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Food habits of the barbastelle bat *Barbastella barbastellus*

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The diet of *Barbastella barbastellus* was investigated through analysis of droppings collected from three maternity roosts in Germany and Switzerland. The results showed a high dominance of moths (Lepidoptera), which accounted for 73–94% of the recovered items by volume. Flies (Diptera), ranging in size from blow flies (Calliphoridae) and large crane flies (Tipulidae) to small Nematocera, were the second most important prey items (4–17%). Prey types recovered also included small numbers of Trichoptera, Neuroptera, Homoptera, Hymenoptera, Coleoptera and spiders (Araneae). The diet of the barbastelle differs from that of most other bats in Europe in the predominance of moths and the corresponding virtual absence of dung beetles (Coleoptera; Scarabaeidae) and midges (Diptera; Chironomidae). Conservation measures for barbastelles should therefore consider facilitation of the diversity and abundance of moths.

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The barbastelle bat (*Barbastella barbastellus* Schreber, 1774) has a wide distribution mainly in Europe, occurring from southern Scandinavia southwards to Morocco and eastwards to Turkey and Caucasus. In southern and central Europe, it is mostly confined to forested upland areas (e.g. Benzal et al. 1991, Zingg 1994). It is considered as a rare bat species in western Europe including Scandinavia and the British Isles (e.g. Baagøe 1981, Stebbings and Griffiths 1986, Lina 1987, Ahlén and Gerell 1989) and appears to be in serious decline in several countries including Switzerland, France, Belgium and Germany (e.g. Stebbings and Griffiths 1986, Richarz 1989, Zingg 1994). It is uncommon but still widespread in Austria (Spitzenberger 1993) and numerous, but possibly declining, in some areas of eastern Europe, where several hibernation sites including hundreds to thousands of individuals still occur (Urbanczyk 1989, Uhrin 1995). The reason for the supposed decline is unknown. The barbastelle is currently listed as endangered or vulnerable in most European countries (Stebbings 1988).

The summer ecology of the barbastelle has not been investigated systematically, and on foraging and diet, only some anecdotal observations have been published. The diet has been reported to consist mainly of moths (Beck 1995), including large species such as *Hepialus humuli* (Gordon 1946), and also flies such as house flies *Musca domestica* (Poulton 1929) and small chironomids, the latter of which may be captured in the air over water (Stebbings 1991).

An investigation of the diet of the barbastelle is highly motivated because "research is urgently required to find ... critical habitats and to find the necessary conservation measures" for this threatened species (Stebbings and Griffiths 1986; p. 82).

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Materials and methods

Droppings were collected in three *B. barbastellus* maternity roosts, all situated behind window shutters of wooden houses. This type of roost seems to be typical of the species in continental Europe (Richarz 1986). The roosts were situated in cultural landscapes, i.e. villages, and surrounded by agricultural land, mostly unfertilized grassland and patches of woodland. The first roost was located c. 200 m a.s.l. in the village of Cunewalde SE of Bautzen, extreme southeastern Germany (51°10′ N, 14°30′ E). The second roost was located c. 500 m a.s.l. in the village of Sachseln at lake Sarnen (region Obwalden), Switzerland (46°52′ N, 08°15′ E). The third roost was located c. 800 m a.s.l. in the village of Frutigen (region Berne), Switzerland (46°35′ N, 07°39′ E). The foraging areas and habitats used by the bats from these colonies are largely unknown.

Before analysis, the droppings were soaked for a few minutes in a mixture of water and ethanol, and were subsequently teased apart using dissecting needles and a pointed tweezer under a binocular microscope. Insect remains were identified to order, or, in the case of Diptera, a little further, by comparison with a sample of whole insects and by use of various field guides to insects including Chinery (1986) and McAney et al. (1992).

For each dropping, the minimum number of each prey type was determined (Swift et al. 1985) and also the approximate volume represented by each type (Whitaker 1988). The frequency of each prey type (percentage of the number of recovered individuals) was obtained by adding the (minimum) number of individuals found in each dropping and dividing the number of individuals of each prey type by the total number recovered. The relative volume represented by each prey type was estimated for each dropping separately, later adding the pecentages, assuming that all droppings represented equal parts of the whole sample (Rydell 1989). The volume gives an estimate of the importance of each prey type in terms of biomass, while frequency gives a picture of the number of items in each category that was pursued and captured. The latter tends to result in an overestimate of the numbers of the larger prey items, because each large item may appear in several droppings.

Results

Moths (Lepidoptera) were by far the most important prey category in all three samples, representing between 73 and 94% of the total volume (Fig. 1) and 61–89% of the number of recovered individuals (Table 1). The second most important prey category was nematoceran flies, including large tipulids as well as several much smaller forms, which together represented 2–13% of the volume and 3–18% of the individuals. There were also some predominantly diurnal brachyceran flies such as house flies and blow flies together with smaller forms of unknown families. Such flies together represented 2–5% of the volume and 6–9% of the insects recovered. Remains of five spiders (Araneae) were also found in one of the samples (Frutigen), representing 3% of the volume of that sample. Other prey types recovered included a lacewing (Neuroptera), three small bugs (Homoptera; Delphacidae and Aphrophoridae), a hymenopteran of unknown affinity, a small beetle (Coleoptera) of unknown affinity and a caddis fly (Trichoptera).

Five insects classified as "undet." (Table 1) occurred in two of the samples. Small remains which probably were parts of cerci suggest that these insects might

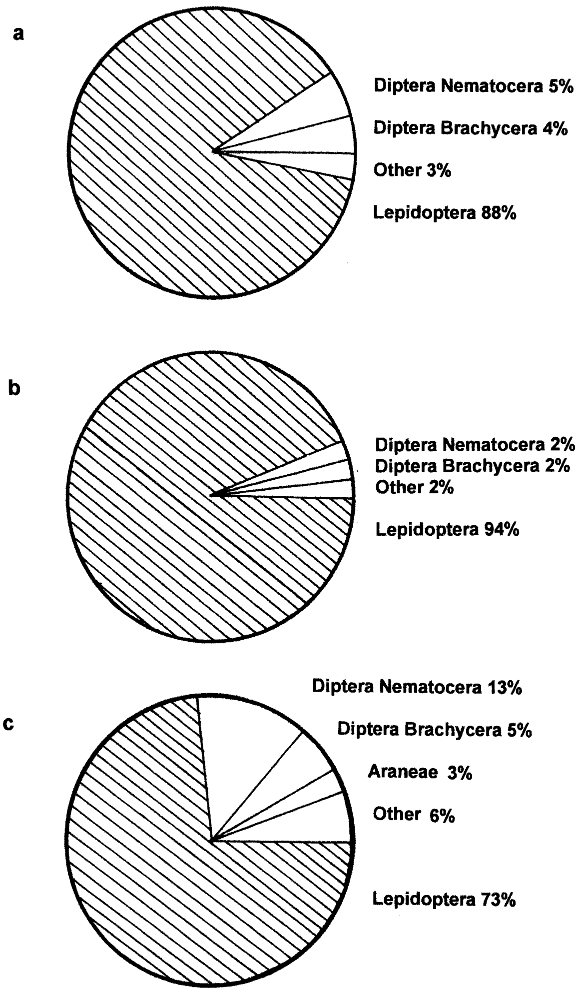

Fig. 1. The diet of *B. barbastellus* from three maternity colonies in a) Bautzen, Germany (N = 40 droppings analyzed), b) Sachseln, Switzerland (N = 80) and c) Frutigen, Switzerland (N = 80) expressed as percentage volume of different food categories recovered from droppings. The hatched areas represent moths (Lepidoptera).

Table 1. The diet of *B. barbastellus* from three maternity colonies in Germany (Bautzen; 40 droppings analyzed) and Switzerland (Sachseln and Frutigen; 80 droppings analyzed for each site), expressed as the minimum number of recovered individuals of each food category (absolute numbers and percentages of totals in parentheses). The ectoparasitic mites and plant material are excluded from the totals.

Prey category	Number (%) of recovered prey individuals Bautzen	Sachseln	Frutigen
Lepidoptera	39 (78.0)	78 (88.6)	68 (61.3)
Diptera, Nematocera	5 (10.0)	3 (3.4)	20 (18.0)
Diptera, Brachycera	4 (8.0)	5 (5.7)	10 (9.0)
Neuroptera	1 (2.0)	0	0
Trichoptera	1 (2.0)	0	0
Homoptera	0	1 (1.1)	2 (1.8)
Coleoptera	0	0	1 (0.9)
Hymenoptera	0	0	1 (0.9)
Undet. insect	0	1 (1.1)	4 (3.6)
Araneae	0	0	5 (4.5)
Acarina (ectoparasites)	(1)	(c. 25)	(1)
Plants	(0)	(0)	(2)
Total	50 (100.0)	88 (99.9)	111 (100.0)

possibly have been either mayflies (Ephemeroptera) or stone-flies (Plecoptera), but more diagnostic parts such as wing fragments or legs were not found.

Small (<1 mm) ectoparasitic mites (Acarina) were also recovered. One dropping in particular contained at least two dozens of these mites. In this particular dropping, the mite remains were mixed with fur but there were no other prey items. Two of the droppings which contained spider and Tipulid remains, respectively, also included plant fragments. Some insect types which are commonly eaten by many other bats in Europe, such as dung-beetles (Coleoptera; Scarabaeidae) and midges (Diptera; Chironomidae) were notably absent.

Discussion

The results largely agree with those of Beck (1995) and also with earlier, mostly anecdotal, observations, in that moths and small dipterans constitute most of the diet, which is also supplemented by calliphorid and muscid flies and a few other, relatively infrequent, forms. However, the high occurrence of moths (c. 70–90% by volume) in the diet of the barbastelle is unusual among bats in Europe. For most others, including aerial-hawking as well as gleaning species, moths do not comprise more than ten percent or so of the diet. This is probably because most moths are difficult to catch due to their tympanate organs (ears), which are sensitive to the ultrasonic echolocation calls used by these bats (c. 20–50 kHz), and the associated evasive flight manoeuvres (Rydell et al. 1995).

A relatively high occurrence of moths (20–80% by volume) also occurrs in the diets of the gleaning long-eared bats of the genus *Plecotus* (Vespertilionidae; Bauerová 1982, Swift and Racey 1983), the flutter-detecting horseshoe bats of the genus *Rhinolophus* (Rhinolophidae; McAney and Fairley 1989, Jones 1990) and the fast flying aerial-hawking bat *Tadarida teniotis* (Molossidae; Rydell and Arlettaz 1994). Although these species use different and variable foraging techniques, all rely on prey detection systems which are based either on passive cues, or on highly modified echolocation calls, which consist of frequencies which are virtually inaudible to tympanate insects including most nocturnal moths (Jones and Rayner 1989, Anderson and Racey 1991). It is not known which type of echolocation calls and which capture technique the barbastelle uses when catching moths. It is possible that it relies on passive listening rather than on echolocation in such situations, but evidence for this is lacking.

Non-flying prey types were relatively few in the diet of the barbastelle and were limited to a few spiders. This seems to suggest that the barbastelle catches most of its prey in flight rather than gleaning them from surfaces, although the moths in particular could have been taken by either method (Anderson and Racey 1991). On the other hand, the spiders and the plant remains that were recovered suggest that a gleaning foraging technique is sometimes used. The plant material had presumably been ingested undeliberately during attacks on insects sitting on or flying near vegetation. The ectoparasitic mites and the associated fur must have been swallowed following grooming.

Although several species of small nematoceran flies were recovered, none of them could be referred to the midge family (Diptera; Chironomidae). Midges are frequently eaten by many species of bats, particularly those that hunt in the vicinity of water (e.g. Swift and Racey 1983, Rydell 1989, 1992a). Furthermore, other forms that normally fly over water such as caddis-flies (Trichoptera), mayflies (Ephemeroptera) and stone-flies (Plecoptera) were rare or absent too. This suggests that the barbastelles investigated here, one colony of which was located next to a lake, did not feed over water to any extent. This seems to be in contrast to the single individual observed by Stebbings (1991), which fed on a swarm of chironomids over a pond in England.

The total absence of dung-beetles (Coleoptera; Scarabaeidae) suggests that the barbastelles did not forage extensively over cattle pastures either. On the other hand, it has been suggested that the barbastelle cannot handle highly chitinous (hard) insects such as dung-beetles, because of its relatively narrow mouth and weak teeth (Schober and Grimmberger 1989). Dung beetles are frequently exploited by many other European bats including aerial-hawking as well as gleaning species (e.g. Rydell 1989, Jones 1990).

The barbastelle has an average wing loading (9.1 N m^{-2}), low aspect ratio (6.0) and short and rounded wingtips. Hence, it would be predicted to fly rather slowly and manoeuvrably and probably stay close to the vegetation most of the time (Norberg and Rayner 1987). Indeed, the flight of the barbastelle has been described as "slow and deliberate" (Gordon 1946) and as "low, often over water, tending to be heavy and fluttering" (Stebbings 1991, p. 130) but also as "fast" and "skilful" (Schober and Grimmberger 1989, p. 176). The flight indoors has been described as "much faster than in *Plecotus auritus* but almost as adroit in narrow quarters" (Ryberg 1947, p. 129). Limited observations of foraging barbastelles (e.g. Welander 1929, Ryberg 1947, Ahlén 1990) suggest that they often fly slowly back and forth along a short route at a height of 4–5 m above the ground, presumably searching for flying insects, sometimes pausing while using almost a hovering flight technique. However, in contrast to many slow flying bat species (Rydell 1992b), barbastelles sometimes feed on insects that aggregate around mercury vapour streetlamps, and at least in this situation they fly relatively fast (Zingg 1994).

The barbastelle uses two contrasting types of echolocation calls while searching for prey; short and relatively weak broad-band frequency-sweeps with maximum intensity at c. 42 kHz, which are similar to those typical of most gleaners, and also pulses which include an initial short narrow-band component at 32 kHz followed by a steep frequency sweep. The latter pulse type is the stronger of the two. Either of the two pulse types used by the barbastelle may occur exclusively or they may alternate, depending on the situation (Ahlén 1981, 1990). The audiogram of the barbastelle shows sensitivity maxima at 20-30 kHz and also around 60 kHz, apparently coinciding with the fundamental and the second harmonic of the stronger of the two pulse types (Konstantinov and Makarov 1981).

The function of the short narrow-band component included in the stronger of the two pulse types is puzzling. Narrow-band components are often used for detection of fluttering insects, which produce "glints" (Schnitzler 1987). However, in the case of the barbastelle, the narrow-band components seem to be too short (c. 1.5 ms; Ahlén 1981) to pick up the glints generated by moving moth wings.

There is no evidence for increased hearing sensitivity at low frequencies, as would have been expected in a gleaning bat (e.g. *Plecotus auritus*; Coles et al. 1989). On the other hand, the barbastelle can apparently emit echolocation pulses through the nose as well as through the mouth (Kolb 1970), a characteristic otherwise found in gleaning and flutter-detecting bats that forage near or within the vegetation, e.g *Plecotus* spp. and *Rhinolophus* spp. The large forward pointing ears strongly enhance the directionality of the hearing (Konstantinov and Makarov 1981), a trait which may also be associated with echolocation in clutter.

In summary, the use of two principal types of echolocation calls as well as limited observations on the flight and foraging of the barbastelle suggest a flexible foraging strategy including aerial-hawking and probabaly also surface gleaning of primarily moths. However, how its flight and echolocation calls relate to a diet consisting mostly of moths remains unexplained. In any case, the barbastelle may be more affected by changes in the abundance and diversity of moths than most other bats in Europe. Conservation measures for barbastelles and their habitats should take this into account.

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