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Factors affecting the distribution pattern of bats in Uppland, central Sweden

Johnny de Jong and Ingemar Ahlén

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Bats were surveyed and insects were trapped in several different habitats to test the hypothesis that insect abundance and types are the most important factors affecting the regional distribution of bats. A bat community of ten species dominated by *Eptesicus nilssoni* and *Pipistrellus pipistrellus* was analysed. The results show that the general pattern of bat distribution in different habitats, and the seasonal changes in habitat utilization, could be explained in terms of the abundance of swarming insects, mainly chironomids. Deciduous woodland near water provided essential habitat in early summer for each bat species. Later on, in July, all species spread out to many different habitats. In autumn street-lamps were an important factor affecting bat distribution.

J. de Jong and I. Ahlén, Dept of Wildlife Ecology, Box 7002, S-750 07 Uppsala, Sweden.

Introduction

Bats are usually unevenly distributed within a region. For instance, from preliminary observations in the Swedish province of Uppland (Ahlén unpubl. data) we know that limited areas, with deciduous woodland, near some lakes, are extremely rich bat habitats. This is in sharp contrast to the open agricultural landscape and conifer dominated forest areas, which are very poor in both terms of species diversity and number of individuals. There were also differences in bat activity within each area during the season. The purpose of this study was to identify factors that may explain the unevenness and the seasonal changes in the distribution pattern of bats in the province of Uppland.

Postulated factors affecting the distribution pattern of local bat fauna include: 1) Predators, 2) Inter and intraspecific competition, 3) Availability of roosting places and hibernation sites, 4) Insect abundance.

There are reasons to regard number 1–3 as being of less importance than number 4 in determining the pattern of distribution. There are no predators specialised upon bats in northern Europe and the enemies of bats in general are relatively few (Gillette and Kimbrough 1970). Competition between and within species can play an important role in the hunting strategies and spacing out in the hunting habitats. However, we find it unlikely that competition is a main factor behind the distribution pattern of the bats on a landscape scale, which is the topic of this paper. One of our best reasons for this view is the regular occurrence of very dense concentrations of all species and all specimens within very small areas. Utilization of foraging habitat may be influenced by roost availability (Kunz 1982, Geggie and Fenton 1985). However, it is common that bats fly several km between their roost and their hunting grounds (Racey and Swift 1985) and hollow trees and suitable buildings are frequent in Uppland. The last hypothesis, that the insect abundance is an important factor, is supported by the fact that the foraging strategy of bats is very energy consuming (Burnett and August 1981, Avery 1985).

Most bats are opportunistic feeders (Fenton 1982), and are quick to exploit swarms of insects. There are only a few examples of bats specialized on certain insect taxa (Buchler 1976, Vaughan 1977, Bauerova 1978, Black 1979). There are however great differences in flight-speed, maneuvrability, ultrasound etc. (Fenton 1982, Baagoe 1987). Each species of bat can only use a

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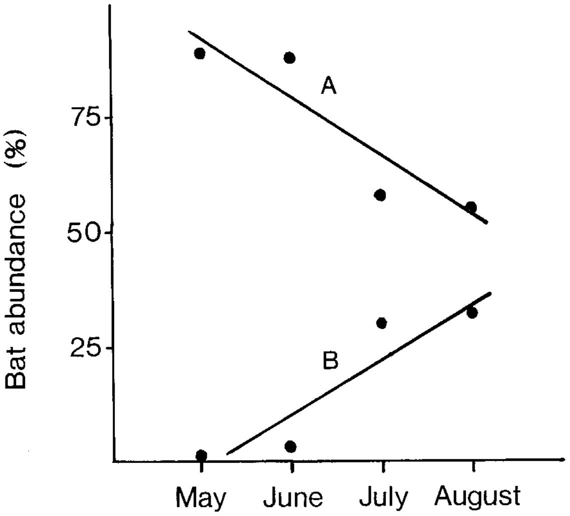

Fig. 1. Proportion of bats occurring in different habitats based on observations in sample plots. A = deciduous woodland near eutrophic lake. B = open habitat (clear-cutting, meadows, fields, pasture). The number of bats in habitat A is significantly higher than the number of bats in habitat B during May and June (U-test, $p < 0.01$, $n = 28$).

limited part of the insect fauna and conversely different bat species need different types (size, flight behaviour, availability) of insects. What then is the right type of insects? This has been examined in a lot of studies, mostly using fecal or stomach content analysis (Black 1972, Anthony and Kunz 1977, Advani 1983, Rydell 1989). Our main hypothesis is that the abundance of insects is the most important factor affecting the regional distribution of bats (Racey and Swift 1985), and out field study is designed to test this idea.

Several factors affect insect abundance: occurrence of breeding or hatching sites, climatic conditions, different types of insect attractants such as streetlamps, flowering trees etc. The local abundance of insects may vary widely, both in time and in space (Black 1974, Anthony and Kunz 1977, Barclay 1985, 1986). Thus, bats should only use certain parts of the environment. Is it possible to find correlations between these factors and bat activity? We attempt to answer this question by conducting a survey of bats and insect trapping in the bats hunting area.

Material and methods

Bats were observed and identified with ultrasound detectors D-940 and D-960 (Ahlén and Pettersson 1985) and by visual observations. It was possible to identify the bats to species except for *Myotis brandti* and *M. mystacinus* which, at the time of the investigation, were considered impossible to separate by their sound (Ahlén 1981). It was also possible to determine if the bats were hunting, based on the detection of feeding buzzes (Griffin et al. 1960).

We surveyed bats in 29 small sites (mean area 0.07 km^2) with different combinations of habitats and located with different types of lakes or wetlands in the vicinity. Each site was visited on at least four occasions from May to August, 1988. Line-transects (Ahlén 1982) were made through eight other areas. Two of these were included deciduous woodland close to lake Mälaren. The other six were located in coniferous forests. The microphone of the bat detector was placed in the open sun-roof or on top of the car-roof, making it possible to hear all individuals flying near the road. Some parts in certain areas had also to be investigated on foot or by using bicycles. In all places special routes were followed on each visit. Positions of bat observations were marked on maps. The line-transects were done during May to 20 September, 1987 and 1988. All our study-areas and line-transects were located within 60 km from Uppsala. During the survey following data were noted: species, number of individuals, type of activity (e.g. hunting), type of habitat where the bats were observed, if there were any other type of habitat nearby and if they were hunting near the substrate (e.g. water, foliage, lamps). Meteorological data, such as temperature, rain, wind direction and wind speed were also taken.

Along three of the line-transects insects were sampled using window-traps and Malaise-traps (Southwood 1966, Kunz 1988) every night. Before the start of each survey the traps were placed 2–5 m above the ground. Four or five traps of each type were used in places where the bats were observed hunting. The traps were taken down a few hours later when the bat survey was finished. Insects were also sampled with sweep-nets on occasions when a lot of bats were hunting in a small area and insect availability was assumed to be critical. The handle of the sweep-net could be extended to 10 m which made it possible to collect insects where the bats were hunting. Sweep-net sampling was done both during 1987 and 1988, while window and Malaise trap sampling was done on 16 occasions 1988.

Results

Altogether 1469 observations of 10 species were made. The most abundant species were *P. pipistrellus* and *P. nilssoni,* and therefore this paper will mainly deal with these two species.

In early summer (May–June), the bats mostly foraged in deciduous and mixed woodland, located near rich wetlands and eutrophic lakes. Later on (July–August) they fed in other habitats including open meadows, area of clear-cuttings and pastures, partially open habitats such as parks and wooded areas, and to coniferous forests and areas located far away from water. Hence, the number of bats hunting in deciduous woodland near eutrophic lakes was significantly greater than the number of bats in open habitats during May and June (U-test, $p < 0.01$, $n = 28$, Fig. 1), but not later in summer.

The importance of eutrophic lakes in May–June was

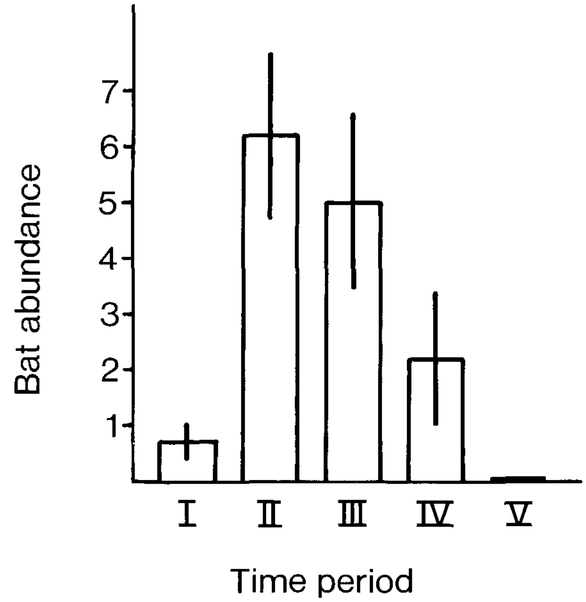

Fig. 2. Abundance of *E. nilssoni* and *P. pipistrellus* hunting along a transect (1200 m) in deciduous woodland near water ($\bar{x} \pm$ S.E.). I = 1–20 May, II = 21 May–30 June, III = 1–31 July, IV = 1–31 August, V = 1–20 September. The difference in insect abundance between period I and II, and between period IV and V is significant (U-test, $p < 0.05$).

also evident from the deciduous woodland-transect (Fig. 2). The figure shows a peak of bat activity hunting near water followed by a decreasing number of bats thereafter.

We divided our 29 study-areas into two groups: A) deciduous and mixed forests near eutrophic lakes or wetlands, B) other habitats. In the first group (A) we found a very high abundance of bats early in the summer. The number of individuals increased rapidly to a peak in early July and many bats remained until September. In the second group (B), the bats arrived later, the abundance was lower and all the bats disappeared quite early (Fig. 3). The results from the line-transect in the coniferous forest also confirm this activity pattern.

At the end of the summer (Aug–Sept) the distribution pattern of bats changed. During this period the bats were very scarce everywhere, except near street-lamps or otherwise illuminated areas. This change of distribution is shown for *E. nilssoni* and *P. pipistrellus* from line-transect in Fig. 4. This figure shows that the street-lamps may also be important in the beginning of the season (May–June).

The results of insect sampling using the Malaise and window traps are shown in Fig. 5. There is a peak in insect abundance in July. The abundance of insects in July is significantly higher (U-test, $p < 0.05$) than in June. Before 20 May insects were very scarce. The number of bat observations was significantly correlated with insect abundance ($r_s = 0.74$, $p < 0.01$, Fig. 6).

More than 90% of the insects sampled with sweep-nets were chironomids of 41 different species. These chironomids were swarming in small patches usually below the canopy of the deciduous woodland. The occurrence of swarming chironomids was often seen to attract a large numbers of bats.

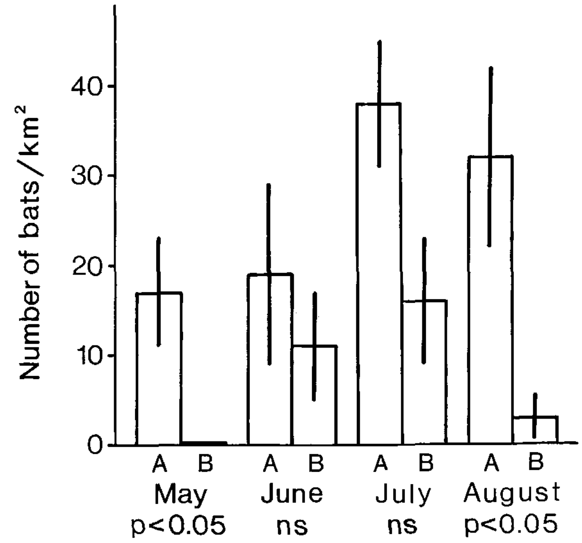

Fig. 3. Abundance of bats ($\bar{x} \pm$ S.E.) in two different types of study-areas. A = deciduous woodland, eutrophic lakes, wetlands. B = open areas, coniferous woodland, dry areas, oligotrophic lakes. There are significantly more bats hunting in type A during May and August.

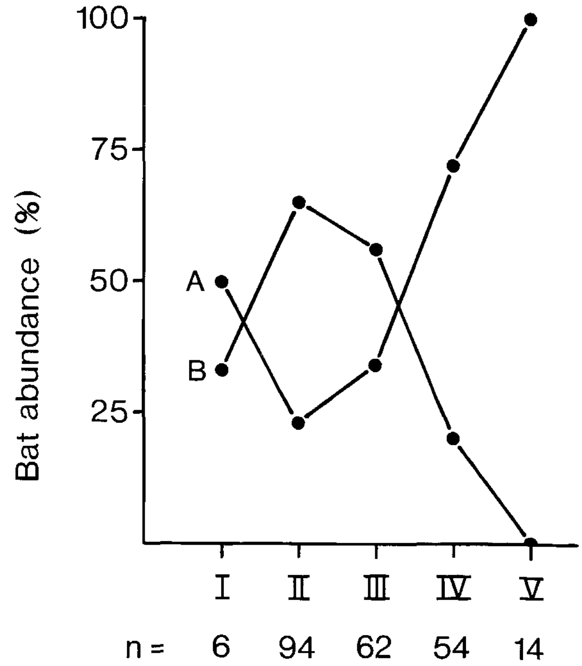

Fig. 4. A: Proportion of bats in the illuminated area. B: Proportion of bats in the dark area. I = 1–20 May, II = 20 May–30 June, III = 1–31 July, IV = 1–31 August, V = 1–20 September. N = number of bat observations.

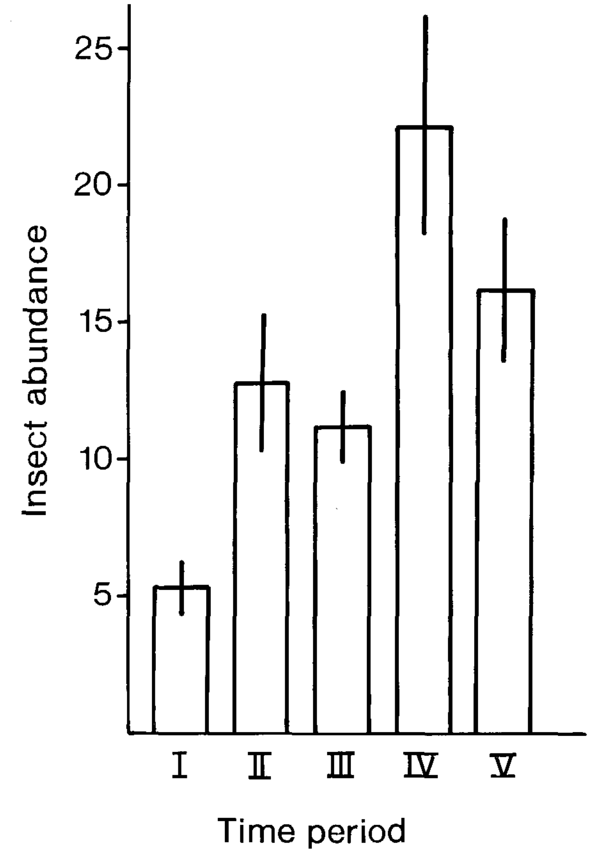

Fig. 5. Insect abundance as number of specimens per sampling ($\bar{x} \pm$ S.E.) during different periods. N = 13. I = 1–20 May, II = 21–31 May, III = 1–30 June, IV = 1–31 July, V = 1–31 August.

Discussion

Our data clearly show that there is an uneven regional distribution of hunting bats and that this pattern change seasonally.

In the early part of the season (May–June) bats hunted only in the deciduous woodland near the lake. Later on, all bats spread out, *E. nilssoni* over all forest types, and *P. pipistrellus* mainly within the deciduous woodland areas. Towards the end of the season (Aug–Sept) bats were more concentrated in the vicinity of street-lamps or other illuminated areas.

Why does the distribution of feeding bats changes during the season? Bats appear to respond to concentrations of insects in deciduous woodland near water during early summer. At this time, insects were scarce except at certain sites, mainly near water, where many of them are hatching. Some specific parts of the deciduous woodland, near the lake shores, were the only localities where insects were abundant. The insects were mainly chironomids which had moved from the lake to the canopy of the deciduous trees where they swarmed in great numbers. Early summer is presumably one of the critical periods for bats, just after hibernation. An abundance of food at this time implies early reproduction which may be important for subsequent survival of young (Racey 1982). All species observed were more or less linked to the deciduous forest near water. This fact shows the importance of these habitats as critical feeding sites for the local bat fauna.

In the middle of the summer (July) more individuals were found hunting, they were present in more types of habitat and were less confined to the lakeshores. They hunted near fields and meadows, and the importance of deciduous woodland decreased. At this time the insect fauna is more diverse and insects are abundant in most habitats.

In September the distribution of hunting bats changed dramatically. Again the bats hunted only in some habitats. At this time however, they were not confined to water, but instead exploited insects in parks and villages with street-lamps. *E. nilssoni* disappeared from the coniferous forests at this time. This is the second critical period for bats, especially the juveniles, because they have to build up their fat reserves before hibernation. It is possible that abundant food in September means high survival during winter (Ransome 1968). During September it becomes dark early in the evening, insects are scarce, and the street-lamps attract insects which bats exploit.

The two most abundant species *P. pipistrellus* and *E. nilssoni* have different flight style, habitat choice and hunting methods. *P. pipistrellus* is very agile and can utilize the insects flying within the canopy. Its ultrasound has a higher frequency and weaker pulses than *E. nilssoni* and this is characteristic of short range-foraging strategy (Barclay 1985). Because of the higher ultrasonic frequencies it is also better at detecting small prey, such as chironomids. *E. nilssoni* is much less agile, has a relatively straight flight, forage in open spaces and emits lower ultrasound frequencies. These differences in hab-

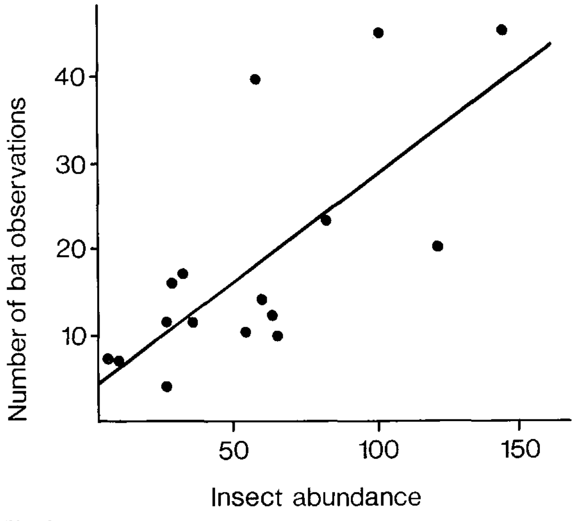

Fig. 6. Correlation between number of bat observations in line transects and insect abundance, $r_s = 0.74$, $p < 0.01$.

itat utilization explain why *P. pipistrellus* can take advantage of the long seasonal activity of insects in the deciduous woodland near water and has its only possibility to survive in areas with such habitats at this latitudes of its northern boundary. Foraging *P. pipistrellus* were observed in such habitats from Mar–Nov, while *E. nilssoni* hunted regularly only from May–Aug. *E. nilssoni* is obviously adapted to survive the long winter by using a short season with great abundance of insects everywhere and a long hibernation period. In the coniferous forest areas the insect activity period was short and *E. nilssoni* was in most cases the only species that occupied these areas. In the earliest part of the season the species was only observed at the chironomid swarming sites in the deciduous woodland.

In summary, this study has shown that there are unique species specific distributional patterns that change throughout the season. Our observations make it possible to predict the abundance and species richness in different parts of the landscape. The data strongly support the hypothesis that availability of insects is the main factor behind these patterns and that landscape elements such as the occurrence of water, deciduous forest and street-lamps are important for insect abundance during critical periods in spring and late summer.

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