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# Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*

Jens Rydell

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Foraging northern bats *Eptesicus nilssoni* were monitored from a car along a 27 km line transect in southern Sweden every week during a 14 month period by means of a bat detector. The number of bats observed along the transect was highly correlated with air temperature, and no bats were observed at temperatures < 6°C. Hence, feeding was infrequent in April and May as well as in September and October and did not occur at all from November to March. In summer, the bats were observed in forest and farmland, but in spring and autumn most bats were detected along rows of street-lights. By attracting insects, artificial lights apparently provide local patches of food for some species of bats during periods which may be critical for their survival and reproduction.

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## Introduction

The northern bat *Eptesicus nilssoni* is a strictly insectivorous (Rydell 1986) vespertilionid which is very common in Scandinavia (Ahlén and Gerell 1990). The females form maternity colonies in heated houses at traditional sites in late May or early June, and give birth about a month later. The maternity roosts are abandoned as the young start to fly in late July or early August (Rydell 1989a and unpubl. data). The northern bat is considered non-migratory (Strelkov 1969), and both sexes hibernate in the study area in small groups in cellars and houses from November to March (Rydell 1989b). Their behaviour during spring and autumn has not been studied.

One aim of this study was to identify the key feeding habitats of the northern bat particularly during spring and autumn. Access to good feeding sites early in the year is critical for successful reproduction of bats at high latitudes (Racey and Speakman 1987, Rydell 1989a). The feeding conditions prevailing in autumn is probably also critical, especially for young bats, since juvenile survival through the first winter is low (Tuttle and Stevenson 1982).

The second aim was to study how the northern bat allocates its feeding efforts at various seasons in relation to weather conditions. In summer, reproducing females maximize their energy budget by restricting their flight activity to relatively warm (> 6°C) evenings, when insect densities exceed a threshold level and feeding is energetically profitable (Rydell 1989a). Can energetic considerations explain the patterns of activity observed at other seasons as well?

## Study area

Flying bats were monitored along roads forming a 27.3 km line transect on the countryside north of the town Ulricehamn in southern Sweden (57°45'N, 13°25'E). This area is situated about 300 m a.s.l. and is characterized by a mixture of coniferous forests, small farms and villages.

The transect was divided into nine sections according to the surrounding habitats. Mature coniferous forests bordered two sections, together comprising 16% of the transect. Farmland, consisting of small fields, pastures

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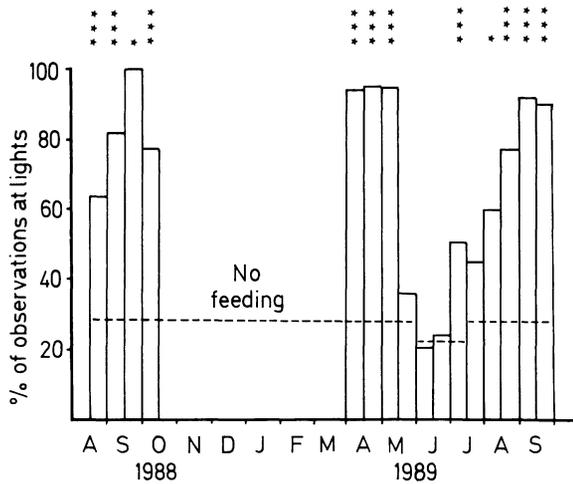


Fig. 3. Percentages of total number of observations each fortnight period that were made in illuminated sections of the transect. The horizontal dashed line shows the frequency expected if distribution of bats was unaffected by street-lights. Asterisks give significance values of differences between observed and expected frequencies ( $\chi^2$ -tests, d.f. = 1,  $p < 0.025^*$  or  $p < 0.001^{***}$ ).

to about 200 Hz after detection of a prey item (Griffin et al. 1960). Statistical analyses were made according to Sokal and Rohlf (1981).

## Results

### Activity patterns

Northern bats were observed along the transect from April to October but only irregularly before the middle of May and after the middle of September (Fig. 1). No bats were detected in winter (November–March).

When the winter months were excluded, evening to evening differences explained 70.5% of the variation, but there were still significant differences between months (one-way ANOVA;  $F = 3.03$ , d.f. = 8 and 36,  $p < 0.005$ ). On average, the highest number of bats were observed in July and August (Fig. 1). There was no significant correlation between the time (in relation to sunset) when I started to drive along the transect and the number of bats observed ( $r_s = -0.23$ ,  $N = 45$ ,  $p > 0.05$ , winter months excluded).

There was a highly significant positive correlation between the number of bats observed each evening and the air temperature ( $r = 0.72$ , d.f. = 53,  $p < 0.001$ , Fig. 2). No bats were active at temperatures  $< 6^\circ\text{C}$ . Evening temperatures remained  $< 7^\circ\text{C}$  throughout the winter ( $md = +3^\circ\text{C}$ , range  $-6$  to  $+6^\circ\text{C}$ ,  $N = 19$ ).

Wind speed also had a significant effect on activity. Fewer bats were observed during evenings with moderate to very strong wind than during evenings with slow

wind or no wind at all (ANCOVA with temperature as covariate; difference in adjusted mean,  $F = 11.2$ , d.f. = 1 and 45,  $p < 0.005$ ). No effects of light rain, mist or moonshine could be detected, but no bats were observed in heavy rain. However, when the temperature was  $11\text{--}15^\circ\text{C}$  (3 evenings), activity was inhibited only temporarily by heavy showers and was resumed as soon as the rain declined in intensity. In contrast, no bats at all were recorded during two evenings when showers of rain coincided with temperatures of  $8\text{--}9^\circ\text{C}$ .

The relationship between the number of bats observed and prevailing air temperature was not significantly different between the spring (April–May), summer (June–July) and autumn (August–October) months (ANCOVA with temperature as covariate: difference in slope,  $F = 2.59$ , d.f. = 2 and 47,  $p > 0.05$ ; difference in adjusted mean,  $F = 0.41$ , d.f. = 0.41, d.f. = 2 and 49,  $p > 0.5$ ).

### Habitat selection

Bat densities (number of observations  $\text{km}^{-1}$ ) did not differ significantly between the sections of the transects which were not illuminated with street-lights (“forest”, “farmland” and “village”) (one-way ANOVA;  $F = 0.70$ , d.f. = 2 and 63,  $p = 0.5$ ). Likewise, the density did not differ significantly between the four villages that were illuminated (one-way ANOVA;  $F = 0.27$ , d.f. = 3 and 92,  $p > 0.5$ ). Hence, the transect could be regarded as composed of a “light” and a “dark” section only.

On average, the density of bats was about five times higher along the illuminated sections of the transect than along the “dark” ones (mean and S.D. were  $1.87 \pm 1.72$  and  $0.38 \pm 0.41$  bats  $\text{km}^{-1}$ , respectively) (one-way ANOVA;  $F = 26.4$ , d.f. = 1 and 72,  $p < 0.001$ ). However, since habitat use varied strongly with the season (see below), densities were about 20 times as high in illuminated sections as in dark ones in spring and autumn ( $2.36 \pm 1.41$  and  $0.11 \pm 0.12$  bats  $\text{km}^{-1}$ , respectively).

Street-lights illuminated 29% of the transect (23% in June and early July, when some lights were not used). Hence, 29 (23)% of the bats were expected to occur in the illuminated sections, if distribution of bats was not affected by presence of lights. During April and May nearly every bat (95%) was observed in the illuminated sections, and the frequency was nearly as high (87%) in September and October (Fig. 3). In summer, however, the situation was very different, with no concentrations of bats near the lights from the middle of May until late June. In July and August the situation varied from evening to evening but, generally, concentrations of bats around street-lights became more apparent for each successive fortnight period (Fig. 3).

## Behaviour of bats foraging near street-lights

When foraging along the illuminated road, the bats flew rapidly straight back and forth, continuing for at least 100 m before turning back. They normally flew several metres from the lights and the surrounding vegetation. The flight level varied from just above the lights (8 m) to more than twice that height. In most cases, several bats used the same part of the road, flying in overlapping flight paths. However, they occasionally established individual feeding territories, which they defended against other individuals by chasing them and simultaneously emitting low frequency (14 kHz) calls.

Many feeding attempts observed were directed towards moths that were visible in the light cone, and consisted of feeding buzzes associated with low dives reaching 1–2 m above the road. During 75 min of observation of bats that foraged alone, 41 feeding attempts were recorded ( $0.55 \text{ min}^{-1}$ ). Attack rates could not be determined when the bats foraged in groups.

## Discussion

### Activity patterns

The number of bats observed each evening was primarily a function of the air temperature, and no bats were observed unless it was at least  $6^{\circ}\text{C}$ . In spring and early summer, this temperature is a threshold, above which flying insects are abundant enough to permit the energy intake to exceed the flight cost, making foraging energetically profitable for a northern bat (Rydell 1989a). Similar observations have been made on winter feeding pipistrelle bats (*Pipistrellus pipistrellus*) in England (Avery 1985).

Reproducing females of bats at high latitudes are apparently reluctant to fly unless they can maintain a positive energy balance by doing so. Instead, they become torpid during periods when feeding is unprofitable (Racey 1973). Due to low insect densities early in the season and increasing energy demands of pregnancy and lactation there is usually no possibility for reproducing females to store energy for more than two or three day's use (Racey and Speakman 1987, Kurta et al. 1989).

The situation may be different in autumn and winter, however, since energy demands are much lower at least for the females. A northern bat (8–15 g) may perhaps be able to store 5 g of fat before hibernation, representing about 200 kJ of available energy, some of which may be used for flight during periods when feeding is unfeasible. However, with a minimum flight cost of about  $7.1 \text{ kJ h}^{-1}$  (calculated according to Norberg 1990), a northern bat would deplete its entire energy store in about 28 h of flight activity, considering the cost of locomotion alone. Profitable feeding conditions only occur infrequently and at unpredictable intervals in autumn and

probably not at all in winter. Therefore, it is likely that the northern bats also in these seasons restrict most of their activities to periods when energy stores can be resupplied more or less immediately. This hypothesis is supported by the current data, if it can be assumed that there is a correlation between aerial insect density and temperature in autumn and winter as there is in spring and summer (Rydell 1989a).

The number of bats detected each evening was highest in July and August. This was expected due to increasing energy requirements associated with pregnancy and lactation in females (Anthony and Kunz 1977, Barclay 1989, Kurta et al. 1989) as well as due to the appearance of juveniles at the feeding sites.

The bat activity in spring and autumn was probably overestimated as compared to summer, because of the seasonal concentrations of bats around the roads. This bias probably masked the seasonal differences to some extent.

### Habitat selection

Wing morphology (Baagøe 1987) and echolocation call characteristics (Ahlén 1981) of the northern bat suggest that it is adapted for straight flight in open habitats and for long-range detection of insects. These suggestions have been substantiated by field observations in summer, when foraging usually takes place along rows of trees or over water (Rydell 1986, Baagøe 1987). The hunting technique used along the illuminated road was very similar to the one previously observed in other habitats.

It is well known that some species of bats are attracted to artificial lights in order to exploit accumulations of insects, particularly moths (Griffin 1958, Bell 1980, Belwood and Fullard 1984, Haffner and Stutz 1985/86, Baagøe 1986, Schnitzler et al. 1987, Barak and Yom-Tov 1989). Significant concentrations of bats were only observed in villages illuminated by street-lights. This supports the hypothesis that the northern bats were attracted to the villages by the lights and not by the houses.

The period between the disappearance of the bats from the street-lights in May and their appearance again in late summer coincided with occupation of maternity roosts (Rydell unpubl. data). In the study area, only a minority of the maternity roosts known (23%,  $n = 13$ ) are situated in villages illuminated with street-lights. Instead, most of them occur in more or less isolated houses in areas without street-lights. Perhaps, there is a movement of bats from illuminated areas in villages to maternity roosts in farmland and forests early in the summer, when street-lights presumably cease to provide insects due to the twilight conditions prevailing around midsummer, and back in late summer as nights become darker again. Unfortunately, this hypothesis can not be

substantiated, since only a few spring and autumn roosts are known.

The use of illuminated areas ceased rather abruptly in May. In contrast, the bats' return to the street-lights in late summer was a more gradual process, perhaps reflecting differential behaviour of adults and juveniles.

Seasonal movements between farmland and urban areas have been observed in *Vespertilio murinus*, another insectivorous bat, in Denmark (Baagøe 1986). This species forms maternity colonies in houses on the countryside in summer, and apparently congregates in towns and cities during the rest of the year.

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