

Unusual echolocation behavior in a small molossid bat, *Molossops temminckii*, that forages near background clutter

Antonio Guillén-Servent · Carlos Ibáñez

Received: 19 May 2006 / Revised: 5 March 2007 / Accepted: 6 March 2007 / Published online: 12 April 2007
© Springer-Verlag 2007

Abstract When searching for flying insects, *Molossops temminckii* uses unusual echolocation calls characterized by upward modulation of frequency vs time (UFM). Call frequency increases asymptotically in the relatively long (~8 ms) pulses from a starting frequency of ~40 kHz to a long narrowband tail at ~50 kHz. When approaching a prey, the bat progressively increases the duration of calls and intersperses in the sequence broadband downwardly frequency-modulated signals with a terminal frequency of about 53 kHz, which totally replaces the UFM signals at the end of the approach phase. The sequence progresses to a capture buzz resembling those from other molossid and vespertilionid bats. The *M. temminckii* wing morphology is characterized by an average aspect ratio and a high wing loading, suggesting that it is more maneuverable than the typical Molossidae but less than typical Vespertilionidae. *M. temminckii* regularly forages near clutter, where it needs to pay attention to the background and might face forward and backward masking of signals. We hypothesize that the UFM echolocation signals of *M. temminckii* represent an adaptation to foraging near background clutter in a not very maneuverable bat needing a broad attention window. The broadband component of the signal might serve for the

perception of the background and the narrowband tail for detection and perhaps classification of prey. Bats may solve the signal masking problems by separating emission and echoes in the frequency domain. The echolocation behavior of *M. temminckii* may shed light on the evolution of the narrowband frequency analysis echolocation systems adopted by some bats foraging within clutter.

Keywords Echolocation · Evolution · Foraging behavior · *Molossops temminckii* · Narrowband signals

Introduction

Echolocation allows bats to get information about the structure of the space where they fly and to detect, classify, and track moving prey or other food resources (Griffin 1958; Simmons and Grinnell 1988; Schnitzler and Kalko 1998). Echolocation systems rely upon signals that are relatively stereotyped within species but diverse in spectral and temporal structure across species. Comparative field studies combined with behavioral and neurophysiological experiments have revealed clear relationships between signal design and characteristics of prey and spatial structure of the foraging habitat (Neuweiler 1983, 1989, 2000; Schnitzler and Kalko 1998). Although evolutionary diversification of echolocation systems is assumed to have happened through adaptation to diverse foraging strategies in habitats differing in spatial structure, there is not a clear understanding on the details of these processes (Schnitzler et al. 2004).

Many aerial hawking insectivorous bats use echolocation pulses with downward modulation of frequency vs time (DFM) when searching for flying prey. In many species, pulse structure is flexible. When searching for prey far from

Communicated by G. Jones

A. Guillén-Servent (✉)
Instituto de Ecología, A. C.,
Km 2.5 Ctra. Antigua a Coatepec #351, Congregación El Haya,
Xalapa 91070 Estado de Veracruz, México
e-mail: antonio.guillen@inecol.edu.mx

C. Ibáñez
Estación Biológica de Doñana (CSIC),
Apartado 1056,
41080 Sevilla, Spain

background clutter, they use long duration DFM narrow-band signals. After a prey is detected, bandwidth increases and duration decreases during the approach maneuver (Griffin et al. 1960). Pulse structure in the search phase also depends on the proximity of the background, calls being long and narrowband when bats fly far from objects and short and broadband when they forage near clutter (Kalko and Schnitzler 1993; Schnitzler and Kalko 1998). Generally, these changes in pulse structure have been explained by the need of avoiding an overlap of emitted calls with echoes (forward masking) and between echoes of prey and background (backward masking; Schnitzler et al. 2003). They are also thought to be a result of a trade-off between the range of detection and resolution in the estimation of the distance to the targets. By concentrating all energy in a narrow frequency band, bats may reduce the effects of atmospheric attenuation and get longer detection distances by stimulating few highly sensitive receptors. However, this comes at the cost of uncertainty in time calculation and broad masking windows. Instead, short broadband pulses stimulate a wide array of cochlear receptors, which probably provide statistical sharpening of echo delay calculations and fine distance and angle estimation. They also provide reduced masking and more spectral information that could be used for the classification of prey and background. However, all this comes at the cost of short range because energy is dispersed in a wide range of frequencies. Echolocation based on DFM signals could be thought of as an adaptive continuum, in which bats foraging regularly far from clutter alter the structure of the pulses according to the distance to background and prey, but bats that always forage near background only rely in very short broadband signals (Neuweiler 1984, 2000; Roverud 1987; Simmons and Grinnell 1988; Schnitzler and Kalko 1998; Siemers and Schnitzler 2004).

Bats in the family Molossidae have been regarded as the archetype of specialization for aerial hawking of flying insects in open air. They usually have relatively small and narrow wings characterized by high values, both of wing loading and aspect ratio. These confer high flight speeds that suit bats for high altitude foraging in open areas and for rapidly commuting long distances to prey swarms (Norberg and Rayner 1987; Marques et al. 2004). However, this capacity comes at the cost of reduced maneuverability that precludes foraging on prey that fly close to vegetation or other substrates because of the risk of colliding with objects in the background (Norberg 1994). The few molossids studied seem to represent the extreme of specialization of echolocation for long distance detection of relatively large prey in open spaces as they use low frequency narrowband calls of very long duration and with very long interpulse intervals (Simmons et al. 1978; Zbinden and Zingg 1986; Heller 1995; Fenton et al. 1998; Mora et al. 2004).

However, the generalizations above are based on only a few detailed studies of echolocation and foraging behavior of a very small sample of species biased towards large body size. Actually, molossid bats show considerable variation in wing morphology. Particularly, some of the smallest Molossidae in the genera *Molossops* and *Mormopterus* have relatively large and broad wings, low wing loading, and widely separated ears that distinguish them from most other ‘typical’ Molossidae, bringing them closer to a more slowly flying and more maneuverable ‘typical’ Vespertilionidae (Smith and Starrett 1979; Freeman 1981; Norberg and Rayner 1987). The wing morphology of those bats suggests that they may forage near clutter, in a way considerably different from that of the typical Molossidae (Willig 1985). Not much is known about the echolocation and foraging behavior of those species, but the specialized wing morphology could be associated with special adaptations in echolocation behavior. This makes them attractive for comparative studies that may shed light on possible evolutionary pathways for echolocation systems when bats face adaptation to different foraging environments.

In this paper, we first describe the echolocation behavior of one of the smallest of these broad-winged Molossidae, the Neotropical species *Molossops temminckii*. We also study the flight morphology and foraging behavior of *M. temminckii* to assess possible correlations with signal structure and echolocation behavior.

Materials and methods

Study site

The study was conducted around El Frío Biological Station, located inside the Hato El Frío, a 68,000-ha ranch, about 150 km west of the city of San Fernando de Apure (7° 48.8' N, 68° 53.99' W, Achaguas municipality, State of Apure, Venezuela). The area is located within the floodplains of the northern Orinoco river basin. The landscape is dominated by seasonally flooded grassland savannah with widely sparse patches of seasonally dry forest restricted to areas of elevated land and river and lake banks (Castroviejo and López 1974). Bats in the area were formerly studied by Ibáñez (1984). Most data for this study were collected between December 1993 and January 1994. A more recent visit to the area in March 2006 allowed completion of the data on echolocation and foraging behavior. All visits took place during the dry season.

The species

Molossops (Molossops) temminckii, with a forearm length of 28–33 mm, is one of the smallest molossid bats (Freeman 1981). It is widely distributed in the dry lowland

areas of South America west of the Andes, from Colombia and Venezuela to Uruguay and Northern Argentina. It roosts underneath tree barks and in crevices in trees and human buildings. It feeds on small insects, mostly coleopterans (Ibáñez and Ochoa 1985; Anderson 1997). We follow Simmons (2005) for genus and species names.

Bat capture, measurements, and wing shape analysis

Bats were captured with mist nets. Sex, age (young or adult; Anthony 1988), reproductive status, forearm length (to the nearest 0.1 mm with a calliper), and body mass (to the nearest 0.1 g, with a spring balance, at least 2 h after capture) were recorded for each bat. Bats were positioned back down and with the right wing and the uropatagium fully stretched on a white acrylic plate printed with a 5×5-cm black line reticule. A photograph was then taken with a camera (Nikon F-801, 60 mm macro lens) with a film plane kept parallel to the plate with the aid of a tripod and bubble levels. Slides were digitized with a film scanner and fed to a SigmaScan software (SPSS Software), where the images were three-point calibrated using the reticule. We measured the wing shape parameters described by Norberg and Rayner (1987). We also calculated the scores on the size-independent principal component equations Q_a (representing aspect ratio) and Q_1 (representing wing loading) from equation 9 in Norberg and Rayner (1987). We then compared the position of *M. temminckii* with those of other vespertilionid and molossid bats presented by Norberg and Rayner (1987) in the wing morphospace. We calculated predicted speed in a straight flight according to the multivariate regression and principal components equations in Table 5 of Norberg and Rayner (1987).

Sound recording and analysis

Wild bats were recorded flying freely in the habitat by using a high-speed instrumentation tape recorder (TEAC XR-5000). The recorder was set at selected locations where bat foraging activity was detected in surveys with ultrasound detectors (D-980, Pettersson Elektronik AB). *M. temminckii* was easily identified with heterodyne detectors (Parsons et al. 2000) by the fast regular rhythm of the calls and the characteristic peak frequency near 50 kHz, with intensity rapidly decreasing and vanishing soon when tuning to upper frequencies and decreasing slowly towards lower frequencies (just the opposite from other vespertilionid and molossid bats). The instrumentation recorder was equipped with a direct recording amplifier connected to a SM2 microphone mounted on a SP2 preamplifier (Ultra Sound Advice). Ultrasound was recorded onto metallic videotapes ran at 76 cm/s to attain near flat frequency response up to 150 kHz. Recordings were played back in the lab at 9.5 cm/s

(corresponding to an eightfold time expansion rate) and digitized at 44.1 kHz, 12-bit sampling rate with a personal computer equipped with a data acquisition PCMCIA card (DAQCard-6062E, National Instruments) using the software BatSound Pro v3.1 (Pettersson Elektronik AB).

Spectrograms were calculated in BatSound Pro using fast Fourier transforms (FFTs) with a Hanning window 512 points long and 96% overlap. Cumulative power spectra of whole pulses were calculated with FFTs over a window covering the whole signal (resolution of frequency and time were 690 Hz and 0.1 ms, respectively). For each pulse in the sequences analyzed, the following parameters were measured: interpulse interval (INTER), from the start of preceding pulse to the start of the present pulse; duration (DUR), from the start to the end of the pulse; starting frequency (FSTART); maximum (for upward modulated calls) or minimum (for downward modulated calls) terminal frequency (FEND); duration of the broadband part of the signal (TBB), conventionally defined as the time from the start of the pulse to the instant at 1 kHz before reaching FEND; frequency at half TBB (FTBB/2); and frequency with maximal intensity in the cumulative power spectrum corresponding to the narrowband part of the call and to the broadband part of the call. Because there was often strong insect background noise, most measurements were taken over the spectrogram, positioning the measurement cursors in the midpoint of the trace at points 30 dB below maximum energy of the pulse. All measurements were taken in milliseconds or kilohertz. After the raw measurements above, the following derived measures were calculated: bandwidth (BW), measured as the absolute difference between FSTART and FEND; mean modulation rate of the broadband part of the signal, measured as $BW - 1 \text{ kHz}/TBB$; and the duty cycle at the pulse level, calculated as $DUR/INTER$.

Changes in the spectral and temporal parameters of the pulses and phases of echolocation behavior were studied by plotting the different variables against time for a selected sample of recordings containing prey capture sequences with good signal to noise ratio. To avoid pseudoreplication, only one pulse per sequence and phase stage was used in the statistical description. A sample of 50 sequences obtained at different locations and dates was selected for the search phase, and another 15 were selected for the approach and capture phases. We tested for differences in selected variables between search phase and approach and post-buzz pulses with two-tailed two-sample *t* tests assuming equal variances. When comparing stages within approach and capture phases of echolocation behavior, we used paired-sample two-tailed *t* tests. The distribution of interpulse intervals during the search phase was assessed after measuring a higher number of pulses from whole sequences. We calculated the predicted interval according to the allometric equation on body mass in Jones (1994). Mean values of variables,

followed by a \pm symbol and the standard deviation, appear in the text between brackets. We computed average (or median for inter-pulse intervals) values for pulses within sequences for statistical comparisons among sites.

Habitat use and foraging behavior

We acoustically surveyed the different habitats available in the study area to assess where *M. temminckii* was foraging. Sampled habitats were as follows: (1) forest, (2) forest edge, (3) park-like areas with dispersed large trees, (4) grassland savannah near the forest (about 150 m in straight line to the forest edge), (5) open savannah far from the forest, and (6) flooding channel bank in the open savannah. Sparse bushes were present in the savannah habitats and along banks of flooding channels. Each habitat was surveyed starting 15 min after sunset along pathways marked during daytime with reflecting tape. The observer captured a sound sample (3 s) and tenfold expanded it in time with a D-980 ultrasound detector (Pettersson Elektronik AB). While the sample was being recorded on tape (30 s; onto metallic tapes with Sony WM-D6C tape recorders), he moved to a new point on the path and repeated the procedure. Two pathways were covered for each habitat type, one for 180 min and the other for 90 min in different evenings. All surveys were done between the 4th and 12th of January 1994. Activity was measured as the number of samples containing the unique (see below) search phase signals of the species. We assessed the evenness of use of different habitats by *M. temminckii* with a chi-square test over a two-way contingency table (factors: habitat and presence/absence of *M. temminckii* echolocation calls). We used chi-square tests over three-way contingency tables (factors were: habitat, species, and presence/absence of echolocation calls) to compare the distribution of the activity of *M. temminckii* among habitats with the pattern shown by all other (high flying) Molossidae in the area together (Ibáñez 1984) and with the Vespertilionidae *Myotis nigricans* and *Eptesicus diminutus*, both species known to forage in background cluttered space (Siemers et al. 2001; own observations). Identification of calls from Molossidae, *M. nigricans*, and *E. diminutus* was based on a reference call library constructed by the authors from hand-released bats in the region (Guillén-Servent and Ibáñez, unpublished data). The low-pitched calls of other Molossidae are unmistakable, as large Vespertilionidae are very rare in the area (Ibáñez 1984), and *M. nigricans* and *E. diminutus* could be readily discriminated from other syntopic Vespertilionidae by their characteristic terminal frequency of the DFM calls at ~ 51 kHz (vs *Myotis albescens* ~ 46 kHz) and ~ 39 kHz (vs *Rhogeessa io* ~ 45 kHz), respectively.

In March 2006, we obtained additional data on the foraging behavior of *M. temminckii* by recording foraging

bats with walkable portable video. The scene was lighted with an infrared illuminator (IRLamp6, Wildlife Engineering), and the image was obtained with a high sensitivity security CCD camera (EXvision, Supercircuits) and recorded onto Digital-8 tapes (Sony) with a digital video walkman (GV-D800, Sony). Echolocation calls were picked up with a U-30 ultrasound detector (Ultra Sound Advice) and recorded directly onto the hard disk of a portable computer (Sony Vaio PCG-4E1L) by using a fast data acquisition PCMCIA card (DAQCard-6062E, National Instruments) controlled by the Recorder v.2.97 software (Avisoft) and operated at 333 kHz sampling rate. The frequency division output of the detector was recorded on the soundtrack of the video tape for synchronization. About 20 h of simultaneous video and high speed recording were obtained in walks starting at sunset and lasting around 2 h each. We surveyed along forest edges, riverbanks, ponds, park-like areas, and open areas, trying to get video imaging of the bats being monitored. Back in the lab, the digital audio recordings were screened for the presence of calls of *M. temminckii*. When the acoustic presence of the species was detected, the corresponding video track was revisited, and the flying behavior of the bat in relation to the surrounding background was described.

Results

Morphometrics and wing shape

We measured ten male and two nonpregnant female adult bats. Females averaged a larger wing area but similar body mass, forearm, and wingspan as males and, consequently,

Table 1 Morphological measurements and wing shape parameters of *Molossops temminckii* from the Hato el Frío

Parameter	Females ($n=2$)	Males ($n=10$)
Forearm (mm)	28.90 \pm 0.57	28.99 \pm 0.57
Body mass (g)	6.30 \pm 0.14	6.19 \pm 0.28
Wingspan (m)	0.221 \pm 0.004	0.222 \pm 0.004
Arm wing length (m)	0.039 \pm 0.001	0.038 \pm 0.001
Hand wing length (m)	0.056 \pm 0.002	0.054 \pm 0.002
Wing area (m ²)	0.00668 \pm 0.00013	0.00632 \pm 0.00022
Arm wing area (m ²)	0.00158 \pm 0.00007	0.00145 \pm 0.00009
Hand wing area (m ²)	0.00125 \pm 0.00008	0.00114 \pm 0.00006
Wing loading (Nm ⁻²)	9.25 \pm 0.02	9.61 \pm 0.40
Aspect ratio	7.34 \pm 0.11	7.78 \pm 0.14
Wing tip length ratio	1.45 \pm 0.03	1.44 \pm 0.06
Wing tip area ratio	0.79 \pm 0.02	0.79 \pm 0.06
Wing tip shape index	1.21 \pm 0.01	1.23 \pm 0.17

Wing shape parameters were calculated as in Norberg and Rayner (1987).

had lower wing loading and aspect ratio. However, the sample was too small for comparison (Table 1). The scores on the size-independent principal components Q_a (representing aspect ratio) and Q_1 (representing wing loading), using the averages of all 12 individuals measured for the input variables in equation 9 in Norberg and Rayner (1987), were 0.456 and 0.956, respectively. These values placed *M. temminckii* in a region of the wing-shaped morphospace out of the fringe of the general area occupied by other Molossidae in Norberg and Rayner's (1987) sample with lower relative wing loading and aspect ratio than them. *Molossops (Neoplatymops) mattogrossensis* was the nearest neighbor of the target species in this morphological space, and it was also outside the polygon defined by other Molossidae (Fig. 1). *M. temminckii* has wing tips relatively as long (high values of wing tip length ratio) but narrower (low values of wing tip area ratio) than most Molossidae listed in Norberg and Rayner (1987; Table 1). Predicted flight speed was 6.3 m/s, both with multivariate regression and principal components equations in Norberg and Rayner (1987).

Echolocation behavior

All descriptions refer to the fundamental harmonic, which was the only harmonic detectable in all the recordings without saturation and with a good signal to noise ratio.

Calls emitted by stationary and hand-released bats We recorded eight bats, both motionless and flying after being hand released, and six more only after being released. While at rest, most individuals emitted mostly pulses with downward linear modulation of frequency vs time, interspersed with some upwardly frequency modulated (UFM) pulses very similar in shape but a little shorter than those used while in search flight (DUR 5.9 ± 1.7 ms, BW 10.7 ± 1.7 kHz, $N=8$). Immediately after being released, all bats broadcasted only UFM pulses with lower frequency of the narrowband part than when held stationary (paired sample $t_{n=8}=2.866$, $p=0.012$, difference 0.99 ± 0.97 kHz). However, there was much variation among individuals in the frequency differences, and these were very close to the resolution limit of our analysis. Four of the bats were recorded when trying to capture flying insects just after being released. These recordings reaffirmed that the “flipping” between UFM and DFM calls during the approach phase was characteristic of *Molossops temminckii* (see below).

Search phase calls During normal foraging flight, *Molossops temminckii* broadcasted UFM echolocation calls with progressively slower modulation rate, which render upward curvilinear sonograms (Figs. 2 and 3a). Frequency increased asymptotically from a minimum starting value around 40.4 kHz to a maximum around 50.4 kHz, for a

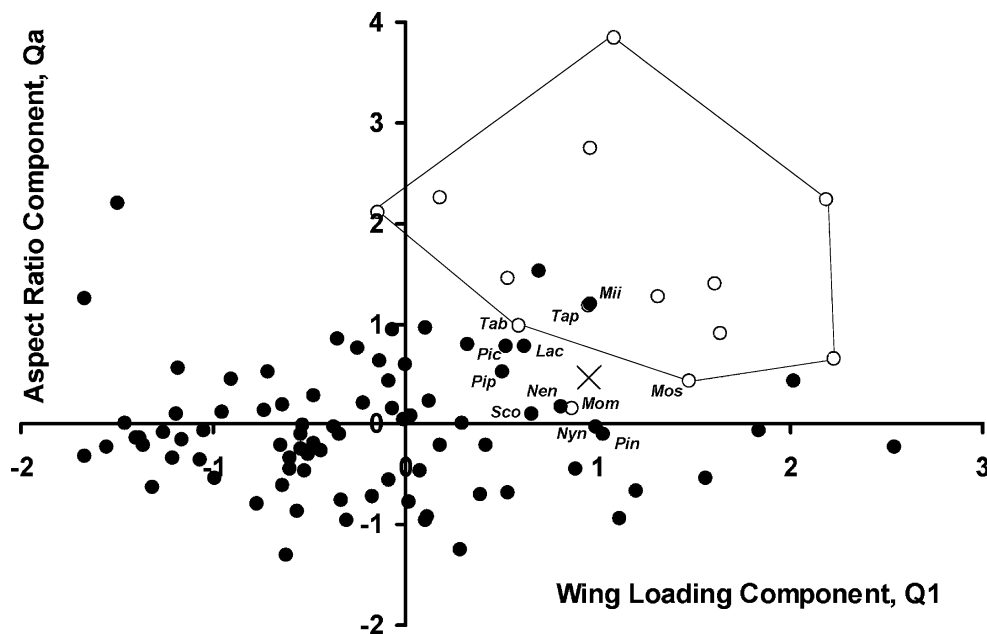
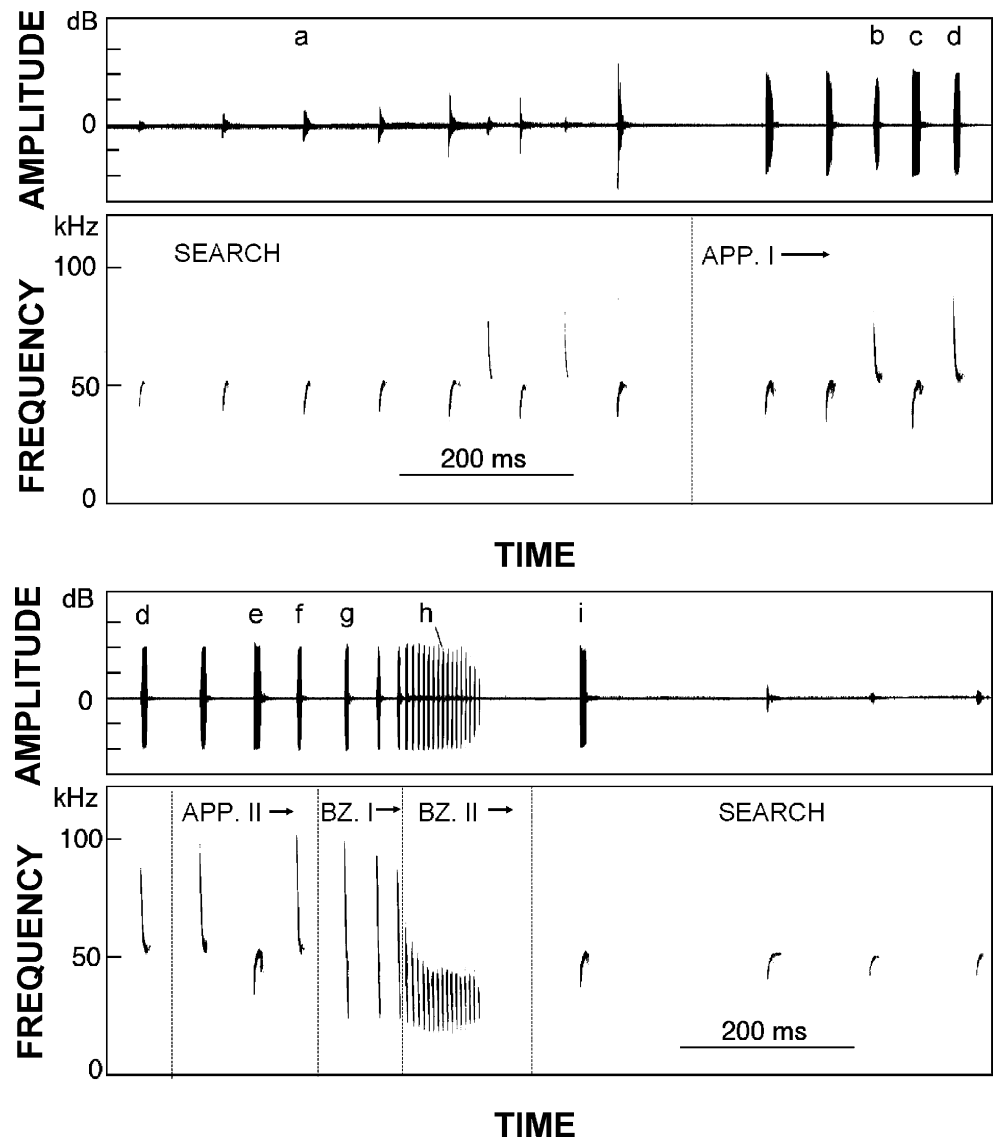


Fig. 1 Wing shape morphospace according to the size-independent principal component equations Q_a (representing aspect ratio) and Q_1 (representing wing loading) as described by Norberg and Rayner (1987). *Molossops (Molossops) temminckii* is represented by an X. Bats originally included in the morphospace by Norberg and Rayner (1987) are plotted as hollow circles (Molossidae) or black circles (Vespertilionidae). The polygon joins the outermost points of the molossid bats with the exception of *Molossops (Neoplatymops)*

mattogrossensis. Species in the vicinity of *M. temminckii* are labelled with the acronyms: *Mii*, *Miniopterus inflatus*; *Tap*, *Tadarida pumila*; *Tab*, *Tadarida brasiliensis*; *Pic*, *Pipistrellus ceylonicus*; *Lac*, *Lasiurus cinereus*; *Pip*, *Pipistrellus pipistrellus*; *Nen*, *Neoromicia nanus*; *Mom*, *Molossops (Neoplatymops) mattogrossensis*; *Sco*, *Scotorepens orion*; *Nyn*, *Nyctalus noctula*; *Pin*, *Pipistrellus nathusii*; and *Mos*, *Molossus sinaloae*

Fig. 2 Example of the echolocation behavior of *M. temminckii* in a sequence of calls from the search phase (SEARCH) through approach I (APP. I), approach II (APP. II), buzz I (BZ. I), buzz II (BZ. II), and back to the search phase after the pause for prey handling. Waveforms are represented in the upper panels and sonograms in the lower ones. Lower case letters in the waveform track identify calls corresponding to the following pulse type and position: **a** search phase UFM, **b** first DFM approach I, **c** last UFM approach I, **d** last DFM approach I, **e** last UFM approach II, **f** last DFM approach II, **g** first LFM buzz I, **h** LFM middle buzz II, and **i** first UFM after buzz. Notice that the search phase subsequence contains two DFM pulses of an aborted approach and a long interpulse interval, a result of one missing emission, just before the start of the approach phase



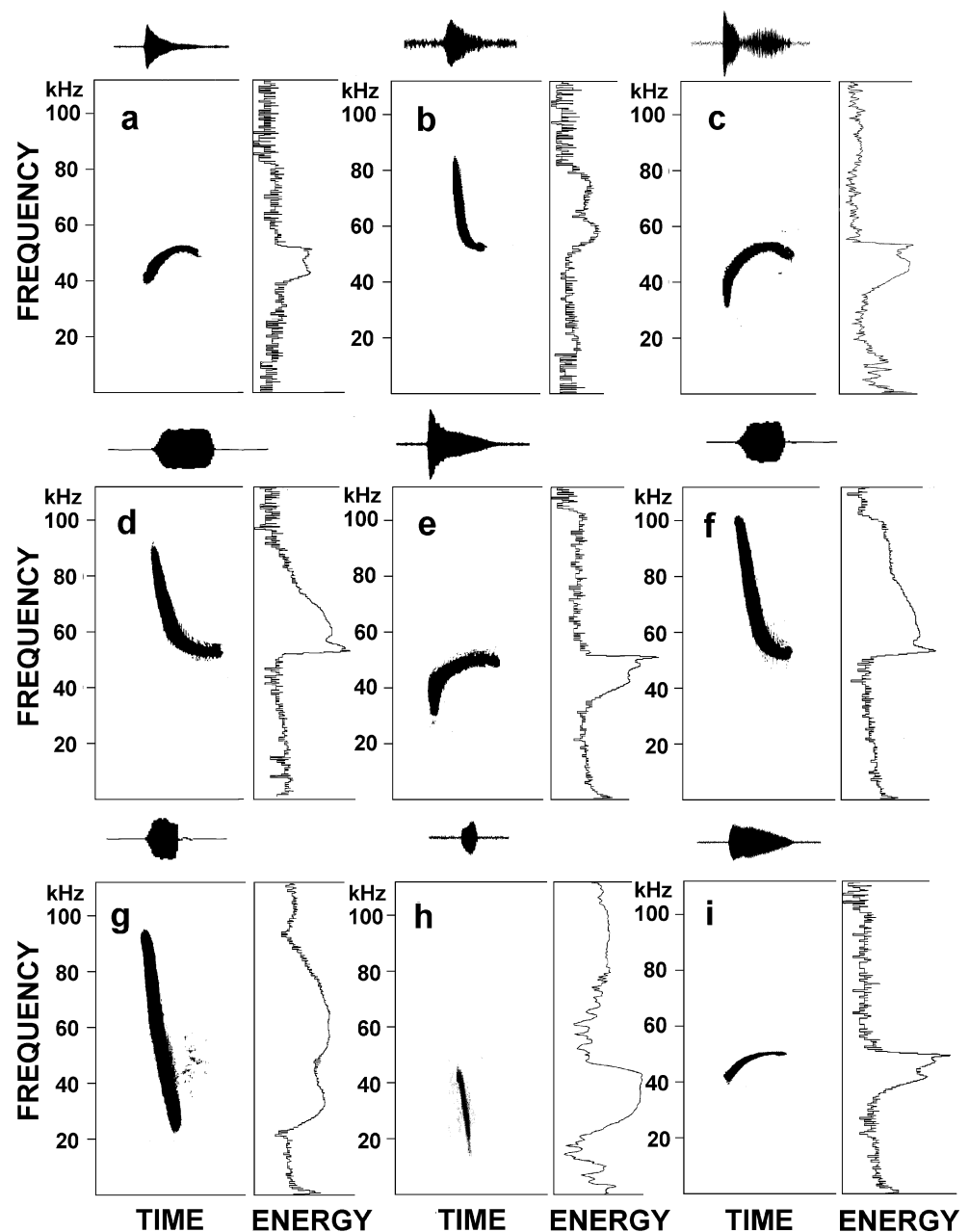
total bandwidth of about 10 kHz. Most frequently, the maximum and the terminal frequency coincide, but sometimes (9 out of 50 sequences) the pulse bent about 1 kHz (1.0 ± 0.8 , $N=9$) downwards at the end (Fig. 3a). This seems to be an individual trait, as all pulses in a given sequence ended similarly. Calls averaged 7.8 ms of duration, half of this time corresponding to the narrowband tail (Table 2). Power spectra of whole pulses always showed two prominent peaks. A very sharp and more intense one (8 dB average above the other in 30 pulses recorded with the microphone near the broadcasting bat) corresponding to the narrowband component and another much broader and shallower one corresponding to the broadband component. However, oscillograms revealed that there was much more instantaneous energy in the broadband component (Fig. 3a,c; Table 2).

Average interpulse interval was 97 ms, somewhat higher than the value of 73.8 ms predicted by body mass allometry

(Jones 1994). The average duty cycle was 8.6%. However, interpulse intervals showed a bimodal distribution ranging from 45 to 215 ms. The first peak (78% of the pulses) median and modal interval midpoint were respectively, 91.7 and 97.5 ms. The second peak (22% of the pulses) median and modal interval midpoint were respectively 170.9 and 162.5 ms, respectively (Fig. 4; Table 2). *Molossops* seems to broadcast one pulse per wingbeat, skipping one emission now and then. A sample of 115 wingbeats observed on video recordings against clear sky showed an average duration of 103 ms.

Search phase calls differed little among sites. For example, there were no significant differences in interpulse interval, duration, or bandwidth (INTER, $t_{n=17,14}=0.10$, $p=0.918$; DUR, $t_{n=17,14}=1.58$, $p=0.126$; BW, $t_{n=17,14}=0.54$, $p=0.590$) between the sequences recorded at the most open recording location positioned between two isolated large trees distant some 80 m from other trees (INTER, 81.2 ± 13.8 ms; DUR, 9.5 ± 0.9 ms; BW, 9.8 ± 1.9 kHz; $N=17$ sequences) and those

Fig. 3 Expanded time traces, sonograms, and power spectra of pulses representing different stages in the echolocation behavior of *M. temminckii*. **a–i** identify position and type of pulses in the sequence displayed in Fig. 2. The time axis total length is 20 ms. Energy is measured in a relative scale of decibels



recorded at a location in the forest edge with considerable more clutter around (INTER, 80.8 ± 7.8 ms; DUR, 9.0 ± 1.9 ms; BW, 9.4 ± 2.2 kHz, $N=14$ sequences). All sequences of search phase signals recorded with various methods at different sites contained exclusively UFM signals, except for the interspersed feeding buzzes and aborted approach sequences.

Echolocation behavior when approaching prey The transition from the search to the approach phase was dramatic because it involved the sudden introduction of DFM pulses, which progressively replaced the UFM pulses of the search phase. Detailed analysis of the changes in the structural characteristic of the pulses and the pattern of emission

allowed the identification of four distinct phases, the first two corresponding to the approach phase of other bats (Fig. 2).

Approach phase I Pulses at the beginning of the phase were mostly UFM, but pulses with an asymptotic decrease of frequency were interspersed progressively within the sequence, resulting in an alternating sequence of both types of calls at the end of the phase (Figs. 2, 4 and 5a). In all analyzed recordings, the start of a pursuit sequence was preceded by a progressive increase in the duration of the UFM pulses (from ~ 8 ms to ~ 10 ms at the end of the phase; $t_{n=50,15} = -4.36$, $p < 0.0001$). DFM pulses that appeared earlier in the sequence were also shorter in average than those near the end of the phase, although this trend was not

Table 2 Characteristics of the echolocation calls of *Molossops temminckii* at different stages during the search, approach, and capture phases of the foraging behavior

Phase	Search phase	Approach Phase I			Approach Phase II		Post buzz
		First DFM	Last UFM	Last DFM	Last UFM	Last DFM	
Pulse type and position	UFM	First DFM	Last UFM	Last DFM	Last UFM	Last DFM	First UFM
Variable							
Interpulse interval	97.0±29.9	57.0±8.3	62.8±19.6	58.9±10.9	46.6±7.3	50.8±8.8	113.7±16.3
Duration	7.8±1.6	7.5±2.0	9.7±0.6	8.1±1.5	8.3±0.7	4.7±1.3	7.1±0.9
Duration broadband	4.0±0.9	4.2±1.1	4.9±0.6	4.5±1.1	4.2±0.5	3.3±0.8	3.1±0.6
Duration narrowband	3.8	3.3	4.8	3.6	4.1	1.4	4.0
Starting frequency	40.4±3.5	76.5±9.2	34.4±5.0	78.2±10.5	33.7±4.3	80.0±12.5	38.4±2.6
Terminal frequency	50.4±1.5	53.4±1.4	50.8±1.4	53.1±1.2	50.2±1.6	51.3±2.2	49.7±1.4
Frequency at TFM/2	47.0±0.5	59.4±2.6	46.9±1.0	59.4±2.6	46.5±1.1	58.4±3.0	46.3±1.1
Peak narrowband	50.4±1.4	54.1±1.3	50.3±1.4	53.8±1.2	49.9±1.4	52.9±2.0	49.4±1.8
Peak broadband	45.1±2.6	57.6±2.0	45.0±1.7	57.1±1.8	44.0±1.5	56.4±3.4	44.8±2.0
Bandwidth	10.3±3.1	24.6±9.6	16.4±5.1	26.6±10.6	16.5±4.3	30.1±12.9	11.4±2.5
MODR (kHz/ms)	2.9±0.8	5.3±1.4	3.1±0.9	5.5±1.5	3.7±1.0	8.6±2.1	3.4±0.7
Duty cycle (%)	8.6±2.7	14.2±2.5	16.6±4.3	14.5±2.8	18.1±3.2	9.5±3.0	6.4±1.2

Sample size was 50 pulses/sequences for the UFM search phase pulses and 15 pulses/sequences for the other phases. Units are in milliseconds for all times and kilohertz for all frequencies. See text for description of variables and phases. Duration of the narrowband part of the signal resulted from subtracting the average duration of the broadband part from the average total duration.

UFM Upward frequency modulated, DFM downward frequency modulated, MODR modulation rate

statistically significant ($t_{n=15}=-1.83$, $p=0.089$). These DFM pulses were shorter than their UFM neighbors (last DFM vs last UFM of approach phase I, $t_{n=15}=-4.02$, $p=0.001$); their terminal frequency was ~3 kHz above (last DFM vs last UFM of approach phase I, $t_{n=15}=11.85$, $p<0.0001$; Figs. 3, 4, and 5), and they covered a much broader band (last DFM vs last UFM of approach phase I, $t_{n=15}=4.26$, $p=0.001$). The starting frequency slowly but progressively decreased in the UFM pulses, and it increased in the DFM pulses. As the terminal frequency remained stable, this resulted in a progressive increase of bandwidth (search phase vs last

UFM of approach phase I, $t_{n=50,15}=-5.60$, $p<0.0001$), which kept the modulation rate almost constant. As the interpulse interval also decreased monotonically during this phase, duty cycle increased to values above 15% (Fig. 5; Table 2).

Approach phase II Spectral and temporal patterns in this phase were close to the approach phase described in other molossid and vespertilionid bats. It was characterized by a progressive decrease in pulse length over a sequence of three to five pulses before the emission of the first pulse

Fig. 4 Histogram of the interpulse intervals of the UFM pulses broadcasted by *M. temminckii* during the search phase of its foraging behavior, $n=20$ sequences, 309 pulses. Predicted interval was calculated according to Jones (1994)

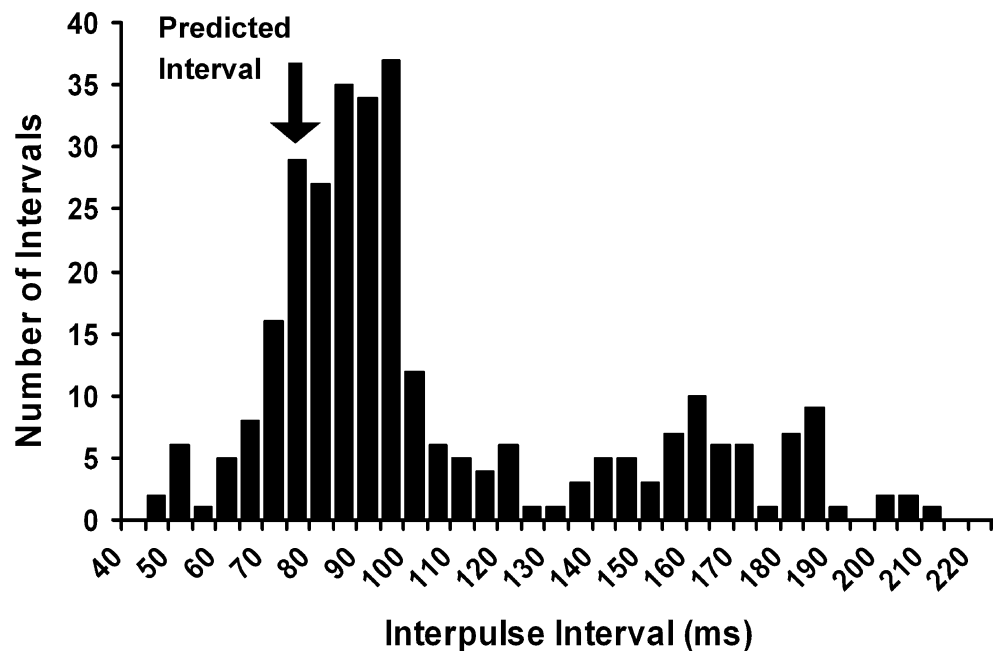
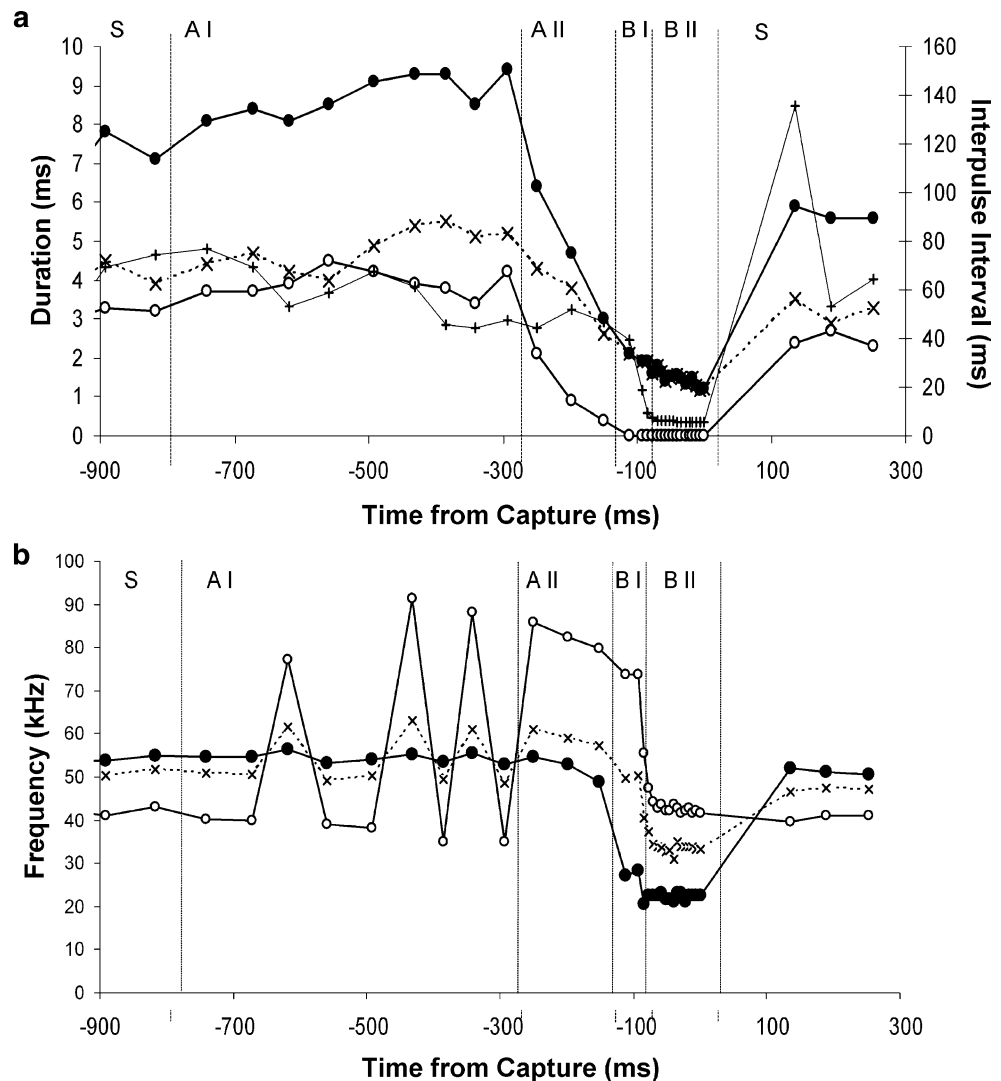


Fig. 5 Temporal and spectral variation of the echolocation call parameters during a hunting sequence of *M. temminckii* (not the same in Fig. 2). Vertical dashed lines mark the limits of the different phases of the echolocation behavior: S, search; A I, approach I; A II, approach II; B I, buzz I; B II, buzz II; and after the last line, beginning of the next search phase. **a** Pulse duration (filled circles), interpulse interval (crosses), and duration of the broadband (X) and the narrowband (hollow circles) components of the signal against time to prey catch at time 0. **b** Starting frequency (hollow circles), terminal frequency (filled circles), and frequency at the middle of the broadband component (X) of the calls against time to prey catch



with a linear downward modulation of frequency that marked the start of the terminal phase or buzz (Fig. 5a). It consisted mostly of DFM pulses (Fig. 2). The one or two UFM pulses that might appear in this phase were longer than their DFM neighbors, but they were still shorter than the UFM pulses in the previous phase (Table 2). Interpulse interval did not change much, and the duty cycle decreased, reaching by the last DFM pulse values near those in the search phase. The shortening of the DFM pulses was mostly due to a steep fall in the duration of the narrowband tail, although the terminal frequency of both types of pulses remained similar to those in the previous phase (Fig. 5a; Table 2). The broadband part of the signal was also progressively shortened, while the starting frequency remained almost unchanged or increased. As a result, the modulation rate increased considerably (Table 2; Fig. 5).

Buzz I We define the start of this phase as the appearance of the first pulse with linear modulation of frequency vs time in the sequence (Fig. 2). Duration progressively shortened

along the two to five pulses of this phase. The interval that separated them also decreased, slowly at the beginning and faster later, which resulted in a sudden drop in the duty cycle at the first pulse followed by a fast increase all the way to the end of the phase (Fig. 5a; Table 3). The start of this phase was also clearly shown in the frequency domain by a sudden drop in the terminal frequency of the pulses. From the nearly invariable values around 51 kHz in the previous phases, the terminal frequency fell below 30 kHz within the first or second pulse of this phase. Because the starting frequency decreased much more slowly, the bandwidth greatly increased at the beginning of this phase, reaching a maximum throughout the echolocation sequence and remained large up to the start of next phase (Fig. 5b; Table 3).

Buzz II The beginning of this phase was marked by a sudden decrease in interpulse interval and a concomitant decrease in the starting frequency of the pulses that caused a drop in the bandwidth (Figs. 2 and 5; Table 3). The phase consists of a

Table 3 Characteristics of the echolocation calls of *Molossops temminckii* at different stages during the capture phase of the foraging behavior

Phase	Buzz I		Buzz II	
	First LFM	Last Buzz I	First Buzz II	Middle
Variable				
Interpulse interval	44.8±7.4	19.7±11.1	9.4±2.2	5.7±0.4
Duration	3.0±0.9	2.5±0.7	2.2±0.5	1.4±0.2
Duration broadband	3.0±0.9	2.5±0.7	2.2±0.5	1.4±0.2
Duration narrowband	0	0	0	0
Initial frequency	76.4±12.5	70.5±11.7	57.2±6.1	43.1±3.2
Max/min frequency	28.2±4.3	25.2±2.7	23.0±2.5	20.6±2.9
F TFM/2	50.5±4.1	47.0±5.2	41.1±2.8	33.6±3.1
Peak narrowband	–	–	–	–
Peak broadband	43.3±6.0	42.3±6.7	35.8±4.6	32.0±4.5
Bandwidth	48.1±15.5	45.3±12.7	34.2±7.1	22.5±3.0
MODR (kHz/ms)	15.7±3.1	17.8±2.2	15.4±1.8	15.3±1.7
Duty cycle (%)	6.8±1.7	16.4±8.1	24.4±6.5	24.5±2.9

Sample size was 15 pulses/sequences per phase. Units are in milliseconds for all times and kilohertz for all frequencies.

LFM Linear frequency modulated, other acronyms as in Table 2.

sequence of 14–28 pulses (16.0±2.9 pulses, $n=40$ buzzes), and it was characterized by the relative stabilization of most parameters that had been changing fast during the previous phase. Interpulse interval, duration, and starting and final frequencies changed very little and uniformly up to the end of the buzz (Fig. 5; Table 3). The pulses typically started with an extremely short element of constant frequency that was not present in the previous phase (Fig. 3h).

After buzz After the buzz, there was a pause in ultrasound emission (113.7±16.3 ms, $n=15$ buzzes), while bats presumably ingested their prey, and before the normal sequence of UFM search phase calls was resumed (Fig. 2). The first pulse after this silent interval was usually a bit shorter, had a relatively longer narrowband tail, and covered a slightly broader band of frequency than regular search phase UFM pulses (Fig. 3i; Table 2).

Habitat use and foraging behavior

M. temminckii was less frequently detected than other Molossidae and the two Vespertilionidae used for comparison. Activity of the species was uneven across habitats ($\chi^2=97.4$, d. f.=5, $p<0.0001$). Bats would concentrate within park-like areas with sparse large trees and along lines of large trees. Some bats were detected along forest edges. The species was seldom detected in sound samples collected in the forest (although ultrasound screening by the canopy could have decreased detectability here) or in the savannah near forest edges and very rarely detected in open areas far from trees and forest, either far or near water. All other species were also more common at the dispersed trees sites, but they used other habitats much more often. This

resulted in a pattern of habitat use significantly different from *Molossops* (other Molossidae, $\chi^2=2365.0$, d. f.=16, $p<0.0001$; *M. nigricans*, $\chi^2=459.0$, d. f.=16, $p<0.0001$; *E. diminutus*, $\chi^2=137.4$, d. f.=16, $p<0.0001$; Table 4). Other Molossidae showed a more even distribution among habitats, being more common than *Molossops* in forest edges and savannah sites near the forest (Table 4).

During our surveys with simultaneous infrared video and ultrasound detection, we only detected *M. temminckii* near groups of large trees. In general, bats were flying along fairly straight paths parallel to the canopy edge at midheight (6–8 m), relatively near the trees (2–4 m). In several instances, the bats were observed flying directly towards the canopy, making a relatively sharp turn to continue flying parallel to it. Bats were also observed flying right above the canopy at 2–3 m above the tree tops. In two occasions, they were observed flying close to the ground (3 m) below the canopy among widely sparse tree trunks. In two instances, we observed the bats with the naked eye before dark and recorded them on the computer while they were flying relatively low (~3 m), describing circles with a radius close to 5 m, once around small trees and houses, and once over grassland 40 m far from the nearest tree.

Discussion

Search phase echolocation behavior

The echolocation behavior of *Molossops temminckii* appears extraordinary when compared with that of other bats. Its most unusual features are the upward modulation of the search calls and the major switching of bandwidth and direction of modulation when approaching and capturing prey.

Table 4 Summary of results of the study of habitat use

Habitat	Total	<i>M. temminckii</i>	Other molossid	<i>M. nigricans</i>	<i>E. diminutus</i>
Forest	486	5 (7.5%)	143 (11.1%)	8 (3.9%)	7 (8.9%)
Forest edge	555	12 (17.9%)	274 (21.2%)	10 (4.9%)	6 (7.6%)
Dispersed trees	571	42 (62.7%)	466 (36.0%)	113 (54.9%)	29 (36.7%)
Savannah near the forest	532	4 (6.0%)	229 (17.7%)	8 (3.9%)	4 (5.1%)
Open savannah	504	2 (3.0%)	104 (8.0%)	39 (18.9%)	25 (31.6%)
Flooding channel bank	508	2 (3.0%)	77 (6.0%)	28 (13.6%)	8 (10.1%)
Total	3,156	67	1,293	206	79

Column Total contains the total number of 3-s sound samples obtained in each habitat. The next columns indicate the number of sound samples containing echolocation calls of the corresponding species or group of species. Figures between brackets correspond to the percentage per habitat of the total positive samples for the species (as the total number of samples is similar across habitats, these figures allow direct comparison of habitat use across species). The total number of positive samples per species is shown in the last row.

The widespread use of downward frequency modulation in bat echolocation calls may have deep roots. Low frequency sounds suffering low atmospheric attenuation travel long distances. However, Rayleigh scattering poses a lower limit to the frequency providing longer detection distance for targets of a specific size. The frequency of the narrowband tail of the DFM echolocation calls used by many bats that forage in open areas is probably set near this limit (Hartley 1989; Barclay and Brigham 1991; Jones 1999; Houston et al. 2004). After prey detection, bats using FM calls obtain more accurate measures of range and angle to their target prey by increasing signal bandwidth (Simmons and Grinnell 1988; Siemers and Schnitzler 2004). To avoid the high-pass filtering of Rayleigh scattering and to get significant echoes of FM signals from tiny targets, bats have to increase the bandwidth by increasing the maximum frequency while keeping the frequency of the narrowband tail of the signal low.

From the mechanical perspective of the vocalization, this transition from narrow to broadband mode while approaching a prey is probably best addressed with downward modulated signals (instead of broadcasting first the narrowband part and then rising the frequency in an upwards FM sweep). Modulating asymptotically, bats get a Doppler tolerant signal as well (Altes and Titlebaum 1970). Additionally, in downward FM signals, the stimulation of the tonotopic receptors of the basilar membrane occurs in the same order in which they are arranged, without low frequency waves travelling first from base to apex and perhaps stimulating the high frequency receptors located near the oval window. *M. temminckii* behavior seems to agree with this logic when it starts using DFM signals when approaching prey. However, why does it use UFM signals during the search phase and most of the approach phase, only to undergo dramatic vocal gymnastics by interspersing both types of signals during the approach maneuver?

When foraging in background-cluttered spaces, bats need detailed information on the structure of such a background. The long narrowband calls used by many

aerial hawking bats in open areas might yield echoes from the background, but backward masking issues may preclude its use close enough to it (Schnitzler et al. 2003). Inaccuracy in range determination, because long narrowband signals provide poor time markers, may also be unacceptable when the bat is facing a risk of collision. Shorter broadband FM signals seem to be useful to locate the background adequately. The echoic areas of particular background objects (branches) and the general planar background (ground, canopy) are much larger than those from flying prey, and they reflect sound instead of reradiating it. Consequently, echoes coming from them do not suffer as much transmission loss owing to spherical spreading and attenuation as it happens with small targets (i.e., Holderied and Helversen 2003). This may compensate for the low energy content of the FM sweep at each frequency, in such a way that broadband FM echoes from the farther background may have similar strength to the echoes coming from a closer prey. This way the bat can adequately locate both kinds of objects and plan its flight path.

We would expect that the transition from narrowband to wideband mode that opens the “background attention window” should happen relatively near the background in relatively maneuverable bats, as they are capable of negotiating flight among objects at close range (Kalko and Schnitzler 1993). However, this transition distance has been estimated at ~5 m for European *Pipistrellus* spp. bats and the neotropical species *Myotis nigricans* (Kalko and Schnitzler 1993; Siemers et al. 2001). *Eptesicus serotinus* also shows a relatively large “critical flight altitude” of 8–10 m for switching between detection modes (Jensen and Miller 1999). These distances are much larger than the combined length of the signal overlap windows caused by forward and backward masking (i.e., $2.72 \text{ m} = 2 \text{ windows} \times [0.008 \text{ s} \times 340 \text{ m/s}] / [\text{two-way sound travel}]$ for the 8-ms or less longest signals of the *Pipistrelles* or 4.08 m for the 12-ms long calls of *E. serotinus*; same references as above). The need for attention to the background might be more

relevant than the potential risk of masking in setting the narrow to wideband transition distance. We might expect that the transition distance would be even larger in faster and less maneuverable bats.

M. temminckii has wing morphology intermediate between some of the slower and more maneuverable of the Molossidae and the fastest and less maneuverable of the Vespertilionidae. The nearest species in the morphospace are vespertilionids with an average to high aspect ratio and high wing loading. According to Norberg and Rayner (1987) and Norberg (1994), and given the wing morphology indexes, *M. temminckii* has greater maneuverability but also greater cost of transport in comparison to other Molossidae. However, it is less manoeuvrable and faster than the high wing loading Vespertilionidae with a similar size [the speed predicted by Norberg and Rayner's (1987) equations was 6.3 m/s vs 5.8 in *Pipistrellus pipistrellus* and 6.2 in *Pipistrellus nathusii*]. Given its flight performance, this species would need to open the 'attention window' at a longer distance from the background than more maneuverable bats do. This need might have been even more extreme in a previous stage in the adaptive process that led the lineage of *M. temminckii* to use a foraging space closer to the background clutter than did its hypothetically more archetypical Molossidae-like ancestors. Bats in the sister genus *Cynomops* (Peters et al. 2002), such as *C. planirostris*, have a very high wing loading and are fast open-air foragers with little maneuverability. *Cynomops*, and consequently its sister *Molossops*, is phylogenetically within the neotropical radiation of molossid bats, from which high-flying paleotropical genera split at more basal nodes (Hooper and Van Den Bussche 2003). Then, any reconstructed common ancestor of *Molossops* and *Cynomops* would have higher wing loading and faster flight than *M. temminckii* (authors' unpublished data).

If the narrowband FM frequency is set at ~51 kHz in *M. temminckii* through a compromise between atmospheric attenuation and Rayleigh scattering, the only possible strategy for increasing ranging distance of background objects while keeping a narrowband element with optimal frequency is to use broadband FM signals with the frequency band below that narrowband element. Producing it by increasing frequency asymptotically from a lower frequency before the narrowband element will generate a Doppler tolerant signal. Asymptotically increasing the tension of the vocal chords along the pulse is perfectly feasible, as some bats, including other molossids, show by producing calls with UFM either for echolocation (i.e., Rhinolophids and some Emballonurids; Kalko 1995; Tian and Schnitzler 1997) or in social contexts (i.e., Kingston et al. 2000; own observations). However, peripheral receptors tuned to these lower frequencies and wired to neural centers capable of processing such echoes will be required for the

signals to remain functional. At least some molossid bats broadcast search phase calls with alternating frequencies (Heller 1995; Fenton et al. 1998; Kössl et al. 1999; Kingston et al. 2003). Among them, *Molossus molossus*, the only one for which neurophysiology data are available, seems to possess the neural requirements for parallel processing of the two frequency bands (Mora et al. 2004). This might work as a preadaptation facilitating separation of function between auditory pathways specialized for processing different signals or components of signals. We hypothesize that the UFM signals used by *M. temminckii* during the search phase provide information for spatial orientation through its upward FM sweep and for detecting prey and perhaps providing some information about its characteristics through the narrowband tail. The stronger instantaneous energy in the FM sweep will further increase detection distance for background objects.

There are parallels in the echolocation behaviors of *M. temminckii* and the vespertilionid bat *Barbastella barbastellus*. Denzinger et al. (2001) reported that the latter species alternates two types of signals during the search phase, both having a bandwidth near 15 kHz. One consists of a relatively long (5–7 ms) narrowband component that ends in a downward FM sweep, while the other is a stronger and shorter (~2.5 ms) FM sweep covering a lower and partially overlapping frequency band. These echolocation signals resemble the UFM calls used by *M. temminckii* in having the narrowband element at the higher frequency end of the FM sweep. Similar to what we propose here, Denzinger et al. (2001) suggested that the lower band signals were specialized for spatial orientation, providing information about the background, while the upper band signals had similar function as the DFM signals with a narrowband tail of other bats (both prey detection and background location). Similar to *M. temminckii*, *B. barbastellus* often forages in background-cluttered space, particularly just above tree crowns (Sierro and Arlettaz 1997), reinforcing the idea of the correspondence between this particular signal structure and the foraging strategy.

Another distinctive feature of the echolocation behavior of *M. temminckii* relative to other open space vespertilionid bats is that its search phase calls are very similar across sites that may differ in spatial structure. Especially noticeable is that the bat broadcasts UFM signals when held stationary and immediately after being released very close to the ground. Instead, other Molossidae and Vespertilionidae only broadcast very steep and short steeply downward frequency modulated signals when stationary or flying in confined spaces (Roverud 1987; Kalko and Schnitzler 1993; Siemers et al. 2001). *M. temminckii* often forages for prey at a distance from the background where it might incur in either forward or backward masking when using the relatively long UFM search calls (signal and clutter overlap windows

for an average 7.8-ms-long search signal is 1.32 m each—total 2.64 m—and gets to 1.65 m—total 3.3 m—for the longer signals of the approach phase). The apparent exclusive use of UFM signals when foraging, despite their evident capacity of producing and analyzing other types of signals, probably indicates that echolocation behavior has become fairly stereotyped to fit a predominant foraging strategy in background cluttered space. This concurs with our habitat survey data.

One possibility for the bat to avoid backward masking is to discriminate between echoes in the frequency domain by using flutter information about the prey carried in the narrowband part of the signal. This would explain the lengthening of the UFM pulses along with the decrease in the interpulse interval and the concomitant increase in duty cycle during the approach phase. This flutter detection capability has been proposed for *Molossus molossus*, which also increases pulse duration and duty cycle during the approach phase but uses DFM signals (Mora et al. 2004). *B. barbastellus* also seems to increase signal duration during the approach phase (Fig. 3b in Denzinger et al. 2001), although the authors did not discuss this detail. Pulses 7.8–10 ms long can encode one complete wingbeat for prey fluttering at 128–100 Hz. *M. temminckii* mostly eats tiny coleopterans less than 4 mm long (our own unpublished data), which may flutter at those rates (Sotavalta 1947). Bats using FM signals are able to discriminate between targets fluttering at different rates, and hipposiderid bats using CF signals of similar duration to the narrowband element used by *M. temminckii* are much better at this task than the former (Sum and Menne 1988; Roverud et al. 1991). We believe that *M. temminckii* has a kind of incipient “acoustic fovea,” dedicated to processing the frequencies around the frequency of the narrowband tail of the echolocation calls. We hypothesize that this has to be more specialized than the cochlear region with an expanded mapping coefficient described for *Tadarida brasiliensis* (Vater and Siefer 1995) or the region of more sensitivity revealed by the peaks in the audiograms of some open space aerial insectivores (i.e., Neuweiler et al. 1984). Spectral analysis in this fovea would allow the bat to detect its prey against clutter and perhaps to get information for its classification. If the bats were able to separate emission and echoes in the frequency domain, they would also avoid forward masking in the narrowband component of the signal more prone to suffer overlap.

Approaching and capturing prey

The transition in perceptual needs during the approach phase is probably similar to what is experienced by other bats hawking in background cluttered space (Kalko and Schnitzler 1998). At close range, broadband FM calls at

higher frequency provide more precise information about the structural characteristics of the prey and about its spatial localization (Simmons and Grinnell 1988; Schnitzler et al. 2003; Siemers and Schnitzler 2004). For example, in *B. barbastellus*, the short lower-band signal disappears along the approach sequence, while the bandwidth of the upper band signals increases by both increasing the starting frequency and lowering the terminal one (Denzinger et al. 2001). In bats using DFM signals during the search phase, the starting frequency and the bandwidth increases during the approach phase (Kalko and Schnitzler 1998). Obviously, the transition between perceptual needs is not sharp, and this explains the extraordinary vocal gymnastics of *M. temminckii*. During the approach phase, the bat is broadcasting two pulses per wingbeat, often alternating UFM and DFM. The alternation between the two types of pulses must involve sudden changes in tension in the vocal chords and precisely alternating asymptotic increase or decrease of that tension, all of which seems a remarkable vocal feat (perhaps matched by the social vocalizations of other bats; i.e., Kingston et al. 2000). We differentiated approach phases I and II according to the trend in the duration of the calls. We believe that prey classification through spectral analysis prevails in approach I and that temporal analysis prevails in approach II.

Evolution of echolocation

The echolocation system of *M. temminckii* may prove relevant to understand the evolution of the echolocation systems based on narrowband frequency analysis. As noted by Fenton et al. (1995), to exploit fluttering prey in clutter, bats must simultaneously detect and track its targets, assess its position relative to the background, and avoid deafening themselves. Relatively maneuverable bats could evolutionarily slide along the adaptive flexibility of the FM echolocation systems and solve this by flying slowly and using low intensity broadband FM signals (i.e., Siemers and Schnitzler 2004). However, for less maneuverable bats, the adaptive pathway might prove more intricate. Narrowband signals and incipient acoustic foveae, having evolved for long distance detection in open areas, may have preadapted these bats for fluttering detection and prey classification. They may need to rely on FM elements of frequency lower than the narrowband detection signals to get information about the background if approaching clutter. Separation of the emitted signal from the incoming echoes in the frequency domain may protect them against self-deafening, opening new adaptive pathways. Perhaps, fast aerial hawking in open air was a necessary intermediate step for the evolution of the narrowband frequency analysis echolocation systems that allowed aerial insectivores to come back to forage in “the forest that early bats once called home.”

Acknowledgment We are most grateful to Carlos Ruiz Benavides, Ariany García, and Esquisa Omaña for their help during field work in Venezuela. The staff at the El Frío Biological Station, particularly Rafael Antelo, Juanma and Julio, provided invaluable logistic support for the field work. The Maldonado family, owner of the ranch “Hato El Frío,” has enforced a reconciled management of the land. This allows the conservation of the natural habitats and the persistence of the rich wildlife that we have been studying. Funding for travel and fieldwork in 2006 was provided by grant no. 39709 from the Mexican National Council for Science and Technology (CONACyT). The research reported here complied with the current laws of the Republic of Venezuela. Michael Smotherman, Winston C. Lancaster, and two anonymous referees made fundamental critical comments on earlier versions of this paper. Charles M. Francis and Leonel Torres helped us in revising the language.

References

- Altes RA, Titlebaum EL (1970) Bat signals as Doppler-tolerant waveforms. *J Acoust Soc Am* 48:1014–1020
- Anderson S (1997) Mammals of Bolivia, taxonomy and distribution. *Bull Am Mus Nat Hist* 231:1–652
- Anthony ELP (1988) Age determination in bats. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats. Smithsonian Institution, Washington, D.C., pp 47–58
- Barclay RMR, Brigham RM (1991) Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *Am Nat* 137(5):693–703
- Castroviejo S, López G (1974) Estudio y descripción de las comunidades vegetales de el Hato El Frío, en los Llanos de Venezuela. *Mem Soc Cienc Nat La Salle* 124:79–151
- Denzinger A, Siemers BM, Schaub A, Schnitzler H-U (2001) Echolocation by the barbastelle bat, *Barbastella barbastellus*. *J Comp Physiol A* 187:521–528
- Fenton MB, Audet D, Obrist MK, Rydell J (1995) Signal strength, timing, and self-deafening: the evolution of the echolocation in bats. *Paleobiology* 21:229–242
- Fenton MB, Arita H, Rautenbach IL, Rydell J, Ortega J, Bouchard S, Hovorka MD, Lim B, Odgren E, Portfors C, Scully B, Syme D, Vonhof MJ (1998) Emergence, echolocation, diet and foraging behavior of *Molossus ater* (Chiroptera: Molossidae). *Biotropica* 30:314–320
- Freeman PW (1981) A multivariate analysis of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. *Fieldiana Zool New Ser* 7:1–173
- Griffin DR (1958) *Listening in the dark*. Yale University Press, New Haven
- Griffin DR, Webster FA, Michael CR (1960) The echolocation of flying insects by bats. *Anim Behav* 8:3–4
- Hartley DJ (1989) The effect of atmospheric sound absorption on signal bandwidth and energy and some consequences for bat echolocation. *J Acoust Soc Am* 85(3):1338–1347
- Heller KG (1995) Echolocation and body size in insectivorous bats: the case of the giant naked bat *Cheiromeles torquatus* (Molossidae). *Le Rhinolophe* 11:27–38
- Holderied MW, Helversen Ov (2003) Echolocation range and wing-beat period match in aerial-hawking bats. *Proc R Soc Lond B* 270:2293–2299
- Hooper SR, Van Den Bussche RA (2003) Molecular phylogenetics of the chiropteran family Vespertilionidae. *Acta Chiropterol* 5:1–63
- Houston RD, Boonman AM, Jones G (2004) Do echolocation signal parameters restrict bats’ choice of prey? In: Thomas JA, Moss CF, Vater M (eds) Echolocation in bats and dolphins. University of Chicago Press, Chicago, pp 339–345
- Ibáñez C (1984) Biología y ecología de los murciélagos del Hato El Frío, Apure, Venezuela. *Doñana Acta Vertebr* 8:1–271
- Ibáñez C, Ochoa JG (1985) Distribución y taxonomía de *Molossops temminckii* (Chiroptera, Molossidae) en Venezuela. *Doñana Acta Vertebr* 12:141–150
- Jensen ME, Miller LA (1999) Echolocating signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. *Behav Ecol Sociobiol* 47:60–69
- Jones G (1994) Scaling of wingbeat and echolocation pulse emission rates in bats: why are aerial insectivorous bats so small? *Funct Ecol* 8:450–457
- Jones G (1999) Scaling of echolocation call parameters in bats. *J Exp Biol* 202:3359–3367
- Kalko EV (1995) Echolocation signal design, foraging habitats and guild structure in six neotropical sheath-tailed bats (Emballonuridae). In: Racey PA, Swift S (eds) Recent advances in bat biology, vol 67. Oxford University Press, London, pp 259–273
- Kalko EKV, 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
- Kalko EKV, Schnitzler H-U (1998) How echolocating bats approach and acquire food. In: Kunz TH, Racey PA (eds) Bat biology and conservation. Smithsonian Institution, Washington, D.C., pp 197–204
- Kingston T, Jones G, Zubaid A, Kunz TH (2000) Social calls in clear-winged woolly bats (*Kerivoula pellucida*) from Malaysia. *Bioacoustics* 11:1–16
- Kingston T, Jones G, Akbar Z, Kunz TH (2003) Alternation of echolocation calls in 5 species of aerial-feeding insectivorous bats from Malaysia. *J Mammal* 84:205–215
- Kössl M, Mora EC, Coro F, Vater M (1999) Two-toned echolocation calls from *Molossus molossus* in Cuba. *J Mammal* 80:929–932
- Marques JT, Rainho A, Carapuço M, Oliveira P, Palmeirim JM (2004) Foraging behaviour and habitat use by the European free-tailed bat *Tadarida teniotis*. *Acta Chiropterol* 6:99–110
- Mora EC, Macías S, Vater M, Coro F, Kössl M (2004) Specializations for aerial hawking in the echolocation system of *Molossus molossus* (Molossidae, Chiroptera). *J Comp Physiol A* 190:561–574
- Neuweiler G (1983) Echolocation and adaptivity to ecological constraints. In: Huber F, Markl H (eds) Neuroethology and behavioral physiology. Springer, Berlin Heidelberg New York, pp 280–302
- Neuweiler G (1984) Foraging, echolocation and audition in bats. *Naturwissenschaften* 71:446–455
- Neuweiler G (1989) Foraging ecology and audition in echolocating bats. *Trends Ecol Evol* 4:160–166
- Neuweiler G (2000) *The biology of bats*. Oxford University Press, Oxford
- Neuweiler G, Singh S, Sripathi K (1984) Audiograms of a South Indian bat community. *J Comp Physiol A* 154:133–142
- Norberg UM (1994) Wing design, flight performance, and habitat use in bats. In: Wainwright PC, Reilly SM (eds) Ecological morphology: integrative organismal biology. Chicago University Press, Chicago, pp 205–239
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos Trans R Soc Lond B* 316:335–427
- Parsons S, Boonman AM, Obrist MK (2000) Advantages and disadvantages of techniques for transforming and analyzing chiropteran echolocation calls. *J Mammal* 81:927–938
- Peters SL, Lim BK, Engstrom MD (2002) Systematics of dog-faced bats (*Cynomops*) based on molecular and morphometric data. *J Mammal* 83(4):1097–1110

- Roverud RC (1987) The processing of echolocation sound elements in bats: a behavioural approach. In: Fenton MB, Racey P, Rayner JMV (eds) Recent advances in the study of bats. Cambridge University Press, Cambridge, pp 152–169
- Roverud RC, Nitsche V, Neuweiler G (1991) Discrimination of wingbeat motion by bats, correlated with echolocation sound pattern. *J Comp Physiol A* 168:259–263
- Schnitzler H-U, Kalko EKV (1998) How echolocating bats search and find food. In: Kunz TH, Racey PA (eds) Bat biology and conservation. Smithsonian Institution, Washington, D.C., pp 183–196
- Schnitzler H-U, Moss CF, Denzinger A (2003) From spatial orientation to food acquisition in echolocating bats. *Trends Ecol Evol* 18:386–394
- Schnitzler H-U, Kalko EKV, Denzinger A (2004) Evolution of echolocation and foraging behavior in bats. In: Thomas JA, Moss CF, Vater M (eds) Echolocation in bats and dolphins. The University of Chicago Press, Chicago, pp 331–339
- Siemers BM, Schnitzler H-U (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* 429:657–661
- Siemers BM, Kalko EKV, Schnitzler H-U (2001) Echolocation behavior and signal plasticity in the neotropical bat *Myotis nigricans* (Schinz, 1821) (Vespertilionidae): a convergent case with European species of *Pipistrellus*? *Behav Ecol Sociobiol* 50:317–328
- Sierro A, Arlettaz R (1997) Barbastelle bats (*Barbastella* sp.) specialize in the predation of moths: implications for foraging tactics and conservation. *Acta Oecologica* 18:91–106
- Simmons NB (2005) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammal species of the world. A taxonomic and geographic reference, 3rd edn, vol 1. The Johns Hopkins University Press, Baltimore, pp 312–529
- Simmons JA, Grinnell AD (1988) The performance of echolocation: acoustic images perceived by echolocating bats. In: Nachtigall PE, Moore PWB (eds) Animal sonar. Plenum, pp 353–385
- Simmons JA, Lavender WA, Lavender RA, Childs JE, Hulebak K, Rigden MR, Sherman J, Woolman B (1978) Echolocation by free-tailed bats (*Tadarida*). *J Comp Physiol A* 125:291–299
- Smith JD, Starrett A (1979) Morphometric analysis of chiropteran wings. In: Baker RJ, Jones KJ, Carter DC (eds) Biology of the bats of the new world family phyllostomatidae, Part III, vol 16. Texas Tech University, Lubbock, pp 1–441
- Sotavalta O (1947) The flight tone (wing-stroke frequency) of insects. *Acta Entomol Fennica* 4–5(4):1–117
- Sum YW, Menne D (1988) Discrimination of fluttering targets by the FM-bat *Pipistrellus stenopterus*? *J Comp Physiol A* 163:349–354
- Tian B, Schnitzler H-U (1997) Echolocation signals of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in transfer flight and during landing. *J Acoust Soc Am* 101:2347–2364
- Vater M, Siefer W (1995) The cochlea of *Tadarida brasiliensis*: specialized functional organization in a generalized bat. *Hear Res* 91:178–195
- Willig MR (1985) Ecology, reproductive biology and systematics of *Neoplattymops mattogrossensis* (Chiroptera: Molossidae). *J Mammal* 66:618–628
- Zbinden K, Zingg PE (1986) Search and hunting signals of echolocating european free-tailed bats, *Tadarida teniotis*, in southern Switzerland. *Mammalia* 50(1):9–25