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Author(s): M. B. Fenton, I. L. Rautenbach, J. Rydell, H. T. Arita, J. Ortega, S. Bouchard, M. D. Hovorka, B. Lim, E. Odgren, C. V. Portfors, W. W. Scully, D. M. Syme, M. J. Vonhof

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Emergence, Echolocation, Diet and Foraging Behavior of *Molossus ater* (Chiroptera: Molossidae)¹

M. B. Fenton

Department of Biology, York University, North York, Ontario M3J 1P3, Canada.

I. L. Rautenbach

Transvaal Museum, P. O. Box 413, Pretoria, South Africa

J. Rydell

Department of Zoomorphology, University of Gothenburg, Medicinaregatan 18, S-41390, Gothenburg, Sweden.

H. T. Arita, J. Ortega

Centro de Ecología, UNAM, Junto a Jardín Botánico Exterior, Ciudad Universitaria, 04510 Mexico DF, Mexico.
and

S. Bouchard, M. D. Hovorka, B. Lim, E. Odgren, C. V. Portfors, W. M. Scully, D. M. Syme, and M. J. Vonhof

Department of Biology, York University, North York, Ontario M3J 1P3, Canada.

ABSTRACT

Between 4 and 16 January 1996, during a period of cool weather, we studied the emergence and foraging behavior of *Molossus ater* at a site near Akumal, in the Yucatan Peninsula in Mexico. The bats, a colony of at least 32 individuals, roosted in a north-facing cinder block wall, and emerged about sunset. Emerging bats were usually clustered in time, while those returning usually were not. Radio-tracking revealed that the bats foraged for short periods (mean 26.8 min) and captures of returning individuals indicated that 27 of 28 had fed, taking, on average, 4.4 g of insects, mainly hydrophilid beetles. On some nights, few or none of the radio-tagged bats emerged from the roost. Calculations concerning the costs of flight and roosting show that they were more than covered by the energy intake the bats achieved. *Molossus ater* have high aspect ratio (8.3–9.1) wings and high wing-loadings of 17.55–24.15 N/m². When searching for prey, these bats produce long (12.3 ms), narrowband (3.8 kHz), echolocation calls that sweep from 27.6–23.8 kHz. Energy was not limiting for these bats at the time of our study.

Key words: food intake; foraging time; free-tailed bats; torpor; Yucatan; Mexico.

THE FORAGING BEHAVIOR OF INSECTIVOROUS BATS can be influenced by a variety of factors partly because different currencies such as energy, time or calcium may constrain an animal's performance (*e.g.*, Barclay 1994). The importance of energy as a limiting currency for insectivorous bats has been inferred from the influence on bats of the distribution of flying insects which, in turn, is affected by weather conditions such as temperature and wind (*e.g.*, Lewis & Taylor 1965, Racey & Swift 1985, Kunz 1988, Rydell 1989). A limiting role for energy is suggested by the tendency of many species of insectivorous bats to exploit the abundance of insects in the period around dusk (Lewis & Taylor 1965, Racey & Swift 1985) even though it can expose them to predators (Fenton *et al.* 1994; Speakman *et al.* 1992, 1995; Jones & Rydell 1995).

Wing morphology and echolocation call design

can affect a bat's access to habitats (Aldridge & Rautenbach 1987, Norberg & Rayner 1987). Bats in the family Molossidae, which comprise > 30 percent of the insectivorous species in the Neotropics and in subsaharan Africa (Fenton 1972), usually have high aspect ratio wings, high wing loading and, when searching for prey, use narrowband echolocation calls, usually with frequencies < 40 kHz (Norberg & Rayner 1987). These morphological features mean reduced maneuverability which should limit flight to more open areas (Aldridge & Rautenbach 1987, Norberg & Rayner 1987). Furthermore, narrowband echolocation calls of lower frequency maximize effective range of prey detection but do not permit assessment of targets in clutter, situations where echoes are returning from objects other than the target of interest (Simmons & Stein 1980, Fenton 1990). Lower frequency calls are presumed to be less effective for detecting smaller prey than are higher frequency calls because of the wavelengths of the

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sounds; the lower threshold of detection is thought to be approximately half of the wavelength (Barclay & Brigham 1991, Jones 1994). However, some bats using narrowband echolocation calls in the 30–10 kHz range, eat smaller insects than expected from call frequencies (10 mm wingspan; *e.g.*, Waters *et al.* 1995) so the relationship between call frequency and prey size is not always clear. Furthermore, bats do not always appear to use their echolocation to its full perceptual capacity (Barclay & Brigham 1994).

Molossids may offset any disadvantages associated with the constraints of wing and echolocation call design in two ways. First, their wing morphology may give them access to a wider range of prey, including high-flying insects (Fenton & Griffin 1997). Second, they may occasionally use diurnal torpor to reduce the cost of thermoregulation. In some vespertilionids, daily torpor minimizes energetic costs during inclement periods (*e.g.*, Audet & Fenton 1988), and some species alternate between torpor and foraging over a larger area (Hickey & Fenton 1996). *Tadarida teniotis* living the year around at 42°N (Switzerland) uses torpor (R. Arlettaz, pers. comm.) as do at least two species of *Molossus* (McNab 1969, Studier & Wilson 1970). The free-running circadian rhythm of *Molossus ater* is affected by ambient temperature (Erkert & Rothmund 1981), also suggesting the use of torpor. The diversity of molossids suggests that specializations for rapid, economical flight is a successful strategy.

Molossus ater, a 30–45 g species, is widespread in the Neotropics (Eisenberg 1989), and although some aspects of its foraging and emergence behavior have been reported by Marques (1986), there are few published details about its behavior. We used radio-tracking, documentation of emergence, analysis of feces, and echolocation calls to study these bats at a site in Akumal, Quintana Roo Province of Mexico (20°25'N, 87°20'W). We examined the bats' responses to the cooler than normal weather conditions (January 1996 mean of 19.8°C versus 30 year average of 22.8°C) associated with the "nortes" (times when it was windy with light rain; Garcia 1981). Specifically, on 5 of 13 nights during our study the minimum temperatures were $\leq 13^\circ\text{C}$, on 2 nights $> 20^\circ\text{C}$. The individuals we studied formed a colony of at least 32 individuals that roosted in hollows in cinder blocks of a building in Akumal. Our study was conducted from 4 to 16 January 1996, a time when it was dark by 1745 h and light by 0615 h (sunset 1727–1734 h) local time.

MATERIALS AND METHODS

We captured bats in mist nets as they departed from or returned to the roost and recorded information about gender and reproductive condition for each individual. Individuals were weighed (± 0.1 g), the lengths of their forearms measured (± 0.5 mm), and their wing outlines traced and areas measured (± 1 mm²) according to the technique of Norberg (1989). Six individuals (1 male, 5 females) received transmitters and collars whose combined mass was 2.3 percent of the bat's body mass. We used collars made of fiber tape (3M) to attach the transmitters, because similar-sized molossids elsewhere quickly groomed off transmitters attached with surgical adhesive (Fenton & Rautenbach 1986). There were no signs of abrasion or lost fur in the neck areas of recaptured radio-tagged bats, suggesting that these collars did not have adverse physical effects. The signals from the transmitters were monitored from dusk to dawn using Lotek (SRX-400) receivers, programmed to scan for the frequency of each radio tag every 15 s (observer present) or every 5 min (data stored in the receiver). We also did some radio tracking with a Merlin Custom 12 receiver. We used five-element Yagi antennae, and observers at the receivers were in continuous contact with walkie talkies.

The timing of emergences and returns of the bats were monitored with a laptop computer programmed to function as an event recorder and to measure events to the nearest 0.1 s. We analyzed files from the event recorder using the Clustan programme of Speakman *et al.* (1992) to assess the extent to which emerging and returning bats were grouped in time. To document time away from the roost by radio-tagged bats, we used two methods: before midnight we manually timed the emergences from and returns to the roost to the nearest min, and after midnight to the nearest 5 min using the Lotek receiver in automatic scan and record mode. We measured the incident light levels outside the roost towards the open sky with a Gossen Mastersix light meter (with diffuser on).

The insects in samples of up to 10 fecal pellets were analyzed to order by volume for each of the bats from which we obtained feces samples (Whitaker 1988). Stools were soaked in water with some ethanol added to reduce surface tension, and teased apart under a dissecting microscope.

We monitored and recorded the echolocation calls of the bats, as they foraged over a soccer pitch or above street lights, using an Anabat V system in conjunction with a laptop computer. Specifically,

TABLE 1. *Wing morphology, flight activity and flight times for radio-tagged bats are compared to the time data for the population of Molossus ater living in the same roost.*

Bat	Aspect ratio	Wingloading in N/m ²	Number of dusk flights/number possible	Mean flight times in min	Mean emergence time \pm min
Male	9.1	24.15	6/9	29.8 \pm 23.1	17:44 \pm 23.7
Female 1	8.3	21.39	5/9	43.0 \pm 24.2	17:41 \pm 13.1
Female 2			6/9	22.7 \pm 57.9	17:42 \pm 6.9
Female 3	8.3	22.66	3/9	35.3 \pm 9.3	17:35 \pm 9.3
Female 4	8.3	20.15	6/9	39.0 \pm 19.3	17:39 \pm 8.0
Female 5	8.7	17.55	5/9	63.0 \pm 9.2	18:03 \pm 10.0
Summary/means (of data from radio-tagged individuals)			31/54	38.2 \pm 22.3	17:45 \pm 13.9
Colony data (all bats emerging from and returning to the colony)			n/a	26.8 \pm 11.7	17:32 \pm 7.1

we used an Anabat II Bat Detector and an Anabat V Zero Crossing Analysis Interface Module.

Data on maximum and minimum temperatures were obtained from a weather station near Tulum, about 23 km south of our study site. Means are reported \pm one standard deviation.

RESULTS

Although 5 to 37 *M. ater* emerged from the colony, we captured just 32 individuals (11 males and 21 females). None of the females was pregnant or lactating. We caught 28 of the 32 bats as they returned from foraging between 1757 h and 1854 h on 15 January. Males were heavier than females and had higher wingloading (Table 1). Bats captured on their returns from foraging on 15 January weighed, on average, 35.3 \pm 4.9 g and 34.2 \pm 4.5 g 2 h later. The weights of bats that had carried transmitters ($N = 5$) averaged 33.5 \pm 2.7 g (excluding transmitter weight) and did not differ significantly ($t = -1.67$, $df = 4$, $P = 0.17$) from those without transmitters ($N = 14$) 35.6 \pm 4.9 g.

The roost faced an open area 32 m by 16 m (unused tennis court) bordered on one side by low (4 m high) buildings, on the others by taller trees and a 2 m high chain link fence. On 16 January at 0800 h local time, the temperature just inside the roost was 21°C when the air temperature outside was 17°C. The bats roosted in the wall that faced north and, during our study, never received direct sunlight. The entrance was situated 4 m above the ground. Emerging bats dropped 1–2 m from the entrance before assuming horizontal flight. Upon levelling out, the bats flew 15–20 m before turning and climbing to avoid the facing building. The bats then climbed to about 50 m

altitude and usually headed off to the SW, almost immediately beginning to forage as indicated by the production of feeding buzzes. Returning bats came in 1–2 m above the ground, directly approaching and swooping up to land on the top of the wall and crawl into the roost entrance. Some returning bats approached the roost on a circular path, flying along within 1 m of the roost wall and circling several times before making the direct approach that resulted in landings.

The bats typically emerged after 1700 h (Table 1) when light levels ranged from 130–210 lux. On the morning of 5 January, the last bat had returned to the roost by 0640 h when the light level was 90 lux. The numbers of bats emerging from the roost ranged from 5 to 37 ($x = 22.4 \pm 9.5$), and individuals began to return to the roost 14–25 min ($x = 18.2 \pm 4.1$ min, $N = 6$ nights) after emergence. Emergences of bats lasted, on average, 1577.6 s, ranging from 459–2288 s and the Clustan analysis revealed that emerging bats were significantly clustered in time on 5 of 6 evenings. Returning bats were significantly clustered on just 2 of 5 evenings.

Radio-tagged bats were followed for a total of 48 bat nights (one bat carrying active transmitter for one night = one bat night), and through the first foraging period of another six bat nights (15 January). On 20 of 48 bat nights, radio-tagged bats did not leave the roost at all, typically when the minimum temperatures were $\leq 13^\circ\text{C}$ and there were strong winds. On two nights (7 and 8 January) none of the radio-tagged bats left the roost although 20 and 5 untagged bats, respectively, emerged from the roost. None of the radio-tagged bats switched roosts during our study.

For 34 bat nights the patterns of emergence and return behavior of radio-tagged individuals

generally resembled those of the colony as a whole (Table 1). The radio-tagged bats invariably made one foraging flight a night, usually at dusk. Two radio-tagged bats made later flights: one departed at 0046 h and returned at 0157 h on 14 January, the other left at 0155 h and returned at 0315 h on 15 January. On these nights, these were the only flights by either of these bats. These patterns of bat activity away from the roost contrast with the pre-dawn return flights we had observed on 5 January.

Our analysis of the echolocation call data shows that foraging bats produced narrowband ($x = 3.8 \pm 0.4$ kHz, $N = 10$ calls) echolocation calls that swept from 27.6 ± 0.7 kHz down to 23.8 ± 0.5 kHz in 12.3 ± 1.7 ms. The average interpulse interval was 402.0 ± 147.6 ms, for a duty cycle of 3.3 percent (122.5 ms of signals in 3746.5 ms). When attacking prey, the bats produced shorter signals (ca 9 ms), with increased bandwidths (ca 15 kHz), sweeping from 38.5–23.5 kHz at intervals of 50–60 ms ($N = 7$ calls).

On 15 January we recaptured five of the six radio tagged bats. The antennae were missing from four of the five transmitters, dramatically reducing the range over which we could track these bats. The female whose transmitter retained an antenna was out of range for 4 min of 113 min total foraging time over the entire study, suggesting that she foraged within 2–4 km of the roost. When there were obvious concentrations of insects at street lights within 5 km of the colony, bats producing calls like those we recorded from *M. ater* foraged there. They emitted both search phase echolocation calls and feeding buzzes, the high pulse repetition rates associated with attacks on insect prey. None of these bats was radio-tagged. Just after emergence, we sometimes observed *M. ater* flying and foraging well above the forest canopy. We also monitored *M. ater* echolocation calls from bats flying well above the streetlights, virtually never venturing below the electric wires suspended above the lights.

Collections of feces from bats returning to the roost revealed that even with short foraging times, most (27 of 28 bats) had eaten (= produced feces). In 2 h an average of 1.1 g of feces (wet weight) was produced. On 15 Jan, the collared male was away from the roost for 80 min and had produced 0.8 g of feces by 2130 h. Comparable data for the radio-tagged females are 71 min—0.9 g; 34 min—0.6 g; 16 min—0.9 g; and 26 min—0 g. Bats returning to the roost after foraging had insect remains in their mouths, but we observed no evidence of insects in cheek pouches as suggested by

Goodwin and Greenhall (1961). The lack of cheek pouches supports the observations of Murray and Strickler (1975).

Analysis of the feces revealed that the bats ate mainly beetles (Table 2), and the incidence of beetles in the feces of bats caught on 15 Jan did not differ significantly between males and females ($t = 0.83$, $df = 4$, $P = 0.45$). The smallest prey were flies with 8 mm wingspans, the largest hydrophilid beetles (*Tropisternus* spp.) with bodies about 15 mm long and wing spans of ca 25 mm. The bats also ate cerambycid, dytiscid, and chrysomelid beetles and at least one dragon fly. Overall, hydrophilid beetles and a few hemipterans accounted for the majority of their prey during the first foraging period on 15 January. Moth remains were notably rare in the feces.

DISCUSSION

Our data on activity patterns of *M. ater* are generally similar to those of Marques (1986) and Erkert (1978). We found that the bats stayed out for shorter periods of time than those reported by Marques (1986; $x = 50.5$ min versus 26.8 min) who observed that some *M. ater* typically left the roost just before dawn, behavior that was rare in our study. The influence of temperature on the daily activity of *M. ater* supports earlier findings (Erkert & Rothmund 1981). Using the weights of stomach contents, Marques (1986) found that the *M. ater* consumed 10.67–19.00 mg of prey/min away from the roost. At 75 percent digestive efficiency (Barclay *et al.* 1991), the rates of food ingestion of known individuals in our study ranged from 0–225.2 mg/min, 40–225.2 mg/min for bats that produced feces. The tendency of tagged bats to remain in the roost for more than one night may support the suggestion that, like other molossids (McNab 1969, Studier & Wilson 1970, Hill & Smith 1984), *M. ater* uses torpor during inclement conditions, explaining the impact of temperature on circadian rhythms (Erkert & Rothmund 1981). This view is supported by the bats roosting in a north-facing wall, the one most sheltered from direct sunlight.

Molossus ater emerged earlier, around sunset, than molossids such as *Tadarida teniotis* (Arlettaz 1990) and *Eumops perotis*, which leave their roosts 40–50 min after sunset (Jones & Rydell 1994). While faster bats tend to emerge earlier, the later emerging molossids use lower frequency echolocation calls and often eat moths (Jones & Rydell 1994). Other bat species that feed on moths also

TABLE 2. *The diets (percent by volume) of Molossus ater captured during this study. For 15 January, the individual bats that were radio-tracked are identified by rt (the male) or the frequency of the transmitter (females). Some insects, Unid, could not be identified to order.*

Date	Bat	Number of stools analyzed	Percent by volume in feces						
			Coleoptera	Hemiptera	Lepidoptera	Diptera	Odonata	Hymenoptera	Unid
5 Jan	male	1	100	0	0	0	0	0	0
7 Jan	male	5	10	46	24	0	0	10	10
	female	3	0	0	33	17	50	0	0
12 Jan	female	10	19	28	12	36	0	0	5
15 Jan	male rt	10	84	9	1	6	0	0	0
	female 799	10	98	2	0	0	0	0	0
	female 983	9	75	19	0	6	0	0	0
	female 897	10	90	5	0	0	0	5	0
	female	3	93	7	0	0	0	0	0
	female	10	99	1	0	0	0	0	0
	female	10	77	11	7	0	0	5	0
	female	7	90	10	0	0	0	0	0
	female	10	93	5	0	0	0	0	3
	female	7	75	1	0	3	0	0	21
	male	10	90	10	0	0	0	0	0
	male	10	94	6	0	0	0	0	0
	male	10	90	5	0	0	0	0	5
	male	8	55	31	0	9	0	0	5
Total/ means		143	74.0	10.9	4.3	4.3	2.8	1.1	2.7

emerge later (e.g., *Lasiurus borealis* and *L. cinereus*) (Hickey *et al.* 1996, Rydell *et al.* 1995). The scarcity of moths in the *M. ater* diet may reflect times of emergence relative to sunset. In this matter, *M. ater* resembles *Tadarida pumila* and *Tadarida condylura*, which also feed mainly on beetles (Fenton *et al.* 1998). The low incidence of moths in *M. ater* feces also could reflect the fact that its echolocation calls are dominated by frequencies to which moth ears tend to be most sensitive (Fenton & Fullard 1979, Rydell *et al.* 1995). Other molossids that commonly feed on moths (e.g., *Tadarida teniotis*) have echolocation calls dominated by sounds < 20 kHz (Rydell & Arlettaz 1994). The situation is complex because both *L. borealis* and *L. cinereus* feeding at lights eat mainly moths (Hickey *et al.* 1996) and both use echolocation calls that are conspicuous to sympatric moths (Acharya 1995).

Emerging *M. ater* were usually significantly clustered in time although we saw no evidence of predators around the roost, unlike the situation facing *T. condylura* and *T. pumila* (Fenton *et al.* 1994). As bats entered and left the narrow roost openings one at a time, clustering on emergence could have reflected a bottleneck effect (Speakman *et al.* 1992). The numbers of obstacles on the approaches to roosts can affect their accessibility to bats.

Vonhof and Barclay (1996) found that four species of vespertilionids (*Myotis evotis*, *Myotis volans*, *Eptesicus fuscus*, and *Lasionycteris noctivagans*) selected roost trees with open access flight paths. This requirement also is suggested by the behavior of *M. ater* departing from and returning to the roost.

What were the energetic gains and metabolic costs of the bats we studied? Insectivorous bats show a range of digestive efficiency from less than 75 percent to over 90 percent depending upon prey type (Barclay *et al.* 1991, Robinson & Stebbings 1993, Webb *et al.* 1993). Assuming 75 percent digestive efficiency of prey mass, the bats which we studied ate an average of 4.4 ± 0.6 g of insects during the time they foraged on 15 January which should have provided 28.5 ± 3.9 kJ of assimilable energy. Geiser's (1988) analysis suggests that, at 30°C, a daily heterotherm like *M. ater* would have a basal metabolic rate of 1.05 ml O₂/g/h, and consume 0.63 kJ/h of roosting, compared to 0.30 kJ/h at 20°C. Estimates of the power required for flight by bats vary widely from 0.375 W for 30 g *L. cinereus* (de la Cueva *et al.* 1995) to 1.43 W for the much smaller (ca 6 g) *Pipistrellus pipistrellus* (Speakman & Racey 1991). On 15 January in 80 min of flight, the male radio-tagged *M. ater* consumed at least 3.2 g of insects, yielding 20.07 kJ of assimilable energy. At the highest roosting

(0.634 kJ/h) and flight costs (1.43 W), this bat covered the cost of its 80 min long foraging flight (6.86 kJ) and obtained enough energy to roost for 20 h at 30°C. The most successful bat, one of the radio-tagged females, obtained 23.29 kJ of assimilable energy from insects in 16 min of flight, covering the costs of flight (1.37 kJ) and 34 h of roosting. If the bats' body temperatures were 20°C, the energy available for roosting is extended to 46 h of roosting for the male, and 73 h for the female. At lower flight or roosting costs, the returns from the foraging flights are even more substantial. These figures could explain the short, infrequent foraging flights we observed.

Our data confirm that *M. ater* has high aspect ratio wings, high wing loading, and uses narrow-band echolocation calls in the 20–30 kHz range. Direct observation and monitoring echolocation calls reveal that this species forages in open areas, situations with minimal clutter. Fecal analyses show that it eats mainly beetles, taking insects with wing spans of at least 8 mm. The bats also forage for short times which usually allowed them to obtain

more than enough prey to cover the costs of flight and basic metabolism. In short, the data support the view that the specializations of molossids for rapid flight in open areas provide them with ready access to more than adequate insect prey, even under unseasonably cool conditions. This presumes that energy is the relevant currency, an assumption that may not be true for lactating females (Barclay 1994).

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