

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 over-

power 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.

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Feathers as indicator of a bat's diet: a reply to Bontadina & Arlettaz

The interpretation of unexpected new findings is inevitably controversial. Our recent description (Ibáñez *et al.* 2001) of the recurrent presence of feathers in the faecal pellets of *Nyctalus lasiopterus* (Schreber 1780) – a typical open hawking insectivorous bat – was no exception. We attribute this presence of feathers to an active hunting behaviour on small migrating birds by the bats. However, Bontadina & Arlettaz (2003) question our interpretation and suggest that the presence of feathers in faeces actually results from the accidental ingestion of free fluttering feathers. Their conclusions appear to be derived, firstly, from a misinterpretation of some of the results shown in our paper particularly regarding the abundance of feathers per faecal pellet and, secondly, from the failure to consider some other evidence described in our paper. Regarding the first point, it is stated in our paper that the majority of the faecal pellets collected contained only one of the items considered in the analysis of the diet of the *N. lasiopterus* (insects, bird feathers and hairs). In fact, it should be clarified that all the pellets assigned to the 'bird feather' category were almost exclusively made up by feather remains and within this category, feathers were never less than 80% of the total volume of the pellet (Fig. 1). Therefore, a frequency of 50% feathers indicates that pellets containing 'feathers only' constituted half of the faecal pellets. More precisely, in the 18 bats netted in their foraging areas that released more than 20 pellets after their capture, 100% of their pellets were made up exclusively by feathers consumed that night, whether that be directly or indirectly. An extreme example was a female that was netted in autumn 3.5 h after sunset, weighing 72 g at the time of capture. This

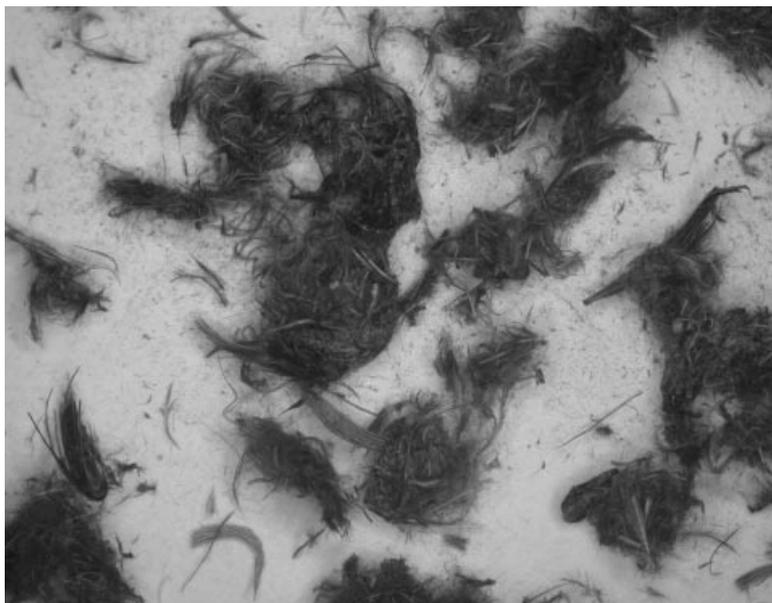


Fig. 1. Dissected faecal pellet of *N. lasiopterus* that comprises 100% feathers in volume.

female produced a total of 64 pellets exclusively made out of feathers in the following 18 h, and had a 61-g body mass at the time of release. Bontadina & Arlettaz's objection – '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' – is then clarified.

Moreover, in our paper we describe that at least one bat was captured gripping feathers in its claws and that fresh-cut wings were found floating in a pond near where the bats were being netted. One explanation for such findings is that the wings were bitten off by the bats, a behaviour that has been documented for other aerial hawking bats feeding on large insects. These observations are not easily explained by Bontadina & Arlettaz's suggestion of an accidental consumption of feathers.

These clarifications made, we can now try to re-analyse the two hypotheses to explain our findings with the evidence at hand. Since there are not, so far, direct observations of the behavioural process that results in the presence of feathers in the pellets, a certain degree of speculation is inevitable. As Bontadina & Arlettaz correctly point out the hypothesis of an active hunting of flying birds opens two main questions: How are the bats able to kill and consume a bird in the air? Why are there no bones in the bats' faeces?

Regarding the first question, a bat overpowering a flying bird that can equal up to 30% of its body mass is certainly a difficult task. In fact, aerial hawking bats normally hunt prey of less than 5% of their body mass (Fenton 1990). Nevertheless, we are still far from fully understanding the actual capacity of bats to adjust to sudden changes of wing loading when flying. For example, the aforementioned female bat would normally have a body mass of less than 50 g at the beginning of spring (Ibáñez *et al.* 2001). However, on the night of capture it had at least 11 g of food in addition to the 11 g increase in its body mass that had already occurred because of prewintering fat accumulation. This is an increase in body mass of over 40% on that particular night in autumn with respect to its body mass in spring, and this without any apparent effect on the bat's flying capacity.

Another factor to be taken into account in this scenario is hunting altitude. It is well documented that some open hawking bats (such as *N. lasiopterus*) can hunt at heights of over 600 m in America, Africa and Australia (Fenton & Griffin 1997; Griffin & Thompson 1982; Williams, Ireland & Williams 1973). Birds, on the other hand, can migrate along a wide range of altitudes, although on average, they fly at over 700 m above ground level (Bruderer 1997). Accordingly, birds and bats could establish contact at this height. These two factors: a high capacity for responding to sudden changes in wing loading and the possibility of contacting birds at high altitude would make it feasible to capture and consume a small bird while losing altitude without risking collision.

Regarding the question of the absence of bones in the faecal pellets, this could result from a partial consumption of the prey, which probably would comprise only the most rewarding parts of the body such as the boneless breast muscles.

Bontadina & Arlettaz suggest that the presence and pattern of feathers in the pellets of the *N. lasiopterus* result from an accidental and erroneous consumption of the feathers dropped in the sky by nocturnally migrating birds. As clarified previously, feathers make up most of the bats' pellets when they are present, and it seems difficult to believe that bats could repeatedly and mistakenly feed almost exclusively on hundreds of feathers, night after night, during the two bird migration periods, especially since these two periods concur with high energetic requirements for the bats; pre-wintering fat accumulation in autumn and pregnancy in spring.

Alternatively, Bontadina & Arlettaz suggest an extra supply of calcium as a possible benefit of the feather intake, since deficiency of this element can be limiting for females during reproduction (Barclay 1995). However, feathers are not particularly rich in calcium and are not actively used as a food supply by any other animal; rather, they are generally discarded. If calcium demand was the reason for feather consumption, a more intense search for feather should then be expected by females than by males, as Barclay (1995) has predicted. Nevertheless, in the five samples in the feeding grounds in northern Spain (La Rioja), males had more feathers in their pellets (90.3%) than females (66.7%). This trend was not statistically significant ($P = 0.41$; Fisher's exact test), although this could be due to the fact that there were only a few sampling days in which both sexes of *N. lasiopterus* were collected.

According to Bontadina & Arlettaz's accidental consumption hypothesis, it would be expected that not only *N. lasiopterus*, but also other open air hawking bats (of any size) would show a similar pattern of feathers in their faeces. Similarly, this result would be expected whether the feathers were consumed accidentally or if they were actively selected for some beneficial effect. However, as Bontadina & Arlettaz point out, only the conspecific bat *N. noctula* (Schreber 1774) has, so far, shown feathers in its pellets, but with a frequency (0.7%) not comparable with *N. lasiopterus*.

Finally, it is hard to envision a 'rain of feathers' such as to allow the rapid ingestion of hundreds of fluttering feathers in just a few hours, an event that would be required to account for the presence of feathers in pellets collected from early evening. Bontadina & Arlettaz suggest large concentrations of resting birds in swamps and marshes as a possible explanation for localized spots of high-density flying feathers. Nevertheless, the collecting localities in northern Spain are all sited in mountains over 800 m where migrating birds do not concentrate to rest.

In an evolutionary context, we do not agree with Bontadina & Arlettaz that a switch from foraging on

high-altitude migrating insects to birds would require bats to 'win' special and sophisticated morphological or physiological adaptation. In fact, there are abundant examples of animals profiting from unusual and short-lasting – but highly profitable energetically – food sources (e.g. bears feeding on red salmon) without any particular adaptations for obtaining these food items. Even more permanent diet shifts can occur with minor or no apparent morphological or physiological changes (Futuyma & Moreno 1988). For instance, badgers change from a rabbit-based diet in southern Spain to an earthworm-based diet in Central Europe without any structural or mechanical change (Martín *et al.* 1995). As Bontadina & Arlettaz indicate: 'from an acoustic viewpoint, detecting a small flying passerine would be similar to locating a large-sized moth'. The combination of a long-range echolocation system and the large size of *N. lasiopterus* could be interpreted in this context, as an exaptation towards this new feeding niche. These kinds of preadaptive processes are considered of major importance in current evolutionary theory (Gould 2002).

In summary, we are aware that available information on the actual feeding behaviour of *N. lasiopterus* is still very limited and that much more work is needed in order to answer fully all the questions raised by the presence of feathers in its faeces. Nevertheless, attributing this presence to the recurrent poor ability of *N. lasiopterus* to discriminate between feathers and moths (during a period of more than half a year!), does not seem to be a very plausible explanation in light of the evidence we have presented and it is of little help in reaching a satisfactory answer to the questions our findings raise.

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