The diet of bats from Southeastern Brazil: the relation to echolocation and foraging behaviour

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ABSTRACT. In this study the incidence of moths and beetles was examined from feces samples of bats that use different foraging behaviors. Twenty sites around the Fazenda Intervales, a Field Research Station located in São Paulo State, in southeastern Brazil were sampled. Feces were collected from bats caught in mist nets, Tuttle Traps or hand nets and, in one case, from beneath a roost. Feces samples were taken from six species of bats: *Micronycteris megalotis* (Gray, 1842), *Mimon bennettii* (Gray, 1838), *Furipterus horrens* (F. Cuvier, 1828), *Myotis riparius* Handley, 1960, *Myotis ruber* (E. Geoffroy, 1806) and *Histiotus velatus* (I. Geoffroy, 1824). To record and describe the frequencies dominating bat echolocation calls, an Anabat II bat detector coupled with an Anabat ZCA interfaces and DOS laptop computers were used. The data show that *Furipterus horrens* feeds extensively on moths, as predicted from the features of its echolocation calls. Gleaning bats, whose echolocation calls are much less conspicuous to moths take a wide range of insect (and other) prey.

KEY WORDS. Chiroptera, diet, echolocation, foraging behaviour, southeastern Brazil

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The interactions between echolocating bats and insects with bat-detecting ears is a particularly enlightening example of the impact that perceptual abilities can have on predator-prev interactions. FULLARD (1987) and RYDELL et al. (1995) described how the frequencies dominating the echolocation calls of bats directly influenced the conspicuousness of these calls to moths. Differences in the conspicuousness of bats' echolocation calls to moths reflects the fact that moth ears are most sensitive to sounds between 20 and 60 kHz (FULLARD 1987: RYDELL et al. 1995). Three categories of bats use echolocation calls that are relatively inaudible to moths or other insects with bat-detecting ears. First are aerial-feeding bats, those that hunt mainly flying insects, and use echolocation calls dominated by frequencies < 20 kHz and which often feed heavily on moths – e.g. Tadarida teniotis (Rafinesque, 1814) RYDELL & ARLETTAZ (1994); Euderma maculatum (J.A. Allen, 1891) FULLARD & DAWSON (1997); Otomops martiensseni (Matschie, 1897) RYDELL & YALDEN (1997). Second are aerial-feeding bats whose calls are dominated by frequencies > 60 kHz - e.g. many rhinolophids and hipposiderids (JONES 1992). Third are gleaning bats whose echolocation calls are relatively inaudible to moths, species that tend to use low intensity echolocation calls (FAURE et al. 1990); for these species, the role of echolocation in their hunting behaviour remains unclear (FENTON et al. 1995).

The purpose of this study was to examine the incidence of moths and beetles in the feces of a sample of bats that use different foraging behaviour. The aerial feeders used echolocation calls dominated by different frequencies (< 20 kHz; 20-60 kHz; > 60 kHz). It was predicted that aerial feeding bats whose echolocation calls are < 20 kHz and > 60 kHz should feed more on moths than species broadcasting between 20 and 60 kHz. Gleaners may show a more variable pattern in the incidence of moths in their diets as reflected in other studies, for example of *Antrozous pallidus* (Le Conte, 1856) (BELL 1982).

Sampling was made over six species of bats: *Micronycteris megalotis* (ALONSO-MEJÍA & MEDELLIN 1991) and *Mimon bennettii* (PEDRO *et al.* 1994; ORTEGA & ARITA 1997) are gleaners, and some observations suggest that *Furipterus horrens* is an aerial feeder (UIEDA *et al.* 1980), but this species has not been studied in detail. Both *Myotis riparius* and *Myotis ruber* also appear to be aerial feeders (unpublished observations) as does *Histiotus velatus* (W.A. Pedro unpublished observations).

MATERIAL AND METHODS

Between 4 and 14 January 1997, twenty sites around the Fazenda Intervales, a Field Research Station located in São Paulo State, in southeastern Brazil (24°16'S; 48°24'W) were sampled. In this area, the vegetation is Atlantic forest (pluvial or rain forest). The Fazenda Intervales station is located in an area of karst where limestone caves provide an abundance of roosts for bats. There is no distinct dry season in the area, although precipitation is lower between May and September than at other times of the year (TRAJANO 1996). The annual rainfall ranges between 1000 and 2000 mm and the mean annual temperature is about 20°C.

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Anabat II bat detector, coupled with an Anabat ZCA interface and DOS laptop computers were used. This system provides no information about the harmonics in the echolocation calls, but indicates the frequencies dominating the calls and the durations of the calls. Echolocation calls of known individuals were recorded from bats flying in the field (light-tagged HOVORKA *et al.* 1996) or in the on site laboratory.

Feces were collected from bats caught in mist nets, Tuttle Traps (TUTTLE 1974) or hand nets and, in one case, from beneath a roost. Feces were examined and analyzed by volume as described by WHITAKER (1988).

RESULTS

The bats here sampled used a range of frequencies in their echolocation calls (Tab. I). While the *Myotis* species and *Histiotus velatus* used high intensity echolocation calls (detectable by the Anabat detector at distances of ≥ 10 m from the bat), the two gleaners (*Micronycteris megalotis* and *Mimon bennettii*) produced echolocation calls of much lower intensity (detectable by the Anabat detector at < 2 m from the bat). The echolocation calls of *Furipterus horrens* (Tab. I) were detectable at ≤ 1 m from the bat by the Anabat detector, probably reflecting their very short durations and the high frequencies in the calls.

Species	Echolacation calls			Foraging mode	Prediction: moths will dominate diet
	Highest kHz	Lowest kHz	Duration in ms		win dominate diet
Furipterus horrens	150	120	<1	unknow	yes
Micronycteris megalotis	94	59	1-2	gleaner	no
Mimon bennettii	180	35	1	gleaner	no
Myotis sp. cf riparius	58	50	4-5	aerial	no
Myotis sp. cf ruber	65	58	5	aerial	no
Histiotus velatus	25	15	5-8	aerial	yes

Table I. The echolocation calls and foraging behaviour of the bats.

The data on foraging behaviour (aerial versus gleaner) and frequencies dominating the echolocation calls lead us to predict that two of the aerial-feeders should prey more often on moths than the other aerial feeders (Tab. I). A total of 137 fecal pellets from the 6 species of bats shown in table II were collected and analyzed.

A c^2 test for heterogeneity or independence reveals that Lepidoptera are significantly more often dominant (> 50% of the volume of insects encountered) in the feces of *Furipterus* and *Histiotus* ($c^2 = 83.87$; df = 3; P < 0.0001) than in the feces of the *Myotis* species or those of the gleaners. There were similar significant differences in the opposite direction for Coleoptera in the feces of *Myotis* and the gleaners versus *Furipterus* and *Histiotus* ($c^2 = 56.67$; df = 3; P < 0.0001). The same pattern of significant differences of Coleoptera and Lepidoptera also prevails when the c^2 test for heterogeneity or independence is performed on a species by species basis ($c^2 = 155.71$, df = 10, P < 0.0001). In all comparisons the differences are significant.

	Bat	Gleaners		
	< 20 kHz	20-100 kHz	> 100 kHz	Gleaners
Number of species	1	2	1	2
Number of bats/ Number of pellets	?/41	7/50	2/20	3/26
Number of insect orders	4	6	1	3
Number of Pellets 100% Lepidoptera	33	6	20	0
Number of Pellets with any Lepidoptera	39	29	20	0
Number of Pellets 100% Coleoptera	0	13	0	15
Number of Pellets with any Coleoptera	4	24	0	26

Table II. The incidence of moths in the feces of bats sampled.

DISCUSSION

The data of this study support earlier predictions about the vulnerability of moths to hunting bats based on the features of bats' echolocation calls and their foraging behaviour (FULLARD 1987; RYDELL *et al.* 1995). However, like other analyses, the methodology here used does not resolve two important questions about bats' diets, namely the nature of the moths eaten by bats and the description of their diets. Are the moths eaten by bats species with functional bat-detecting ears or those that are deaf or lacking ears? Earless and deaf moths show different patterns of flight (some deaf moths are flightless) behaviour that could influence their exposure to aerial-feeding bats (MORRILL & FULLARD 1992). The prevalence of Coleoptera in the feces of some species of bats also could complicate generalizations about the vulnerability of beetles to aerial-feeding bats, because some species have bat-detecting ears (YAGER & SPANGLER 1997).

The data indicate that *Furipterus horrens* feeds extensively on moths as predicted from the features of its echolocation calls which would be virtually inaudible to moths with hearing-based defenses. The same degree of specialization does not extend to *Histiotus velatus* whose calls are probably more conspicuous to moths than those of *Furipterus*, but less so than those of the aerial-feeding *Myotis* that were studied. Gleaning bats, whose echolocation calls are much less conspicuous to moths (*e.g.* FAURE *et al.* 1990) also take a wide range of insect (and other) prey.

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