Leisler's Noctule *Nyctalus leisleri* (Kuhl, 1817)

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Common Names

English	Leisler's bat, lesser noctule
German	Kleiner Abendsegler
French	Noctule de Leisler
Spanish	Murciélago nóctulo pequeño
Italian	Nottola di Leisler
Russian	Малая вечерница

Taxonomy, Systematics and Paleontology

The Leisler's bat *Nyctalus leisleri* (Kuhl, 1817) is one of the six described species of the Nyctalus genus and one of the four found in continental Europe. It was first discovered by Johann Ph. A. Leisler. His student Heinrich Kuhl published the first description in the monography "die deutschen Fledermäuse" (1871), where he renamed it from *Vespertilio dasykarpos* ("hairy bat") to *V. leisleri,* nowadays *N. leisleri* after his teacher. The larger noctule bat, *N. noctula*, is found sympatrically with *N. leisleri* across its European range except for Ireland, while *N. lasiopterus* and *N. aviator*, also larger species, are distributed across southwestern Europe, the Near East, and North Africa. A subspecies, *N. leisleri verrucosus*, is confined to the islands of Madeira (Palmeirim 1991), while the closely related *N. azoreum*, endemic to the Azores Archipelago, has been described as a separate species (Palmeirim 1991; Salgueiro et al. 2004, 2007). These smaller species, along with *N. leisleri*, share the karyotype 2n = 44 (Volleth 1992).

Fossil records of *N. leisleri* are rare but resemble the extant species in their measurements. The oldest have been found in southern Spain and stem from the mid-Pleistocene of Las Granjas and the lower Pleistocene of Cueva del Agua (Sevilla 1989). It has also been reported from the Neolithic layers at Dowel Cave in England (Yalden 1986).

Current Distribution

It is distributed from Ireland in western Europe eastwards through central Europe as far as the Urals, Afghanistan, Western Himalayas, and Central China (Dietz et al. 2009; Horáček et al. 2000) from sea level to 2400 m (Juste and Paunović 2016). The Northern edge of its range runs across Scotland, as far north as Nairn in the northeast (Haddow and Herman 2000; National Biodiversity Network 2019), and along the European mainland up to approximately 57°N. They are largely absent from Scandinavia including Denmark, with only a few records from southern Sweden (Juste and Paunović 2016). The species has also been recorded from offshore installations and islands in the North Sea (Boshamer and Bekker 2008). To the south, there are records from northwest Africa, including Morocco and Tunisia, as well as the Canary Islands and Madeira (on Tenerife and La Palma only) (Juste and Paunović 2016). It is absent from southwestern Italy and Sicily, Southeastern Spain, but found in Sardinia (Mucedda 1997) and Elba island (Vergari and Dondini 1998), and Greece and Turkey to the southeast (Miric and Paunovic 1997; Albayrak 2003) and is present on Crete (Benda et al. 2008) and Cyprus (Benda et al. 2007). Figure 1 Illustrates the distribution.

Generally, densities of the species are low, except in Ireland, where it is relatively common and widespread.

Fig. 1 Distribution of Leisler's Noctule. Distribution is based on the IUCN Red List of Threatened Species. Version 2017-2 updated to include recent records available in the literature as of May 2019. (Map template: © Getty Images/iStockphoto)

Description

Size and Morphology

A medium-sized bat with rounded ears and a mushroom-shaped tragus. It can be distinguished from other *Nyctalus* species by its smaller size. It weighs on average 13–18 g, with a forearm length of between 40.5 and 47.1 mm, and a wingspan of between 26 and 32 cm (Dietz et al. 2009). However, in addition to measurements of forearm length indicating that females are usually larger than males, there also appears to be some regional variation (Roche et al. 2014; Perrin 1988). Anecdotal data also indicate different ear length between sexes.

Photograph by © Austin Hopkirk

Photography by © Billy Clarke

The fur is generally dark brown and bicolored, being darker at the base and lighter, red-brown towards the tip. *Nyctalus leisleri* is often described as having a "lion's mane" with long shaggy fur around the shoulders and upper back which can be raised in excited males. Fur is often darker in autumn after the molt. Fur on the ventral side is very similar to the dorsal fur and only slightly lighter on the throat. The visible skin is dark, almost black, with only the bottom and the outer edge of the ear clearly lighter colored. *Nyctalus leisleri* has long narrow wings and is also known as the "hairy-armed bat," with fur extending onto the forearm and wing. The tail emerges from the uropatagium 1–2 mm. Aspect ratio is 7.0, wing load 15.2 ± 2.62, which makes *N. leisleri* a fast flyer with low maneuverability (Norberg and Rayner 1987). Flight is usually straight and fast with brief stooping flights. The wings are clearly brought under the body during the downstroke (Vesey-Fitzgerald 1949).

Apart from its size, it is very similar to the larger congener *N. noctula*, but *N. leisleri* appear less compact, have darker, shaggier fur, and more delicate thumbs and feet. *Nyctalus leisleri* and *N. noctula* can also be distinguished by the number of facial vibrissae (*N. leisleri*: 6; *Vibrissae labii superiores*, *N. noctula*: 7–8) (Haffner and Ziswiler 1989). The skull shape is very similar to *N. noctula* apart from size, but smoother and more rounded, the *crista lambdoidae* are only weakly developed. No sexual dimorphism in skull morphology reported, but this may be due to small sample size.

Dentition

The dental formula in *N. leisleri* is 2 1 2 3 (upper), 3.1.2.3 (lower) = 34. Isup small and almost of equal size; C1 robust, no grooves on the labial and lingual aspects; P4 subrectangular; M1–M3 with paraloph and metaloph; M3 quite reduced; surfaces of P2 and P4 nearly equal size; M1–M3 with robust cingulum, nyctalodont; talonid of M3 slightly reduced (Menu and Sige 1971; Sevilla and Lopez-Martinez 1986; Sevilla 1988).

In *N. leisleri* males, the baculum is Y-shaped with proximal end clearly split, similar in shape to other *Nyctalus* species. However, in contrast to the other *Nyctalus* species, the distal end is never split but bulbous with only a slight dent (Lanza 1959; Bree et al. 1967; Hanäk and Elgadi 1984).

Physiology

The existence of buccal pads has been described in both male and female *N. leisleri* (Lanza 1956a; Harrison 1958). Present in the commissure of mouth, they are formed from thickened cells of the mucus membrane lining the upper labio-gingival fornix and release a fatty secretion (Lanza 1956b). These appear larger in males and with seasonal variation shown to coincide with the active breeding season and is more evident in males (Dondini et al. 2003). This supports a hypothesis that these pads serve a reproductive function, probably via the pheromone-like secretion and visual communication (Dondini et al. 2003).

Genetics

A molecular genetic study sheds some light on the evolutionary relationships among the smaller *Nyctalus* species, N. *leisleri* (2n = 44, Volleth, 1992), *N. azoreum* (2n = 44, Volleth, 1992), and *N. leisleri verrucosus* (2n = 44, Volleth, 1992) (Boston et al. 2015). It demonstrates the existence of two distinct mitochondrial DNA (mtDNA) haplotypic groups for these species across Europe. A western group includes *N. leisleri* populations from Ireland and Britain, and populations of *N. azoreum*; the eastern group is found across the European range including Ireland and Britain, North Africa, and populations of *N. leisleri verrucosus* from Madeira. This study suggests that these island endemics represent isolated populations derived from two mtDNA haplogroups. These probably diverged in allopatry during the last glacial maxima in Europe; one giving rise to populations in the Azores, Ireland, and Britain; and the other to all other European populations, including the British Isles and Madeira (Boston et al. 2015).

Regional differentiation and limited gene flow has been observed between populations of *N. leisleri* across the major geographical areas of Ireland and Britain and mainland Europe using mtDNA and nuclear microsatellites (Boston et al. 2015).

Relatedness among females within a maternity colony is lower during pregnancy and lactation, increasing as roost sizes decrease once the young are weaned (Nad'o et al. 2017). Roost switching is likely to be high, with a fission-fusion social system described, and males appear to be the more dispersive sex (Boston et al. 2012; Nad'o et al. 2017).

Life History

Reproduction

The reproductive cycle of *N. leisleri* is typical of temperate bat species. Mating takes place at or near the wintering sites when the females return from migration. It is thought to take place from late August through hibernation (Ohlendorf 1983; Červený and Bürger 1989; Schmidt 1989; Ohlendorf and Scheidt 1996) with a peak in August when the testes reach maximum size (8.5–9.5 mm in length, Schmidt 1989). In Italy, mating started in late August and ends by mid-October (see Dondini and Vergari 2009). In Greece, the main reproductive period is thought to take place later in September (von Helversen and von Helversen 1994). Males have been observed to establish and defend territories by calling from tree holes or buildings as well as during flight to attract females (von Helversen and von Helversen 1994; Ohlendorf and Scheidt 1996). These calling sites can be the same as the day roosts, but not always (von Helversen and von Helversen 1994). The same calling roosts are used in consecutive nights. The territories are then visited by females, which results in the formation of harems of several females to a single male. In a research conducted in Italy, it has been observed that most males are present with only one female. Only a small number of males exceed six females. The maximum size of a harem was 1 male and 11 females (see Dondini and Vergari 2009). Fertilization is delayed until the following spring after the hibernation period. A short second mating period can be observed in April (Cerveny and Bürger 1989). After April, the females then aggregate in maternity colonies (in migratory populations at the summering sites). Males spend the summer solitary or in bachelor groups of up to 11 individuals (Cerveny and Bürger 1989; Schmidt 1989) Nursery colonies typically consist of 20–50 individuals and can comprise over 100 individuals. The largest colony has been reported from West Cork, Ireland, with 800–1000 individuals (O'Sullivan 1994). These include mothers and their young, juveniles, and a few adult males (Boston et al. 2012).

The placenta is saucer-shaped and is situated antimesometrically relative to the uterus. It is hemochrial, i.e., the maternal endothelium of the capillaries is lost relatively early during the development of the embryo (Gopalakrishna and Karim 1979). Typically, a single pup is born in June or early July after a gestation period of around 70–75 days. Observations of two pups per gestation have been made in Germany (Abelencev et al.

1956) and Ireland (Barrett-Hamilton 1910). Pups are born within 1–3 weeks of each other but the timing of this can vary from year to year as well as geographically (Kurskov 1981; Abelencev et al. 1956; Ohlendorf 1983; Lichacev 1980) from mid-June (Belarus and Ukraine) to early July (Germany). A nursing female was found in May on the Canary Islands (Trujillo and Barone 1991).

Ontogeny and Lifespan

The milk teeth (di 2/3, dc 1/1, dp 2/2, total: 22) are almost completely present at birth (Matthews 1950; Lichotop 1990). The eyes and auditory channels open between day 4 and day 5. Permanent teeth begin to emerge between day 15 and 17, and this process is completed by day 29 (Kozurina 1995). Young are generally weaned and able to fly within 3–5 weeks (Kozurina 1995; Abelencev et al. 1956) and are fully grown after about 2 months (Kurskov 1981). The growth of the forearm and phalanges is completed in mid-August in Germany, but at this stage, the juveniles are still lighter than adults (Schmidt 1989). The most important factor affecting growth of *N. leisleri* and other bats in the temperate zones appears to be the roost temperature. Nursery colonies in Germany were found on south-exposed slopes and above the levels reached by dense and cold fog (Ohlendorf 1983). Young start to produce isolation calls on the first day. These early calls contain nine harmonics, with an initial frequency of 14 kHz, an end frequency of 12.6 kHz and a duration of 14.2 ms (Kozurina 1995). By day 17, the calls typically last 5.6 ms and the beginning and end frequency have risen to 29.3 and 17.9 kHz. Typical orientation-FM-pulses appear after day 12. On day 17, they begin to dominate the call repertoire (mean duration 0.9 ms, beginning frequency 37.3 kHz, end frequency 17.1 kHz). After day 25, the calls resemble those of adults. Sexual maturity, as in other temperate bats, is thought to occur after 1–2 years (Altringham 2001), with some evidence that both sexes appear capable of reproducing in their first year (Boston et al. 2012).

The average lifespan of the Leisler's bat is not known for certain but is probably around 7 years, although they could live for up to 15–20 years (Hayden and Harrington 2000). An individual ringed as an adult in Italy in 1996 was recaptured 10 years and 5 months later (Dondini G and Vergari S., pers. com.), while an injured adult female rescued in 2002 and kept in captivity remains alive in 18 years later at the writing of this chapter (Hopkirk A, pers. com.)

Habitat and Diet

Habitat Selection

Typically found to be foraging in habitats associated with deciduous and coniferous woodlands, as well as in open areas, over rivers, lakes or pastures, and around streetlights in parts of its range (Vaughan 1997; Shiel et al. 1999; Waters et al. 1999; Russo and Jones 2003; Russ et al. 2003). In Austria, for example, about half of the investigated localities were in mixed oak-forests, the other half in forests dominated by beech, pine, and/or fir (Spitzenberger 1992). In North Africa, it can be found in natural forests dominated by *Juniperus excelsior*, *Cupressus sempervirens*, *Quercus faginea*, *Q. suber*, *Q. ilex*, and *Q. canariensis* (Hanak and Gaisler 1983; Ibanez 1988). Its densities are highest in areas with large numbers of old trees (Heise 1982; Leger et al. 1986; Červený and Bürger 1989; Schmidt 1989; Ibanez et al. 1992). In the Bialowieza primeaval forest, *N. leisleri* is one of the species most commonly captured in nets along streams (Rachwald et al. 2001). However, the species can also be found in large cities such as London, Berlin, Vienna, or Warsaw (Mickleburgh 1987; Klawitter 1975; Haensel 1992; Lesiński 1983, Spitzenberger 1990).

Diet

Their diet depends on the local habitat and season and varies geographically (summarized in Vaughan 1997). Frequent prey are small to medium-sized insects (e.g., Nematocera,

Trichoptera, Coleoptera, and Lepidoptera) (Beck 1995; Vaughan 1997; Shiel et al. 1998, 1999; Waters et al. 1999; Fuhrmann et al. 2002). Insects with aquatic larvae (Ephemeroptera, Trichoptera, Chironomidae/Ceratopogonidae, Culicidae) often make up an important part of the diet. In England, Ireland, and Germany (Shiel et al. 1998), there is a major pastoral prey component, indicated mainly by *Scathophaga stercoraria*, Scarabaeoidea and associated Acari, while in parts of Germany and England dominated by arable farming insects of the families Lepidoptera, Hemerobiidae, Chrysopidae, and Ichneumonidae are also important. A record from the Krim of caterpillars (Konstantinov et al. 1976) as well as of prey collected from tree bark in the Ukraine (Abelencev et al. 1956) indicated that the species is also capable of gleaning; however, in the latter case, this was attributed to an emergency strategy under unfavorable weather conditions. In captivity, *N. leisleri* has been recorded to eat up to 70 mealworms in a single meal (Whitaker 1907). Food remains in the intestinal tract for an average of 54 min in captivity and up to 82.5% of the food are assimilated (Kovtun and Zukova 1986). Faces are pale to medium brown, rarely black, thicker than those of *Pipistrellus nathusii* and much thinner than those of *N. noctula* (Schmidt 1989).

Spatial Movements

It is during the spring to autumn period, with the formation of nursery roosts, that activity and behavior of *N. leisleri* are best understood. During this period, *N. leisleri* are known to switch roosts every few days, with an average distance of 700 m between roost sites (Ruczyński et al. 2010). Bats return to the same roosts, or network of roosts throughout the breeding season as well as in subsequent years (Boston et al. 2012; Nad'o et al. 2017), which indicates that Leisler's bats are able to maintain social bonds only over a single season (Nad'o et al. 2017).

The activity of *N. leisleri* leading up to and during hibernation is less known. In continental Europe, *N. leisleri* is often migratory, travelling long distances between summer roosting sites broadly in northeastern Europe and hibernation sites in southwestern Europe (Hutterer et al. 2005; Alcalde et al. 2013). The longest movement known in Europe is 1567 km, with a female ringed in Dresden, Germany, being recaptured near Burgos, Spain (Ohlendorf et al. 2000). Numerous shorter migrations have been recorded between Germany and Spain, France, Austria, and Switzerland as a result of over 70 years of data compiled from banding studies (Hutterer et al. 2005). Individuals ringed in Russia have been recovered in Turkey (1245 km) (cited in Panyutin 1980), another ringed in Italy was recovered 2 years later in Poland (960 km) (Dondini et al. 2012), while in Slovakia, a single bat was recovered after a journey of 339 km from Poland (Krzanowski 1960). However, some individuals do not migrate but remain reproduce and hibernate at locations where winters are milder including Germany and Switzerland (Gebhard 1984; Von Helversen et al. 1987; Kulzer et al. 1987; Roer 1989; Kuhner-Ryser 1990), and there is some evidence to suggest the same is true in Ireland (Boston et al. 2015).

Behavior

Roost Selection

Nyctalus leisleri roosts mainly in tree cavities, preferring rot holes, and other natural cavities (90% of those observed in Białowieża Forest) to cavities made by woodpeckers (Ruczyński and Bogdanowicz 2005). Preference for oaks and ashes, over hornbeam and alder has been observed in mixed woodland stands (Ruczyński and Bogdanowicz 2008), but the species has also been observed roosting in other species of tree, e.g., sweet chestnut, beech, sycamore lime, or pine (Spada et al. 2008; Ruczyński and Bogdanowicz 2008). In the Netherlands, summer roosts are predominantly in cracks under the bark and cavities of red oak and beech (Limpens and Bongers 1991; Lina et al. 1982). On the Canary Islands, *N. leisleri* roosts in tree cavities, as well as crevices in walls and rocks (Trujillo and Barone 1991). *Nyctalus leisleri* selects cavities at heights between 9 and 26 m, but on average 19 m above

the ground and prefers roost sites within old deciduous or wet woodlands over young or medium aged and coniferous ones (Ruczyński and Bogdanowicz 2005). Older records from the Ukraine (at least 2 m above ground; Abelencev et al. 1956), central Poland (2.8–7.5 m; Lesiński 1983), and the Czech Republic (2–8 m; Červený and Bürger 1989) report lower roosting heights. *Nyctalus leisleri* selects warmer cavities and those situated close to forest gaps (Ruczyński 2006; Ruczyński and Bogdanowicz 2005). Roosts can also be found in buildings (Shiel et al. 1999; Waters et al. 1999; Mitchell-Jones et al. 1999), and bat boxes are readily used also by nursery colonies, especially in coniferous but also in deciduous forests (Spoelstra 1997; Corbet and Harris 1991; Hausser 1996). In Poland and the Ukraine, about 4% of bats found in boxes are *N. leisleri* (Kowalski and Lesiński 1994). They prefer boxes that offer a low horizontal slit-shaped entrance of 15–18 mm length (Haensel and Naef 1982). *Nyctalus leisleri* is thought to hibernate in hollow trees, buildings, and occasionally in rock crevices (Roer 1989; Schober and Grimmberger 1989; Kuhner-Ryser 1990; Mayle 1990); however, data are limited.

Hibernation typically lasts from October to March as single individuals or in small colony (Roer 1989; Kuhner-Ryser 1990), sometimes until the middle of April or even the first week of May (Blackmore 1964). The heart beat frequency of *N. leisleri* during induced hibernation stabilizes at 17–25 bpm (Kulzer 1967). The ECG is identical to that of an awake bat except all components are stretched. An influence of the *Nodus sinoatrialis* and an increase of the T-P-intervals during the cold period has been noted (Kulzer 1967).

Foraging Behavior

Nyctalus leisleri has long narrow wings adapted to high (>70 m) fast flight (Russ and Montgomery 2002), with commuting speeds of up to 40–48 km hr^{-1} (Shiel and Fairley 1999). They are an aerial hawking species, catching insects on the wing. They can be observed flying just above the canopy and around street lights or higher, but they also fly low over forest ponds and creeks, where they can be caught in nets (Barta 1976; Hanak and Gaisler 1983; Masson and Sagot 1987; Ibanez 1988). They cover distances of up to 5.8 km from the roost during foraging (Waters et al. 1999), with a home range (minimum convex polygon) of 7.4 km^2 (max. 18 km^2).

Strong wind and low temperatures completely interrupt foraging activity (Abelencev et al. 1956; Whiteley and Clarkson 1985). Rain, as long as it is not too strong, seems less inhibitory (McAney and Fairley 1990) although they can cause temporary return to the roost. In Ireland, *N. leisleri* often show bimodal nightly activity taking advantage of increased insect numbers at dusk and dawn, while resting in between these times in night roosts (Shiel et al. 1998). In Białowieża Forest, Poland, only one noticeable peak of activity was observed, from 9 pm to 10 pm. Subsequently, the bats spent progressively less time outside their roosts and a second peak was only faintly visible. Bats emerge early from the roosts, the first ones even before sunset (Shiel and Fairley 1999; Ruczyński et al. 2017). During pregnancy, females emerge later than during lactation. Average activity duration during pregnancy is on shorter (132 min) than during lactation (190 min). Duration of bat activity is significantly affected by the interactive effect of temperature and reproductive period. As the temperature increases, the length of time that animals spend outside the roost almost linearly extends during pregnancy while during lactation, duration of activity increased at moderate temperature and decreased when ambient daily temperature exceeded 21 °C (Ruczyński et al. 2017).

Echolocation and Social Calls

Nyctalus leisleri produce FM/QCF calls, which are up to 20 ms-long with end frequency 21–30 Khz (Russo and Jones 2002; Vonhelversen and Vonhelversen 1994; Zingg 1988). The intervals between search pulses follow a bimodal distribution with a higher mode at 192 ms and a weaker one at 294 ms (Zingg 1988).

Echolocation calls can be confused with calls of *N. noctula*, *Eptesicus serotinus*, *E. nilssonii*, and *Vespertilio murinus,* especially when bats are active nearby obstacles such as vegetation or street lamps. *Nyctalus noctula* has usually lower end frequency, while that of *E. nilssonii* higher and *E. serotinus* calls are usually more strongly frequency-modulated in the initial part (Dietz et al. 2009). Regional variations among continental European, British, and Irish populations of *N. leisleri* have been described (Buckley et al. 2011).

The "advertisement song" of *N. leisleri* is produced by stationary as well as flying individuals to attract conspecifics (Zingg 1988; Vonhelversen and Vonhelversen 1994). Pfalzer and Kusch (Pfalzer and Kusch 2003) describe a range of social calls produced by *N. leisleri* in five different ecological and behavioral situations: in mating roosts, in maternity roosts, during flight, in foraging habitats, and in distress situations. Due to structure, these social calls were divided into four general types (including more subtypes): A (squawk), B (repeated, trill), C (curved, cheep), and D (complex, song). In the mating roost, calls of type C2 are used; in maternity roosts, type A, B2, and C1; during flight, type B1, C1, C2, and D; in the foraging habitat, type B1 and D; and in distress situations, bats produce calls of type B.

Parasites and Diseases

A number of ectoparasites have been recorded in this species, including species of mites, bugs, ticks, fleas, and flies. In a study in Slovakia (Kaňuch et al. 2005), ectoparasites were recorded in 56.5% of examined bats and comprised seven arthropod species; the most common were the mites *Spinturnix helvetiae* (55.4%) and *Steatonyssus spinosus* (31.3%). Mites were also common in Moldavia where *Macronyssus flavus* was found on 95% of the bats, *Steatonyssus spinosus* on 26.3%, *Spinturnix acuminatus* on 23.9%, and *Calcarmyobia miniopteris* on 4.8% (Andreijko 1973). Bats carried up to 278 on a single individual, most of them *M. flavus*. *Spinturnix helvetiae* was newly described from *N. leisleri* in Switzerland (Deunff et al. 1986). Also reported was a tick, *Argas vespertilionis* in Spain (Estrada-Pena et al. 1988), Germany (Walter 1996), and Bulgaria (Beron 1973). At least four species of fleas occur on *N. leisleri*: *Ischnopsyllus intermedius* (e.g., Aellen 1960; Hurka 1976; Peus 1978; Walter 1996), *I. octactenus* (Smit 1957; Sleeman and Smiddy 1994), *I. variabilis* (Hurka 1963a, b), and *Nycteridopsylla longiceps* (George 1957; Sleeman and Smiddy 1994). Moldavian individuals were infested with fleas (*I. intermedius*), bugs (*Cimex lectularius, C. pipistrelli*), and flies (*Nycteribia pedicularia*; Abelencev et al. 1956). Two species of bugs have been reported from Germany (*C. dissimilis and C. lectularius*). Pregnant females were the most infested. Ectoparasitic flies *Nycteribia latreillii* and *Nycteribia* (Acrocholidia) *vexata* were recorded for the first time in this species. *Nyctalus leisleri* also carries endoparasites, predominantly trematodes. These include *Plagiorchis vespertilionis* (Matskasi 1967), *Lecithodendrium linstowi* (e.g., Merkusava 1971; Andreijko 1973; Tkac 1995), *Parabascus semisquamosus* (Andrejko 1973), *Prosthodendrium atelleni* (Tkac et al. 1985), *P. chilostomum* (Matskasi 1967; Tkac 1995), *Pycnoporus megacotyle* (Tkac et al. 1985), *P. heteroporus* (Matskasi 1967), and *Ophiosacchulus mehelyi* (Tkac 1995). The trematode *Lecithodendrium linstowi* was found in 28.6% of all Moldavian *N. leisleri* in a study (Andrejko 1973). In addition, at least six species of nematodes occur in *N. leisleri*: *Molinostrongylus skrjabini*, *M. vespertilionis, Capillaria italica, Skrjabinocapillaria eubursata, Ascarops strongylina* (larvae), and *Physocephalus sexalatus* (larvae; e.g., Meszaros 1966; Merkusava 1971; Andreijko 1973; Durette-Desset and Chabaud 1975; Tkac 1995). Cestodes in *N. leisleri* include *Vampirolepis acuta* (Tkac 1995). Five out of eight investigated *N. leisleri* in Great Britain carried the protozoan *Trypanosoma* (*Schizotrypanum*) sp. (Gardner et al. 1987). This parasite is transmitted by the bat-specific bug *Cimex pipistrelli* and lives in the bloodstream of the host. It is thought to be harmless for bats (Gardner et al. 1987). Rabies has not been observed in *N. leisleri* to date (Muller et al. 2007; Nieuwenhuijs 1992; Vos et al. 2007; Schatz et al. 2013).

Population Ecology

Equal numbers of males and females are found as juveniles (Stebbings 1977; but see Lichacev 1980, who found more females in Moscow over the duration of several years). In adults, the proportion of females versus males can vary from extreme rarity of females with <1.215 (Russia; Abelencev et al. 1956), 1:48 (Greece; von Helversen and Weid 1990), and 1:16 (NE-Germany and Moscow; Heise 1982; Lichacev 1980) to more females with 4:1 (Czech Republic; Gaisler 1975). However, these numbers may largely be due to a seasonal effect of females migrating northeast in the summer in combination with the timing of data collection. Monitoring of a mating site in Italy over a 15-year period found remarkable numerical fluctuations, which were particularly evident in the number of females (Vergari and Dondini 2011). Accurate population estimates or trends are unknown. Generally considered rare but can be locally common in some regions (e.g., Białowieża Forest; Rachwald et al. 2001). In Brandenburg, Germany, a local density of 4.2 females/km^2 has been estimated. In Ireland, populations are estimated to be stable or increasing with between 73,000 and 130,000 individuals (Roche et al. 2014).

Conservation Status

IUCN Red List 2013: LC (Least Concern) with an unknown population trend; Red List of the European Union 2007: LC (Least Concern); EU Habitats Directive, Annex IV.

Management

Threats to its survival include declines in insect populations, due to the intensification of agriculture; loss of roost sites, through tree felling, intolerance of homeowners, and inappropriate building practices.

The association of *N. leisleri* with cavities in large, old, dying or dead trees inevitably brings them into direct conflict with the interests of forest managers (Ruczyński et al. 2010), at particular risk are the maternity colonies.

A significant negative effect of proximity to wind turbines on activity for *N. leisleri* has been observed (Barre et al. 2018). Isotopic geo-location reveals that wind turbines kill bats not only of sedentary local populations but also of distant populations, thus having potentially a negative impact beyond political borders for migratory species such as *N. leisleri* (Voigt et al. 2012).

Several species prey on *N. leisleri*, but none of them regularly as far as is known. The most common predator is the cat (*Felix catus*). Birds that prey on *N. leisleri* are the barn owl (*Tyto alba*), tawny owl (*Strix aluco*), long-eared owl (*Asio otus*), little owl (*Athene noctua*), and eagle owl (*Bubo bubo*; e.g., Uttendörfer 1943; Abelencev et al. 1956; Schmidt and Topal 1971; Ruprecht 1990; Libois 1983; Noblet 1988; Mitev 1995; Il'in 1988). However, all of these are thought to prey on other bats more frequently than on *N. leisleri*. Anecdotal reports are also available of predation by the hooded crow (*Corvus corone corax*; Abeljencev et al. 1956) and the Wadi racer in Afghanistan (*Coluber rhodorachis;* Schätti 1984).

Future Challenges for Research and Management

There is observed lability in the selection of roosting habitat by bats. It appears that Leisler's bats are able to respond to changes in their environment by changing their roost site preferences and could occupy habitat previously considered less suitable (Ruczyński et al. 2010); however, the level of flexibility these bats can exhibit is unknown, as therefore is the impact of ongoing climate change.

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