Functional Ecology 2003
17, 141–145

Forum

A heap of feathers does not make a bat's diet

Ibáñez *et al*. (2001) reported predation by Greater Noctule bats *Nyctalus lasiopterus* (Schreber 1780), the largest European bat species, upon nocturnally migrating passerines in Spain. The authors collected hundreds of faecal pellets at one maternity roost and from bats mist-netted in their foraging areas. In the faeces, they found numerous insect fragments, an usual prey for noctules, but also feathers. Overall, 45% of faecal samples contained feathers whereas up to 70% of the individual bats captured had swallowed feathers. The occurrence of feathers furthermore coincided, temporally and geographically, with the main periods of passage of nocturnally migrating birds, either in spring or in autumn. The authors concluded that 'the greater noctule is the first known bat regularly preying on passerines during their seasonal migration'.

Massively relayed by a large panel of media worldwide, including top scientific journals (Clarke 2001; Shouse 2001), the sensational news had the effect of a 'media bomb'. Although eating birds is well documented for gleaning bats (i.e. species capturing their prey from surfaces) (Fenton 1990; Pavey & Burwell 1997), this recent finding appears especially peculiar as it would represent the first evidence of an aerial-hawking bat species preying on birds in flight. Unlike carnivorous bat species preying on vertebrates, which show specific morphological adaptations for slow and manoeuvrable flight in cluttered habitats (Norberg & Fenton 1988), noctule bats are fast-flying species foraging in the open air. Their sonar system differs from that of gleaning bats. Consisting of low-frequency, high-intensity echolocation calls of long duration separated by long pulse intervals, it is suited for detecting relatively large airborne targets at great distances (Jones 1995). From the acoustic viewpoint, detecting a small flying passerine would be similar to locating a large-sized moth.

Nyctalus lasiopterus is reported to have an average body mass of 48 g in Spain (Ibáñez *et al*. 2001). The size of the 10 most frequent bird species which migrate at night (Jenni & Naef-Daenzer 1986, Figure 4) to the south lies between 6 and 90 g. Ibáñez *et al*. (2001) name two species of passerines that might have been eaten by *N. lasiopterus*: *Phylloscopus sibilatrix* has a body mass of 7–12 g and *Erithacus rubecula* of 16–22 g (Glutz von Blotzheim 2001). The capture on the wing of such prey, about one-third of the body mass of its predator (*vs* up to 5–10% for a large-sized insect), appears a complicated task. First, Greater Noctules lack the enlarged tail membrane, feet and claws that enable gleaning species to seize their prey. Second, it is difficult to envision how Greater Noctules could overpower their bird prey by capturing them directly with their jaws, even with the aid of the wing membranes. Anyway, even with such features, the capture of massive prey in the air would definitely be compromised by the specific aerodynamic constraints induced by this foraging situation. Based on his own experience with carnivorous bat species, M. B. Fenton (personal communication) could imagine prey for *N. lasiopterus* with a body mass of up to 10 g, but not more than 15 g.

As far as we know, noctule bats, prior to ingestion, prepare their prey mainly on the wing. They would have few opportunities, again because of ecomorphological constraints, to do it from a perch like gleaning species. Preparing a bird on the wing before consumption seems a real challenge. When eating insects, bats usually discard the main unprofitable parts of the exoskeleton, such as antennae, wings, elytras or legs, by chewing them off. Ingesting a bird, however, would require removal of most feathers, and, last but not least, the separation of muscles, the nutritionally interesting tissues, from parts of the endoskeleton such as bones. It is very unlikely that this might be achieved in flight!

The original paper does not report any bone fragments in the faeces, which is in this context particularly astonishing. In comparison, indigestible parts of the exoskeleton of arthropods are regularly found in faeces in other studies – even among species investing considerable additional time to handle their prey (this is how faecal analyses enable bat diet identification; Whitaker 1988). As there is definitely no way to perfectly separate meat from bones of vertebrate prey, either in flight or at perch, bats cannot fully avoid ingesting unprofitable parts. As a consequence, if birds were a major prey, one would at least have expected the occurrence of bones in bats' diet from time to time.

In addition, it is strange that no faecal sample comprised solely feathers, although such a big, profitable prey as a passerine would have enough feathers to make up 100% of the volume of numerous faecal pellets. Ibáñez *et al*. (2001) gave figures on occurrence frequency of prey category, a traditional semiquantitative way of presenting dietary data. Yet, by their very characteristics, occurrence frequencies are not estimations of prey category by volume. For instance, when it is said that the occurrence frequency of feathers in individual faecal samples amounted to 50%, it means that about half of the individuals captured in the field had remains of feathers in their faeces; but each bat may well have ingested only a single feather, among dozens of other prey! In the absence of fully quantitative data on prey category it remains difficult to judge the actual proportion of feathers in the diet. Interestingly, previous faecal analyses carried out in *Nyctalus noctula*, another aerial-hawking bat species closely related to *N.*

lasiopterus, also occasionally revealed feathers (Gloor, Stutz & Ziswiler 1995). They found (S. Gloor, personal communication) feather remains in 3 out of 435 faecal pellets (frequency 0·7%). Two of these pellets contained feathers by 90% volume, another by 10%. However, because of their smaller body size (*c*. 25 g, i.e. about the body mass of a passerine, *vs* 50 g for the Greater Noctule), nobody could even have imagined and suggested that noctules may prey on birds!

But why were there feathers in the faecal pellets of Greater Noctule bats if predation upon birds seems so unlikely? We suggest that Greater Noctule bats, as their smaller relatives, simply capture feathers fluttering in the open air by chance. A passing bat may be easily attracted by a small stone thrown in the air, if the stone appears ahead and along the bat's main flight trajectory. Even successive attempts to attract the same individual bat this way continue to elicit its reaction in a very stereotypical manner. In fact, this poor ability to discriminate between profitable and unprofitable targets is characteristic of the short FM echolocation signals typical of aerial-hawking bats such as noctules. If bats so easily confuse targets as different as a stone and an insect, one may imagine how easily they could confuse airborne feathers with flying insects! Yet, whereas stones are rejected as false prey before ingestion, it might be easier for a bat to eat a feather instead of rejecting it once it is stuck in its mouth. Notice that, according to Barclay (1995), feathers might even possibly be ingested on purpose as a source of calcium, a limiting mineral in bat diet. In consequence, the positive correlation between the occurrence of feathers in bats' diet and the amount of migrating birds in southern Spain might simply mask the fact that more feathers are fluttering in the air at the period of bird migration, which seems furthermore to coincide with the periods when several bird species are moulting; for instance, passerines such as *Acrocephalus scirpaceus*, *Sylvia communis* and *Muscicapa striata* migrate while still moulting (Schaub & Jenni 2000). Interestingly, noctule bats readily exploit sudden, massive occurrences of swarming insects which often concentrate above marshes, swamps or ponds, which are traditional night-roosting habitats for millions of birds at the time of migration. Under these circumstances, the chances to accidentally capture flying feathers would be numerous.

The study by Ibáñez *et al*. (2001) certainly improves our knowledge of this rare and mysterious bat species by presenting the most comprehensive dietary investigation of the species so far. It also convincingly refutes the hypothesis that Greater Noctule bats may prey upon birds visiting their cavernicolous roosts (Dondini & Vergari 2000). However, has the Greater Noctule bat actually won the evolutionary arms race by starting to exploit an extraordinary, and by bats long neglected, feeding niche: the millions of nightly migrating passerines? If so, how could it ultimately have bypassed the numerous constraints imposed by such a highly innovative foraging tactic in terms of morphological and physiological adaptations? Referring to the principle of parsimony, we are more inclined to believe that the Greater Noctule might simply be bound by limited resolution of its echolocation calls, and condemned to catch feathers mistakenly.

Acknowledgements

We thank S. Gloor for the data on the diet of *Nyctalus noctula*. M. B. Fenton, P. Christe and an anonymous referee improved the manuscript by their valuable comments.

References

Barclay, R.M.R. (1995) Does energy or calcium availability constrain reproduction by bats? *Ecology, Evolution and Behaviour of Bats, Symposia of the Zoological Society of London*, Vol. 67 (eds P.A. Racey & S.M. Swift), pp. 245–258. Zoological Society of London, London.

Clarke, T. (2001) Bats eat birds on the wing. *Nature [nature.com, online]*, 7 August 2001.

Dondini, G. & Vergari, S. (2000) Carnivory in the greater noctule bat (*Nyctalus lasiopterus*) in Italy. *Journal of Zoology London* **251**, 233–236.

Fenton, M.B. (1990) The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology* **68**, 411–422.

Gloor, S., Stutz, H.-P. & Ziswiler, V. (1995) Nutritional habits of the noctule bat *Nyctalus noctula* (Schreber, 1774) in Switzerland. *Myotis* **32–33**, 231–242.

Glutz von Blotzheim, U.N. (2001) *Handbuch der Vögel Mitteleuropas auf CD-ROM*. Vogelzug Verlag, Wiebelsheim.

Ibáñez, C., Juste, J., García-Mudarra, J.L. & Agirre-Mendi, P.T. (2001) Bat predation on nocturnally migrating birds. *Proceedings of the National Academy of Sciences of the USA* **98**, 9700–9702. DOI: 10·1073/pnas.171140598.

Jenni, L. & Naef-Daenzer, B. (1986) Vergleich der Fanghäufigkeit von Zugvögeln auf dem Alpenpass Col de Bretolet mit Brutbeständen im Herkunftsgebiet. *Ornithologischer Beobachter* **83**, 95–110.

Jones, G. (1995) Performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. *Journal of Zoology London* **237**, 303–312.

Norberg, U.M. & Fenton, M.B. (1988) Carnivorous bats? *Biological Journal of the Linnean Society* **33**, 383–394.

Pavey, C.R. & Burwell, C.J. (1997) The diet of the diadem leaf-nosed bat *Hipposideros diadema*: confirmation of a morphologically-based prediction of carnivory. *Journal of Zoology London* **243**, 295–303.

Schaub, M. & Jenni, L. (2000) Body mass of six long-distance migrant passerine species along the autumn migration route. *Journal für Ornithologie* **141**, 441–460.

Shouse, B. (2001) Whoosh, pow! Batman eats Robin. *Science Now [online]*, 6 August 2001.

Whitaker, J.O. (1988) Food habits analysis of insectivorous bats. *Ecological and Behavioral Methods for the Study of Bats* (ed. T.H. Kunz), pp. 171–189. Smithsonian Institution Press, Washington.

F. BONTADINA and R. ARLETTAZ
Division of Conservation Biology, Zoological Institute, University of Bern, Baltzerstrasse 6, CH–3012 Bern, Switzerland
E-mail: fabio.bontadina@swild.ch