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# Low-frequency echolocation enables the bat *Tadarida teniotis* to feed on tympanate insects

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## SUMMARY

The European free-tailed bat, *Tadarida teniotis*, forages in uncluttered airspace by using intense narrow-band echolocation calls with low frequency (11–12 kHz), and feeds on relatively large flying insects, mainly (90% by volume) of the tympanate orders Lepidoptera and Neuroptera. The use of low-frequency echolocation calls without strong harmonics appears to be a specialization for long-range detection of large, tympanate insects, which are less well represented in the diet of most other aerial-hawking bats. The results provide evidence in support of the allotonic frequency hypothesis, i.e. that use of echolocation calls with frequencies above or below the best hearing of tympanate insects is an adaptation to increase the availability of these insects.

## 1. INTRODUCTION

Predation pressure from echolocating bats seems to be the primary reason for the evolution of tympanal organs (ears) in members of the major families of nocturnal moths (Lepidoptera), i.e. Noctuidae, Notodontidae, Geometridae, Pyralidae and Sphingidae, and also in at least one family of lacewings (Neuroptera; Chrysopidae). These hearing organs are tuned to the acoustic frequencies used by most bats, usually between 20 kHz and 50 kHz (see, for example, Miller 1984; Fullard 1987), and elicit evasive flight manoeuvres when exposed to sound pulses containing these frequencies (see, for example, Roeder 1967; Miller & Olesen 1979; Surlykke 1988). Moths with intact tympanal organs stand much higher chances (ca. 40%) of surviving attacks by aerial-hawking bats than deafened moths (Roeder 1967; Acharya 1992).

The European free-tailed bat, *Tadarida teniotis* (Rafinesque 1814), is a large (25–50 g) molossid that searches for prey during fast and straight flight in open air and by use of comparatively long (ca. 15 ms), intense, narrow-band echolocation pulses with most energy between 11 kHz and 12 kHz (Zbinden & Zingg 1986; Arlettaz 1990). Use of such low-frequency pulses for echolocation is unusual among bats, presumably because their long wavelength (3 cm) makes them unsuitable for detection of small prey items (Pye 1980; Möhl 1988), and therefore suggests a specialization on relatively large, tympanate insects. To test this, we analysed the diet of *T. teniotis* from Europe and also, for comparison, from a site in Central Asia.

## 2. METHODS

Droppings were collected under *Tadarida teniotis* roosts situated in a high building at Sisteron in southeastern France (44° 11' N, 05° 57' E) in April 1989 (Arlettaz 1993), and also

from bats captured in mist nets in the Duvachan Pass (850 m above sea level) in the Osh Province of Kirghizstan, Central Asia (40° 22' N, 72° 31' E), in September 1992.

The droppings were soaked in a mixture of water and ethanol, and subsequently teased apart under a binocular microscope. Insect remains were identified to order, and in some cases to family, by comparison with a sample of whole insects and by the use of various field guides to insects and keys to faecal analysis (see, for example, Whitaker 1988; McAney *et al.* 1992). Droppings (100) from the French locality were analysed, as were 50 from the locality in Kirghizstan. Hence each dropping was assumed to represent 1% and 2% (1/100 and 1/50), respectively, of the samples by volume. For some droppings which contained more than one prey category, the approximate proportion (by volume) of each was estimated visually (Whitaker 1988).

## 3. RESULTS

Both samples showed a dominance of lepidopteran remains, which comprised 68% and 87% of the volume for the European and Central Asian samples, respectively (figure 1). Lepidopteran remains in the form of scales, as well as chitinous parts, were present in every individual dropping examined. Further classification of Lepidoptera into families was not possible because diagnostic remains such as wings, mouthparts and antennae were rarely found.

In the European sample, Neuroptera, mostly of the family Hemerobiidae, comprised 24% of the volume, and was hence the second most important prey category. In the sample from Central Asia, however, neuropterans were rare, and only 0.2% of the remains were of this order. Instead, an unidentified hemipteran was the second most common prey item in this sample (12%).

Other insect orders such as Trichoptera, Diptera, Coleoptera and Hymenoptera were also recovered, but these taxa together represented only 4% of the

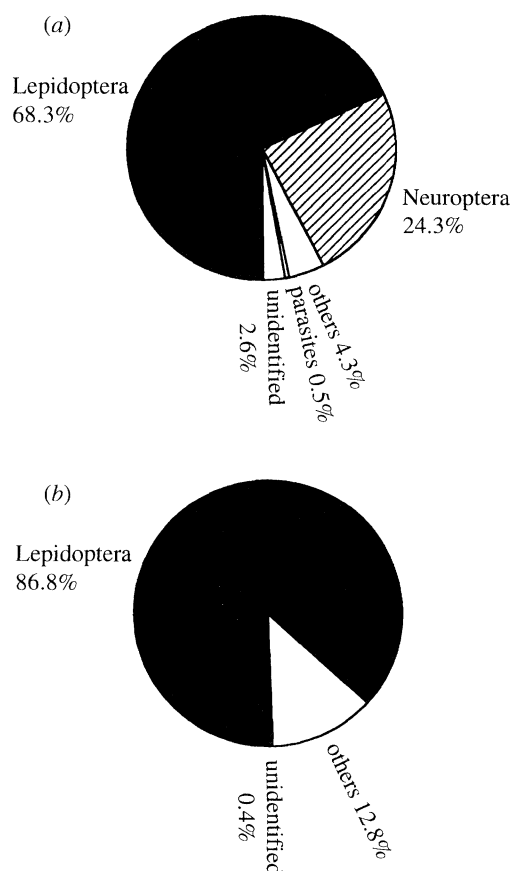


Figure 1. The diet (% volume) of *Tadarida teniotis* as determined from faeces (a) collected under a roost in southeastern France and (b) from bats mistnetted in Kirghizstan.

European sample and 0.4% of the Central Asian one (figure 1). Some ectoparasitic mites (Acari), which presumably had been ingested during grooming, were also recovered from the European sample (0.5%).

Disregarding the mites, the smallest insects encountered were the Neuroptera (Hemerobiidae) referred to above, which have body lengths of approximately 5 mm and wingspreads of 15 mm. A few wing fragments, legs and antennae from other insects suggests that many of these prey items were much larger.

#### 4. DISCUSSION

Many bat species are believed to overcome the defence systems of tympanate insects by using detection strategies which are less conspicuous to the prey, for example, by using echolocation pulses of low intensity or with frequencies above the insects' hearing ranges, thereby minimizing the insects' detection distance (Novick 1977; Fenton & Fullard 1979; Faure *et al.* 1990; Jones 1992), or by ceasing sound emission and relying on passive listening and vision instead (see, for example, Bell 1982, 1985; Anderson & Racey 1991; Faure & Barclay 1992). Such strategies have the disadvantage of a relatively short detection range, and hence reaction time for the bat, however, due to initial

low pulse intensities and increased atmospheric attenuation of high-frequency sound (Lawrence & Simmons 1982), and are therefore used mainly by relatively slow-flying, manoeuvrable bats, some of which glean their prey from surfaces.

Fast-flying, aerial-hawking bats require high-intensity echolocation pulses and also relatively low frequencies, which suffer less severe attenuation losses, to compensate for the longer detection distances and reaction times required in such situations (Barclay 1986; Barclay & Brigham 1991). However, such pulses are very conspicuous to tympanate insects unless the frequencies fall below their best hearing range (Novick 1977; Fenton & Fullard 1979; Fullard 1987).

In *T. teniotis*, no less than 93% of the European sample and 87% of the Central Asian sample was composed of remains of the orders Lepidoptera (moths) and Neuroptera (lacewings). Most nocturnal moths and at least some lacewings possess ears sensitive to bat echolocation calls. The high incidence of these insects in the diet is in sharp contrast to other species of large or medium-sized aerial-hawking bats in the Palearctic for which the diet has been analysed systematically. For these species (i.e. *Eptesicus serotinus*, *E. nilssonii*, *Vespertilio murinus*, *Nyctalus noctula*, *N. leisleri*), which all search for prey by use of narrow-band echolocation calls with frequencies between 20 kHz and 30 kHz (Ahlén 1981), either dipterans or dung beetles (Scarabaeidae) are the most important prey items. These insects do not possess defence mechanisms against bat predation, as far as is known. Moths represent less than 20%, and usually less than 10%, of the diet of these species (Sologor 1980; Bauerová & Ruprecht 1989; Rydell 1989, 1992; Sullivan *et al.* 1993; Catto *et al.* 1994; Jones 1994). A similar situation seems to apply to comparable North American species, e.g. *Eptesicus fuscus* (Brigham & Saunders 1990), *Lasius cinereus* (Whitaker & Tomich 1983; Barclay 1985), *Lasionycteris noctivagans* (Barclay 1985) and *Nycticeius humeralis* (Whitaker & Clem 1992), although, when feeding around streetlamps, these bats may sometimes subsist almost entirely on moths (see, for example, Belwood & Fullard 1984; Hickey & Fenton 1990). However, insect ears evolved in habitats which were free of streetlamps, and therefore a lit road may not be the appropriate place to test the outcome of the evolutionary arms race between bats and tympanate insects. Artificial lights interfere with the moths' flight behaviour, and probably make them easier targets than they would be in other, more natural, situations (Rydell & Racey 1994).

There are few other low-frequency bats for which the diet is adequately known. One example, however, is the North American aerial-hawking species *Euderma maculatum*, which provides a case similar to that of *Tadarida teniotis*, as it also feeds in open habitats and uses low-frequency (11 kHz) echolocation calls when searching for prey (Leonard & Fenton 1983). This species, too, feeds primarily on moths (Wai-Ping & Fenton 1989).

*Tadarida teniotis* is a large, fast-flying bat, and its ability to catch moths may not only depend on its echolocation call frequency but perhaps also on its

flight speed. However, two lines of evidence suggest that the echolocation call frequency, not flight speed, is of primary importance: (i) among aerial-hawking bats, *Euderma maculatum*, which also feeds extensively on moths, is a relatively slow-flying, manoeuvrable species, very different from *T. teniotis* (Leonard & Fenton 1983); (ii) other large, fast-flying species, e.g. *Nyctalus* spp., which use higher frequencies, do not feed on moths to the same extent as *T. teniotis*.

Disregarding observations made near streetlamps, the difference in moth exploitation between *Tadarida teniotis* and *Euderma maculatum*, which use low frequencies, and other Palaearctic and Nearctic aerial-hawking bats, which use higher frequencies is good evidence that tympanate insects avoid predation by aerial-hawking bats because of their hearing abilities. The evidence therefore supports the 'allotonic frequency hypothesis', i.e. that use of low-frequency echolocation calls during search flight is an adaptation to increase the availability of tympanate insects by minimizing the distance at which the insects can detect the bat (Novick 1977; Fenton & Fullard 1979; Fullard 1987).

The fact that bat species which use low-frequency echolocation calls, such as *T. teniotis* and *E. maculatum*, are comparatively rare components of their respective bat faunas, and hence contribute little to the total selective pressure on insects in these areas, is also consistent with this hypothesis (Fullard 1987).

Although the echolocation calls used by many aerial-hawking bats during the search phase usually include strong harmonics (see, for example, Ahlén 1981; Habersetzer 1981; Barclay 1986; Kalko & Schnitzler 1993; Surlykke *et al.* 1993), this is apparently not the case in species which use low frequencies, such as *Tadarida* spp. and *Euderma maculatum* (Simmons *et al.* 1978; Leonard & Fenton 1983; Barclay 1986; Zbinden & Zingg 1986). This observation is also consistent with the allotonic frequency hypothesis because second or higher harmonics would fall within the best hearing range of many tympanate insects.

The use of low-frequency echolocation in *Tadarida teniotis*, and probably also in some other large, aerial-hawking bats, may thus be considered as a specialization for echolocation of relatively large tympanate insects in the open air, a prey type which appears to be less available to other aerial-hawking bats. The combination of low echolocation call frequency (long wavelengths) and fast flight also involves a considerable cost, however, because small insect, such as dipterans, which are often the most abundant, are no longer available (Pye 1980; Möhl 1988; Barclay & Brigham 1991). The specialization on tympanate insects by use of low frequencies thus reduces the available food spectrum, and hence the flexibility in prey choice, considerably.

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## REFERENCES

- Acharya, L. 1992 Are ears valuable to moths flying around lights? *Bat Res. News* **33**, 47.
- Ahlén, I. 1981 *Identification of Scandinavian bats by their sounds*. Uppsala: Swedish University of Agricultural Sciences, Department of Wildlife Ecology.
- Anderson, M. E. & Racey, P. A. 1991 Discrimination between fluttering and non-fluttering moths by brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* **46**, 1151–1155.
- Arlettaz, R. 1990 Contribution à l'éco-éthologie du Molosse de Cestoni, *Tadarida teniotis* (Chiroptera), dans les Alpes valaisannes (sud-ouest de la Suisse). *Z. Säugetierk.* **55**, 28–42.
- Arlettaz, R. 1993 *Tadarida teniotis*' tail. *Myotis* **31**, 155–162.
- Barclay, R. M. R. 1985 Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. *Can. J. Zool.* **63**, 2507–2515.
- Barclay, R. M. R. 1986 The echolocation calls of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats as adaptations for long- versus short-range foraging strategies and the consequences for prey selection. *Can. J. Zool.* **64**, 2700–2705.
- Barclay, R. M. R. & Brigham, R. M. 1991 Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *Am. Nat.* **137**, 693–703.
- Bauerová, Z. & Ruprecht, A. L. 1989 Contribution to the knowledge of the trophic ecology of the parti-coloured bat, *Vespertilio murinus*. *Folia Zool.* **38**, 227–232.
- Bell, G. P. 1982 Behavioral and ecological aspects of gleanings by the desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* **10**, 217–223.
- Bell, G. P. 1985 The sensory basis of prey location by the California leaf-nosed bat *Macrotus californicus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* **16**, 343–347.
- Belwood, J. J. & Fullard, J. H. 1984 Echolocation and foraging behaviour in the Hawaiian hoary bat *Lasiurus cinereus semotus*. *Can. J. Zool.* **62**, 2113–2120.
- Brigham, R. M. & Saunders, M. B. 1990 The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. *NW Sci.* **64**, 7–10.
- Catto, C. M. C., Hutson, A. M. & Racey, P. A. 1994 The diet of *Eptesicus serotinus* in southern England. *Folia Zool.* (In the press.)
- Faure, P. A. & Barclay, R. M. R. 1992 The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. *Anim. Behav.* **44**, 31–39.
- Faure, P. A., Fullard, J. H. & Barclay, R. M. R. 1990 The response of tympanate moths to the echolocation calls of a substrate gleanings bat, *Myotis evotis*. *J. comp. Physiol. A* **166**, 843–849.
- Fenton, M. B. & Fullard, J. H. 1979 The influence of moth hearing on bat echolocation strategies. *J. comp. Physiol. A* **132**, 77–86.
- Fullard, J. H. 1987 Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In *Recent advances in the study of bats* (ed. M. B. Fenton, P. A. Racey & J. M. V. Rayner), pp. 244–272. Cambridge University Press.
- Habersetzer, J. 1981 Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*. A field study. *J. comp. Physiol. A* **144**, 559–566.
- Hickey, M. B. C. & Fenton, M. B. 1990 Foraging by red

- bats (*Lasiurus borealis*): do interspecific chases mean territoriality? *Can. J. Zool.* **68**, 2477–2482.
- Jones, G. 1992 Bats vs moths: studies on the diets of rhinolophid and hipposiderid bats support the allotonic frequency hypothesis. In *Prague studies in mammalogy* (ed. I. Horaček & V. Vohralík), pp. 87–92. Prague: Charles University Press.
- Jones, G. 1994 Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. *J. Zool. Lond.* (In the press.)
- Kalko, E. K. V. & Schnitzler, H.-U. 1993 Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.* **33**, 415–428.
- Lawrence, B. D. & Simmons, J. A. 1982 Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. acoust. Soc. Am.* **71**, 585–590.
- Leonard, M. L. & Fenton, M. B. 1983 Habitat use by spotted bats (*Euderma maculatum*, Chiroptera: Vespertilionidae): roosting and foraging behavior. *Can. J. Zool.* **61**, 1487–1491.
- McAney, C. M., Shiel, C. B., Sullival, C. M. & Fairley, J. S. 1992 *The analysis of bat droppings*. London: Mammal Society.
- Miller, L. A. 1984 Hearing in green lacewings and their responses to the cries of bats. In *Biology of Chrysopidae* (ed. M. Canard, Y. Semeria & T. R. New), pp. 134–139. Hague: Junk Publishers.
- Miller, L. A. & Olesen, J. 1979 Avoidance behavior in green lacewings. I. Behavior of free flying green lacewings to hunting bats and ultrasound. *J. comp. Physiol. A* **131**, 113–120.
- Möhl, B. 1988 Target detection by echolocating bats. In *Animal sonar: processes and performance* (ed. P. E. Nachtigall & P. W. B. Moore), pp. 435–450. New York: Plenum Press.
- Novick, A. 1977 Acoustic orientation. In *Biology of bats*, vol. 3 (ed. W. A. Wimsatt), pp. 73–287. New York: Academic Press.
- Pye, J. D. 1980 Echolocation signals and echoes in air. In *Animal sonar systems* (ed. R. G. Busnel & J. F. Fish), pp. 309–354. New York: Plenum Press.
- Roeder, K. D. 1967 *Nerve cells and insect behavior*, 2nd edn. Cambridge, Massachusetts: Harvard University Press.
- Rydell, J. 1989 Food habits of northern (*Eptesicus nilssonii*) and brown long-eared (*Plecotus auritus*) bats in Sweden. *Holarct. Ecol.* **12**, 16–20.
- Rydell, J. 1992 The diet of the parti-coloured bat *Vespertilio murinus* in Sweden. *Ecography* **15**, 195–198.
- Rydell, J. & Racey, P. A. 1994 Streetlamps and the feeding ecology of insectivorous bats. In *Ecology, evolution and behaviour of bats* (ed. P. A. Racey & S. M. Swift) (*Symp. zool. Soc. Lond.*). (In the press.)
- Simmons, J. A., Lavender, W. A., Lavender, B. A., Childs, J. E., Hulebak, K., Rigden, M. R., Sherman, J., Woolman, B. & O'Farrell, M. J. 1978 Echolocation by free-tailed bats 9 *Tadarida*). *J. comp. Physiol. A* **125**, 291–299.
- Sologor, E. L. 1980 K izutjeniyu pitaniya *Vespertilio serotinus*. In *Voprosy teriologii. Rukokryliye* (ed. V. E. Sokolov), pp. 188–190. Moscow: Akademia Nauk.
- Sullivan, C. M., Shiel, C. B., McAney, C. M. & Fairley, J. S. 1993 Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentonii* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. *J. Zool.* **231**, 656–663.
- Surlykke, A. 1988 Interaction between echolocating bats and their prey. In *Animal sonar: processes and performance* (ed. P. E. Nachtigall & P. W. B. Moore), pp. 551–566. New York: Plenum Press.
- Surlykke, A., Miller, L. A., Möhl, B., Andersen, B. B., Christensen-Dalsgaard, J. & Jørgensen, M. B. 1993 Echolocation in two very small bats from Thailand: *Craseonycteris thonglongyai* and *Myotis siligorensis*. *Behav. Ecol. Sociobiol.* **33**, 1–12.
- Wai-Ping, V. & Fenton, M. B. 1989 Ecology of spotted bats: roosting and foraging behaviour. *J. Mamm.* **70**, 617–622.
- Whitaker, J. O. Jr 1988 Food habit analysis of insectivorous bats. In *Ecological and behavioral methods for the study of bats* (ed. T. H. Kunz), pp. 171–189. Washington, D.C.: Smithsonian Institution Press.
- Whitaker, J. O. Jr & Clem, P. 1992 Food of the evening bat *Nycticeius humeralis* from Indiana. *Am. Midl. Nat.* **127**, 211–214.
- Whitaker, J. O. Jr & Tomich, P. Q. 1983 Food habits of the hoary bat, *Lasiurus cinereus*, from Hawaii. *J. Mamm.* **64**, 151–152.
- Zbinden, K. & Zingg, P. 1986 Search and hunting signals of echolocating European free-tailed bats, *Tadarida teniotis*, in southern Switzerland. *Mammalia* **50**, 9–25.

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