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Echolocation behavior and signal plasticity in the Neotropical bat *Myotis nigricans* (Schinz, 1821) (Vespertilionidae): a convergent case with European species of *Pipistrellus*?

Abstract We used both field and flight cage observations to investigate the echolocation and foraging behavior of the seldom studied, small, aerial insectivorous bat *Myotis nigricans* (Vespertilionidae) in Panama. In contrast to its temperate congeners, *M. nigricans* foraged extensively in open space and showed an echolocation behavior well adapted to this foraging habitat. It broadcast narrowband echolocation signals of 7 ms duration that enhance the chance of prey detection in open space. Because of rhythmical alternations of signal amplitude from signal to signal in our sound recordings of search signals in open space, we conclude that the bats scanned their environment with head movements, thereby enlarging their search volume. In edge-and-gap situations, and in the flight cage, *M. nigricans* introduced an initial broadband component to its search calls. In the field and in the flight cage, *M. nigricans* hawked for prey in aerial catches; gleaning was never observed. *M. nigricans* demonstrates call structures, such as narrow bandwidth and rather long signals adapted to foraging predominantly in open space. Moreover, call structure is highly plastic, allowing *M. nigricans* to forage in edge-and-gap situations also. These adaptations in call structure and plasticity have evolved convergently at least twice within the genus *Myotis*. Finally, *M. nigricans* echolocation and foraging behavior parallels that of the small, aerial, insectivorous pipistrelle bats (Vespertilionidae), which are not closely related to *M. nigricans* but forage in similar habitats.

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Introduction

Among Chiroptera, mouse-eared bats (*Myotis*, Vespertilionidae) represent the largest genus, with more than 80 species worldwide (Koopman 1994). To date, all field studies of *Myotis* species indicate that they feed predominantly on arthropods. They use mostly broadband (>40 kHz bandwidth) downward-frequency-modulated echolocation signals in the search phase (literature summarized in Table 1). Short, broadband signals are generally accepted to be well suited for foraging for insects flying close to substrates. This signal type improves separation of prey echoes from background targets and permits precise determination of the position of background targets to avoid collision (e.g., Simmons and Stein 1980; Neuweiler 1990; Schnitzler and Kalko 1998). Field studies have shown that many *Myotis* species forage close to substrates in highly cluttered or background-cluttered space. Within these spaces, however, *Myotis* species exploit a diverse range of niches. They take prey by gleaning it from the ground or from the vegetation, by "trawling" from water surfaces, or by hawking in the air (Table 1). Classically, *Myotis* is subdivided into subgenera (e.g., Koopman 1994), with the subgenus *Myotis* comprising the gleaning species, *Leuconoë*, the trawling species, and *Selysius*, those that mostly catch prey in mid-air (Table 1). Molecular systematics, however, suggests that the subgenera do not reflect close phylogenetic relationships but rather represent species showing similar ecomorphs that have evolved convergently several times in different parts of the world (Ruedi and Mayer 1999).

To date, most field studies of *Myotis* have focused on species from temperate regions and information on echolocation and foraging behavior of tropical *Myotis* is scarce. Here we present the first detailed study of the echolocation behavior of a Neotropical *Myotis*. First ob-

Table 1 Mean values of search call parameters summarized from published field studies on echolocation in *Myotis* species. Note that the parameter means obscure the high degree of situation-specific variability in call parameters that can by found in any of the species. This table, therefore, must be interpreted with caution. Where reported, the mode of prey capture (*G* gleaning, *A* aerial, *T* trawling) and observed distance of the recorded (foraging) bats to the background is given. Classification into "subgenera" is according to Koopman (1994); note that the "subgenera" probably do not reflect close phylogenetic relationships, but, rather, similar ecomorphs (Ruedi and Mayer 1999) [*SF* starting frequency, *PF* peak frequency, *TF* terminal frequency, *BW* bandwidth (* when BW was not given in the respective paper, we calculated it by subtracting TF from SF), *PD* pulse duration, *PI* pulse interval]

Species distribution	Distance bat to background	Prey capture	SF (kHz)	PF (kHz)	TF (kHz)	BW (kHz)	PD (ms)	PI (ms)	Reference
"Subgenus" *Myotis*: the gleaning ecomorph									
M. auriculus North America		G	97	66	54	43*	Max. 2		Fenton and Bell (1979, 1981)
M. bechsteinii Europe		G, A	111; 112	51; 73	34; 42	77*; 70*	2.5; 2.1	97	Vaughan et al. (1997a); Parsons and Jones (2000)
M. emarginatus Europe		G, A	105; 94	–	25; 43	79; 51	1.0; 2.8	26; 77	Schumm et al. (1991)
M. evotis North America	<1 m	G, A	100–60	58–45	49–31	69 max.*	2.7–0.3		Faure and Barclay (1994)
M. nattereri Europe	For the most part 20 cm–2.5 m from vegetation	A, G	99; 102; 121	51; 48; 67	23; 20; 31	76*; 82; 90*	2.3; 2.0; 3.4	77; 68	Vaughan et al. (1997a); Siemers and Schnitzler (2000); Parsons and Jones (2000)
M. septentrionalis North America	Several centimeters from a screen porch	G, A	107		49	58	2.4	55	Miller and Treat (1993)
M. thysanodes North America			49	34	31	18*	Max. 8		Fenton and Bell (1981)
"Subgenus" *Leuconoë*: the trawling ecomorph									
M. adversus Australia	About 9 cm above water surface	T, A	84	47	36	48*	4.5	68	Jones and Rayner (1991)
M. dasycneme Europe and Asia	About 26 cm above water surface	T, A	48	35	28	20*	18	117	Britton et al. (1997)
M. daubentonii Europe and Asia	Within 30 cm of water surfaces or >2 m away from clutter	T, A	90–95		25	47; 50–70	3.1; 5.0	67	Jones and Rayner (1988); Kalko and Schnitzler (1989)
M. lucifugus North America	Cruising altitude ca 12 m <1 m above water; other surfaces: >1 m	T, A	90; 79		40; 39	50*; 40*	5.6	50–100	Buchler (1980); Saunders and Barclay (1992)
M. riparius Neotropics		A	58		50	8*	4–5		Fenton et al. (1999)
M. ruber Neotropics		A	65		58	7*	5		Fenton et al. (1999)
M. volans North America	>1 m from surfaces	A	89; 94	46	40; 39	49*; 55*	10; Max. 4.4		Fenton and Bell (1979, 1981); Saunders and Barclay (1992)
M. yumanensis North America			64		48	16*	3.2		O'Farrel et al. (1999)
"Subgenus" *Selysius*: the aerial-feeding ecomorph									
M. brandtii Europe and Asia			86; 101	48; 55	34; 36	52*; 65*	3.1; 3.8	88	Vaughan et al. (1997a); Parsons and Jones (2000)
M. californicus North America		A	67	43	37	30*	Max. 6		Fenton and Bell (1979, 1981)
M. ciliolabrum North America			62		40	12*	3.5		O'Farrel et al. (1999)
M. leibii North America			55	44	41	14*	Max. 5		Fenton and Bell (1981)
M. mystacinus Europe and Asia			86; 112	51; 73	34; 42	52*; 70*	2.5; 2.1	97	Vaughan et al. (1997a); Parsons and Jones (2000)
M. nigricans Neotropics	>5 m	A	62	54	51	11	7.2	106	This study; for complete data see Table 2
M. siligorensis Southeast Asia	More than some meters, 2–5 m above ground	A		66		2.4	5.4	71	Surlykke et al. (1993)

servations in Panama indicated that search signals of the small *Myotis nigricans* differ considerably from those of its temperate congeners. In contrast to temperate *Myotis*, which typically produce short, wideband search signals, search signals recorded from *M. nigricans* are often more shallow modulated and of smaller bandwidth. The shape of *M. nigricans* search signals more closely resembles search calls of the similar-sized, temperate pipistrelle bats (Vespertilionidae: *Pipistrellus*) and those of the Palaeotropical *M. siligorensis* studied by Surlykke et al. (1993) than those of temperate *Myotis* species.

These differences in signal structure could reflect differences in habitat use and foraging behavior between *M. nigricans* and temperate *Myotis*. Currently, much attention is being paid to the relationship of echolocation signal structure to foraging habitats of bats, both within and between species (for reviews see Fenton 1990; Neuweiler 1990; Schnitzler and Kalko 1998; Schnitzler and Kalko, in press). Long and narrowband (i.e., shallow-modulated) signals are typically used by bats when foraging for insects in open space. Shorter, broadband signals are produced when using echolocation for foraging for prey closer to vegetation. Bats that use passive cues to perceive prey in and on vegetation also use broadband signals for orientation in space. Under discussion is the degree to which signal structure reflects phylogenetic relationships and the extent to which it evolved in response to physical and prey-related constraints imposed by the ever-changing settings in which bats evolved and diversified.

The objective of our study in Panama was to assess the signal inventory of *M. nigricans* both in the field and in a flight cage and to link signal structure to possible differences in habitat use and foraging behavior in comparison to temperate *Myotis*. In particular, we wanted to find out whether the comparatively long and narrowband search signals of *M. nigricans* are associated with foraging in open space, a behavior not known in temperate *Myotis*, at least not from the Eurasian region. The apparent similarities in call structure between *M. nigricans* and similar-sized European pipistrelle bats raises questions about the degree of convergent evolution in call structure between this Neotropical *Myotis* and the pipistrelles. The "vocal plasticity hypothesis" predicts that similarities in echolocation behavior and species' call inventories have evolved convergently under similar ecological constraints from an unknown ancestral inventory (Schnitzler at al., in press). We used the data from *M. nigricans* to test this prediction and to answer the following questions. Can the similarities in call structure between *M. nigricans* and pipistrelles be interpreted as adaptations to similar environmental constraints? Conversely, can the differences in echolocation behavior between *M. nigricans* and temperate *Myotis* be explained by different foraging strategies?

Methods

Study site

Data were collected from 25 January to 20 February 1999 on Barro Colorado Island (BCI), the field station of the Smithsonian Tropical Research Institute, in Panama (9°9′ N, 79°51′ W). The 16-km² island is between 30–170 m above sea level. It is covered by tropical, semi-deciduous moist forest in several successional stages (Foster and Brokaw 1990). Rainfall is seasonal, with about 90% of the total annual rainfall (2,623 mm) falling during the wet season between the end of April and the first half of December (Windsor et al. 1990; Paton 2000). In 1998–1999, the rainy season ended late, and the dry season began on 18 January 1999 (Panama Canal Commission, in Paton 2000), 1 week prior to the beginning of this study.

Animals and species identification

M. nigricans is abundant on BCI and is commonly found roosting in crevices, lofts, and attics of the laboratory buildings (Wilson 1971; personal observations). Species identification in the field was achieved by visual observation and sound analyses. With the exception of *M. riparius* (see Fenton et al. 1999), which is very rare on BCI, *M. nigricans* is the only small bat on BCI broadcasting downward-frequency-modulated signals with terminal frequencies between 48–55 kHz. Many mist-netting nights over the past years and the capture of bats from roosts exclusively revealed *M. nigricans* and never *M. riparius* in the area where the recordings were made (Kalko et al. 1996). Characteristic parameters (terminal and peak frequency) of echolocation calls recorded from *M. nigricans* in the flight cage matched well with the field recordings (Table 2) and serve a posteriori as additional confirmation of our species identification in the field.

For experiments in the flight cage, three adult non-reproductive females were taken from their roosts during the day, and after the experiments were returned to the capture site in the wild. Animals were kept under a natural light regime, housed in a small cage during the day and fed mealworms either during the behavioral experiments or by hand to maintain their weight. The species was identified according to Reid (1997) and a key by C.O. Handley (unpublished): small *Myotis* with brownish underparts and smooth dorsal fur that distinguishes it unambiguously from the sympatric, wooly-haired *M. riparius*.

Field recording sites and definition of habitat type

Following a study on pipistrelles by Kalko and Schnitzler (1993), we classified two habitat types for foraging *M. nigricans*. *M. nigricans* hunts in an edge-and-gap situation when it flies closer than about 5 m to the vegetation or less than about 5 m above the ground. In contrast, a bat hunts in open space when it flies more than 5 m from vegetation and higher than 5 m above the ground. We selected three field sites for simultaneous recording and observation of foraging *M. nigricans*: two edge-and-gap sites and one site in open space. One of the edge-and-gap sites was a rectangular 10×20 m forest gap around a 6×8 m artificial pond with closed canopy. The other, equally rectangular edge-and-gap site, measuring 20×5 m, was between a two-story dormitory and an adjacent forest edge. We recorded *M. nigricans* flying in open space in the upper part of the laboratory clearing above an open field of approximately 60×30 m. A 30-m-high radio-tower at the edge of the field, with regularly spaced horizontal bars at 3-m height intervals, was used as a reference to estimate the bats' flight height above ground. Sequences broadcast by the bats at the two edge-and-gap sites (i.e., always closer than 5 m to vegetation), were categorized as "edge-and-gap sequences." Sequences from bats at the open-space site flying higher than 5 m over the ground and further than about 5 m from vegetation were considered as "open-space sequences."

We started the observations shortly before dusk (around 1900 hours local time) and stopped when the bats activity level dropped, usually between 2200 hours and midnight. The data presented here stem from eight nights of observation.

Echolocation behavior

Bats on straight or circular flight paths without abrupt course deviations were assumed to be searching for prey. Accordingly, their echolocation calls were classified as search signals. Only search-call sequences from visually observed bats were used for further analysis.

When bats were abruptly deviating from their flight path, e.g., by diving downwards, we concluded that they were approaching prey and had started to emit approach signals. We took the simultaneous onset of an almost monotonic decrease in pulse duration and pulse interval and, whenever obvious, also a distinct increase in bandwidth (>29 kHz in open-space sequences) as our criterion for the start of the approach sequence. Based on consistent signal patterning, we discriminated a buzz or terminal group at the end of the approach sequence of *M. nigricans* as buzz 1 (drop of pulse interval below 20 ms followed by almost monotonic decrease in pulse interval) and buzz 2 (sudden drop of terminal frequency below 36 kHz; Figs. 5, 6).

Sound recording and analysis

Echolocation calls were recorded with a custom-built ultrasonic microphone and a transient recorder (Department of Animal Physiology, University of Tübingen). The time-expanded signals were recorded with a WM-DC6 Sony Walkman. For analysis, the signals were digitized and processed through a Fast Fourier Transformation (FFT; 256 points, Hanning window; FTTs calculated with 93.75% time overlap; software: Sona-PC; B. Waldmann, University of Tübingen). Equipment and analysis is described in detail elsewhere (Siemers and Schnitzler 2000). Sound duration and pulse interval were measured from the time signal. Starting frequency and terminal frequency were determined from the sonagram representation at about 25 dB below the peak frequency (i.e., frequency with most energy) of each signal. We only considered the first harmonic for measurements, because it contained most of the signal energy in all phases including search, approach, and buzz.

Out of six CrO_2 tapes, each comprising 90 min of time-expanded signal (i.e., 36 min of real-time signal), a total of 75 sequences with 1,937 calls were selected for further analysis. For each call, we determined starting frequency, peak frequency, terminal frequency, relative amplitude at peak frequency, bandwidth, pulse duration, and pulse interval.

Behavioral observations in the flight cage

To study echolocation and prey capture behavior of *M. nigricans* under controlled conditions, we presented mealworms (*Tenebrio molitor*; whole and halved larvae) suspended on nylon threads 0.06 mm in diameter to the bats in a flight cage (4×4.5 m with 2.1 m height). This manner of presentation was chosen to mimic natural airborne prey. To investigate the importance of arthropod-specific cues for prey detection, rubber dummies (electrical shrink-wrap tubing ranging from 1.6 mm diameter and 1 mm length to 2.4 mm diameter and 18 mm length) were offered to the bats in a similar way. Simultaneous video and sound recordings were made with one bat at a time flying in the flight cage. We started the observations in the flight cage at the main activity time of the bats, around 1930 hours local time and stopped when the bats activity level dropped, usually between midnight and 0200 hours. The data presented were obtained on six different nights. The flight cage was situated in the rainforest interior and has a natural light regime. Observations were conducted in the dark with infrared illumination.

Video recording

Behavior of the animals in the flight cage was videotaped (Orion Combi 600 LCD recorders) with CCD video cameras (Sanyo, VC 1950; 50 half-frames/s) under stroboscopic infrared illumination in temporal synchrony with sound recordings. Synchronization was achieved by writing a sync-signal into the sound recording memory array for every video frame. Additionally, a video-time code (VITC-code) was written into the video frames (electronics custom-made; Department of Animal Physiology, University of Tübingen). Video sequences were digitized (HaSoTec, Fledermaus 1.5) and the bat behavior was analyzed frame by frame with a time resolution of 20 ms.

Statistics

Statistics were calculated using Excel 97 for Windows and Systat 7.0 for Windows. For statistical comparison of calls emitted in different situations, call parameters were averaged for each search sequence or for each sub-phase of approach sequence; i.e., only one data point per sequence or sub-phase was used in order to minimize possible effects of pseudoreplication inherent to many field studies of bat echolocation. Because the sequence-wise means of the call parameters were not normally distributed in all cases (Kolmogorov-Smirnov test under Lilliefors adaptation, $P<0.05$), non-parametric statistics (Mann-Whitney U-test and Kruskal-Wallis test; significance level $P<0.05$) were used to compare the data sets of means. For analysis of the flight cage recordings, each of the three bats contributed similar amounts of data (two search sequences with ten calls each per individual from 2 nights and three to four approach sequences from 2 nights). We did not compare the call parameters between the sub-phases (initial approach, buzz 1, buzz 2) of the approach sequence statistically, because categorization of calls into sub-phases was not independent of call parameters. In the Results section, data are given as the mean±SD.

Results

Field studies

Search and prey capture behavior

Peak flight activity of *M. nigricans* was observed between 1 and 3 h after dusk, i.e., between 1930 and 2130 hours local time. In the two edge-and-gap situations, the bats flew on ellipsoid flight paths at distances of about 2–5 m from the vegetation. In the open-space situation, the bats flew straight through the clearing, mostly between 10–15 m above ground and at least 5 m from the surrounding forest edge. When pursuing and capturing prey, the bats frequently deviated from their search flight trajectory, typically heading downward to intercept the target. We never observed *M. nigricans* in slow or hovering flight close to vegetation and we did not see it gleaning prey from substrates.

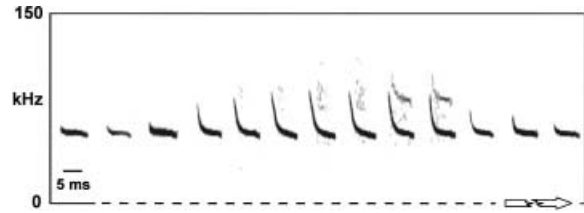#### *Search calls in edge-and-gap situations versus open space*

M. nigricans broadcasts downward-frequency-modulated echolocation signals (Fig. 1 a, b). The average call of an edge-and-gap sequence showed larger bandwidth than
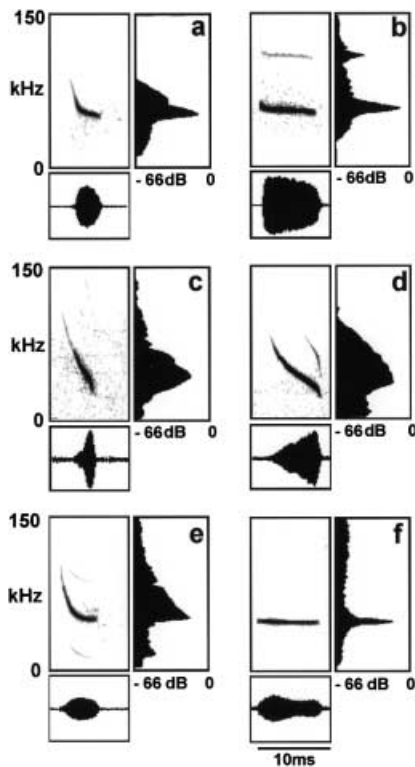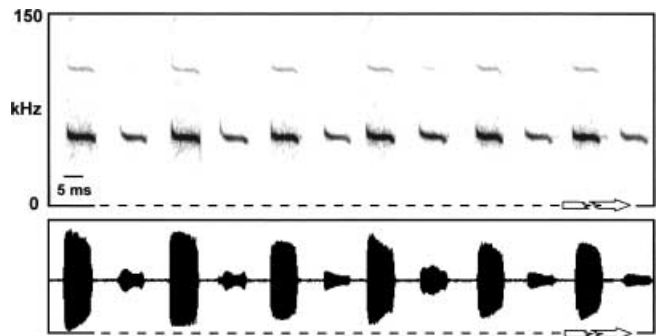
Fig. 1 Sonagrams, averaged power spectra, and time signals of typical search calls broadcast in edge-and-gap situations (*left columns*) and in open space (*right columns*) for *Myotis nigricans* (**a,b**), *M. brandtii* (recorded in Höhreute, southern Germany) (**c,d**),and from *Pipistrellus pipistrellus* (recorded in Mössingen, southern Germany) (**e,f**). *M. nigricans*, *M. brandtii*, and *P. pipistrellus* are of roughly similar size. The *M. brandtii* open-space call (**d**) shows the typical sigmoidal frequency time course seen in many *Myotis* search signals, including an initial steep, middle shallow, and terminal steep component. All open-space calls shown here are about 7 ms long. However, *M. nigricans* (**b**) and *P. pipistrellus* (**f**) broadcast calls of ≤10 kHz bandwidth in open space, whereas the representative *M. brandtii* call has a bandwidth of 65 kHz (**d**). High bandwidth in edge-and-gap calls is achieved by adding an initial broadband component to the shallow element in *M. nigricans* (**a**) and *P. pipistrellus* (**e**), whereas *M. brandtii* (**c**), in addition to increasing starting frequency, increases modulation rate in all three signal components. Thus, in both bandwidth and frequency time course, the search signals of *M. nigricans* (**b**) resemble *Pipistrellus* search calls (**f**) more closely than those of many temperate *Myotis* (e.g., **d**)

Fig. 2 Call sequence in sonagram representation of an individual *M. nigricans* flying from open space into an edge-and-gap situation and back into open space, showing the gradual transition of search call structure. Note that pulse intervals have been cut out!

Fig. 3 Representative *M. nigricans* call sequence from open space in sonagram and oscillogram representation. The amplitude of subsequent calls alternated in a distinct pattern between strong and faint. Note that pulse intervals have been cut out!

*Alternating pulse amplitude in open space*

In all 20 sequences that we analyzed for the open-space situation, the amplitude of adjacent calls alternated in a distinct pattern between strong and faint (133 of 153 subsequent call pairs; Pearson χ^2: $P<0.0001$, 1 df. We defined a sequence to begin with the strongest of the first two calls, and calculated amplitude differences between call 1 and 2, 3 and 4, and so on, for each sequence. The first call pair of each sequence was excluded from statistical analysis because the amplitude of the first call was not independent of our definition of the beginning of a sequence. Example in Fig. 3). All recordings were made from the ground with the bats passing between 5–20 m above the microphone, which pointed straight upward (90° to ground). Amplitude differences between succeeding signals ranged from 0.1 to 47 dB. We found a systematic change in amplitude difference in association with the bats' proximity to the microphone in most sequences, when using the absolute amplitude of the stronger call of a pair as a measure of distance of the bat to the microphone (Fig. 4). In our edge-and-gap recordings and in the flight cage recordings, amplitude alternations were less distinct.

Calls while approaching and capturing prey

As a general pattern, bandwidth of the first harmonic was high in the initial approach sequence and in buzz 1
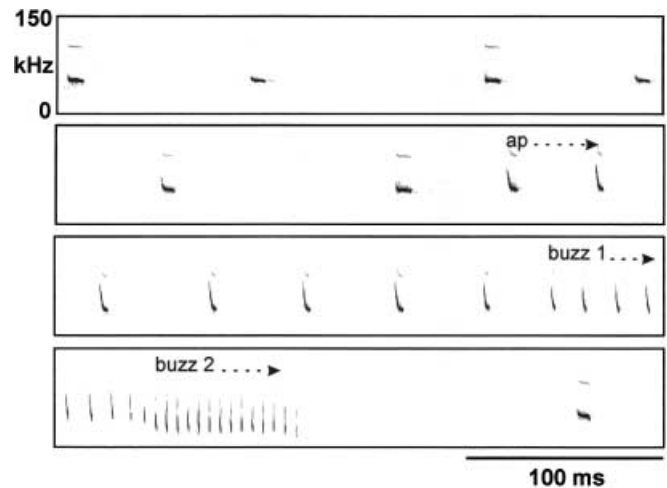
the average call of an open-space sequence ($P<0.0001$; Mann-Whitney *U*-test; 25 edge-and-gap and 20 open-space sequences), largely due to a higher starting frequency (Table 2, Fig. 1). Pulse duration and pulse interval were significantly shorter in edge and gap than in open space (Table 2). Bandwidth of open-space calls averaged 10.6±2.0 kHz and reached lowest values around 4 kHz. When flying from open space into an edge-and-gap situation and back, individual *M. nigricans* gradually changed their echolocation calls from the typical shallow-modulated open-space call to the broadband signal structure observed in edge-and-gap situations and back again (Fig. 2).

	Open space	Edge and gap	Mann-Whitney U	Flight cage
Starting frequency (kHz)	61.5±2.3 (55.5–84.4)	95.4±4.7 (76.9–110.2)	$P<0.0001$	111.1±5.7 (96.4–120.7)
Peak frequency (kHz)	54.2±0.4 (51.7–61.1)	55.0±1.2 (51.4–65.6)	$P<0.05$	57.4±0.9 (54.0–68.2)
Terminal frequency (kHz)	50.9±0.6 (48.0–54.0)	51.6±1.1 (47.6–56.2)	$P<0.05$	50.3±1.5 (46.9–54.0)
Pulse duration (ms)	7.2±0.3 (5.8–8.1)	4.3±0.5 (2.5–6.3)	$P<0.0001$	2.2±0.3 (1.3–2.9)
Pulse interval (ms)	106.2±11.2 (70.4–241.2)	67.6±13.1 (30.5–219.8)	$P<0.0001$	53.7±6.7 (41.5–79.7)
Number of calls (sequences) analyzed	372 (20)	430 (25)		60 (6); 1/3 from each of the three bats
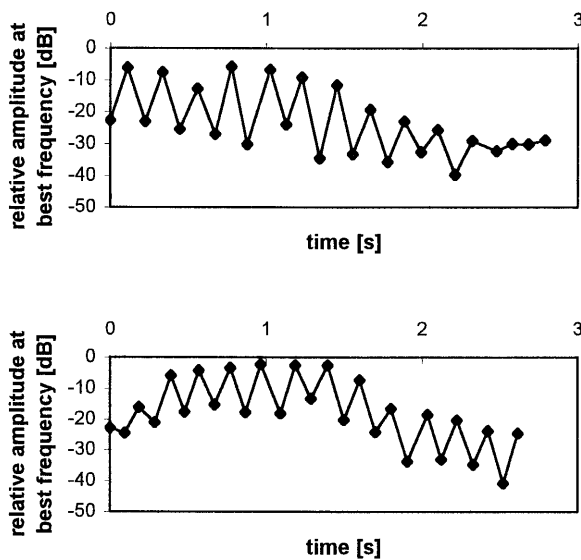
Fig. 4 In open-space search sequences, the difference between a strong and the subsequent faint call often changed systematically with the amplitude of the strong call; i.e., with proximity of the bat to the microphone. This pattern is in accordance with the hypothesis that when hunting in open space, *M. nigricans* scans its environment with head movements

Fig. 5 Example of a call sequence recorded during prey capture in open space. The transition from search phase to approach phase (*ap*) is clearly marked by an increase in bandwidth. At the end of the approach phase, *buzz 1* and *buzz 2* can be distinguished

and was reduced in buzz 2 (Fig. 5, Table 3). Terminal frequency decreased slightly from initial approach sequence to buzz 1 and then dropped sharply at the onset of buzz 2. The second, and sometimes also the third, harmonic became apparent in buzz 2 (Fig. 5). Pulse length and pulse interval decreased throughout the approach sequence and showed nearly constant minimum values in buzz 2 (Fig. 5, Table 3). Before the bats started emitting search calls again, they paused on average 110–120 ms after buzz 2. In edge-and-gap situations, initial approach calls were somewhat shorter and had lower terminal frequencies (Table 3). Buzz 1 and buzz 2 calls from the two situations, however, were similar in frequency parameters and especially in pulse duration and pulse interval.

Flight cage observations

Search and prey capture behavior

On the first night, the bats were released together. They immediately started to explore the 4×4.5 m flight cage. They spent much time on the wing, but they did not attack the tethered mealworms. On the second night in captivity, they readily approached and caught the tethered mealworms. They also repeatedly attacked tethered plastic prey dummies and apparently mistook them for prey. On 2 consecutive nights, two individual bats attacked the dummies 99 and 108 times, respectively. The bats never tried to glean mealworms or the tailless whip-scorpions (Arachnida: Amblypygi) that crawled on the floor and the walls of the flight cage. They only performed aerial catches. Prey was caught with the inter-femoral membrane and then taken with the mouth (*n*=10; Fig. 6a). In search flight, wingbeat rate varied between 10–15 Hz, as determined from video sequences (*n*=10).

Table 3 Call parameters summarized for the three sub-phases of approach phase recorded from *M. nigricans*, with, in the last two rows, the number of calls per sub-phase and sub-phase length. While closing in on the target, the animals shortened the pulse duration and pulse interval; starting and peak frequency dropped sharply in buzz 2 (only the first harmonic is considered here). To minimize pseudoreplication in a statistical comparison between approach phase calls in open space, edge and gap, and the flight cage, call parameters were averaged for each call sequence and the three data sets of means were subjected to Kruskal-Wallis tests. Data are represented by the mean±SD of the averaged sequences and the range (minimum–maximum) of the whole, unaveraged data set with *P*-values for the Kruskal-Wallis test (significance level: *P*<0.05) (*OS* open space, *EG* edge and gap, *F* flight cage)

	Initial approach phase	Buzz 1	Buzz 2
Starting frequency (kHz)	OS: 94.2±8.1 (81.4–111.1) EG: 99.5±6.0 (82.1–114.0) F: 106.6±4.6 (91.1–116.2) *P*<0.01	OS: 92.4±6.2 (66.4–109.9) EG: 93.8±9.2 (66.4–112.9) F: 104.1±5.7 (80.9–114.0) *P*<0.01	OS: 53.2±4.5 (41.2–84.4) EG: 50.0±5.8 (30.7–92.6) F: 47.3±3.1 (31.1–89.6) *P*=0.1545
Peak frequency (kHz)	OS: 56.0±1.0 (53.6–61.5) EG: 55.6±1.5 (51.4–63.0) F: 56.6±1.3 (52.9–60.7) *P*=0.2054	OS: 57.2±1.0 (45.4–63.4) EG: 56.8±4.7 (46.9–70.5) F: 56.3±1.4 (51.0–62.6) *P*=0.3862	OS: 37.2±1.6 (31.9–45.4) EG: 36.6±2.8 (22.8–55.1) F: 34.6±1.4 (25.9–54.4) *P*=0.0509
Terminal frequency (kHz)	OS: 53.2±1.1 (49.5–)57.4 EG: 50.5±0.8 (44.4–55.1) F: 46.5±0.5 (42.4–51.0) *P*<0.0001	OS: 47.9±3.0 (37.5–57.4) EG: 44.0±1.5 (37.1–53.2) F: 43.4±1.5 (36.4–47.6) *P*<0.05	OS: 26.4±1.3 (22.5–33.4) EG: 24.4±1.2 (18.7–36.0) F: 20.6±1.0 (15.4–36.0) *P*<0.001
Pulse duration (ms)	OS: 4.4±0.6 (2.0–6.0) EG: 3.1±0.8 (1.4–7.0) F: 1.6±0.3 (0.9–3.0) *P*<0.0001	OS: 1.2±0.2 (0.4–2.2) EG: 1.2±0.4 (0.4–2.8) F: 1.1±0.2 (0.6–1.5) *P*=0.3309	OS: 0.5±0.1 (0.2–0.9) EG: 0.5±0.1 (0.2–1.1) F: 0.6±0.1 (0.3–1.0) *P*<0.01
Pulse interval (ms)	OS: 56.0±12.4 (16.5–67.0) EG: 40.2±3.6 (20.0–63.7) F: 32.9±3.8 (18.6–63.1) *P*<0.0001	OS: 10.6±0.9 (5.5–16.04) EG: 11.9±2.2 (6.5–28.5) F: 14.2±1.3 (7.8–20.0) *P*<0.05	OS: 5.4±0.1 (5.1–5.8) EG: 5.5±0.2 (5.0–7.9) F: 5.4±0.2 (4.9–9.4) *P*=0.4440
Pause after buzz 2 (ms)			OS: 119±40 (83–166) EG: 111±58 (30–240) F: 192±82 (117–392) *P*<0.01
Number of calls (sequences) analyzed	OS: 33 (4) EG: 71 (10) F: 126 (10)	OS: 32 (4) EG: 86 (10) F: 49 (10)	OS: 53 (4) EG: 175 (10) F: 213 (10) from three bats
Number of calls per sub-phase	OS: 8.3±1.5 (7–9) EG: 7.1±4.9 (2–16) F: 13.3±4.9 (5–18) *P*<0.05	OS: 8±1.4 (6–9) EG: 8.6±9.0 (3–33) F: 4.9±0.9 (3–6) *P*=0.4968	OS: 13.3±1.5 (11–14) EG: 17.5±8.4 (9–38) F: 20±5.8 (11–30) *P*=0.1176
Sub-phase length (ms)	OS: 438±181 (284–405) EG: 263±210 (44–683) F: 429±169 (165–627) *P*=0.1236	OS: 80±21 (53–98) EG: 102±132 (25–467) F: 60±15 (31–84) *P*=0.0702	OS: 66±8 (54–71) EG: 91±47 (43–209) F: 110±25 (68–152) *P*<0.05

The bats reduced flight speed before capture. Wingbeat rate increased to 12–16 Hz about 1 m prior to touching prey (*n*=6).

Echolocation

Search calls were recorded while the bats were circling in the flight cage when no prey was presented. On average, these calls were 2.2 ms long and covered a bandwidth of 61 kHz (Table 2). Terminal and peak frequency were similar to those of the field recordings (Table 2). The pulse interval was about 54 ms. Thus, the bats typically emitted two calls per wingbeat in search flight in the laboratory.

Approach sequences in the flight cage (Fig. 6b) were similar to those recorded in the field, although some small but significant differences between approach sequences in open space, edge-and-gap situations, and the flight cage were found (Table 3). Terminal frequency was lower in the flight cage than in the field in all three sub-phases. At the beginning of the approach phase, pulse duration and pulse interval were lower in the flight cage than in the field. Synchronized sound and video recordings showed that the bats stopped emission of buzz 2 one to two half-frames (i.e., 20–40 ms) before touching prey (*n*=7; example in Fig. 6).

Discussion

We found *M. nigricans* foraging in two different habitat types. As expected, the search calls differed between

Fig. 6a,b Example of prey capture in the flight cage. **a** Flight path redrawn from video images. The bat captures a mealworm (*m*) in the uropatagium (*arrow*) and retrieves it with the mouth. Video half-frames are numbered consecutively. A half-frame was taken every 20 ms. **b** Call sequence recorded in temporal synchronization with **a**. Numbers correspond to bat's position in **a**
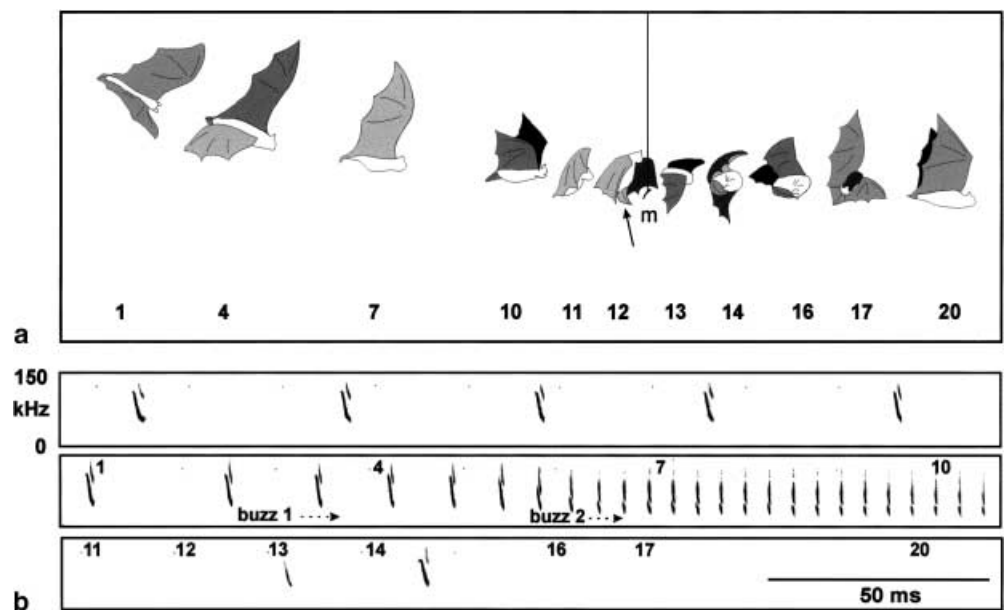
open-space and edge-and-gap situations. In addition, signal structure and pattern changed in a characteristic way during approach and (attempted) capture of prey.

M. nigricans adapted search call parameters to habitat type

In edge-and-gap situations, *M. nigricans* broadcast short, broadband search signals, whereas in open space, it used longer and more shallowly modulated search calls. Clearly, ground recordings of high-flying bats have to be interpreted with caution (Jensen and Miller 1999) because some signal information might be lost due to atmospheric attenuation. However, the narrow bandwidth of the search signals of *M. nigricans* emitted in open space is unlikely to be a recording artifact, because even in calls with a very good signal-to-noise ratio, no broadband signal component was detectable (see Fig. 3 for an example). A bat, by definition, forages in "uncluttered space" when it does not react to background targets by changing call parameters in its echolocation behavior (Schnitzler and Kalko 1998). *M. nigricans* only reacted to the background by increasing bandwidth and shortening pulse duration (to below the average 7.2 ms; Table 2) when approaching vegetation or the ground about as close as 5 m. Thus, our definition of "open space" for foraging *M. nigricans* (>5 m of background) indeed corresponds to "uncluttered space" in the above sense for this bat species. This transition distance is equal to that found for similar-sized *Pipistrellus* spp. that use open-space search signals of similar duration (Kalko and Schnitzler 1993), but is smaller than the 8–10 m "critical flight altitude," at which the four- to fivefold heavier *Eptesicus serotinus* starts reacting acoustically to the ground (while using 12-ms-long signals; Jensen and Miller 1999). Bats are thought to keep an overlap-free

window open between the emitted signal and returning clutter echoes by shortening pulse length when searching closer to the background to increase the chance of prey detection (e.g., Kalko and Schnitzler 1993; Schnitzler and Kalko 1998).

Typically, insectivorous bats emit short, broadband calls in cluttered environments and longer, narrowband calls in uncluttered space (for reviews see Neuweiler 1989, 1990; Fenton 1990; Schnitzler and Kalko 1998; Schnitzler and Kalko, in press). This is in accordance with the hypothesis that short, broadband calls improve the discrimination of prey from background targets (e.g., vegetation) and the characterization of background targets, whereas long, narrowband calls are well suited for detection of targets (reviewed in Schnitzler and Kalko 1998). In addition, long, narrowband signals are well suited to deliver some flutter information, i.e., "acoustic glints," imprinted onto the echoes by fluttering insects (reviewed in Moss and Schnitzler 1995). The duty cycle (percentage of time in which signals are emitted) of *M. nigricans* in open space was $7.0\pm0.7\%$ (*n*=20 sequences with 352 calls). Assuming a prey wingbeat frequency of 100 Hz, a bat would on average perceive 7 glints/s (duty cycle×prey wingbeat frequency), i.e., nearly 1 glint per pulse. This rather high average perceived glint rate is similar to that expected for other vespertilionids hunting in open space (Schnitzler 1987). Acoustic glints might increase the distance at which an insect can be detected by increasing the echo amplitude.

We conclude that the long, narrowband signals of *M. nigricans* are well adapted to open-space foraging. We assume that *M. nigricans* makes more use of open space than most of its temperate congeners (Table 1). However, owing to the variability in its signal design, *M. nigricans* is also perfectly capable of aerial foraging with short, broadband signals in edge-and-gap situations and even in the cluttered environment of a flight cage.

Alternating search call amplitude in open space: evidence for scanning movements?

In our open-space recordings, the amplitude of subsequent search calls alternated in a distinct pattern between strong and faint. We hypothesize that the observed pattern does not reflect changes in the emission level, but is, instead, an effect of head movements made by the bat to scan its environment during search flight. We assume that the bats move their heads during search flight in a regular manner, thereby emitting one call toward the microphone, one away, and so forth. Depending on the direction of call emission by the bat and on the direction of the microphone, one would expect a systematic change in amplitude difference in association with the bats' proximity to the microphone, as we indeed found. The alternation of emission level without head movements seems a less probable alternative explanation, because it would result in a constant amplitude difference between strong and faint calls, irrespective of the bats' position relative to the microphone.

Scanning movements can be advantageous for a bat hunting in open habitat, by enlarging its search volume. This holds especially true for bats using comparatively high call frequencies with high directionality, like *M. nigricans*. Scanning movements are known from perch-hunting rhinolophids (e.g., Jones and Rayner 1989), and are suggested for *Lasionycteris noctivagans* (Barclay 1986), *Pipistrellus* sp. (Kalko 1995a), and *E. serotinus* (Jensen and Miller 1999) on the basis of alternating pulse amplitude.

Prey capture in active mode

In the flight cage, the animals performed aerial catches; they did not show any gleaning attempts. This fits well with our field observations and corroborates our hypothesis that *M. nigricans* is an aerial-foraging species. In contrast, many temperate *Myotis* habitually glean prey from vegetation and the ground or trawl prey from water surfaces (e.g., Thompson and Fenton 1982; Jones and Rayner 1988; Kalko and Schnitzler 1989; Jones and Rayner 1991; Schumm et al. 1991; Miller and Treat 1993; Faure and Barclay 1994; Arlettaz 1996a, 1996b; Britton et al. 1997; Swift 1997). As *M. nigricans* captured silent, non-moving tethered mealworms and plastic dummies in the dark, we assume that they can perceive prey by echolocation alone; i.e., in active mode. Passive acoustic, visual, or flutter cues ("acoustic glints," see above) were not necessary for prey perception under flight cage conditions. This does not preclude, however, that such cues are used in some situations in the field. We conclude that the freshly caught animals in our experiments took any airborne reflector of a certain (small) size as potential prey as long as they could separate it from background.

When approaching and capturing prey, *M. nigricans* produced an approach sequence typical for aerial hawk-ing vespertilionids that localize prey by echolocation during the approach (e.g., Griffin et al. 1960; reviewed in Kalko and Schnitzler 1998). Very short and broadband calls are generally accepted to provide good localization of a target and the high repetition rate is thought to provide good temporal resolution for tracking prey (e.g., Simmons and Stein 1980; Neuweiler 1990; Kalko and Schnitzler 1998). A clearly subdivided buzz, as in *M. nigricans*, is found in many other *Myotis* species (e.g., Kalko and Schnitzler 1989; Jones and Rayner 1991; Surlykke et al. 1993; Siemers and Schnitzler 2000) and in European pipistrelles (Kalko 1995a), whereas this subdivision is less conspicuous or lacking in other bat genera.

"Vocal plasticity"

Convergent evolution of similar echolocation inventories by bats using similar niches is known from several examples and suggests rigid physical constraints on echolocation in animals (e.g., Schnitzler and Henson 1980; Fenton 1990; Neuweiler 1990; Surlykke et al. 1993; Schnitzler and Kalko 1998; Schnitzler and Kalko, in press). According to the "vocal-plasticity hypothesis," species call inventories evolved from an unknown ancestral inventory under the selective pressure of specific ecological conditions (Schnitzler et al., in press). This hypothesis assumes that the anatomical structures and physiological processes underlying signal generation are, in an evolutionary perspective, highly flexible, presumably permitting fast evolutionary change. Below, we first explore the divergence of the signal inventory of *M. nigricans* from those of most other *Myotis*. We then address convergence in signal structure that we, based on the aforementioned studies, expect to find, by comparing small vespertilionids with similar ecologies (aerial feeding) both within and outside the genus *Myotis*.

Comparison within the genus *Myotis*

The echolocation behavior of *M. nigricans* differs in one main respect from those of most of the hitherto studied *Myotis*: the search calls we recorded in open space are of very narrow bandwidth in comparison to those of other *Myotis* (Table 1). Many other *Myotis* species produce broadband signals with changing steepness, i.e., with a sigmoidal frequency-time course (Jones and Rayner 1991), even when flying in open space (e.g., *M. brandtii*; Fig. 1d). The example in Fig. 1d depicts this sigmoidal call type with an initial steep component, a middle, more shallowly modulated component, and a steep final element. All known signal inventories of *Myotis* species, including intra- and interspecific signal plasticity, can be derived from this basic, sigmoidal type by changing duration and bandwidth of the three components.

Looking at the differences in habitat use and echolocation behavior within *Myotis*, the genus forms a contin-

uum of adaptations to various ecological constraints. On one side are the species of "subgenus"/ecomorph *Myotis* that are adapted to forage in narrow space and to glean prey from vegetation (Table 1). They use very short, broadband signals (Table 1), where the middle, shallowly modulated component is lacking, to detect prey very close to vegetation by echolocation (Siemers and Schnitzler 2000) or for spatial orientation, while they rely on passive acoustic cues to perceive prey in clutter (e.g., Faure and Barclay 1994).

At the other end of the continuum, we find species adapted to open-space foraging such as *M. siligorensis* from Thailand (Surlykke et al. 1993; data summarized in Table 1) and *M. nigricans*, both grouped into the "subgenus" *Selysius*. They broadcast longer, narrowband signals in open space, with a prominent shallow component in the middle and vestigial initial and final steeper components. The open-space calls of *M. siligorensis* are somewhat shorter in duration than those of *M. nigricans* (5.4 ms as opposed to 7.2 ms). Because *M. siligorensis* (2.3–2.6 g; Surlykke et al. 1993) is smaller than *M. nigricans* (4.3 g; Kalko et al. 1996), this fits well with the general rule that pulse duration scales with body mass within those Vespertilionidae that produce narrowband signals (Jones 1999). The similarities in open-space search calls of *M. siligorensis* and *M. nigricans* are also likely the result of convergent or at least parallel evolution within the genus *Myotis*, and are not indicative of a close phylogenetic relationship between the two species (Ruedi and Mayer 1999, personal communication). The European representatives of *Selysius* use a broadband signal even in open situations (Table 1, Fig. 1d), and we thus assume that they are not especially adapted to open-space foraging. In contrast, some North American *Selysius* species sometimes show calls of lower bandwidth (Table 1). Based on our data on *M. nigricans*, we would predict that these species also show extensive open-space foraging.

Other *Myotis* species forage at low heights over water ("trawling bats") in relatively fast flight and are attributed to a third "subgenus"/ ecomorph *Leuconoë*. They use search calls of intermediate bandwidth and duration (Table 1). As an exception, signals of 10-kHz bandwidth or less have been reported for *M. dasycneme* when foraging far from the shore (Britton et al. 1997). Smooth water surfaces reflect little clutter echo when ensonified from an acute angle (Boonman et al. 1998) and are thus acoustically comparable to open space, when echo-cluttering river banks and other structures are far from bat and prey. In this situation, narrowband signals are well suited for prey detection (Schnitzler and Kalko 1998). Interestingly, calls of low bandwidth have also been found in two Neotropical *Leuconoë* species that are suggested to be mainly aerial-feeding and hence not trawling bats (*M. riparius* and *M. ruber*: Fenton et al. 1999; data summarized in Table 1).

Convergence in signal design and foraging behavior with pipistrelle bats

We find many similarities in foraging behavior, flight style, and habitat use of *M. nigricans* and European pipistrelles, which also hunt in edge-and-gap and in open habitats (Kalko and Schnitzler 1993; de Jong 1995; Vaughan et al. 1997b). Most European pipistrelles are similar in size to a little bigger than *M. nigricans* (Schober and Grimmberger 1998). European pipistrelles and *M. nigricans* belong to two different genera of vepertilionid bats. Based on the "vocal plasticity hypothesis," we expect similarities in echolocation behavior to have evolved convergently under these similar ecological constraints. Indeed, pipistrelles use narrowband signals in open space (Kalko and Schnitzler 1993; example in Fig. 1f) that are similar in duration, bandwidth and, for similar-sized *Pipistrellus* species, even in peak frequency to those of *M. nigricans*. Much like *M. nigricans*, pipistrelles shorten pulse duration and introduce an initial broadband signal component when within 5 m of vegetation (Kalko and Schnitzler 1993; example in Fig. 1e). As in *M. nigricans*, there also is evidence for scanning movements in *Pipistrellus* when foraging in the open (Kalko 1995a).

However, whereas the Neotropical *M. nigricans* strongly resembles pipistrelle bats in its echolocation behavior and habitat use, temperate-zone *Myotis* living sympatrically with pipistrelle bats show distinct differences. For example, in European bat communities, pipistrelles generally forage further from substrate than sympatric *Myotis* species. Pipistrelles perform aerial catches (Kalko 1995a) in contrast to many *Myotis* that glean prey from surfaces (Table 1). In Neotropical communities, *M. nigricans* exploits a niche similar to that of (European) pipistrelles. As the genus *Pipistrellus* is absent south of Honduras, which corresponds roughly to the northern distribution limits of *M. nigricans* (Koopman 1993; Reid 1997), it is suggestive to assume ecological vicariance between the two taxa. To explore this suggestion, further information will be required on the foraging behavior of the two (North) American *Pipistrellus* species (whose generic status is under debate; J. Gaisler, personal communication).

M. nigricans has to share its aerial hunting habitat with many other bat species in the Neotropics, specifically from the families Vespertilionidae (i.e., *Eptesicus*, *Lasiurus*) and Emballonuridae (i.e., *Centronycteris*, *Cormura*, *Peropteryx*, and *Saccopteryx*), the latter using echolocation calls of quite different structure (e.g., Kalko 1995b; Kalko et al. 1996). In the Neotropics, gleaning insectivorous bats of the family Phyllostomidae producing multiharmonic frequency-modulated calls use niches similar to those of European *Myotis* (e.g., Kalko et al. 1996). It would be most interesting to study the foraging and echolocation behavior of the remaining *Myotis* species that occur in Central and South America (at least 18 more species, mostly attributed to the *Selysius* and *Leuconoë* types; Koopman 1993) to see how they fit into the

local communities of bat species within the species-rich Neotropics.

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