

Wing morphology, echolocation calls, diet and emergence time of black-bearded tomb bats (*Taphozous melanopogon*, Emballonuridae) from southwest China

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We studied the wing morphology, echolocation calls, diet and emergence time of the black-bearded tomb bat (*Taphozous melanopogon*) from May to October 2006 in Guangxi Province, southwest China. *Taphozous melanopogon* has wings with high aspect ratio, high loading and pointed wing-tip shape-characteristics associated with fast flight in open space. This species usually produces low-intensity, low frequency, and frequency-modulated (FM) calls usually containing up to four harmonics, with most energy in the second (or sometimes third) harmonic. The diet of this species consists mostly of Lepidoptera and Hemiptera. Timing of evening emergence is correlated with the time of sunset. This is the first study to describe the flight and echolocation behavior of this species in China, and opens the way for future studies of its biology.

Key words: flight morphology, echolocation calls, diet, emergence time, *Taphozous melanopogon*, southwest China

INTRODUCTION

Wing morphology and echolocation call design can affect a bat's access to habitat (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987). The wing morphology of bats can be used to predict flight behavior and feeding niches (Norberg and Rayner, 1987). A higher aspect ratio usually corresponds with greater aerodynamic efficiency and lower energy expenditure in flight, and wing loading is considered to be positively correlated with flight speed and negatively correlated with manoeuvrability and agility (Norberg and Rayner, 1987). Generally, bats characterized as having (i) high wing loadings, high aspect ratios and high wingtip shape indices fly fast in open area, (ii) high wing loadings, average aspect ratios and average wing tip shape indices fly in and around the edges of vegetation in background-cluttered space, and (iii) low wing

loadings, average or low aspect ratios and pointed wing tip shape indices fly in highly-clutter space (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987). Many bats use echolocation calls to orientate and locate prey (Fenton, 1995; Schnitzler and Kalko, 1998). The structure of echolocation calls has been shown to be associated with niche partitioning in bat communities (Norberg and Rayner, 1987; Zhang *et al.*, 2005). Generally, bats with high aspect ratio wings with high wing loadings, and therefore reduced manoeuvrability, use narrow band echolocation calls at relatively lower frequency (usually less than 40 kHz) in more open area when they were searching for prey (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987). Moreover, the use of lower frequency and/or narrower band echolocation calls can increase the range of prey detection in open areas (Simmons and Stein, 1980; Norberg and Rayner, 1987). Because of their

shorter wavelength, higher frequency echolocation calls can be more effective for detecting smaller insects than lower frequency echolocation calls. However, the relationship between call frequency and prey size is not always coincident, as it has been shown that bats producing narrow band echolocation calls at lower frequencies also feed on smaller prey (Waters *et al.*, 1995).

Insectivorous bats are voracious predators but many species must compete for food and reproductive opportunities in spatially constrained, resource limited habitats. Therefore, effective resource partitioning is an important factor within bat communities, and must be included in any discussion of ecological interactions among bats (Kunz and Fenton, 2003).

The timing and patterns of nocturnal activities of bats can be affected by many factors, such as sunset and sunrise (Erkert, 1982; Welbergen, 2006), food availability (Erkert, 1982), weather (McAney and Fairy, 1988; Kunz and Anthony, 1996; Lee and McCracken, 2001), temperature (Kunz and Fenton, 2003), colony size and reproductive status (Korine *et al.*, 1994), potential predators (McWilliam, 1989; Speakman, 1991) and social context (Welbergen, 2006). Time of evening emergence is also one mechanism for avoiding competition between species of bats (Swift and Racey, 1983).

The black-bearded tomb bat (*Taphozous melanopogon* Temminck, 1841) is a medium-sized, aerially-foraging emballonurid with a forearm length of 63–68 mm. This species is widespread and occurs over much of south and southeast Asia (Bates and Harrison, 1997; Bates *et al.*, 2000; Simmons, 2005). *Taphozous melanopogon* commonly resides in urban areas, in areas with limestone caves, and in sea caves, and often coexists with other bat species such as *Scotophilus heathii*. It shows little geographical variation in morphology across its range (Medway, 1983; Bates and Harrison, 1997; Bates *et al.*, 2000; Simmons, 2005). Previous studies of *T. melanopogon* have focused on circadian rhythms (Subbarai and Chandrashekar, 1978), wing shape (Norberg and Rayner, 1987), external morphology (Bates *et al.*, 2000), and foraging and roosting habits (Zubaid, 1990); information on other aspects of its behavior and ecology are lacking.

To better understand this widespread bat, we investigated its wing morphology, echolocation calls, diet, and emergence time. We also investigated the pattern of emergence to see how many times the bats returned to the cave throughout the night.

Finally, we relate the diet of *T. melanopogon* to its echolocation calls and wing morphology.

MATERIALS AND METHODS

Study Site

The study took place from May to October 2006 in the vicinity of Bidi Cave (25°16.684'N, 111°20.914'E) near Guilin City in Guangxi Province, southwest China. The colony resides in a limestone cave, within a karst landscape typical of the region. The cave is surrounded by shrubbery, arbors, villages, lakes, and farmland. This region is subtropical, with an annual mean temperature of 19.3°C, and annual precipitation averaging 1900 mm with seasonal variation. The cave has two entrances, with one (about 20 m above the ground) used by *T. melanopogon* and the other one (about 3 m above the ground) used by *Myotis siligorensis*. The cave housed about 350 individuals of *T. melanopogon* and several *M. siligorensis* during the study period.

Wing Morphology Measurements

Bats were captured with mist nests as they returned to the caves after nightly foraging. When a bat was captured, we noted the time and kept it on its own in a cotton bag before transporting all captured bats back to the lab. Bats were sexed, aged, and the reproductive condition of females noted. Juvenile bats were differentiated from adults by the degree of fusion of the epiphyses at the metacarpal-phalangeal joints and were excluded from this study to avoid inconsistent body mass estimates (Black, 1974; Norberg and Rayner, 1987; Anthony, 1988). Pregnant females were also excluded from the study to avoid bias in estimates of wing-loading caused by increased body mass (Anthony, 1988; Zhang *et al.*, 2007).

Wing measurements were taken from adult males and non-pregnant females. Body masses (M) were determined using a spring balance (Q/CYA 41-1996, Shanghai, China) to the closest 0.1 g. Forearm length was measured to be the nearest 0.1 mm using dial calipers (c3000110, Measuring and Cutting Tool Works, Guilin, China). Wing tracings were made by tracing around the extended right wing and right half-tail, and right half-body on a plain sheet of graph (Thabah *et al.*, 2007; Zhang *et al.* 2007). Areas were calculated by counting panes on the graph papers (accuracy 1 mm²). Aspect ratio (A), wing loading (WL), and wing tip shape index (I) were calculated following Zhang *et al.* (2007) and Norberg and Rayner (1987). We also categorized aspect ratio, wing loading and wing tip shape index as low, average or high, following Jennings *et al.* (2004): 1. Aspect ratio: low ≤ 6.1 , average = 6.1–7.3, high ≥ 7.3 ; 2. Wing loading (N \times m⁻²): very low ≤ 6.45 , low = 6.45–7.5, average = 7.5–10.3, high ≥ 10.3 ; 3. Wingtip shape index: low ≤ 1.3 , average = 1.3–1.9, high ≥ 1.9 .

Echolocation Calls

After measuring the morphological parameters, the bats were taken to a temporary field laboratory and their echolocation calls were recorded. Echolocation calls were recorded for each bat using an ultrasound detector (D980, Pettersson Elektronik AB, Uppsala, Sweden) at a distance of approximately 1 m as the bat flew freely in nearly-dark condition after being

released from the hand. Time-expanded calls were digitized to a computer at sampling rate of 44.1 kHz with 16-bits precision and analyzed using the software Batsound (version 3.10, Pettersson Elektronik AB, Uppsala, Sweden). Power spectra and spectrograms were produced using 512-point Fast Fourier Transforms (FFT) with a Hanning window, giving a frequency resolution of 200 Hz.

For each bat, 5–10 sequential calls were analyzed, and the mean value for each measured parameter was used in later analyses. For each call, we measured the general dominant frequency (DF, kHz), start-frequency (Start-F, kHz) and end-frequency (End-F, kHz) of each harmonic, pulse duration (PD, ms), inter-pulse interval (IPI, measured from the start of one call to the start of the next call, ms) and duty cycle (DC, %). DF was measured from power spectra, Start-F and End-F from spectrograms, and PD and IPI from oscillograms following Zhang *et al.* (2007). On the basis of DC values, each bat was placed into one of three categories: low ($\leq 5\%$), average (5–10%), and high ($\geq 10\%$) based on Jennings *et al.* (2004).

Dietary Analysis

Insects potentially available to the bats were captured with light traps (GYZ250, Foshan, China) in known feeding areas over 1 week at monthly intervals from around sunset (18:40–19:20 h) to just after midnight (00:30 h). Captured insects were placed in plastic bottles containing ether and were taken to a laboratory for identification. Insects were identified to order (Zheng and Gui, 1999) and abundance as calculated by volume percentage (V%, the numbers of each order as a percentage of the total numbers of insects captured). Insects were identified using a reference collection (Black, 1974).

Bat feces were collected directly from underneath the day-roost in the morning, at monthly intervals, two hours after the bats had returned. When the bats' convergence position was confirmed, 5–10 fecal pellets collected from underneath the convergence position were classified as one sample. Samples were preserved in 96–100% alcohol. Fecal samples were teased apart with needles and tweezers after they had softened. Insect remains were observed under a low power dissecting microscope (10 \times magnification) and identified to order (Zhang *et al.*, 2005) and compared with potential insects captured by light trapping in the field. Prey composition and volume percentage was estimated visually to the nearest 5% for insects in the diet and from light trap samples. Frequency of occurrence of the different categories of prey was also evaluated for each fecal sample (Whitaker, 1988; Zhang *et al.*, 2005).

Monthly variation in the diet was compared by using a χ^2 -test. For calculation of food abundance in feces, all droppings collected from underneath the roost were analyzed. We used the Shannon-Wiener Index to calculate food abundance, where P_i is the proportion of the frequency of occurrence of each insect taxon captured (following Leslie *et al.*, 2002).

Timing of Emergence

To minimize disturbance of the bats, field work took place at intervals of one or two weeks near the 30 m high entrance of Bidi Cave which is about 1.2 m in height and 1 m diameter. Because of the size of the entrance, the fact that it was only used by *T. melanopogon*, and because bats did not return to the cave for at least two hours after leaving, bats could be reliably counted by eye as they left at dusk and returned at dawn.

Bats were counted at a distance of approximately 3 m from the cave mouth.

Observations began just before dusk, between 18:30–19:00 h depending on the time of year. Counts were carried out by two people, with the first person counting the numbers of bats emerging per minute, and the second person timing and recording observations. When no bats emerged after an interval of 15–20 minutes, counting ceased. Returning observations initiated at 23:00 h, and we defined the onset of returning as the time when bats began returning in a continuous column while no or few bats were leaving the cave. When no bats returned after an interval of 20 minutes, we considered that returning had ended. We also visually estimated cloud cover and wind speed at a location near the cave on each evening when emergence counts were conducted.

RESULTS

Wing Morphology

We captured a total of 86 bats, 71 of which were adults, including 37 males and 34 non-reproductive females. The average values of body mass (M), forearm length (FA), wingspan (B), wing area (S), aspect ratio (A), wing loading (WL), tip area ratio (T_s), tip length ratio (T_l) and wing tip shape index were 22.9 ± 2.3 g, 64.9 ± 1.7 mm, 368.3 ± 12.3 mm, 17857.5 ± 1626.8 mm², 7.64 ± 0.58 , 12.72 ± 1.09 N \times m⁻², 0.52 ± 0.05 , 1.18 ± 0.06 and 0.79 ± 0.12 , respectively. *T*-tests were used to compare M, FA, B, S, A, WL, T_s , T_l and I between males and females, yielding no significant differences between sexes (see Table 1).

Echolocation Calls

We were able to obtain high quality recordings from 12 of the 71 adult bats captured. Because sample size was low and no significant differences were detected between males and females for morphology measurements, data from echolocation calls from males and females were pooled.

Taphozous melanopogon usually produced low frequency, medium duration, modulated (FM) calls containing up to four harmonics with most energy in the second or sometimes third harmonics (Fig. 1). The average values of the Start-F and End-F of the 1st harmonic, the Start-F and End-F of the 2nd harmonic, the Start-F and End-F of the 3rd harmonic, Start-F and End-F of the 4th harmonic, general dominant frequency (DF), pulse duration (PD), inter-pulse interval (IPI), and duty cycle (DC) were as follows: 15.34 ± 0.96 kHz, 10.36 ± 2.72 kHz; 30.14 ± 2.58 kHz, 22.72 ± 2.62 kHz; 46.34 ± 4.34 kHz, 34.27 ± 7.53 kHz; 59.41 ± 2.28 kHz, 46.59 ± 2.11 kHz; 30.10 ± 3.41 kHz; 7.87 ± 1.74 ms; 61.43 ± 50.36 ms; 17.21 ± 10.42 , respectively.

TABLE 1. Morphological measurements of male ($n = 37$) and female ($n = 34$) of *T. melanopogon*. The means \pm SD (range in the parentheses) are shown. Abbreviations used are: n , numbers of bats; M, body mass; FA, forearm length; B, wing span; S, wing area; A, aspect ratio; WL, wing loading; S_{hw} , hand wing area; S_{aw} , arm wing area; L_{hw} , length of hand wing; L_{aw} , length of arm wing; T_s , S_{hw}/S_{aw} ; T_1 , L_{hw}/L_{aw} ; I, wing tip shape index [= $T_s/(T_1 - T_s)$]

Wing parameters	Males		Females		P-level (<i>t</i> -test)
	$\bar{x} \pm SD$	min-max	$\bar{x} \pm SD$	min-max	
M (g)	22.5 \pm 2.5	17.4–26.8	22.9 \pm 2.1	18.2–26.7	0.48
FA (mm)	64.6 \pm 1.8	61.6–68.8	65.3 \pm 1.5	60.0–67.4	0.07
B (mm)	366.9 \pm 9.4	340.6–383.0	369.4 \pm 14.3	339.4–393.4	0.44
S (mm ²)	17,769.6 \pm 1,539.3	14,614–20,996	17,929.8 \pm 1,715.1	14,236–20,600	0.70
A	7.62 \pm 0.53	6.47–9.19	7.66 \pm 0.63	6.59–9.01	0.78
WL (N \times m ⁻²)	12.79 \pm 1.06	10.76–15.53	12.67 \pm 1.12	10.50–15.21	0.69
T_s	0.52 \pm 0.06	0.41–0.62	0.51 \pm 0.05	0.44–0.66	0.59
T_1	1.18 \pm 0.06	1.10–1.33	1.18 \pm 0.07	1.09–1.38	0.98
I	0.80 \pm 0.14	0.52–1.12	0.77 \pm 0.10	0.57–1.02	0.35

Diet

From June to October 2006, we captured 5,579 insects belonging to 17 orders (also including spiders) at known bat foraging areas. Of these potential prey taxa, Lepidoptera was the most abundant (49.76%), followed by Coleoptera (12.18%), Diptera (9.99%), Orthoptera (8.85%), Homoptera (6.77%), Hemiptera (4.87%), Odonata (2.7%), Hymenoptera (1.7%) and Trichoptera (1.1%). Other orders representing less than 1% of the sample included Neuroptera (0.73%), Dermaptera (0.57%), Phasmida (0.29%), Blattaria (0.02%), Isoptera (0.01%), Aranaea (0.01%), Megaloptera (0.006%) and Mantodea (0.003%).

A total of 344 fecal samples was collected from the day roost and analyzed. In total, eight

insect orders were detected. Lepidoptera was the most abundant order in the diet (100%, percent frequency), followed by Hemiptera (19.42%), Diptera (11.06%), Coleoptera (1.67%), Orthoptera (0.65%), Odonata (1.05%), Hymenoptera (0.26%), and Neuroptera (0.22%).

Lepidoptera represented the largest proportion of potential insect prey throughout the study period, although large variation was recorded (from 58.41% to 30.13%). Proportions of Diptera (16.74%), Homoptera (12.53%), and Orthoptera (15.44%) peaked in August while the proportion of Lepidoptera (30.13%) decreased sharply during this period. The proportion of Hemiptera increased gradually from 2.24% to 12.83% from June to October, compared to Coleoptera, which decreased slowly from 15.80% to 9.63% in during the same period. Proportions of

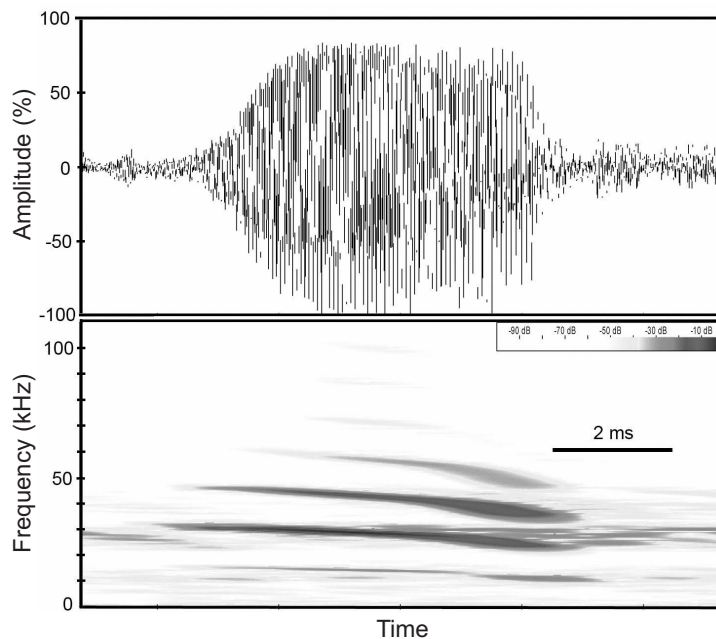


FIG. 1. Waveform and sonogram (512 FFT in Hanning Window) of a typical echolocation pulse from *T. melanopogon*

TABLE 2. Monthly variation (in %) in diet and prey abundance (potential arthropods, mainly insects), and values of the Shannon-Wiener diversity index were calculated from frequency of occurrence. Diet is the frequency of occurrence of each insect taxon in fecal samples. Abundance (Abund.) of each insect taxon is relative to total numbers of arthropods belonging to taxa consumed. The numbers of fecal samples and total numbers of insect taxa captured by light are shown in parentheses

Arthropod taxa	June		July		August		September		October	
	Diet (70)	Abund. (483)	Diet (70)	Abund. (926)	Diet (71)	Abund. (2,214)	Diet (53)	Abund. (1,582)	Diet (80)	Abund. (374)
Lepidoptera	100.0	58.4	100.0	51.1	100.0	30.1	100.0	48.9	100.0	55.6
Coleoptera	22.6	15.8	14.1	11.7	0.0	10.0	0.0	8.5	0.0	9.6
Diptera	32.1	3.8	73.2	12.6	1.4	16.7	4.3	9.3	0.0	5.4
Orthoptera	3.8	10.2	0.0	5.1	0.0	15.4	0.0	12.2	0.0	4.1
Homoptera	0.0	3.7	0.0	7.3	0.0	12.5	0.0	5.8	0.0	1.9
Hemiptera	60.4	2.2	63.4	3.8	15.7	6.7	22.9	8.3	7.5	12.8
Odonata	3.8	1.2	16.9	2.1	0.0	4.3	0.0	4.4	0.0	6.7
Hymenoptera	3.8	0.6	9.9	1.9	0.0	2.3	0.0	2.1	0.0	3.2
Trichoptera	0.0	0.6	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0
Neuroptera	0.0	0.2	5.6	1.3	0.0	0.8	0.0	0.4	0.0	0.0
Dermoptera	0.0	0.4	0.0	0.8	0.0	0.9	0.0	0.0	0.0	0.0
Phasmida	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Blattaria	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isoptera	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aranea	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Megaloptera	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mantodea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Shannon-Wiener Index	2.21		2.23		2.71		2.36		1.76	

Hymenoptera and Odonata in the diet remained the same over the study period.

The diet of *T. melanopogon* showed monthly variation ($\chi^2 = 423.0, d.f. = 4, P < 0.001$). Except for the Lepidoptera, no prey item represented > 50% frequency of occurrence between August and October. However, Hemiptera accounted for > 50% frequency of occurrence in June and July, and Diptera accounted for > 50% frequency of occurrence in July only.

The Shannon-Wiener diversity index (Table 2) indicated that in terms of prey abundance, the diet of *T. melanopogon* was more homogeneous in June

and July than in August and September. This diversity declined again in October.

Time of Emergence

From May to September 2006, emergence times were noted on 14 nights (including three all-night counts). Between 23–341 individual bats emerged on any one night. On average, bats began leaving the cave 31.7 ± 16.6 min after sunset. Emergence ended on average 104.7 ± 51.2 min after sunset. Time of evening emergence was strongly correlated with the time of sunset ($r^2 = 0.77, n = 14, P < 0.001$), but no

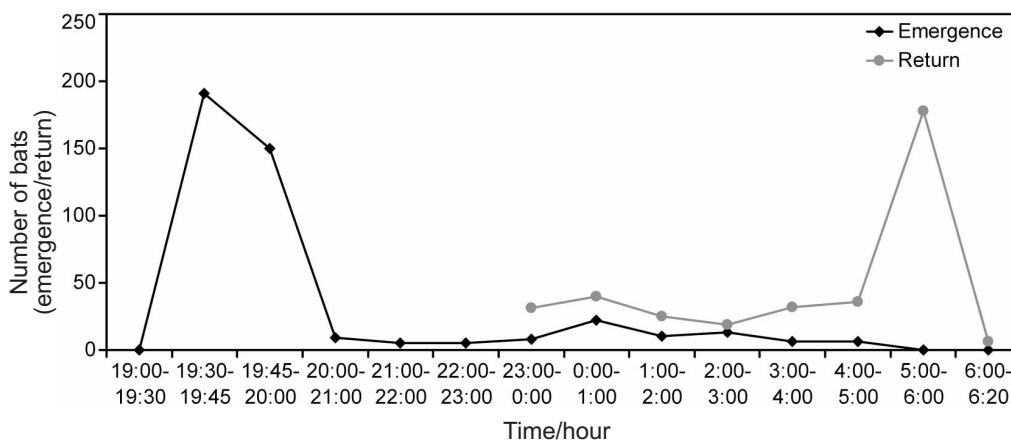


FIG. 2. Numbers of *T. melanopogon* out of roost on 31st July/1st August 2006. Sampling intervals for emergence were every 15 min from 19:30 to 20:00 (no bat left the roost between 19:00–19:30) and every hour from 20:00 to 06:00; for return, every hour from 23:00 to 06:00, with observations ending at 06:20

relationship was found between the time of emergence ending and time of sunset ($r^2 = 0.39$, $n = 14$, $P > 0.05$). The overall monthly effect on evening emergence was significant (ANOVA, $F = 6.57$, $d.f. = 4$, $P < 0.01$ — Fig. 2). Rates of emergence (number of bats per minute) varied significantly by month (0.53, 1.12, 5.24, 1.58, and 0.78 from May to September, respectively). In July and August, bats emerged at a fairly rapid rate, but this declined sharply in September. Meanwhile, bats left the cave significantly earlier on clear evenings compared with cloudy evenings (4.5 ± 7.2 min, 15.5 ± 0.7 min, respectively; ANOVA, $F = 12.41$, $d.f. = 13$, $P < 0.05$). In addition, on the three nights when the entrance was watched continuously from dusk until dawn, *T. melanopogon* showed a unimodal pattern of emergence and return each night (e.g., Fig. 2).

DISCUSSION

Wing Morphology

Norberg and Rayner (1987) calculated a very high wing loading, $25.9 \text{ N} \times \text{m}^{-2}$, for *T. melanopogon*. Our findings differ from those of Norberg and Rayner (1987), with average wing loadings of $12.72 \text{ N} \times \text{m}^{-2}$. The reason for this difference is probably because the body masses and wing areas of bats measured by Norberg and Rayner (1987) were respectively heavier (39.1 g) and smaller ($14,800 \text{ mm}^2$) than ours (22.9 g and $17,858 \text{ mm}^2$, respectively).

Theoretical relationships between wing morphology, flight behavior, forage strategies and forage habitats among bat species have been suggested (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Fenton, 1990; Jennings *et al.*, 2004; Jones *et al.*, 2006; Zhang *et al.*, 2007). For *T. melanopogon*, aspect ratio and wing loading were high, wing-span was long, while tip length ratio, tip area ratio and wing tip shape index were low. These features suggest an ability to fly fast in open areas, over treetops, and along the edge of forest or semi-cluttered habitats. However, bats with high aspect ratio wings (relatively longer, narrower wings) and wing loadings (relatively smaller wing area) have reduced maneuverability, thus potentially limiting them to relatively uncluttered habitats. For high maneuverability, the wings should have a relatively large wing area, shorter wingspan and lower aspect ratio (Norberg and Rayner, 1987). A relatively long wingspan and high aspect ratio enables *T. melanopogon* to fly fast with reduced energy,

an advantageous ability for a bat that flies over long distances (e.g., *Miniopterus natalensis* — Mills and Hess, 1997).

Taphozous melanopogon has small wing tip shape indices (pointed wingtips), which benefit them when they are flying in confined spaces, as through the small entrance to Bidi cave. In fast-flying bats, the tip length ratio should be low, and when the wingspan is relatively short and wingtip frequency is high, wingtip and wing tip shape index should be relatively low (Norberg and Rayner, 1987). More agile bats tend to have relatively pointed wingtips (low T_s), low wing tip shape index and high aspect ratio wings (Norberg and Rayner, 1987). These features are completely consistent with the wing shape of *T. melanopogon*.

Echolocation Calls

Low frequency calls of relatively long wavelength allow bats to detect large and distant targets (Heller, 1995; Schnitzler and Kalko, 1998). However, some very small insects (such as Diptera) are also commonly found in the diet of bats using these calls, despite the wavelength of the bats' echolocation calls being longer than the body length of the target (e.g., Houston *et al.*, 2004). The largest vesperilionid bat, the fast-flying *Ia io*, also eats some small insects (Thabah *et al.*, 2007). *Ia io* produced low-frequency calls and with most energy concentrated in a relatively bandwidth when they were searching for prey. Although the calls of *T. melanopogon* were relatively short for an open-air forager, they do appear to be suited to detection of distant targets. The calls of *T. melanopogon* flying in the wild may be much longer than those recorded in this study due to the nature of our recording method; bats were flown in a confined space. Echolocation calls of *T. melanopogon* were characterized as broadband multi-harmonic FM sweeps of low-intensity, long duration, long inter-pulse interval and high duty cycle — features that may indicate that this species is adapted to long-range detection when searching for prey by fast hawking in open areas and/or detecting relatively large prey (Simmons and Stein, 1980).

Diet

Collecting potential insect prey with light traps provides a biased picture of insect availability within a local community because these traps effectively attract positively-phototactic insects only. Nevertheless, they remain the most effective trapping device

for estimating absolute and relative abundance of insect species (Black, 1974). And though there may be differences in capture susceptibility across all insect orders, light traps are still useful in that they can provide important information on seasonal abundance, diversity, and activity patterns within insect orders (e.g., Black, 1974; Arlettaz, 1996). Insects caught in light traps can also be easily categorized and preserved as reference material which allows for the identification of fragmentary remains recovered from bat feces (Zhang *et al.*, 2005).

Fecal analysis is a reliable method for estimating the diet of bats because insect fragments, especially wings and legs, remain partially intact in bat feces (Kunz and Whitaker, 1983; McAney *et al.*, 1991; Sample and Whitmore, 1993; Zhang *et al.*, 2005). Our light trapping results showed that Lepidoptera and Coleoptera were the most abundant insect orders captured in a foraging area used by our study population. Fecal analysis showed Lepidoptera to be the most common element in the diet, which may suggest that this bat forages for prey opportunistically. However, although beetle-eating is common amongst many different species of insectivorous bats (e.g., Freeman, 1979; Griffith and Gates, 1985; Warner, 1985; Zubaid, 1988), we found that *T. melanopogon* consumed hemipteran and dipteran insects disproportionately more, and Coleoptera disproportionately less, than expected based on our light-trapping results. This result suggests that *T. melanopogon* may be a somewhat selective or specialized feeder. Our results differ from those presented by Zubaid (1990), who found that in peninsular Malaysia *T. melanopogon* is a generalized feeder, with no particular group of insects dominating in the diet. This is unsurprising, as we might expect variability in the feeding habitats of such a widespread species across widely-dispersed localities with different climates. Furthermore, Zubaid (1990) examined the diet of *T. melanopogon* in October and November 1986, and March and May 1987, while our study took place from June to October 2006. Our results as presented suggest that temporal variation in the local composition and abundance of prey may be a critical factor in shaping the diet of *T. melanopogon*.

Emergence

Nocturnal activity patterns of many species of bats have been reported previously, e.g., for *Antrozous pallidus* (O'Shea and Vaughan, 1977), *Pipistrellus pipistrellus* (Bullock *et al.*, 1987; Speakman

et al., 1995), *Molossus molossus* (Chase *et al.*, 1991), *Eptesicus serotinus* (Catto *et al.*, 1995), *Myotis lucifugus* (Kunz and Anthony, 1996), *Chalinolobus tuberculatus* (O'Donnell, 2000), and *Tadarida brasiliensis mexicana* (Lee and McCracken, 2001). These authors found that nocturnal activities were tightly synchronized with respect to sunset and/or sunrise. Our study likewise showed that the timing of evening emergence is linked closely to the timing of sunset. The rate at which *T. melanopogon* emerged varied across months. Rates of emergence (bats per minute) may be linked with energetic demands and reproduction. Rates increased in June when the bats were reproductively active, were highest in July and August when juveniles became volant, and declined again in September as maternity groups dispersed.

Taphozous melanopogon showed a unimodal pattern of foraging at night, and this might be affected by the size of roost entrance and predation risk (Speakman *et al.*, 1999). This species emerged from the daytime roost in rapid succession, not as a continuous serpentine stream. The results of this study also confirmed that this species was active throughout the night. For example between 19:00 h and 23:00 h, activity levels within the roost were high and bats left the roost with few returning within 2 h of initial emergence. Between 23:00 h and 04:00 h small cluster of bats returned to the roost but left again after only 3–5 minutes. Between 04:00 h and 06:00 h, individual bats began returning to the roost, flying inside the cave for a short time before settling.

Many questions remain regarding the basic biology of *T. melanopogon*, including the timing of pregnancy and lactation, timing of departure from and return to the cave by different reproductive classes, how patterns of emergence vary seasonally, and foraging patterns of juveniles, to name but a few.

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