of individuals (Rydell 1992a, 1993b; Snit’ko 2007). These colonies include both parous and non-parous females, but no adult males have been identified in the colonies (Kosonen 2013; Rydell 1989; Tress et al. 1989). Whereas males disperse in their first year, females show high maternity roost fidelity; more than 70% of females return to the colony they were born in (Rydell 1989; Tress et al. 1989).

Females usually breed for the first time at the age of three years, but may have their first pups already in their first full summer (Dietz and Kiefer 2016). Among the breeding females, older individuals maintain a higher body mass and are in better condition compared to younger individuals. There is a stable, age-determined dominance hierarchy among individuals in the maternity colony (Rydell 1993b).

During pregnancy, the weight of the females may increase by up to 50%, from eight to twelve grams, which significantly increases the females’ flight costs. To compensate for the increased energy expenditure, pregnant females concentrate their feeding flights to the hours of the night when insect, especially dipteran, abundance is at its highest and foraging is energetically most profitable (Duvergé et al. 2000; Rydell 1989, 1992b, 1993b).

Female foraging flights during pregnancy typically extend only a few hundred meters from the maternity roost; later, after the birth of the young, lactating females start to extend their foraging flights further away from the roost (de Jong 1994; Rydell 1989). Foraging flight distances of up to several kilometers from the roosts have been recorded (de Jong 1994; Kosonen 2013).

Parasites and Diseases

Ectoparasites

The northern bat is host to several parasitic flea species, such as *Ischnopsyllus hexactenus, I. obscurus* (Scheffler et al. 2010, 2012, 2016), *I. intermedius, I. simplex, I. octactenus* and *I. variabilis* (Krištofík and Danko 2012). Parasitic mites found in northern bats include *Spinturnix kolenatii* (Krištofík and Danko 2012; Scheffler et al. 2010, 2012, 2016), *S. plecotina* (Stanyukovich 1997), *Macronyssus* spp. (Scheffler et al. 2010, 2012), *Leptotrombidium russicum* (Haitlinger and Ruprecht 1992), *Trombicula* spp. (Scheffler et al. 2012), *Steatonyssus spinosus* (Scheffler et al. 2016), and *Ornithonyssus pipistrelli* (Orlova et al. 2016). Northern bats are also hosts to bedbugs (*Cimex* sp.) (Orlova et al. 2015; Scheffler et al. 2016).

In Poland, a study investigating the parasitic loads of swarming bats found that male northern bats had a lower prevalence (20.4%, $N = 152$) of mites compared to females (55.9%, $N = 34$), but the prevalence of mites differed significantly between years (Piksa et al. 2011). Lilley et al. (2014) examined the parasitic loads for 12 northern bats and found a mite prevalence of 25%, with a mean intensity (number of mites/infested individual) of 1.7 mites, and a louse fly prevalence of 8.3% with a mean intensity of 1.

Diseases

A study investigating the causes of death for bats in Germany found that of the 17 northern bats dissected for a study, seven had organ lesions, two had died of trauma, one had suffered from a bacterial infection and the remaining seven bats had died of other causes (such as pulmonary edema, anemia, dehydration, hypoglycemia, hypo-/hyperthermia), or the cause of death could not be determined. The main histo-pathological findings for northern bats were mild to moderate interstitial pneumonia, mild to severe enteritis, and inflammatory cell infiltrates in the liver. Bacterial infections were determined to be caused by *Enterococcus faecium*. The prevalence of lung lesions in northern bats was high compared to other species (76.5%) (Mühldorfer et al. *2011*). While northern bats have been confirmed to develop clinical signs of the fungal disease known as white-nose disease in some cases (Zukal et al. *2014*), there have been no reports of mortality. This is most likely due to the hibernation temperature of the northern bat falling outside the optimal growth range of the fungus (Verant et al. *2012*; Wermundsen and Siivonen *2010*).

Several studies have tested northern bats for European bat lyssaviruses, but none of the tested bats have been found positive for the virus or antibodies (Botvinkin et al. *2003*; Nokireki et al. *2013*; Schatz et al. *2013*). However, northern bats may act as reservoirs to some other viruses and bacteria that can affect human health. Veikkolainen et al. (*2014*) tested three northern bats for *Bartonella* , a gram-positive group of bacteria that includes several species considered to be zoonotic. The study found *Bartonella* spp. from the peripheral blood of one of the northern bats as well as from ectoparasites collected from the individual. Kivistö et al. (*2019*) found beta-coronaviruses in 2 out of 36 northern bat fecal samples.

Population Ecology

Because the northern bat usually gives birth to one, or at most two pups per year, the potential for rapid population growth is small. However, while the species may potentially be preyed upon by several different predators, it is probably not a significant item in the diet of any other species. For example, pellets of tawny owls (*Strix aluco*) have been found to contain remnants of northern bats, but these only constitute approximately 1% of their diet (Lesiński et al. *2009*; Obuch *2011*). Other known avian predators of the northern bat are barn owl (*Tyto alba*) (Ruprecht *1979*), Ural owl (*Strix uralensis*) (Jäderholm *1987*; Korpimäki and Sulkava *1987*), long-eared owl (*Asio otus*) (Mihály and Anna *2016*), short-eared owl (*Asio flammeus*) (Mikkola *1983*: 372), and merlin (*Falco columbarius*) (Frafjord *2012*); in addition, Rydell (*1992a*) has observed predation attempts by Tengmalm's owl (*Aegolius funereus*) and sparrowhawk (*Accipiter nisus*). Mammalian predators include pine marten (*Martes martes*) (Pulliainen and Ollinmäki *1996*) and, in Siberia, sable (*Martes zibellina*) (Khritankov and Shishikin *2001*). Domestic cats are also a cause of mortality, especially for newly-weaned young (details from Finnish museum of Natural History Mammal collection http://tun.fi/HR.1329).

Karlsson et al. (*2006*) conclude that the bats at high latitudes, such as the northern bat, have not been exposed to nocturnal predation, and therefore have not evolved nocturnal antipredatory responses, such as lunar phobia.

Conservation Status

The northern bat is classified as a globally Least Concern species in the IUCN Red Data list (Coroiu *2016*). It is widely distributed and abundant in its distribution range in northern Fennoscandia, Russia, and northern Asia, but closer to the edges of the distribution range, where the species becomes rare, e.g., in Germany, its conservation status is Endangered. Recent declines in population size in Sweden (Rydell et al. *2020*) suggest the status of the species should be re-evaluated in the more northern parts of its range. In Europe, the northern bat is protected under Annex IV (a) of the EU Council Directive (92/43/EEC) on the conservation of natural habitats and of wild fauna and flora.

Management

Several challenges for management are mentioned in the UNEP/EUROBATS publication, “Guidance on the conservation and management of critical feeding areas and commuting routes for bats” (Kyheröinen et al. *2019*). Based on studies by de Jong et al. (de Jong and Ahlén *1991*; de Jong *1994*) and Nummi et al. (*2011*), the management of areas, such as water bodies, beaver flowages, and deciduous forests close to maternity colonies (up to 5 km) with high insect production, are mentioned as a key to the conservation and management of the species. Also, although feeding at street lights is common for the species (Rydell *1992b*), the maintenance of natural habitats, such as forests and grasslands will remain essential to the survival of the species, because urban areas might not remain profitable with the removal of insect-attracting Hg-lighting (Rydell et al. *2020*; Haupt et al. *2006*).

The UNEP/EUROBATS-publication also mentions mitigation programs in conjunction to wind farm construction as a future challenge for management. Indeed, collisions have been documented at wind farms (Ahlén *2002*; Rydell et al. *2010a*, *b*, *2016*; Aminoff *2014*). Bats may be attracted to wind turbines in pursuit of insects (Rydell et al. *2010b*, *2016*). The northern bat’s habit of foraging above treetop height, i.e., at altitudes of up to and exceeding 100 m, and frequently in close vicinity of the turbine rotors, makes it vulnerable to fatal rotor collisions (Ahlén *2002*; Rydell et al. *2010a*, *b*, *2016*; Blomberg *2016*). The northern bat is therefore classified as a “high-risk species” at wind farms (Rydell et al. *2010a*, *2016*).

There is a need for more robust monitoring programs to understand the population dynamics of the northern bat. Alarmingly, a study by Rydell et al. (*2020*) estimated a 59% decline in the northern bat population in southern Sweden between 1988 and 2017. The activity of northern bats has declined more along sections of their transects with artificial street lighting compared to sections without lighting, and the authors attribute this further reduction to the switch from mercury-vapor lights to LED-lights. Mercury-vapor lighting produces light in the UV-range of the spectrum, which makes these street lights attractive to insects (Wakefield et al. *2018*). The northern bat benefitted from the mercury-vapor street lights for several decades with increased food availability, which most likely resulted in a population increase. Even though the findings of the study clearly demonstrate the effect of lighting, the authors conclude that they cannot exclude other contributing factors, such as the intensification of forestry practices and changes in agriculture, which both could affect the availability of prey insects. Furthermore, since 1988, the northern bat has been replaced by the soprano pipistrelle (*Pipistrellus pygmaeus*) as the most common bat species in southern Sweden, with two other species, Nathusius' pipistrelle (*Pipistrellus nathusii*) and common pipistrelle, having established themselves, and increased their distribution range between the two time-points. In this light, one has to also consider the effects of inter-species competition and climate-change on the decrease in occurrence of the northern bat in southern Sweden.

Future Challenges for Research and Management

Research challenges for the future are mostly focused on the poorly known critical areas of the biology of the northern bat. These include understanding the full distribution range of the species, the multiple factors determining the occurrence of the species, potential competition with other species expanding their range, the extent of gene flow between populations (including more isolated populations), taxonomical issues related to the status of populations and more in-depth details on behavior, preferences, and physiology related to hibernation and thermoregulation in general. With the impending climate change looming, these areas in the biology of the northern bat need clarification for the evaluation of the risks the future holds for the species.

Acknowledgments

We thank Tanya Troitsky and Mariina Gunther for help with measuring northern bat samples in the collections of the Finnish Museum of Natural History, Vitali Razumov and Axel Donning for help with translating Russian and German language literature and Kio Kohonen for searching for northern bat remains from owl nests. We would also like to thank Jens Rydell and Johnny de Jong for their valuable comments on the chapter, and Niclas Fritzén, Harry Lehto, and Katarina Meramo for the beautiful photographs they provided us for this chapter.

References

Ahlén I (1981) Identification of Scandinavian bats by their sounds. Rapp Sver Lantbruksuniv Instit Viltekol 6, 58 pp

Ahlén I (2002) Fladdermöss och fåglar dödade av vindkraftverk. Fauna och Flora, Stockholm 97:14–22

Ahlén I (2011) Fladdermusfaunan i Sverige – arternas utbredning och status. Kunskapsläget 2011. Fauna och Flora 106:2–19

Ahlén I, Baagøe HJ, Bach L (2009) Behavior of Scandinavian bats during migration and foraging at sea. J Mammal 90:1318–1323. https://doi.org/10.1644/09-MAMM-S-223R.1

Aminoff S (2014) Vindkraftens inverkan på fladdermöss i Finland – en pilotstudie om undersökningsmetoderna I finländska förhållanden. Master’s thesis, University of Helsinki, Helsinki, Finland

Anděra M, Hanák V (2007) Atlas of the mammals of the Czech Republic–a provisional version. V. bats (Chiroptera) – Part 3 (in Czech). Natl. Mus. Prague

Anufriyev AI (2008) Wintering and winter sleep of bats in Yakutia. Vestnik of M. K. Ammosov Yakutsk State University 5:5–9

Anufriev A, Revin Y (2006) Bioenergetics of hibernating bats (Chiroptera, Vespertilionidae) in Yakutia. Plecotus Al 9:8–17

Arthur L, Lemaire M (2015) Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope, Méze, 544 pp

Artyushin IV, Bannikova AA, Lebedev VS, Kruskop SV (2009) Mitochondrial DNA relationships among North Palaearctic *Eptesicus* (Vespertilionidae, Chiroptera) and past hybridization between common serotine and northern bat. Zootaxa 2262:40–52. https://doi.org/10.11646/zootaxa.2262.1.2

Artyushin IV, Kruskop SV, Lebedev VS, Bannikova AA (2018) Molecular phylogeny of serotines (Mammalia, Chiroptera, *Eptesicus*): evolutionary and taxonomical aspects of the *E. serotinus* species group. Biol Bull 45:469–477. https://doi.org/10.1134/S1062359018050035
CrossRef

Atanassov CL, Naegeli H-U, Zenke G, Schneider C, Kramarova LI, Bronnikov GE, Van Regenmortel MHV (1995) Anti-lymphoproliferative activity of brown adipose tissue of hibernating ground squirrels is mainly caused by AMP. Comp Biochem Physiol C Pharmacol Toxicol Endocrinol 112:93–100. https://doi.org/10.1016/0742-8413(95)00000-3
CrossRef

Baagøe HJ (2007) Nordflagermus *Eptesicus nissonii* (Keyserling & Blasius, 1839). In: Baagøe HJ, Jensen TS (eds) Dansk pattedyratlas. Gyldendal, Copenhagen, pp 82–83

Baagøe HJ, Bloch D (1993) Bats (Chiroptera) in the Faroe Islands. Fróðskaparrit 41:83–88

Baranovoj GL, Gromova IM (1981) Katalog mlekopitayuschchikh SSSR Pliotsen-sovremennost (Catalog of the mammals of USSR). Pliocene-resent. Nauka, Leningrad, 456 p

Barataud M (2015) Acoustic ecology of European bats. In: Species, identification, study of their habitats and foraging behaviour. Biotope, Mèze, 340 p

Belkin VV, Panchenko DV, Tirronen KF, Yakimova AE, Fedorov FV (2015) Ecological status of bats (Chiroptera) in winter roosts in eastern Fennoscandia. Russ J Ecol 46:463–469. https://doi.org/10.1134/S1067413615050045
CrossRef

Belkin VV, Ilyukha VA, Khizhkin EA, Fyodorov FV, Yakimova AE (2019) Studies of the bat fauna (Mammalia, Chiroptera) in the green belt of Fennoscandia. Works Karelian Sci Cent 5:17–29. https://doi.org/10.17076/eco1079
CrossRef

Benda P, Ivanova T, Horá I, Hanák V (2003) Bats (Mammalia: Chiroptera) of the eastern Mediterranean. Part 3. Review of bat distribution in Bulgaria, 114 p

Benda P, Faizolâhi K, Andreas M, Obuch J, Reiter A, Ševčík M, Uhrin M, Vallo P, Ashrafi S (2012) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 10. Bat fauna of Iran. Acta Soc Zool Bohemicae 76:163–582

Bennett KD, Tzedakis PC, Willis KJ (1991) Quaternary refugia of north European trees. J Biogeogr 18:103–115. https://doi.org/10.2307/2845248
CrossRef

Blomberg AS (2016) Tuulivoiman lepakoille aiheuttamat riskit ja niiden lieventäminen Suomessa. Master's thesis, University of Turku, Turku

Blomberg AS, Vasko V, Meierhofer MB, Johnson J, Eeva T, Lilley TM (2021) Winter activity of boreal bats. Mammalian Biology 101:609–618. https://doi.org/10.1007/s42991-021-00111-8

Bobrinskoj NA (1926) Predvaritelnoje soobshtchnie o letutchikh myshach (Chiroptera) iz Centralnoj Azii (Note préliminaire sur les chiropteres de l'Asie Centrale) (in Russian with a summary in French). Compt Rendus Acad Sci URSS A:95–98

Boshamer JPC, Bekker JPC (2008) Nathusius' pipistrelles (*Pipistrellus nathusii*) and other species of bats on offshore platforms in the Dutch sector of the North Sea. Lutra 51:17–36

Botvinkin AD, Poleschuk EM, Kuzmin IV, Borisova TI, Gazaryan SV, Yager P, Rupprecht CE (2003) Novel lyssaviruses isolated from bats in Russia. Emerg Infect Dis 9:1623–1625. https://doi.org/10.3201/eid0912.030374
CrossRef

Bouma HR, Strijkstra AM, Boerema AS, Deelman LE, Epema AH, Hut RA, Kroese FGM, Henning RH (2010) Blood cell dynamics during hibernation in the European ground squirrel. Vet Immunol Immunopathol 136:319–323. https://doi.org/10.1016/j.vetimm.2010.03.016

Bruijn Z (2004) Vondst noordse vleermuis in Nederland. Zoogdier 15:18

Bukhnikashvili A, Gazaryan S, Kandaurov A, Natradze I, Rakhmatulina I, Yavruyan E (2009) Current Status of Chiroptera Conservation in the Caucasus (Zazanashvili N, Mallon D, eds.) Status and protection of globally threatened species in the Caucasus 98–105. Tbilisi: CEPF, WWF. Contour Ltd, pp 232

Bykhovets HM, Petrov AH (2019) First observation of the northern bat (*Eptesicus nilssonii* Keyserling et Blasius, 1839, Vespertilionidae, Chiroptera) in the tundra (city of Vorkuta, Republic of Komi). Herald Institute of Biology, Komi Scientific Center, Ural Branch of the Russian Academy of Sciences 4:36–37. [in Russian] https://doi.org/10.31140/j.vestnikib.2019.4(211).5

Coroiu I (2016) *Eptesicus nilssonii*. The IUCN red list of threatened species. e.T7910A22116204. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T7910A22116204.en. Downloaded on 9 February 2020

Currat M, Ruedi M, Petit RJ, Excoffier L (2008) The hidden side of invasions: massive introgression by local genes. Evolution 62:1908–1920. https://doi.org/10.1111/j.1558-5646.2008.00413.x
CrossRef

Datzmann T, Dolch D, Batsaikhan N, Kiefer A, Helbig-Bonitz M, Zöphel U, Stubbe M, Mayer F (2012) Cryptic diversity in Mongolian vespertilionid bats (Vespertilionidae, Chiroptera, Mammalia).

Results of the Mongolian-German biological expeditions since 1962. Acta Chiropterologica 14:243–264. https://doi.org/10.3161/150811012X661594

Davis WH, Cawein MJ, Hassell MD, Lappat EJ (1967) Winter and summer circulatory changes in refrigerated and active bats, *Myotis lucifugus*. J Mammal 48:132–134.
https://doi.org/10.2307/1378178
CrossRef

de Jong J (1994) Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. Mammalia 58:535–548.
https://doi.org/10.1515/mamm.1994.58.4.535
CrossRef

de Jong J, Ahlén I (1991) Factors affecting the distribution pattern of bats in Uppland, Central Sweden. Holarct Ecol 14:92–96

Degerbøl M (1935) Flagermus (Chiroptera). In: Manniche ALV, editor. Danmarks pattedyr. København: Gyldendalske Boghandel, Nordisk Forlag. Gyldendalske Boghandel, Nordisk Forlag, København

Dietz C, Kiefer A (2016) Bats of Britain and Europe. Bloomsbury Publishing, pp 316–319

Dolch D, Batsaikhan N, Thiele K, Burger F, Scheffler I, Kiefer A, Mayer F, Samjaa R, Stubbe A, Stubbe M, Krall L, Steinhauser D (2007) Contributions to the Chiroptera of Mongolia with first evidences on species communities and ecological niches. 287. Erforsch Biol Ress Mongolei 10:407–458. ISSN:0440-1298

Duvergé PL, Jones G, Rydell J, Ransome RD (2000) Functional significance of emergence timing in bats. Ecography 23:32–40. https://doi.org/10.1111/j.1600-0587.2000.tb00258.x
CrossRef

Eklöf J, Svensson AM, Rydell J (2002) Northern bats, *Eptesicus nilssonii*, use vision but not flutter-detection when searching for prey in clutter. Oikos 99:347–351
CrossRef

Ellerman JR, Morrison-Scott TCS (1951) Checklist of Palaearctic and Indian mammals 1758 to 1946. British Museum (National History), London, 747 p

Fadeeva TV, Kruskop SV (2008) Rudimentary small upper premolars in the northern bat, *Eptesicus nilssoni* (Vespertilionidae, Chiroptera). Russ J Theriol 7:77–80

Frafjord K (2012) Observations of a merlin (*Falco columbarius*) hunting northern bats (*Eptesicus nilssonii*) in midnight sun (northern Norway), Nyctalus (N.F.) 17:107–111

Frafjord K (2013) Influence of night length on home range size in the northern bat *Eptesicus nilssonii*. Mamm Biol 78:205–211
CrossRef

Fritzén N, Hägg J (2020) Valsörarnas biologiska station – verksamhetsberättelse för år 2019. OA-Natur 22:3–17

Fukui D, Agetsuma N, Hill D (2004) Acoustic Identification of Eight Species of Bat (Mammalia: Chiroptera) Inhabiting Forests of Southern Hokkaido, Japan: Potential for Conservation Monitoring. Zoological Science 21:947–955. https://doi.org/10.2108/zsj.21.947

Gaisler J (1959) Příspěvek ke srovnávacímu studiu létacího aparátu netopýrů. Zool Listy 8(1):37–62

Gajdošík M, Gaisler J (2004) Diet of two *Eptesicus* bat species in Moravia (Czech Republic). Folia Zool 53:7–16

Gorobeyko UV, Kartavtseva IV (2018) Karyology of the bats from the Russian Far East. Cytogenet Past Present Furth Perspect. https://doi.org/10.5772/intechopen.78767

Greenaway F, Hill D (1987) First British record of the Northern Bat (*Eptesicus nilssonii*). J Zool 215:357–358

Haarsma A-J, Siepel H (2013) Macro-evolutionary trade-offs as the basis for the distribution of European bats. Anim Biol 63:451–471. https://doi.org/10.1163/15707563-00002424
CrossRef

Haitlinger R, Ruprecht A (1992) Parasitic arthropods (Siphonaptera, Diptera, Acari) of bats from western part of the Białowieża Primeval Forest. Nyctalus 3:315–319

Hanák V, Horáček I (1984) Zur südgrenze des areals von *Eptesicus nilssoni* (Chiroptera: Vespertilionidae). Ann Nat Hist Mus Wien Ser B Bot Zoo 88/89:377–388

Haupt M, Schmidt S (2007) Small scale activity patterns of *Eptesicus nilssonii* – an indication of habitat preference or interspecific processes. Acta Chiropterologica 9:503–516. https://doi.org/10.3161/1733-5329(2007)9[503:SSAPOE]2.0.CO;2
CrossRef

Haupt M, Menzler S, Schmidt S (2006) Flexibility of habitat use in *Eptesicus nilssonii*: does the species profit from anthropogenically altered habitats? J Mammal 87:351–361. https://doi.org/10.1644/05-MAMM-A-193R1.1
CrossRef

Havenstein N, Langer F, Stefanski V, Fietz J (2016) It takes two to tango: phagocyte and lymphocyte numbers in a small mammalian hibernator. Brain Behav Immun 52:71–80. https://doi.org/10.1016/j.bbi.2015.09.018
CrossRef

Heller K-G, Volleth M (1984) Taxonomic position of "*Pipistrellus societatis*" Hill, 1972 and the karyological characteristics of the genus *Eptesicus* (Chiroptera: Vespertilionidae). J Zool Syst Evol Res 22:65–77. https://doi.org/10.1111/j.1439-0469.1984.tb00563.x
CrossRef

Hoofer SR, Van Den Bussche RA, Horáček I (2006) Generic status of the American Pipistrelles (Vespertilionidae) with description of a new genus. J Mammal 87:981–992. https://doi.org/10.1644/05-MAMM-A-425R1.1

Horáček I (1982) K poznání glaciálních poměrů v krasu severního Bulharska [Notes on the glacial-time environment in Northern Bulgaria]. Československý Kras 32:95–103

Horáček I, Hanák V, Gaisler J (2000) Bats of the Palearctic region: a taxonomic and biogeographic review. Presented at the European Bat research symposium, Proceedings of the VIIIth European bat research symposium, Krakow, pp 11–157

Hůrka L (1967) Okologische Beobachtungen in der Wochenstube von *Eptesicus nilssoni*, Keyserling et Blasius,1839 in der Tschechoslovakei. Zool Listy 16:193–197

Hutterer R, Ivanova T, Meyer-Cords RL (2005) Bat migration in Europe: a review of banding data and literature. Naturschutz und Biologische Vielfalt. Federal Agency for Nature Conservation, 180 p

Ijäs A, Kahilainen A, Vasko VV, Lilley TM (2017) Evidence of the migratory bat, *Pipistrellus nathusii*, aggregating to the coastlines in the northern Baltic Sea. Acta Chiropterologica 19:127–139. https://doi.org/10.3161/15081109ACC2017.19.1.010
CrossRef

Ilyukha VA, Antonova E, Belkin VA, Uzenbaeva L, Khizhkin E, Sergina S, Ilyina T, Baishnikova I, Kizhina A (2015) The eco-physiological status of hibernating bats (Chiroptera) in the north of the European distribution range. Acta Biol Univ Daugapilsiensis 15:75–94

Imaizumi Y (1953) A new species of *Eptesicus* from Japan (Mammalia; Chiroptera). Bull Nat Sci Mus 33:91–95

Jäderholm K (1987) Diets of the Tengmalm’s owl *Aegolius funereus* and the Ural owl in central Finland. Ornis Fenn 64:149–153

Jánossy D (1986) Pleistocene vertebrate faunas of Hungary, vol 8, 1st edn. Elsevier Science, 206 p

Jensen ME, Miller LA, Rydell JJ (2001) Detection of prey in a cluttered environment by the northern bat *Eptesicus nilssonii*. J Exp Biol 204:199–208
CrossRef

Jére C, Simon L, Bücs SL, Csosz I, Barti L, Szodoray-Parádi F, Dóczy A (2018) The distribution of the northern bat *Eptesicus nilssonii* (Keyserling & Blasius, 1839) in Romania. North-West J Zool 14:130–134

Jo YS, Baccus JT, Koprowski JL (2018) Mammals of Korea: a review of their taxonomy, distribution and conservation status. Zootaxa 4522:1–216. https://doi.org/10.11646/zootaxa.4522.1.1

Juste J, Benda P, Garcia-Mudarra JL, Ibáñez C (2013) Phylogeny and systematics of old world serotine bats (genus *Eptesicus*, Vespertilionidae, Chiroptera): an integrative approach. Zool Scr 42:441–457. https://doi.org/10.1111/zsc.12020
CrossRef

Kalabukhov NI (1985) Spyachka mlekopitayushchikh [Hibernation of mammals]. Nauka, Moscow, pp 194–233

Kaňuch P, Danko Š, Celuch M, Krištín A, Pjenčák P, Matis Š, Šmídt J (2008) Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe). Mamm Biol 73:147–155. https://doi.org/10.1016/j.mambio.2006.12.001
CrossRef

Karlsson B-L, Eklöf J, Rydell J (2006) No lunar phobia in swarming insectivorous bats (family Vespertilionidae). J Zool 256:473–477. https://doi.org/10.1017/S0952836902000511

Kawai K, Tiunov MP, Kondo N, Antipin MA, Boiko VN, Ohtanishi N, Dewa H (2014) Bats from Kunashir and Iturup Island. Bulletin of the Hokkaido University Museum 7:74–81

Keyserling A, Blasius J (1839) Uebersicht der Gattungs- und Artcharactere der europäischen Fledermäuse. Arch für Naturgesch 5:293–331

Khritankov AM, Shishikin AS (2001) Natural enemies of the bats in Central Siberia. Trudy gosudarstvennogo zapovednika Stolby 95–102

Kishida K (1932) Proposition of a new specific name for the lesser Korean serotine. Lansania, Tokyo 4:1–2

Kivistö I, Tidenberg E-M, Lilley T, Suominen K, Forbes KM, Vapalahti O, Huovilainen A, Sironen T (2019) First report of Coronaviruses in northern European bats. Vector-Borne Zoonotic Dis 20:155–158. https://doi.org/10.1089/vbz.2018.2367
CrossRef

Kizhina A, Uzenbaeva L, Antonova E, Belkin V, Ilyukha V, Khizhkin E (2018) Hematological parameters in hibernating *Eptesicus nilssonii* (Mammalia: Chiroptera) collected in northern European Russia. Acta Chiropterologica 20:273–283. https://doi.org/10.3161/15081109ACC2018.20.1.021
CrossRef

Knolle F (1981) Zur Beschreibung der Nordfledermaus (*Eptesicus nilssoni*). Myotis 18-19:197–198

Kolenati FA (1858) Eine neue Österreichische Fledermaus. Sitzungberichte Kais Acad Wiss Mat.-Naturwissensaftliche Kl. Wien 29:250–256

Korpimäki E, Sulkava S (1987) Diet and breeding performance of Ural owls *Strix uralensis* under fluctuating food conditions. Ornis Fenn 64:57–66

Kosonen E (2013) On the trail of the Northern Bat: a radio-tracking study of the northern bat (*Eptesicus nilssonii*) colony in southwestern Finland. Rep Turku Univ Appl Sci 150:1–29

Kovalchuk L, Mishchenko V, Chernaya L, Snitko V, Mikshevich N (2017) Haematological parameters of pond bats (*Myotis dasycneme* Boie, 1825 Chiroptera: Vespertilionidae) in the Ural Mountains. Zool Ecol 27:168–175. https://doi.org/10.1080/21658005.2017.1305153
CrossRef

Krištofík J, Danko S (2012) Arthropod ectoparasites (Acarina, Heteroptera, Diptera, Siphonaptera) of bats in Slovakia. Vespertilio 16:167–189

Kruskop SV, Borisenko AV, Ivanova NV, Lim BK, Eger JL (2012) Genetic diversity of northeastern Palaearctic bats as revealed by DNA barcodes. Acta Chiropterologica 14:1–14.
https://doi.org/10.3161/150811012X654222
CrossRef

Krzanowski A (1977) Weight classes of palearctic bats. Acta Theriol (Warsz) 22:365–370
CrossRef

Kulzer E, Nelson JE, McKean JL, Möhres FP (1970) Untersuchungen über die Temperaturregulation australischer Fledermäuse (Microchiroptera). Z Für Vgl Physiol 69:426–451.
https://doi.org/10.1007/BF00333769
CrossRef

Kurtén B (1968) Pleistocene mammals of Europe. Weidenfeld & Nicolson, 336 p

Kyheröinen E-M, Aulagnier S, Dekker J, Dubourg-Savage M-J, Ferrer B, Gazaryan S, Georgiakakis P, Hamidovic D, Harbusch C, Haysom K, Jahelkova H, Kervyn T, Koch M, Lundy M, Marnell F, Mitchell-Jones A, Pir J, Russo D, Schofield H, Syvertsen PO, Tsoar A (2019) Guidance on the conservation and management of critical feeding areas and commuting routes for bats. UNEP/EUROBATS, Bonn

Lapini L, Dorigo L, Zagmajster M, Asta A (2015) Distribution of two alpine-boreal bat species, *Eptesicus nilssonii* (Keyserling & Blasius, 1839) and *Vespertilio murinus* (Linnaeus, 1758), in Friuli Venezia Giulia region. Gortania Bot Zool 36:115–121

Lebl K, Bieber C, Adamík P, Fietz J, Morris P, Pilastro A, Ruf T (2011) Survival rates in a small hibernator, the edible dormouse: a comparison across Europe. Ecography 34:683–692. https://doi.org/10.1111/j.1600-0587.2010.06691.x
CrossRef

Lechler E, Penick GD (1963) Blood clotting defect in hibernating ground squirrels (*Citellus tridecemlineatus*). Am J Physiol-Leg Content 205:985–988. https://doi.org/10.1152/ajplegacy.1963.205.5.985
CrossRef

Lempiäinen A (2014) Mitochondrial DNA diversity of the Northern Bat (*Eptesicus nilssonii*) in the northern Palearctic. Master’s thesis, University of Helsinki, Helsinki

Lesinski G, Fuszara E, Fuszara M, Lesny D, Popczyk B, Ruprecht AL (2008) The occurrence of the northern bat, Eptesicus nilssonii (Keyserling & Blasius, 1839), in Warsaw and its vicinity, Central Poland. Nyctalus (N.F.) 2–3:137–141

Lesiński G, Gryz J, Kowalski M (2009) Bat predation by tawny owls *Strix aluco* in differently human-transformed habitats. Ital J Zool 76:415–421. https://doi.org/10.1080/11250000802589535
CrossRef

Lilley TM, Stauffer J, Kanerva M, Eeva T (2014) Interspecific variation in redox status regulation and immune defence in five bat species: the role of ectoparasites. Oecologia 175:811–823. https://doi.org/10.1007/s00442-014-2959-x
CrossRef

López-Baucells A, Burgin CJ (2019) 197. Northern serotine *Eptesicus nilssonii.* In: Handbook of the mammals of the world, bats. Lynx Edicions, Barcelona, pp 851–852

Lučan RK (2007) New findings of the Northern Bat (*Eptesicus nilssonii*) in Romania. Lynx (Praha) 38:107–108

Lyman CP, Chatfield PO (1955) Physiology of hibernation in mammals. Physiol Rev 35:403–425. https://doi.org/10.1152/physrev.1955.35.2.403
CrossRef

Markova AK, van Kolfschoten M, Bohncke S, Kosintsev P, Mol J, Puzachenko A, Simakova A, Smirnov N, Verpoorte A, Golovachev I (2008) Evolution of the European ecosystems during the Pleistocene-Holocene transition (24-8 Kyr BP): an introduction. KMK Scientific Press, Moscow

Martinoli A, Nodari M, Mastrota S, Spada M, Preatoni D, Wauters LA, Tosi G (2007) Recapture of ringed *Eptesicus nilssonii* (Chiroptera, Vespertilionidae) after 12 years: an example of high site fidelity/Recapture d'un *Eptesicus nilssonii* (Chiroptera: Vespertilionidae) bagué après 12 ans: un exemple de fidélité à un site. Mammalia 70:331–332. https://doi.org/10.1515/MAMM.2006.058
CrossRef

Masing M (1981) Nahkhiirte talvitumisest madalatel õhutemperatuuridel. Eesti Lood 12:760–764

Masing M (1983) On the hibernation of bats in Estonia. Myotis 20:5–10

Masing M, Lutsar L (2007) Hibernation temperatures in seven species of sedentary bats (Chiroptera) in northeastern Europe. Acta Zool Litu 17:47–55. https://doi.org/10.1080/13921657.2007.10512815
CrossRef

Masing M, Poots L, Randla T, Lutsar L (1999) 50 years of bat-ringing in Estonia: methods and the main results. Plecotus 2:20–32

Mayer F, von Helversen O (2001) Cryptic diversity in European bats. Proc R Soc Lond B Biol Sci 268:1825–1832. https://doi.org/10.1098/rspb.2001.1744
CrossRef

Michaelsen T, Olsen O, Grimstad K (2013) Roosts used by bats in late autumn and winter at northern latitudes in Norway. Folia Zool 62:297–303. https://doi.org/10.25225/fozo.v62.i4.a7.2013
CrossRef

Middleton N, Froud A, French K (2014) Social calls of the bats of Britain and Ireland. Pelagic Publishing, Exeter, 200 pp

Mihály E, Anna K (2016) Adatok az erdei fülesbagoly (Asio otus) táplálkozásának denevérfaunisztikai vonatkozásaihoz (A szerzök ajánlásával Schmidt Egonnak.) Calandrella 17–18:138–144

Mikkola H (1983) Owls of Europe. T & A D Poyser, Calton

Miller GS (1907) The families and genera of bats. Bull U S Natl Mus 57:1–282

Miller GS (1912) Catalogue of the mammals of western Europe in the collection of the British Museum. Trustees of the Britissh Museum, London, pp 1019

Miroposlki V (2001) Autumn record of *Eptesicus nilssonii* in the Kyiv region. Novit Theriol 6:114

Mosansky A, Gaisler J (1965) Ein Beitrag zur Erforschung der Chiropterenfauna der Hohen Tatra. Bonn Zool Beitr 16:249–267

Mühldorfer K, Speck S, Kurth A, Lesnik R, Freuling C, Müller T, Kramer-Schadt S, Wibbelt G (2011) Diseases and causes of death in European bats: dynamics in disease susceptibility and infection rates. PLoS One 6:e29773. https://doi.org/10.1371/journal.pone.0029773
CrossRef

Naďo L, Lőbbová D, Hapl E, Ceľuch M, Uhrin M, Šara M, Kaňuch P (2019) Highly selective roosting of the giant noctule bat and its astonishing foraging activity by GPS tracking in a mountain environment. Mamm Res 64:587–594. https://doi.org/10.1007/s13364-019-00446-1
CrossRef

Nilsson S (1836) Illuminerade figurer till Skandinaviens fauna (Illuminated figures to the fauna of Scandinavia), pt 17, Lund

Nokireki T, Huovilainen A, Lilley T, Kyheröinen E-M, Ek-Kommonen C, Sihvonen L, Jakava-Viljanen M (2013) Bat rabies surveillance in Finland. BMC Vet Res 9:174. https://doi.org/10.1186/1746-6148-9-174
CrossRef

Norberg UM, Rayner MV (1987) Ecological morphology and flight in bats (Mammalia: Chiroptera), wing adaptations, flight performance, foraging strategy and echolocation. Philos Trans R Soc Lond B 316:335–427
CrossRef

Nummi P, Kattainen S, Ulander P, Hahtola A (2011) Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. Biodivers Conserv 20:851–859.
https://doi.org/10.1007/s10531-010-9986-7
CrossRef

Nyholm ES (1983) Pohjanlepakko. In: Koivisto I (ed) Suomen Eläimet 1: Nisäkkäät. Weilin+Göös, Espoo, pp 101–102

Obuch J (2011) Spatial and temporal diversity of the diet of the tawny owl (*Strix aluco*). Slovak Raptor J 5:1–120
CrossRef

Orlova MV, Zhigalin AV, Khritankov AM (2015) New findings of ectoparasites of bats (Chiroptera: Vespertilionidae) in Southern Siberia. Entomol Rev 95:681–686.
https://doi.org/10.1134/S0013873815050127
CrossRef

Orlova MV, Kazakov DV, Zakhahrov ES, Troeva IS, Vladimirov LN (2016) The first data on bat ectoparasites (Acarina, Insecta) in the Baikal region and Yakutia (eastern Siberia). Check List 12:1–7. https://doi.org/10.15560/12.4.1943
CrossRef

Paksuz S, Paksuz E, Özkan B (2009) White blood cell (WBC) count of different bat (Chiroptera) species. Trak Univ J Sci 10:55–59

Pauza D, Pauziene N (1998) Bats of Lithuania: distribution, status and protection. Mamm Rev 28:53–68
CrossRef

Pavlinić I, Tvrtković N (2003) The presence of *Eptesicus nilssonii* and *Vespertilio murinus* in the Croatian bat fauna confirmed. Nat Croat Period Musei Hist Nat Croat 12:55–62

Petersen A, Jensen J-K, Jenkins P, Bloch D, Ingimarsson F (2014) A review of the occurrence of bats (Chiroptera) on islands in the north east Atlantic and on North Sea installations. Acta Chiropterologica 16:169–195. https://doi.org/10.3161/150811014X683381
CrossRef

Pfeiffer B, Mayer F (2013) Spermatogenesis, sperm storage and reproductive timing in bats. J Zool 289:77–85. https://doi.org/10.1111/j.1469-7998.2012.00970.x
CrossRef

Piksa K, Nowak J (2002) Noteworthy records of northern bat *Eptesicus nilssonii* (Chiroptera: Vespertilionidae) in the Tatra Mountains. Acta Zool Cracoviensia 45:321–324

Piksa K, Skwarek M, Siuda K (2011) Argasid and spinturnicid mite load on swarming bats in the Tatra Mountains, Poland. Folia Parasitol (Praha) 58:322–325. https://doi.org/10.14411/fp.2011.033
CrossRef

Pocora I, Pocora V, Baltag E, Cuza A (2008) The structure and the dynamics of a hibernation mixed colony of bats (Chiroptera) from an old gallery mine (Rarău mountains – Romania). Analele Ştiinţ. Ale Univ „Al Cuza" Iaşi Biol Anim 54:227–235

Popov VV, Pandurska R (2000) Late Quaternary mammals (Mammalia: Insectivora, Chiroptera, Lagomorpha, Rodentia, Carnivora) from Filipovska Cave (Western Bulgaria) and the problems of the biostratigraphy of the cave sediments. Karst Sofija 1:129–135

Pulliainen E, Ollinmäki P (1996) A long-term study of the winter food niche of the pine marten *Martes martes* in northern boreal Finland. Acta Theriol 41:337–352
CrossRef

Reddick RL, Poole BL, Penick GD (1973) Thrombocytopenia of hibernation. Mechanism of induction and recovery. Lab Investig J Tech Methods Pathol 28:270–278

Reznik G, Reznik-Schüller H, Emminger A, Mohr U (1975) Comparative studies of blood from hibernating and nonhibernating European hamsters (*Cricetus cricetus* L). Lab Anim Sci 25:210–215

Rigotti A (2007) Absorption, transport, and tissue delivery of vitamin E. Mol Aspects Med 28:423–436. https://doi.org/10.1016/j.mam.2007.01.002
CrossRef

Ruprecht AL (1979) Bats (Chiroptera) as constituents of the food of barn owls Tyto alba in Poland. Ibis 121:489–494

Ryberg O (1947) Studies on bats and bat parasites. 1. Svensk Natur, 319 pp

Rydell J (1986a) Foraging and diet of the northern bat *Eptesicus nilssoni* in Sweden. Ecography 9:272–276. https://doi.org/10.1111/j.1600-0587.1986.tb01219.x
CrossRef

Rydell J (1986b) Feeding territoriality in female northern bats, *Eptesicus nilssoni*. Ethology 72:329–337. https://doi.org/10.1111/j.1439-0310.1986.tb00633.x

Rydell J (1989) Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. Oecologia 80:562–565. https://doi.org/10.1007/BF00380082
CrossRef

Rydell J (1990) Behavioural variation in echolocation pulses of the northern bat, *Eptesicus nilssoni*. Ethology 85:103–113

Rydell J (1992a) Occurrence of bats in northernmost Sweden (65°N) and their feeding ecology in summer. J Zool 227:517–529. https://doi.org/10.1111/j.1469-7998.1992.tb04412.x
CrossRef

Rydell J (1992b) Exploitation of insects around streetlamps by bats in Sweden. Funct Ecol 6:744–750. https://doi.org/10.2307/2389972
CrossRef

Rydell J (1993a) *Eptesicus nilssonii*. Mamm Species 430: 1–7. https://doi.org/10.2307/3504128

Rydell J (1993b) Variation in foraging activity of an aerial insectivorous bat during reproduction. J Mamm 74:503–509. https://doi.org/10.2307/1382411
CrossRef

Rydell J (1993c) Variation in the sonar of an aerial-hawking bat (*Eptesicus nilssonii*). Ethology 93:275–284

Rydell J, Strann K-B, Speakman JR (1994) First record of breeding bats above the Arctic Circle: northern bats at 68–70°N in Norway. J Zool 233:335–339. https://doi.org/10.1111/j.1469-7998.1994.tb08597.x
CrossRef

Rydell J, Bach L, Dubourg-Savage MJ, Green M, Rodrigues L, Hedenström A (2010a). Bat mortality at wind turbines in northwestern Europe. Acta Chiropterologica 12:261–274. https://doi.org/10.3161/150811010X537846

Rydell J, Bach L, Dubourg-Savage MJ, Green M, Rodrigues L, Hedenström A et al (2010b) Mortality of bats at wind turbines links to nocturnal insect migration?. Eur J Wildl Res 56:823–827. https://doi.org/10.1007/s10344-010-0444-3

Rydell J, Bogdanowicz W, Boonman A, Pettersson S, Suchecka E, Pomorski JJ (2016) Bats may eat diurnal flies that rest on wind turbines. Mamm Biol 81:331–339. https://doi.org/10.1016/j.mambio.2016.01.005

Rydell J, Eklöf J, Fransson H, Lind S (2019) Long-term increase in hibernating bats in Swedish mines – effect of global warming? Acta Chiropterologica 20:421–426. https://doi.org/10.3161/15081109ACC2018.20.2.012

Rydell J, Elfström M, Eklöf J, Sánchez-Navarro S (2020) Dramatic decline of northern bat Eptesicus nilssonii in Sweden over 30 years R Soc open sci 7191754191754. https://doi.org/10.1098/rsos.191754

Sachanowicz K, Ciechanowski M, Piksa K (2006) Distribution patterns, species richness and status of bats in Poland. Vespertilio 9:151–173

Salari L, Kotsakis T (2011) Late Pleistocene and Holocene bats of Latium (Central Italy). Il Quat Ital J Quat Sci 24:121–129

Salari L, Kotsakis T (2017) Late Pleistocene bat assemblage with *Eptesicus nilssonii* from Grotta del Fossellone (southern Latium, central Italy). Lpine Mediterr Quat 30:125–136

Schatz J, Fooks AR, McElhinney L, Horton D, Echevarria J, Vázquez-Moron S, Kooi EA, Rasmussen TB, Müller T, Freuling CM (2013) Bat rabies surveillance in Europe. Zoonoses Public Health 60:22–34. https://doi.org/10.1111/zph.12002
CrossRef

Scheffler I, Dolch D, Ariunbold J, Batsikhan N, Abraham A, Thiele K (2010) Ectoparasites of bats in Mongolia (Ischnopsyllidae, Nycteribiidae, Cimicidae and Spinturnicidae). 304. Erforsch Biol Ress Mongolei 11:367–381

Scheffler I, Dolch D, Ariunbold J, Stubbe A, Abraham A, Thiele K (2012) Ectoparasites of bats in Mongolia, Part 2 (Ischnopsyllidae, Nycteribiidae, Cimicidae and Acari). 315. Erforsch Biol Ress Mongolei 12:135–151

Scheffler I, Jargalsaikhan A, Bolorchimeg I, Stubbe A, Stubbe M, Abraham A, Thiele K (2016) Bat ectoparasites of Mongolia, Part 3. 341. Erforsch Biol Ress Mongolei 13:395–408

Schneeberger K, Czirják GÁ, Voigt CC (2013) Measures of the constitutive immune system are linked to diet and roosting habits of Neotropical bats. PLoS One 8(1):e54023. https://doi.org/10.1371/journal.pone.0054023
CrossRef

Schnitzler H-U, Kalko EKV (2001) Echolocation by insect-eating bats. BioScience 51:557–569. https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2
CrossRef

Schober W, Grimmberger E, Stebbings RE (1989) A guide to bats of Britain and Europe. The Hamlyn Publishing Group Ltd., London, 224 pp

Shpak A (2018) Hibernating bat species of Belarus: results of the work of the Minsk bat contact centre. Theriol Ukr 16:156–162. https://doi.org/10.15407/pts2018.16.156
CrossRef

Siivonen Y, Wermundsen T (2008) Characteristics of winter roosts of bat species in southern Finland. Mammalia 72:50–56. https://doi.org/10.1515/MAMM.2008.003
CrossRef

Smirnov DG (2018) Comparative trophic niche analysis of *Pipistrellus nathusii* and *Eptesicus nilssonii* (Chiroptera, Vespertilionidae) in conditions of Samarskaya Luka. Nat Sci Ecol 4:28–41

Smirnov DG, Vekhnik VP, Kurmaeva NM, Shepelev AA, Il'in VY (2008) Spatial structure of the community of bats (Chiroptera: Vespertilionidae) hibernating in artificial caves of Samarskaya Luka. Biol Bull 35:211–218. https://doi.org/10.1134/S1062359008020167
CrossRef

Snit'ko VP (2007) Seasonal spatial differentiation of sex groups in populations of resident bat species (Chiroptera, Vespertilionidae) in the Southern Urals. Russ J Ecol 38:334–340. https://doi.org/10.1134/S1067413607050074
CrossRef

Solomonov NG, Anufriev AI, Solomonova TN (2010) Mechanisms of hibernation in small mammals of Yakutia. Cryobiology 61:397. https://doi.org/10.1016/j.cryobiol.2010.10.120

Speakman JR, Webb PI, Racey PA (1991) Effects of disturbance on the energy expenditure of hibernating bats. J Appl Ecol 28:1087–1104. https://doi.org/10.2307/2404227
CrossRef

Speakman JR, Rydell J, Webb PI, Hayes JP, Hays GC, Hulbert IAR, McDevitt RM (2000) Activity patterns of insectivorous bats and birds in northern Scandinavia (69° N), during continuous midsummer daylight. Oikos 88:75–86. https://doi.org/10.1034/j.1600-0706.2000.880109.x
CrossRef

Spitzenberger F (1986) Die Nordfledermaus (*Eptesicus nilssoni* Keyserling & Blasius, 1839) in Österreich. Mammalia austriaca 10 (Mammalia, Chiroptera). Ann Naturhist Mus Wien Ser B Bot Zool 87:117–130

Spurrier WA, Dawe AR (1973) Several blood and circulatory changes in the hibernation of the 13-lined ground squirrel, *Citellus tridecemlineatus*. Comp Biochem Physiol A Physiol 44:267–282. https://doi.org/10.1016/0300-9629(73)90479-9
CrossRef

Stanyukovich MK (1997) Keys to the gamasid mites (Acari, Parasitiformes, Mesostigmata, Macronyssoidea et Laelaptoidea) parasitizing bats (Mammalia, Chiroptera) from Russia and adjacent countries. Rudolstädter Naturhistorische Schriften 7:13–46

Strelkov PP (1986) The Gobi bat (*Eptesicus gobiensis* Bobrinskoy, 1926), a new species of chiropteran of Palaearctic fauna [In Russian]. Zool Zhur 65:1103–1108

Szilagyi JE, Senturia JB (1974) Erythrocyte changes in the hibernating woodchuck (*Marmota monax*). Cryobiology 11:478–481. https://doi.org/10.1016/0011-2240(74)90116-3
CrossRef

Taake K-H (1985) Einige verhaltensökologische Aspekte der Räuber-Beute-Beziehungen europäischer Fledermäuse (Chiroptera). Zeitschr Säugetierk 50:202–208

Thollesson M, Norberg U (1991) Moments of inertia of bat wings and body. J Exp Biol 158:19–35
CrossRef

Tidenberg E-M, Liukko U-M, Stjernberg T (2019) Atlas of Finnish bats. Ann Zool Fenn 56:207–250
CrossRef

Tiunov M, Kosmach A, Alexeeva E (1992) On the formation of the bat fauna in the south of the Soviet Far East. In Horáček I, Vohralík V (eds.) Prague studies in mammalogy. Charles University Press, Prague, pp 201–211

Toffoli R, Culasso P, Locatelli AG, Giraudo L (2016) Bats of Alpi Marittime Nature Park (North West Italy) and Site of Community Importance IT1160056: distribution and status. Nat Hist Sci Atti Soc It Sci Nat Mus Civ Stor Nat Milano 3:3–13

Tress J, Bornkessel G, Fischer J, Henkel F (1989) Beobachtungen an einer Wochenstubengesellschaft der Nordfledermaus (*Eptesicus nilssoni* [sic]) in Südthüringen. Wiss Beitr Univ Halle 20:189–200

Uhrin M, Hapl E (2004) Prehľad stavovcov (Vertebrata) Muránskej planiny Review of vertebrates (Vertebrata) of the Muránska Planina Mts. Reussia 1:311–332

Uhrin M, Benda P, Lučan R, Miková E, Rendoš M, Horáček I (2014) Noteworthy bat records from Romania. Vespertilio 17:197–213

Uzenbaeva L, Belkin V, Viktor I, Aleksandra K, Yakimova A (2015) Profiles and morphology of peripheral blood cells in three bat species of Karelia during hibernation. J Evol Biochem Physiol 51:342–348. https://doi.org/10.1134/S0022093015040109
CrossRef

Vasko V, Blomberg AS, Vesterinen EJ, Suominen KM, Ruokolainen L, Brommer J, Norrdahl K, Niemelä P, Laine V, Santangeli A, Lilley TM (2020) Feasting under the midnight sun: habitat use in forest-dwelling boreal bats. Ecol Evol 10:4164–4174

Veikkolainen V, Vesterinen E, Lilley T, Pulliainen AT (2014) Bats are reservoir hosts of the human bacterial pathogen *Bartonella mayotimonensis*. Emerg Infect Dis 20:960–967
CrossRef

Verant ML, Boyles JG, Waldrep Jr W, Wibbelt G, Blehert DS (2012) Temperature-dependent growth of Geomyces destructans, the fungus that causes bat white-nose syndrome. PLoS ONE 7(9):e46280. https://doi.org/10.1371/journal.pone.0046280

Vesterinen EJ, Puisto AIE, Blomberg A, Lilley TM (2018) Table for five, please: dietary partitioning in boreal bats. Ecol Evol 8:10914–10937. https://doi.org/10.1002/ece3.4559
CrossRef

Vintulis V, Pētersons G (2013) Root cellars are important winter roosts for brown long-eared bats (*Plecotus auritus*) and northern bats (*Eptesicus nilssonii*) in Latvia. Mammalia 78:85–91. https://doi.org/10.1515/mammalia-2012-0104
CrossRef

Volleth M, Bronner G, Göpfert MC, Heller K-G, von Helversen O, Yong H-S (2001) Karyotype comparison and phylogenetic relationships of *Pipistrellus*-like bats (Vespertilionidae; Chiroptera; Mammalia). Chromosome Res 9:25–46. https://doi.org/10.1023/A:1026787515840
CrossRef

Wakefield A, Broyles M, Stone EL, Harris S, Jones G (2018) Quantifying the attractiveness of broad-spectrum street lights to aerial nocturnal insects. J Appl Ecol 55:714–722. https://doi.org/10.1111/1365-2664.13004
CrossRef

Wermundsen T, Siivonen Y (2010) Seasonal variation in use of winter roosts by five bat species in south-east Finland. Cent Eur J Biol 5:262–273. https://doi.org/10.2478/s11535-009-0063-8
CrossRef

Widerin K, Reiter G (2017) Bat activity at high altitudes in the Central Alps, Europe. Acta Chiropterologica 19:379–387. https://doi.org/10.3161/15081109ACC2017.19.2.014
CrossRef

Widerin K, Reiter G (2018) Bat activity and bat migration at the elevation above 3,000 m at Hoher Sonnblick massif in the Central Alps, Austria (Chiroptera). Lynx New Ser 49:223–242.
https://doi.org/10.2478/lynx-2018-0017
CrossRef

Wolk E, Bogdanowicz W (1987) Hematology of the hibernating bat: *Myotis daubentoni*. Comp Biochem Physiol A Physiol 88:637–639. https://doi.org/10.1016/0300-9629(87)90675-X
CrossRef

Woloszyn BW (1987) Pliocene and Pleistocene bats of Poland. Acta Palaeontol Pol 32:3–4

Yoshiyuki M (1989) A systematic study of the Japanese Chiroptera. Natl Sci Mus Monogr Natl Sci Mus Tokyo 7:242

Yoon MH (2010) Vertebrate fauna of Korea: Bats. Flora and Fauna of Korea 5(1):123

Zukal J, Bandouchova H, Bartonicka T, Berkova H, Brack V, Brichta J, Dolinay M, Jaron KS, Kovacova V, Kovarik M, Martínková N, Ondracek K, Rehak Z, Turner GG, Pikula J (2014) White-nose syndrome fungus: a generalist pathogen of hibernating bats. PLoS One 9:e97224.
https://doi.org/10.1371/journal.pone.0097224
CrossRef