Bat predation on nocturnally migrating birds

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Bat predation on birds is a very rare phenomenon in nature. Most documented reports of bird-eating bats refer to tropical bats that occasionally capture resting birds. Millions of small birds concentrate and cross over the world's temperate regions during migration, mainly at night, but no nocturnal predators are known to benefit from this enormous food resource. An analysis of 14,000 fecal pellets of the greater noctule bat (*Nyctalus lasiopterus*) reveals that this species captures and eats large numbers of migrating passerines, making it the only bat species so far known that regularly preys on birds. The echolocation characteristics and wing morphology of this species strongly suggest that it captures birds in flight.

Activity patterns in birds and bats differ considerably, and ecological and behavioral interactions between the two groups are rare (1). Millions of Palaearctic birds fly seasonally across the Mediterranean, mainly at night, north and south between summer and winter quarters (2). During their migrating journeys, birds concentrate and stop over in large numbers in the Mediterranean region. Only two diurnal birds of prey (*Falco eleonorae* and *Falco concolor*) show specific adaptations to feed on migrating birds in this area (3, 4). Surprisingly, no nocturnal predators are known to prey on migrating birds. At least a few bat species would be expected to exploit this food resource, as the order exhibits a remarkably wide range of lifestyles and foraging strategies, as well as a high diversity of echolocation calls (5) and flight behaviors. However, predation on birds has been reported from only three or four of the dozen known carnivorous bat species (6, 7), these being mainly large tropical bats that occasionally capture resting birds by using a gleaning foraging strategy. Bats have never been known to chase birds in flight. The first report of bird predation by a bat in temperate regions was of the greater noctule (*Nyctalus lasiopterus*) (8), one of the rarest and least known mammals in Europe. We here report the regular occurrence of bird predation by this species, based on the analysis of fecal pellets. The echolocation capabilities and wing morphology of the greater noctule adapt it to chase and capture of birds in flight.

Materials and Methods

We examined over 14,000 fecal pellets of *N. lasiopterus* collected in two ways. First, fecal pellets were collected between August 1998 and October 2000 from 170 individual *N. lasiopterus* netted over water courses mainly in a mountainous area of La Rioja (northern Spain; 100 bats) and as they returned to their tree-roosts in a city-park in Seville (Andalusia, southern Spain; 70 bats). The bats were individually kept in cloth bags until the next evening and thereafter sexed, weighed, measured, and released at the site of capture. Only ten bats yielded no feces and a total of 2,347 pellets was collected. Second, samples of fecal pellets were collected every 10 days from May to October 1999 under a maternity colony of around 80 *N. lasiopterus* that roost under three palms (*Washingtonia filirifera*) at the zoological gardens in Jerez de la Frontera (Andalusia, southern Spain). For each sample up to a maximum of 7 g of dried material was randomly selected from the fecal pellets gathered under each palm. A total of 11,815 fecal pellets, of the over 150,000 collected, were sampled and analyzed. No fecal pellets were obtained during the bats' hibernation period from December to February. The fecal pellets were dried and examined for presence of insects, bird feathers, and hair, using standard procedures. Most of the pellets showed mainly one of these items, to which the pellet was assigned. Between three and six hairs per pellet were identified by using a local reference hair collection and identification manuals (9, 10).

To characterize flying traits, the wings of twelve netted bats were outlined and the aspect ratio (the square of the wingspan divided by the wing area) and wing loading (weight divided by the wing area, corrected by the cubic-root of the body mass) were estimated (6, 11).

Echolocation calls (750 ms per sample) were captured in the field with ultrasound bat detectors D-960 (Pettersson Elektronik, Uppsala) in time-expanded mode (10×), and recorded onto metal-XR Sony tapes with a Sony Walkman DC6 cassette recorder. Recordings were analyzed with a Kay DSP 5500 Sonagraph (Kay Elemetrics, Pine Brook, NJ). Time parameters (duration and pulse interval) were measured with a 0.3-ms resolution on a sonogram. Frequency parameters were measured in the power spectrum built with 512 point fast-Fourier transform of each complete pulse. Peak frequency was defined as the frequency with the strongest energy. Bandwidth was measured as the difference between the -15 dB high-frequency and the -15 dB low-frequency cut-offs with regard to peak frequency. For all parameters, mean $\pm$ 1 SD was calculated. Field identification of echolocation calls was based on previous recordings of hand-released individuals.

Results and Discussion

Insects were present all year around in the bats' fecal pellets. Feathers showed two seasonal peaks, and hairs (identified as belonging to *N. lasiopterus*) were found in 2.2% of the fecal pellets (Fig. 1). Both sets of samples showed abundant bird remains (as much as 70% of the netted bats and 45% of the fecal pellets) during the migration periods of birds in March–May and August–November, but there were virtually no bird remains (0–1%) during June–July (Fig. 1).

The proportion of feathers in samples collected at the bat colony was significantly correlated ($r_S = 0.738$, $P = 0.035$) with the presence of small migrating passerines in this region of Spain (12) during the migration period (Fig. 1*B*). The pattern in this roosting colony even reflected the first peak corresponding to the earliest trans-Saharan birds crossing the area in mid September (12). In addition, the proportion of feathers in the bats netted in La Rioja increased corresponding to increases in the number of migrating birds through August (Fig. 2). The delay in the increases in the proportion of feathers in autumn between the two sampling sites (700 km apart) is consistent with the earlier massive passage of migrants at the northern site (Fig. 1*B*). These results show that the greater noctule is the first known bat regularly preying on passerines during their seasonal migration.

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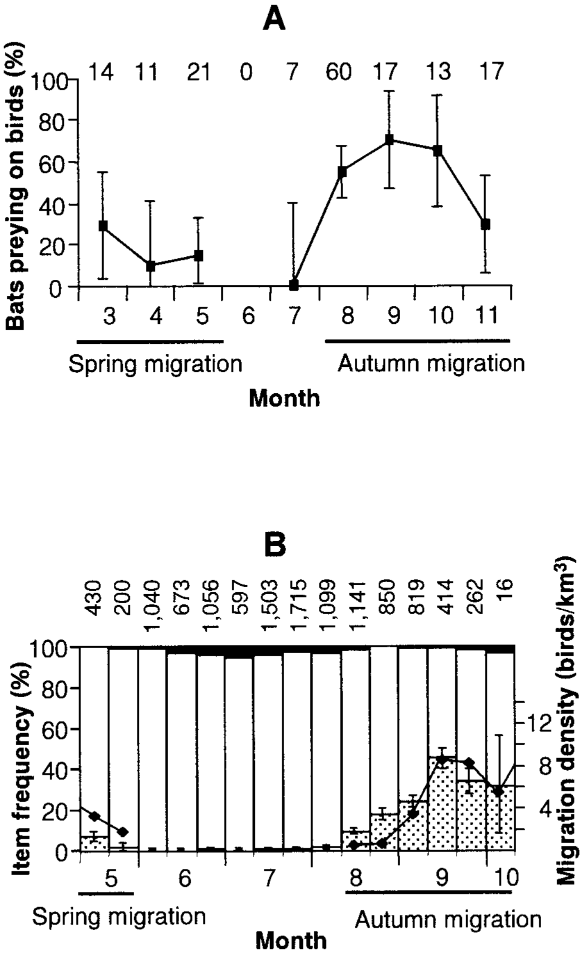

Fig. 1. (*A*) Percentage (±95% confidence interval) of netted bats from La Rioja, northern Spain, and Andalusia, southern Spain, showing feathers in their fecal pellets. The number of individuals captured are shown above the line. (*B*) Proportions (percentage of presence in fecal pellets ±95% confidence interval) of insects (white), feathers (gray), and hair (black) found in fecal pellets sampled under a roosting colony of greater noctules at the zoological gardens in Jerez de la Frontera (southern Spain). Numbers of fecal pellets examined per sample are shown above columns. Black lines indicate the nocturnal migration density of small passerines along the migration periods, tracked by radar at Vélez-Málaga, 180 km from the bat locality (12).

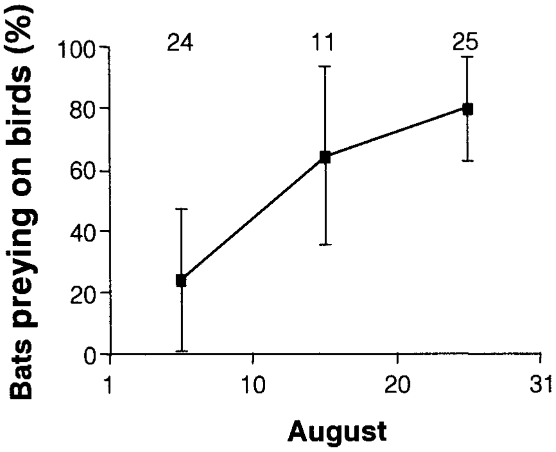

Fig. 2. Percentage of bats netted at 10-day intervals during August that show feathers in their fecal pellets in La Rioja, northern Spain (±95% confidence interval). The number of bats captured in each time period is shown above the line.

Habitat characteristics and foraging strategy constrain echolocation and flight performance of bats and specific echolocation parameters and wing characteristics are associated to each habitat and feeding strategy (5, 11, 13). Carnivorous bats that use a combination of ground/foliage gleaning and a perched hunting strategy show typical wing morphology (relative wing loading < 36, and aspect ratio < 6.3) corresponding to low speed and highly maneuverable flights in cluttered habitats (6). The greater noctule has a very different relative wing loading (41.8 ± 3.9; $n = 12$) and aspect ratio (7.2 ± 0.3, $n = 12$), indicating fast and poorly maneuverable flight in open areas.

The frequency, amplitude, and time parameters of the echolocation calls are modeled according to the information required for prey detection and flight in each characteristic habitat (5, 13). Because of their foraging strategy, the known carnivorous bats use short (pulse duration < 1 ms), low-intensity and high-frequency (peak frequency > 50 kHz) echolocation calls (6). Nevertheless, the echolocation calls of the greater noctule in 13 sequences analyzed are long calls (pulse duration 12.3 ± 3.1 ms, $n = 47$) and show a low frequency (peak frequency 18.8 ± 1.5 kHz, $n = 46$; Fig. 3). These characteristics (together with others such as long-pulse interval 319.7 ± 95.9 ms, $n = 35$; and narrow bandwidth 7.5 ± 3.7 kHz, $n = 33$) are suited for long-range target detection in open air, and are not compatible with short-range prey detection in cluttered habitats (5). Thus, wing morphology and echolocation characteristics of the greater noctule clearly support that this species chases airborne prey in the open and does not hunt birds with a gleaning strategy as was suggested (8).

N. lasiopterus might perhaps catch birds in boxes when they are searching for roosts (8). However, this is unlikely to explain the observed pattern because the proportion of feathers in the bat fecal pellets is minimal in spring, when the number of birds breeding in boxes is at its peak. In addition, only feathers were found in feces, and never the remains of other common box-dwelling vertebrates (e.g., bats, geckos, and mice) typically found in feces from gleaning carnivorous bats (e.g., *Nycteris grandis, Vampyrum spectrum*, *Chrotopterus auritus*) (6, 14).

The known carnivorous bats accumulate remains under perching sites where the prey are carried and consumed. In contrast, none of our netted bats was caught carrying a bird and bird

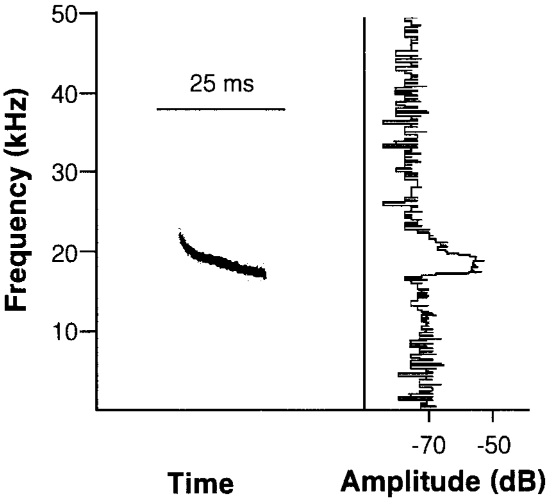

Fig. 3. Sonogram (*Left*) and power spectrum (*Right*) of a typical echolocation call of the greater noctule, *N. lasiopterus*. Pulse duration is 18.2 ms and peak frequency is 19.2 kHz.

remains were never found under the bat colony. However, two fresh and recently cut passerine wings (*Erithacus rubecula* and *Phylloscopus sibilatrix)* were recovered on the ground during the nocturnal netting of bats, and one greater noctule carried in its claws feathers identified as belonging to *E. rubecula*. These observations strongly suggest that *N. lasiopterus* handles and eats birds in flight just as aerial-hawking bats normally do with insects. The greater noctule can approach and surprise the birds without being detected, because its echolocation frequency is far above the "auditory space" (0.5–6.0 kHz) of the birds (15).

The greater noctule is the largest European bat (body mass = 47.9 ± 0.41 g, $n = 155$; forearm = 64.4 ± 1.52 mm, $n = 170$; wingspan = 450 ± 23.3 mm, $n = 12$) and one of the largest aerial-hawking bats in the world; thus, it should be able to easily overpower small passerines flying at night. The congeneric *Nyctalus noctula* flies at around 500 m above the ground in autumn, most probably to feed on migratory insects (16), and the free-tailed *Tadarida teniotis*, another large aerial-hawking bat from the Mediterranean region, is reported to hunt migratory insects in mountain passes (17). Switching from a diet of large flying insects to one of small flying birds should not require any specific adaptations in the wing morphology or echolocation system of *N. lasiopterus*, apart from the size increase. In fact, the smaller congeneric, but morphologically similar, *Nyctalus leisleri* and *N. noctula* are well known, fast-flying, aerial-hawking insectivorous bats with wing morphology and echolocation characteristics consistent with this feeding strategy (11, 16, 18, 19).

As a rough estimate, 5,000 million West and Central Palaearctic passerines migrate toward trans-Saharan Africa across the Mediterranean basin in autumn (2). Although these birds use a broad-front migration, important migratory streams concentrate in the Iberian Peninsula (e.g., migration intensity across Iberia is twice that across the Balearic islands; ref. 12). This huge migration occurs during 7 out of approximately 9 months of bat activity; therefore, a diet switch would be highly advantageous. Whether large aerial-hawking bats from other temperate/subtropical zones in the route of migrating birds (e.g., *Eumops underwoodii* in America or *Ia io* in Southeast Asia) also make use of this food resource remains to be investigated. Finally, this finding opens new perspectives to the study of evolutionary interactions between birds and bats. Particularly, it raises new questions about the selective impact of predation and possible behavioral and ecological responses of passerines to this new selective pressure during migration.

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1. Fenton, M. B. & Flemming, T. H. (1976) *Biotropica* **8,** 104–110.
2. Moreau, R. E. (1972) *The Palaearctic–African Bird Migration Systems* (Academic, London).
3. Alerstam, T. (1993) *Bird Migration* (Cambridge Univ. Press, Cambridge, U.K.).
4. Orta, J. (1994) in *Handbook of the Birds of the World, Vol. 2: New World Vultures to Guineafowl*, eds. del Hoyo, J., Elliot, A. & Sargatal, J. (Lynx Edicions, Barcelona), p. 266.
5. Schnitzler, H. U. & Kalko, E. (1998) in *Bat: Biology and Conservation*, eds. Kunz, T. H. & Racey, P. A. (Smithsonian Inst. Press, Washington, DC), pp. 183–196.
6. Norberg, U. M. & Fenton, M. B. (1988) *Biol. J. Linn. Soc.* **33,** 383–394.
7. Pavey, C. R. & Burwell, C. J. (1997) *J. Zool.* **243,** 295–303.
8. Dondini, G. & Vergari, S. (2000) *J. Zool.* **251,** 233–236.
9. Tupinier, Y. (1973) *Period. Biol.* **75,** 93–95.
10. Teeriuk, B. J. (1991) *Hair of West European Mammals: An Atlas and Identification Key* (Cambridge Univ. Press, Cambridge, U.K.).
11. Norberg, U. M. & Rayner, J. M. V. (1987) *Philos. Trans. R. Soc. London B* **316,** 335–427.
12. Bruderer, B. & Liechti, F. (1999) in *Proc. Int. Ornithol. Congr., Durban*, eds. Adams, N. & Slotow, R. (BirdLife South Africa, Johannesburg), pp. 1983–1999.
13. Fenton, M. B. (1990) *Can. J. Zool.* **68,** 411–422.
14. Gardner, A. L. (1977) in *Biology of Bats of the New World Family Phyllostomatidae, part II*, eds. Baker, R. J., Jones, J. K., Jr., & Carter, D. C. (Spec. Publ. Mus. Texas Tech Univ., Lubbock, TX), pp. 293–350.
15. Dooling, R. J., Lohr, B. & Dent, M. L. (2000) in *Comparative Hearing: Birds and Reptiles*, eds. Dooling, R. J., Popper, A. N. & Fay, R. R. (Springer, New York), pp. 309–359.
16. Kronwitter, F. (1988) *Myotis* **26,** 23–85.
17. Arlettaz, R. (1990) *Z. Säugetierk.* **55,** 28–42.
18. Baagøe, H. J. (1987) in *Recent Advances in the Study of Bats*, eds. Fenton, M. B., Racey, P. & Rayner, J. M. V. (Cambridge Univ. Press, Cambridge, U.K.), pp. 57–74.
19. Waters, D. A., Rydell, J. & Jones, G. (1995) *Behav. Ecol. Sociobiol.* **37,** 321–328.