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The diet of the Noctule bat *Nyctalus noctula* in Latvia

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Abstract

As indicated by the diet, noctule bats in an agricultural landscape in Latvia feed mostly near or over water; catching predominantly larger non-tympanate insects such as Trichoptera, Ephemeroptera, Coleoptera, and Hemiptera and also Lepidoptera, Neuroptera, and Diptera in smaller numbers. The diet reflects limitations on the echolocation call system and flight characteristics of this large, fast-flying bat. The smallest insects in the diet (ca. 9 mm wingspan) conform in size with what is theoretically predicted, although they are taken in rather small amounts. Therefore, the minimum prey size is probably set by perceptual constraints.

Key words: Chiroptera, echolocation, insects, predation

Introduction

The common noctule (*Nyctalus noctula* Schreber, 1774) is a large (30 g) aerial-hawking insectivorous bat common throughout most of Europe, ranging northward to about 60° N in Scandinavia. Being relatively large with high wing loading (Norberg and Rayner 1987), this bat would be expected to feed on mostly large prey; because it flies fast and uses low frequency (18–26 kHz; Zbinden 1989) echolocation calls to increase the detection range. This would suggest that it probably cannot prey on insects as small as most nematoceran dipterans, which can only be detected over very short distances (Barclay and Brigham 1991).

Previous observations suggest that the noctule specialises on very large insects such as crickets and large scarabaeid beetles (Poulton 1929; Cranbrook and Barrett 1965). However, more recent investigations of this and closely related species indicate that they also feed on small insects such as chironomids (Jones 1995; McKenzie and Oxford 1995; Waters et al. 1995). Thus, the latter observations challenge the earlier reports. It is also possible that the fauna of larger insects were impoverished in urban and intensively farmed areas of southern England where the latter studies were conducted, and that the bats may have responded to nontypical situations prevailing over farm ditches and around street lights.

Other recent studies in continental Europe suggest that the noctule preferentially forages over water, when available, and near street lamps (Kronwitter 1988; Rachwald 1993), feeding mostly on relatively large insects such as mayflies, caddis flies and moths (Gloor et al. 1994; Beck 1995). The purpose of the present study was to investigate the diet of the common noctule in two farmland areas of Latvia, each with high habitat diver-

sity, including several lakes and rivers, and where street lamps are few. This study is the first to investigate the diet of bats in the Baltic area.

Material and methods

Faeces were collected in tree roosts used by colonies of noctules in a small-scale farming landscape (pasture, arable fields, and coniferous and mixed woodlands) of eastern Latvia. The first sample was obtained from a woodpecker hole in a pine (*Pinus silvestris*) in Rucava Village, 10 km east of Lake Pape (56°11′ N, 21°03′ E) in September 1992. The second sample came from a hollow lime tree (*Tilia cordata*) at Janopole, 7 km SSE of Rezekne (56°28′ N, 27°23′ E). In this case, the droppings were collected in June 1995, while bats occupied the roost. The two roosting holes were both situated about 5 m above the ground and within flight distance of lakes and rivers, which we judged to be suitable for foraging. The first roost was located near lake Pape and 4–5 km from the Sventaja River. The second roost was located within 10 km of several small lakes and ponds and about 12 km from Lake Raznas.

The faecal pellets were kept frozen until they were analysed. The droppings were soaked in a mixture of water and ethanol for a few minutes and then teased apart using needles and pointed tweezers under a Wild M5 binocular (dissecting) microscope at 12-40 X magnification. The prey remains were identified according to order ar family by using various field guides (e.g. CHINERY 1986; MCANEY et al. 1991) and a collection of whole insects. The proportions (by volume) of each prey category were estimated for each dropping separately, and the percentages were then averaged. Due to the many potential biases involved in this method (KUNZ and WHITAKER 1983; ROBINSON and STEBBINGS 1993), the percentages should only be regarded as a rough estimate of the dietary composition. We also include the frequency of occurrence of each prey category (the percentage af the faecal pellets in which the category was found). This measure may be less biased, but on the other hand gives almost no indication of the relative importance of the various prey categories. Since it does not add to 100%, it is virtually useless for statistical (comparative) purposes (WHITAKER 1988).

Results

Both samples consisted almost entirely of insects that normally occur near water, suggesting that the bats mostly foraged over lakes and ponds, several of which occurred in the vicinity of the roosts. The first faecal sample (from Rusava) was dominated by beetles (Coleoptera), mainly or exclusively medium-sized water beetles (family Hydrophilidae) and diving beetles (Dytiscidae), together representing 64% of the sample by volume (Tab. 1). The second most important prey category was caddis flies (Trichoptera), mostly af the family Limnephilidae. Moths (Lepidoptera), mayflies (Ephemeroptera), small flies (Di-

Table 1. Recovered remains (%) of arthropod taxa from droppings of *Nyctalus noctula* collected in two tree holes in Latvia. One hundred droppings were analysed from each of the two localities.

Prey category	Locality 1		Locality 2	
	% volume	% frequency	% volume	% frequency
Trichoptera	24	39	36	60
Coleoptera	64	62	2	10
Lepidoptera	4	7	13	28
Ephemeroptera	4	7	13	31
Hemiptera	3	4	15	29
Neuroptera	0	0	9	15
Diptera	2	5	7	16
Siphonaptera	0	0	0	1
Acarina	0	3	0	1

ptera, mostly Chironomidae) and water bugs (Hemiptera; Heteroptera) were also obtained from this sample, but only in small amounts (2–4% each). Among the water bugs, members of the family Corixidae were the most frequent. Three of the faecal pellets included parasitic mites (Acarina), which probably were ingested inside the roost following grooming of the fur. This may also apply to bed bugs (*Cimex* sp.), which were recovered from one of the droppings.

In the second sample (from Rezekne), the diet was even more diverse, but like the first sample, it consisted almost entirely of insects that normally occur over water. This sample was dominated by caddis flies (Trichoptera, mostly Limnephilidae), comprising 36% of the sample, but also included large amounts of moths (Lepidoptera; 13%), mayflies (Ephemeroptera; 17%), bugs (Hemiptera, including Corixidae; 15%) and brown lacewings (Neuroptera, Hemerobiidae; 9%). Diptera represented only 7% of this sample. One flea (Siphonaptera) must have been ingested during grooming, like the ectoparasites found in the first sample.

To obtain a rough idea of the size of some of the prey items, the length of some wings which were recovered from the faecal samples more or less whole, were measured. Among the caddis flies, the wings (N = 10) were 5–13 mm long, indicating total wingspans of the smallest specimens of just over 1 cm. The mayflies were apparently of similar size, as recovered wings (N = 2) were 5–6 mm long. This also applies to beetles (5 and 10 mm; N = 2). The wings of small flies (Diptera) were 4–6 mm long (N = 6), again indicating wingspans of around 1 cm for the smallest specimens.

Discussion

The diet of the noctule is varied. In England it is dominated by farmland insects, such as *Geotrupes*, *Aphodius*, and *Melolontha* beetles (Coleoptera; Scarabaeidae), crane-flies (Diptera; Tipulidae), dung flies (Diptera; Scatophagidae) and moths (Lepidoptera) (Jones 1995; McKenzie and Oxford 1995). In Germany and Switzerland, caddis flies (Trichoptera), mayflies (Ephemeroptera) and true bugs (Hemiptera; Heteroptera) were also included in the diet, as well as non-biting midges (Diptera; Chironomidae), suggesting that the bats in these cases fed near or over water (Gloor et al. 1994; Beck 1995). The apparent difference in the diet of noctules between England and central Europe may perhaps be related to differences in geology and landscape. ln southern England, lakes or large rivers are relatively scarce, while they may form a dominant part of the countryside further east and north on the European mainland, where glaciations have been more prevalent.

Insects that emerge from water surfaces, such as mayflies, caddis flies, and chironomids, are important prey for many aerial-hawking bats in Europe and elsewhere. However, some aquatic insects appear to be more important as bat food than others, for reasons that are not clear. For example, Daubenton's bats *Myotis daubentonii* (Kuhl, 1819) and common pipistrelles *Pipistrellus pipistrellus* (Schreber, 1774), two of the most common species in northern Europe, frequently feed over water (Swift and Racey 1983; Racey and Swift 1985), where they consume large numbers of chironomids but surprisingly few caddis flies, mayflies, and other larger insects (Swift et al. 1985). A very similar situation applies to the northern bat *Eptesicus nilssonii* (Keyserling and Blasius, 1839) and the particoloured bat *Vespertilio murinus* Linné, 1758, which also catches mainly small insects when foraging over water in Scandinavia (Rydell 1986, 1992 a). Likewise, Leisler's bat *Nyctalus leisleri* (Schreber, 1774), feeds mainly on chironomids and yellow dung flies (*Scatophaga* spp.) in England and Ireland (Sullivan et al. 1993; Waters et al. 1995). The noctules caught many more of the larger insects than any of the other species, as might have been expected, but they also caught occasional flies with wingspans of about 1 cm or half a wavelength of the search phase echolocation calls (20 kHz translates to a wave-

length of 22 mm). This minimum prey size corresponds precisely with those recorded by Jones (1995) for noctules in England. It also corresponds with the minimum prey sizes recorded for the other species, in the sense that the smallest prey had wingspans a little less than half a wavelength of their echolocation calls. It is also very similar to the sizes expected based on experiments and theory (Waters et al. 1995), suggesting that the minimum prey size is determined by perceptual constraints rather than by considerations based on optimal foraging (Anthony and Kunz 1977; Barclay and Brigham 1991).

Smaller bats such as the pipistrelles are able to catch large aquatic insects including mayflies and caddis flies, although they catch them only in small numbers (Swift et al. 1985), suggesting that handling large prey is not a problem even for small bats. However, we suspect that the availability of larger insects that occur near water not only are constrained by the hunting and handling technique of the bats and the absolute abundance of the prey but also by the behaviour of the insects. Many mayflies and caddis flies are predominantly diurnal or crepuscular, and may only be available to bats that emerge and start to forage early in the evening. In northern Europe, the noctule is always the first bat to appear, half an hour before the pipistrelle and almost an hour before Daubenton's bat, on average (Jones and Rydell 1994). Hence, the noctule would, therefore, be expected to encounter more crepuscular and diurnal insects than any of the other bat species.

Moths were caught much less frequently by the Latvian noctules than by those in England and central Europe. Most nocturnal moths are tympanate, and may thus be well adapted to avoid high intensity echolocating bats such as noctules (Roeder 1967), although moths seem to be at a relative disadvantage near streetlamps (Rydell 1992 b), where noctules often forage (Kronwitter 1988). It is possible that the difference in moth utilisation between Latvia and most of western Europe reflects the relative scarcity of street lamps in the east.

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Zusammenfassung

Die Nahrung des Abendseglers Nyctalus noctula in Lettland

Die Nahrungsanalyse des Abendseglers aus der Kulturlandschaft Lettlands zeigt an, daß dieser hauptsächlich in der Nähe von Wasser oder an der Wasseroberfläche jagt. Er fängt große Insekten ohne Tympanalorgane, größtenteils Trichoptera, Ephemeroptera, Coleoptera und Hemiptera, in geringer Anzahl aber auch Lepidoptera, Neuroptera und Diptera. Die Nahrung spiegelt die Begrenzung des Echoortungssystemes und der Morphologie der Flügel dieser großen, schnellfliegenden Art wieder. Die kleinsten Insekten in der Nahrung (ca. 9 mm Flügelspannweite) stimmen größenmäßig mit dem überein, was theoretisch detektierbar ist, obwohl so kleine Insekten verhältnismäßig selten gefangen werden. Die angewandten Wellenlängen scheinen die Untergrenze für die Größe der Beute festzulegen.

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