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Exploitation of insects around streetlamps by bats in Sweden

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Summary

1. Nine species of insectivorous bats in southern Sweden were monitored with a bat detector to assess which species regularly forage around streetlamps and which do not. Only the fast-flying species that use long-range echolocation systems (*Nyctalus noctula*, *Vespertilio murinus*, *Eptesicus nilssonii* and occasionally *Pipistrellus pipistrellus*) did, whereas *Myotis* spp. and *Plecotus auritus* did not.

2. Bats foraging near streetlamps were monitored with a bat detector from a car. Bat density along illuminated roads was 1–5 km⁻¹. More than 90% of the bats detected were *E. nilssonii*.

3. In and around a small town, *E. nilssonii* was predominantly found in residential and rural parts, and avoided areas without trees. *Vespertilio murinus*, in contrast, was observed in all habitats. The difference was probably related to differences in the foraging behaviour of the two species.

4. The attractiveness to insects by streetlamps was determined photographically. The various lamp types attracted insects in relation to the amount of short wavelengths emitted. Bats were attracted to the same lamp types as insects.

5. The gross energy intake of *E. nilssonii* foraging around streetlamps was more than twice as high (0.5 kJ min⁻¹) as previously recorded in woodlands (0.2 kJ min⁻¹) but slightly lower than over pastures where dung beetles occurred (0.6 kJ min⁻¹).

6. The results have implications for the conservation of bats. Generally, the fast-flying species will probably be least likely to suffer from a general decline in insect abundance. Priorities should therefore be given to the needs of the slow-flying bat species.

Key-words: Bat conservation, echolocation, foraging behaviour, habitat use, urban ecology

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Introduction

Flying vertebrates vary considerably in size and wing shape, and the variation is strongly correlated with manoeuvrability and flight speed and hence with the use of space (Norberg 1990). For insectivorous bats, size and wing shape are also correlated with the structure of echolocation calls. Generally, bat species with long and narrow wings fly fast, use long and powerful echolocation calls suited for long-range detection of insects in the open air, while those with short and broad wings are manoeuvrable, fly slowly and use echolocation pulses suitable for short-range detection of insects near vegetation or close to water surfaces (Neuweiler 1989).

The feeding success of aerial insect predators depends both on the abundance of insects and their distribution in space and time (Racey & Swift 1985).

Bats and swallows, for instance, often tend to exploit insects that for one reason or another occur in swarms (Griffin 1958; Fenton & Morris 1976; Gould 1978; Shields & Bildstein 1979; Bell 1980; Turner 1982; Belwood & Fullard 1984; Kronwitter 1988). Artificial light sources attract insects, which sometimes form dense aggregations. Indeed, because of streetlamps, bats frequently feed in villages and even in urban and suburban areas (Fenton, Merriam & Holroyd 1983; Geggie & Fenton 1985; Haffner & Stutz 1985/86; Baagøe 1986; Furlonger, Dewar & Fenton 1987; Schnitzler *et al.* 1987; Barak & Yom-Tov 1989; Rydell 1991).

The aim of this study was to investigate the relationship between streetlamps, insects and foraging bats in southern Sweden. Specifically, the following questions were addressed: (1) Which bat species take advantage of streetlamps and which do not, and how is the exploitation of streetlamps related to the flight style and echolocation calls of bat species? (2)

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How does the spectrum of the light source and the structure of the surroundings influence the attractiveness of streetlamps to insects and bats? (3) Do bats really benefit energetically from the occurrence of streetlamps?

At present, several European bat species show declining population trends. In many cases, the most likely reason for this is a decline in the abundance of certain insects, due to changing agricultural practices (Stebbins 1988). In contrast to many other habitats, illuminated streets and roads may attract insects and hence provide a resource for bats that is likely to persist. Hence, the extent to which different bat species may take advantage of streetlamps is an important conservation issue.

Study area

The study was carried out in the province of Västergötland in south central Sweden in April and early May and from late July to early October 1990 and 1991. In Sweden, summer nights are not really dark around the summer solstice, except in overcast weather. Therefore, artificial lights attract few nocturnal insects and hence bats from late May to mid-July (Rydell 1991).

Bats were monitored on foot in a small-scale farmland area called Valle (about 7500 ha; 58°25'N, 13°40'E). Part of this area is maintained as nature reserves for protection and management of structurally diverse and biologically rich mixtures of deciduous woodlands, lakes and farmland. Bats were also monitored from a car in and around the town of Ulricehamn (57°45'N, 13°25'E), where insects around streetlamps were also monitored. This town has c. 10000 inhabitants. Its surroundings are biologically less diverse than Valle, and consist mostly of coniferous forests and oligotrophic lakes. During the preliminary part of the study, bats were also monitored from a car in some other villages and towns in the same province.

Materials and methods

MONITORING OF BATS

Bats were monitored by two methods, both based on a D-960 ultrasound detector (Pettersson Elektronik, Uppsala, Sweden), which is equipped with three different monitoring systems: a heterodyne (tuned) mode, a frequency division (broadband) mode and a time expansion mode. The latter system relies on a digital memory. In combination with a cassette tape recorder, this system is equivalent, in practice, to a high-speed tape recorder.

The first objective was to identify which species of bats exploited insects around streetlamps. I searched on foot through 35 selected plots (each about 0.5 ha)

representing different foraging habitats away from streetlamps (forests, woodlands, pastures, arable fields and lakes) and eight plots in small villages with streetlamps. By eye and the bat detector (visual observations facilitated by the relatively good light conditions prevailing at 58°N in summer), the minimum number of each bat species that foraged in each plot during 30-min periods was estimated. Two or more observations of the same species in a plot were scored as one bat unless the observations were made more or less simultaneously and hence must have represented different individuals. Hence, the number of bats scored for each plot is an underestimate of the true number. Each plot was searched once. Foraging in all species, except *Plecotus auritus* Linnaeus 1758, was defined by the occurrence of 'feeding buzzes', i.e. the marked increase in echolocation pulse repetition rate associated with prey captures (Griffin, Webster & Michael 1960), and/or quick deviations from a more or less straight flight path. Since *Plecotus auritus* sometimes catches insects without the emission of such feeding buzzes (Anderson & Racey 1991), it was assumed that all individuals of this species were foraging when encountered.

To simultaneously monitor all bat species, the detector was set in the broadband mode (frequency-division by 10). In some cases, where species identity was not immediately evident, pulses were recorded via the time expansion system on a cassette tape recorder (Sony TC-D5M) for later analysis. *Myotis* spp. could not always be identified to species. All species of this genus were therefore considered together. To verify which *Myotis* species were actually present, the entrances to underground quarters, mines and cellars were mist netted on eight nights during the swarming period (August) in 1991. Sixty *Myotis* of four species were caught (41 *M. daubentoni* (Kuhl, 1819), 12 *M. brandtii* (Eversmann 1845), five *M. mystacinus* (Kuhl 1819) and two *M. nattereri* (Kuhl 1818).

The subsequent monitoring of bats around streetlamps was concentrated on *Nyctalus*, *Vespertilio* and *Eptesicus*. To maximize sampling efficiency, these species were monitored simultaneously from a moving car. The detector was pointed obliquely upwards through the side window, while the car was driven at 40–50 km h⁻¹. This speed allowed each individual bat to be detected and separated. Since broadband monitoring included too much of the noise generated by the moving car, the narrow-band (heterodyne) mode of the detector was used in this case. The detector was tuned to 27 kHz, which permitted frequencies between approximately 22 and 32 kHz to be detected. Hence, the three species could be monitored simultaneously, and were distinguished by differences in pitch and pulse repetition rate. The detection distance was about 50 m for *E. nilssonii* (Keyserling & Blasius 1839) and probably a little

longer for *V. murinus* Linnaeus 1758 and *N. noctula* (Schreber 1774) (Ahlén 1981, Rydell 1991).

Repeated (13 evenings) detector monitoring was made from the car along a 27.4 km transect, composed of 18 sections, each 0.5–3.1 km long and all bordered by streetlamps, in the town of Ulricehamn. Each section was classified as 'urban' (i.e. near the town centre; mostly buildings, much traffic, very little vegetation), 'industrial' (mostly small industries surrounded by open areas, little vegetation except a few trees), 'residential' (mostly one- or two-storey houses, parks and gardens) or 'rural' (farmland and forest, relatively few buildings). For each section, the following were determined: the type of streetlamp (spectrum); the fraction of the section that was bordered by trees (an index of wind exposure); the density (no. km⁻¹) of buildings within 100 m from the road (an index of roost availability); the mean distance from the town centre (an index of noise and pollution level).

MONITORING OF INSECTS

Relative insect densities around streetlamps were determined photographically, using a Nikon camera with a 105-mm lens and a Metz 60 CT-4 electronic flash at a distance of about 10 m from the light. Ektachrome 100 ASA 24×36 mm slide film was used and $f=5.6$. Focus was on the lamp. Some photographs were also taken midway between two lamps and at lamps which were switched off temporarily. The numbers of insects visible as white dots on the film were counted. No attempt was made to distinguish between different types or sizes of insects. Most photographs were taken within 150 m from street-crossings, where two types of lamps were available in more or less the same place. In most cases, three adjacent lamps were photographed in each locality (street). One photograph was taken per lamp.

Three types of streetlamps occurred in the study area: 125 W Hg lamps which give a bluish white light, 100 W high-pressure Na lamps with a light orange light and 100 W low-pressure Na lamps with deep-orange light. The spectrum of each of these is shown in Fig. 1. The lamps were situated 7–8 m above the ground. The distance between adjacent lamps was normally 30 m near the town centre and 50 m in the surrounding residential and rural areas.

OBSERVATIONS OF BATS AND INSECTS

Insects and foraging bats (*E. nilssonii*) were observed in the vicinity of a maternity roost near Ulricehamn. The bats, all adult females, were captured in mist nets when they emerged from the roost at dusk and were marked with rings (Lambournes Ltd, Birmingham, UK) covered by reflective tapes in individual colour combinations (Rydell 1986).

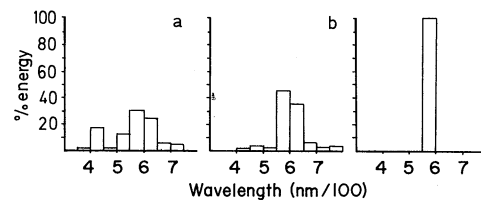


Fig. 1. Spectra of the three types of streetlamps used in the study area. (a) White (Hg), (b) light-orange (high-pressure Na) and (c) deep-orange (low-pressure Na) lamps. These data were kindly provided by Osram AB, Stockholm.

When the bats fed on large insects (moths or dung beetles), what they caught could normally be seen. The attack rates were determined with the bat detector and a stop watch during 2–5-min samples. An attack was defined by a sudden change in flight direction immediately followed by a feeding buzz. The capture success was determined by watching a specific insect until it was attacked by a bat. The fates of moths around streetlamps could usually be seen easily, but attacks on beetles were more difficult to follow visually. In this case, successful captures were either scored after seeing the bat catching the beetle or, in most cases, after hearing the bat chewing the insect immediately after the attack. These observations were made during 15 nights in July and early August (the lactation period of the bats).

Samples of the insect species that were observed to be attacked by the bats were collected with a hand net on the nights when the observations were made. They were dried in an oven at 70°C and then weighed on an electronic balance. Energy content of these insects was assumed to be 22 J mg⁻¹ (Krebs & Avery 1985).

STATISTICS AND NOMENCLATURE

Where the data obtained were not normally distributed, non-parametric statistics were used (Siegel & Castellan 1988). ANOVA was performed on log-transformed data (Wilkinson 1990). Nomenclature of bats follows Corbet & Harris (1991) and that of insects follows Chinery (1986).

Results

SPECIES OF BATS FEEDING AT STREETLAMPS

The broadband monitoring revealed a minimum of 140 foraging bats of six genera (probably nine species). Four of the species [*N. noctula*, *V. murinus*, *E. nilssonii* and *Pipistrellus pipistrellus* (Schreber 1774)] foraged around streetlamps, but one of them (*Pipistrellus pipistrellus*) was observed to do so only once (Fig. 2). *Myotis* spp. (probably four species) and *Plecotus auritus* were only observed away from streetlamps. The differential use of streetlamps by the various bat species (genus) was highly significant ($\chi^2=40.2$, $df=5$, $P<0.001$).

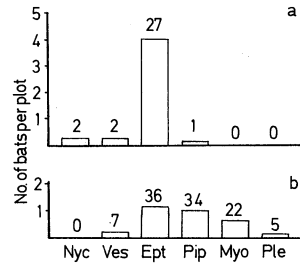


Fig. 2. The minimum number of foraging bats per 0.5-ha plot in Valle, south Sweden, in August 1991 as indicated by observations with a bat detector and visually in (a) villages with streetlamps ($n=8$ plots) and (b) other habitats away from streetlamps ($n=35$ plots). Each plot was searched once for 30 min. The bat species are *Nyctalus noctula* (Nyc), *Vespertilio murinus* (Ves), *Eptesicus nilssonii* (Ept), *Pipistrellus pipistrellus* (Pip), *Myotis* spp. (Myo) and *Plecotus auritus* (Ple). The numbers above the bars represent the total number of foraging bats observed.

Eptesicus nilssonii was by far the most numerous species in the illuminated areas, comprising 86% of the observations ($n=37$). Several individuals were present in each of the eight plots (Fig. 2).

DISTRIBUTION OF BATS IN RELATION TO LAMP TYPE AND SURROUNDING HABITAT

During a preliminary survey along 20.2 km of road through nine villages (0.4–2.9 km per village), each illuminated either by white (Hg) or orange (Na) lights, a total of 61 bats were observed (3.0 bats km^{-1}). Of these, 58 (95%) were *E. nilssonii*. This species occurred in seven (78%) of the villages. *Nyctalus noctula* was only detected once and *V. murinus* twice (two villages). Bat density differed considerably between the villages illuminated by white (Hg) lamps ($n=7$) and those illuminated by orange (Na) ones ($n=2$); on average 5.52 and 0.52 bats km^{-1} , respectively ($t=1.95$, $df=8$, $P=0.088$; Fig. 3). Hence, preliminary data seemed to suggest

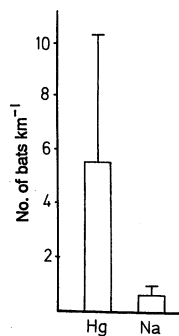


Fig. 3. Density (mean+SD) of foraging bats in villages illuminated by white (Hg) and orange (Na) streetlamps ($n=7$ and 2, respectively) in the province of Västergötland, south Sweden, as indicated by bat detector observations from a moving car. *Eptesicus nilssonii* represents 95% of the observations ($n=61$).

that variation in bat density among the villages might have been influenced by the type of streetlamps present or, alternatively, by a habitat characteristic associated with it.

This hypothesis was further examined by repeated (13 times) monitoring of bats along a 27-km transect in the town of Ulricehamn. In this case, lamp type as well as several other habitat characteristics were recorded for each of 18 sections of the transect. Altogether, *E. nilssonii* was detected 342 times (91% of the observations) and *V. murinus* 34 times (9%) (Fig. 4). *Nyctalus noctula* was not observed.

The average density of bats along the transect was highest in summer (July–August; 1.82 bats km^{-1}) followed by autumn (September–October; 1.13 bats km^{-1}) and spring (April; 0.64 bats km^{-1}). These differences are not significant ($P>0.05$, $df=2$, Kruskal–Wallis test). In the following analysis, therefore, data were pooled across seasons.

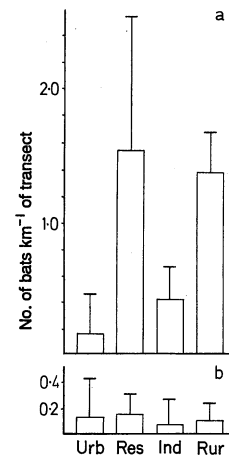


Fig. 4. Density (mean+SD) of foraging (a) *Eptesicus nilssonii* and (b) *Vespertilio murinus*, as indicated by a bat detector from a car moving along a transect ($n=13$), in urban (Urb), residential (Res), industrial (Ind) and rural (Rur) parts of a small town in south Sweden.

On average, *E. nilssonii* was about five times more abundant in the residential and rural sections of the transect, i.e. areas including woodlands, parks or gardens, as compared to the urban and industrial sections, where little natural vegetation remained ($P<0.001$, $df=3$, Kruskal–Wallis test). This was not the case for *V. murinus*, which was found at a similar density throughout the town and the surrounding rural areas ($P>0.05$, $df=3$, Kruskal–Wallis test).

The average density of *E. nilssonii* in each section of the transect was positively associated with the short-wavelength content of the streetlamps ($r_s=0.678$, $n=18$, $P<0.005$; three lamp types) and also with the occurrence of trees ($r_s=0.657$, $n=18$, $P<0.005$). It was not associated with the density of buildings or the distance from the town centre

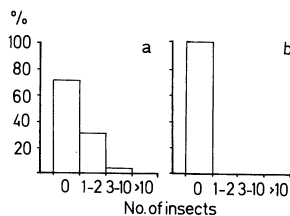


Fig. 5. Frequency distribution of insect densities around (a) white streetlamps ($n=23$) and (b) 20–30m away from streetlamps ($n=23$) in April and May as determined from flash photographs.

($P>0.05$). A two-way ANOVA confirmed that bat density was associated both with lamp type ($F=3.91$, $df=2$ and 13 , $P<0.05$) and the presence of trees ($F=10.40$, $df=1$ and 13 , $P<0.01$; the interaction term was not-significant).

The occurrence of *V. murinus* was not associated with any of the four habitat variables ($P>0.05$). Likewise, occurrence of the two bat species was not associated ($r_s=0.222$, $n=18$, $P>0.05$).

DISTRIBUTION OF INSECTS IN RELATION TO THE TYPE OF STREETLAMP

Insects were attracted to streetlamps. Among the spring samples, insects were more often visible on the photographs taken towards the lamps than on those taken in the same manner midway between two adjacent lamps (30% and 0%, respectively, $n=23$ in both cases: $\chi^2=8.5$, $df=1$, $P<0.01$; Fig. 5).

The photographs taken in late summer and autumn showed a similar result, but since insects were much more abundant at this time of the year, a more detailed analysis could be made. Insects were visible around 52% ($n=113$) of the lamps that were in use and the corresponding frequency for switched-off lamps was 17% ($n=12$) ($\chi^2=5.5$, $df=1$, $P<0.05$). The number of insects per lamp also differed significantly between these two groups. At five street-crossings, where some lamps were in use and some were switched off, the lamps in use always attracted more insects than the ones which were switched off (0.2–26.5 and 0.0–0.3 insects per lamp, respectively, $P=0.03$, Wilcoxon's Signed Ranks test).

The different lamp types attracted insects differently ($\chi^2=17.6$, $df=6$; Fig. 6). Insects were most abundant around the white (Hg) lamps, but also

occurred with rather high frequencies around the light-orange lamps (high pressure Na). At 13 street-crossings, where both white and light orange lamps occurred, the white ones attracted most insects (0.3–49.0 and 0.0–9.5 insects per lamp, respectively, $P=0.002$, Wilcoxon's Signed Ranks test). Deep-orange lamps (low pressure Na) did not attract insects. In fact, the number of insects visible around these lamps was as low as around lamps which were switched off ($\chi^2=1.65$, $df=1$, $P=0.20$).

OBSERVATIONS OF INSECTS AND FORAGING BATS

To determine if streetlamps could affect the energy intake of bats, I observed *E. nilssonii* foraging at two regularly used feeding sites, situated within 200m of a maternity roost: (a) along a row of streetlamps where moths (mostly *Cerapteryx graminis* Linnaeus) occurred and (b) over a pasture, away from the streetlamps, where dung beetles (*Aphodius* spp. and *Serica brunnea* Linnaeus) were found in abundance.

The gross energy intake, assuming that whole insects were eaten, was high (0.5–0.6 kJ min^{-1}) both over the pasture and around the lamps. Dung beetles were fairly large and also relatively easy to catch (100% capture success). Although the moths were even larger, they escaped from the approaching bats in most cases (only 36% capture success) (Table 1).

Discussion

Various species of bats (genus in the case of *Myotis* spp.) showed different tendencies to feed around streetlamps in the study area. In fact, the percentage of the observations that were made near lamps (Fig.

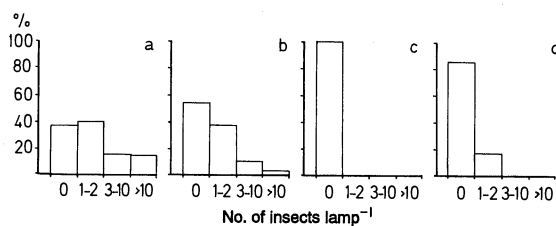


Fig. 6. Frequency distribution of insect densities around (a) white ($n=52$), (b) light-orange ($n=52$), and (c) deep-orange ($n=9$) streetlamps and (d) streetlamps that were switched off ($n=12$) as determined from flash photographs taken between July and October.

Table 1. Gross energy intake of female *Eptesicus nilssonii* as estimated from close observations of insects and bats foraging near streetlamps and over pastures 100–200m from the lamps

Feeding site	Prey type	Attack rate (min^{-1})	Capture efficiency (%)	Prey mass (mg dry weight)	Gross energy intake (kJ min^{-1})
Street	Moths	1.58 ($n=34$)	35.7 ($n=56$)	40.0	0.50
Pasture	Beetles	2.62 ($n=24$)	100.0 ($n=24$)	10.0	0.58

2) were correlated with the species' (genus') average wing loading [ranked after the data in Norberg & Rayner (1987); $r_s=0.88$, $n=6$, $P<0.05$], the average speed in straight flight [ranked after data in Baagøe (1987); $r_s=0.84$, $n=6$, $P<0.05$], the duration of the most common echolocation pulses used in search flight [ranked after data in Ahlén (1981); $r_s=0.93$, $n=6$, $P<0.05$] and the most common pulse repetition rate in search flight [ranked after data in Ahlén (1981); $r_s=-0.93$, $n=6$, $P<0.05$]. These correlations imply that only those species that fly relatively fast and straight and use echolocation pulses suited for long-range detection of insects were likely to be found near the streetlamps. The relatively slow-flying, manoeuvrable species, that use short-range detection foraging strategies, in this case the *Myotis* and *Plecotus* species, did not feed around the lamps at all.

Eptesicus nilssonii and *V. murinus* were frequently encountered near the lamps in the study area and *N. noctula*, as well as most *Pipistrellus* spp., are known to exploit streetlamps elsewhere (Haffner & Stutz 1985/86; Schnitzler *et al.* 1987; Kronwitter 1988; Barak & Yom-Tov 1989). The wing shapes and echolocation pulses of all these species are suited for foraging in straight flight in relatively open areas (Norberg & Rayner 1987). *Eptesicus nilssonii* normally forages below tree-top level and hence may take advantage of the wind shelter formed by trees. This is in contrast to *V. murinus* and *N. noctula* (Baagøe 1987).

Of the pipistrelles, only *Pipistrellus pipistrellus* occurred in the study area and it was only once encountered near streetlamps. However, this species is known to feed around streetlamps in areas with little competition from other species that use a similar foraging technique, e.g. other *Pipistrellus* species (Haffner & Stutz 1985/86). In the present case, it might, therefore, have been competitively excluded from the streets by the larger and commoner *E. nilssonii*.

The energy intake of *E. nilssonii* that fed on moths at streetlamps and of those feeding on dung beetles over the pasture was more than twice as high as the energy intake of the same bats feeding on dipterans (0.2 kJ min^{-1}), as they do during most of the summer (Rydell 1989). Illuminated streets and roads seem to be relatively profitable for bats that are adapted to exploit this habitat.

Urban parts of big cities presumably have depleted insect faunas (Taylor, French & Woiwod 1978; Frankie & Ehler 1978), and few bats may be able to survive there (Geggie & Fenton 1985; Kurta & Teramino 1992). On the other hand, the situation may be very different in small towns and villages, since insects may be attracted from surrounding habitats over the relatively short distances involved.

The results of this study should have implications for conservation of bats in Europe and elsewhere.

Bats of the genera *Nyctalus*, *Vespertilio*, *Eptesicus* and *Pipistrellus* seem to suffer less from a general decline in insect abundance than bats of the genera *Myotis* and *Plecotus*. There is limited evidence that *E. nilssonii*, *V. murinus* and *P. pipistrellus* populations in northern Europe have increased recently (Zukal & Gaisler 1989; Ahlén & Gerell 1990; Speakman *et al.* 1991a,b), and it is tempting to speculate that the relative success of these species is at least in part an effect of an increased number of streetlamps. At present, there is little evidence of population declines in any *Nyctalus*, *Vespertilio*, *Eptesicus* or *Pipistrellus* species in northern Europe, with the possible exception of *N. noctula*, which depends on tree holes for roosting. In contrast, population declines are frequently recorded in several *Myotis* and *Plecotus* species (e.g. Stebbings 1988; Speakman *et al.* 1991a).

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