

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.

Acknowledgements

We thank M. Delibes, J. Figuerola, R. Jovani and D. Serrano for earlier comments on the manuscript and Jane Orr for improving the English version.

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.
- Bontadina, F. & Arlettaz, R. (2003) A heap of feathers does not make a bat's diet. *Functional Ecology* **17**, XX–XX.
- Bruderer, B. (1997) The study of bird migration by radar. Part 2: major achievements. *Naturwissenschaften* **84**, 45–54.
- Fenton, M.B. (1990) The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology* **68**, 411–422.
- Fenton, M.B. & Griffin, D.R. (1997) High-altitude pursuit of insects by echolocating bats. *Journal of Mammalogy* **78**, 247–250.
- Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics* **19**, 207–233.

- Gould, S.J. (2002) *The Structure of Evolutionary Theory*. Harvard University Press, Cambridge.
- Griffin, D.R. & Thompson, D. (1982) High altitude echolocation of insects by bats. *Behavioral Ecology and Sociobiology* **10**, 303–306.
- 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* **98**, 9700–9702.
- Martín, R.A., Rodríguez, A. & Delibes, M. (1995) Local feeding specialization by badgers (*Meles meles*) in a Mediterranean environment. *Oecologia* **101**, 45–50.
- Williams, T.C., Ireland, L.C. & Williams, J.M. (1973) High altitude flights of the free-tailed bat, *Tadarida brasiliensis*, observed with radar. *Journal of Mammalogy* **54**, 807–821.

C. IBÁÑEZ, J. JUSTE and
J. L. GARCÍA-MUDARRA
Estación Biológica de Doñana (CSIC), Apdo 1056,
41080 Sevilla,
Spain
E-mail: ibanez@ebd.csic.es

P. T. AGIRRE-MENDI
Departamento de Biología Animal,
Universidad de Alcalá de Henares,
28871 Alcalá de Henares,
Madrid,
Spain

