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Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico

J. Rydell[1]*, H. T. Arita[2], M. Santos[2], and J. Granados[2]

[1] Zoology Department, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden
[2] Instituto de Ecología, Universidad Nacional Autónoma de Mexico (UNAM), Apartado Postal 27–3 (Xangari), CP 58089 Morelia, Michoacán, Mexico

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Abstract

The echolocation calls of insectivorous bats of the northern Yucatan Peninsula, Mexico, with the exception of the phyllostomids and molossids, are presented. The aim is to provide a catalogue of bat sounds that can be used for acoustic inventories of insectivorous bats using the Pettersson heterodyne and time-expansion bat detectors. The acoustic method can be used alone or in combination with inventories based on mist-netting, a method more suitable for the low-intensity echolocators (mainly the phyllostomids), which are difficult to monitor acoustically. The insectivorous species of the Yucatan are generally easy to identify by their echolocation calls, particularly when combined with visual observations of foraging bats at dusk.

Key words: conservation, echolocation, inventories, tropics, ultrasound, insectivorous bats

INTRODUCTION

The bats (order Chiroptera) usually comprise 40–50% of the mammalian species in tropical habitats, and hence constitute a considerable and important component of the biodiversity (Findley, 1993; Voss & Emmons, 1996). Neotropical bat communities are particularly diverse, containing up to 70 species and including all types of diets and functional roles (Simmons & Voss, 1998). Recent research has shown that bats are suitable to be used as indicator species to document habitat disturbance in Neotropical forest areas (Fenton, Acharya *et al*., 1992; Moreno & Halffter, 2000).

Diversity of neotropical bats is traditionally monitored by mist-netting, as this method is reasonably efficient for detecting gleaning species and other low-intensity echolocators, such as frugivores, nectarivores, sanguivores and some phyllostomid insectivores (Kunz & Kurta, 1988). However, the method is relatively inefficient in the case of aerial insectivores, particularly emballonurids, molossids and most vespertilionids. Aerial insectivores therefore tend to be underrepresented in most bat surveys based on mist-netting. However, because most aerial insectivores forage by using high-intensity echolocation calls, they can be identified and monitored with relative efficiency by acoustic methods. A combination of the traditional mist-netting procedure and the use of ultrasound detectors seems to be the best strategy to estimate and monitor tropical bat diversity (Rautenbach, Fenton & Whiting, 1996). The use of echolocation calls to conduct inventories of insectivorous bats in the Neotropics is hindered at present by a poor knowledge of the details and the variation in the echolocation calls of most species.

The purpose of this work is to present an acoustic library of the aerial insectivorous bats known to occur in the state of Yucatan, Mexico (Arita, 1997), thereby facilitating acoustic inventories of bats in this and neighbouring areas. In this paper we include insectivorous species except the six species of molossids (*Molossus ater, Molossus sinaloe, Nyctinomops laticaudatus, Eumops glaucinus, Eumops bonariensis* and *Promops centralis*, see Bowles *et al*., 1990). The molossids are high-flying bats that use highly variable echolocation calls. They will be treated separately.

MATERIALS AND METHODS

Study sites

Most recordings and observations of bats were made in the vicinity of Mérida, northern Yucatan, during 7 10-day sessions in 1997–1999, covering both the wet- and

*All correspondence to: Jens Rydell.
Email: jens.rydell@zool.gu.se

the dry season. The Yucatán Peninsula consists of a flat limestone plateau, typically containing caves, water-filled sinkholes ('cenotes') and other features of a karstic terrain. The habitat around Mérida is dry, deciduous woodland mixed with agricultural patches (Arita & Vargas, 1995; Arita, 1996, 1997). Recordings were made near cenotes or along trails and in openings in the woodland and also in parks or over swimming-pools in the city of Mérida.

With the exception of *Natalus stramineus* and *Mormoops megalophylla* all species were recorded as they foraged unconstrained in their natural habitats. *Natalus stramineus* emits echolocation calls of such a low intensity that we were unable to record or even detect them acoustically in outdoor settings, although we observed them visually. This species was recorded as single individuals flying either inside the hotel room (measuring *c.* 5 × 4 × 2.5 m) or in a larger (*c.* 10 × 5 × 4 m), straw-roofed building situated in the Botanic Garden of the Center for Scientific Research (CICY) in Mérida.

In addition to the recording from Mérida and vicinity, observations and recordings of *Peropteryx macrotis* were also made in the vicinity of Ticum and Oxkutzcab, located in the Sierra de Ticul in the southern part of the state of Yucatan. Also *M. megalophylla* and *N. stramineus* were recorded as several individuals flew inside a cave 1.5 km south of Hoctún, *c.* 35 km east of Mérida (see Arita, 1996 for a description of the site). Additionally we observed and recorded *Rhogeessa aeneus* around a light post over a forest trail and *Pteronotus davyi* and *Pteronotus parnellii* at a country road lit by orange streetlights near Akumal in the state of Quintana Roo in the eastern part of the Yucatan Peninsula 2–15 January 1996.

Capture and measurements

Bats were captured in mist-nets set over water holes, near roosts in caves or in their feeding places. They were identified to species using Medellin, Arita & Sánchez (1997) and Reid (1997). The data presented here are from individuals that were recorded immediately before or after they had been captured and identified to species, and whose foraging behaviour had been observed continuously in the meantime. All captured individuals were sexed, weighed to the nearest 0.1 g with an electronic, portable balance, and forearms (FA) were measured to the nearest 0.1 mm with an electronic caliper. A silhouette of each individual was drawn and used to measure the wing area by means of a digital planimeter. Wing-morphology parameters were then derived following Norberg & Rayner (1987): wing loading (WL; mass × gravity / wing and body area, in N/m^2) and aspect ratio (AR; wing span^2 / wing area), and are presented as means of the individuals caught. Bats were not marked and handling was restricted to what was necessary for identification and measurements. Individuals were released immediately. Weight data are presented as means for males and non-pregnant females.

Recording and sound analysis

Bats were recorded using bat detectors D960 and D980 (Pettersson Elektronics, Uppsala, Sweden), which are equipped with digital memories (0.75 and 3.0 s for the 2 versions, respectively), permitting time-expanded (10 ×) recodings that retain the full harmonic content of the original signal. The recordings were stored on a Sony Walkman Professional or a TC D-5 M tape recorders. The recordings were analysed with Bat Sound software (Pettersson Elektronics, Uppsala, Sweden) at a sampling rate of 44 100 Hz and a Hanning window. FFT size was 512 for sonagrams and 4096 for power spectra.

The echolocation data were analysed and are presented sequence by sequence, each sequence representing an independent recording (usually a different site except for the indoor recordings of *N. stramineus*). This illustrates the variation between: (1) individuals; (2) recording situations (e.g. the distance between the bat and the microphone); (3) adaptive variation related to foraging habitats, such as distance to obstacles and amount of acoustic clutter (e.g. Rydell, 1990; Kalko & Schnitzler, 1993; Obrist, 1995).

RESULTS

Peropteryx macrotis

Single individuals of this small (FA = 44.2 mm, mass = 6.1 g, *n* = 10), but fast-flying (WL = 5.9 N/m^2, AR = 7.6), cave-dwelling emballonurid was observed foraging 2–10 m above the ground around tree canopies in farmland habitats, along trails and other openings in forest and in gardens. The echolocation calls are always short (5–9 ms) but intense CF-pulses, that usually start and/or end in shallow down-sweeps. Most energy is in the second harmonic at *c.* 38–40 kHz (Table 1, Fig. 1), when bats fly alone. When they hunt in small groups, however, the CF-frequency shifts by *c.* 2 kHz up or down (sequence 7). In straight flight the pulse repetition rate is usually regular at *c.* $7\,s^{-1}$, but sometimes lower (by a factor of two or three) or higher, and, because the pulse duration remains about the same, the duty cycle becomes highly variable. Individuals released from hand flew away quietly and only started to echolocate as they began to forage.

Mormoops megalophylla

This medium-sized (FA = 53.4 mm, mass = 14.8 g, *n* = 11), fast-flying (Bateman & Vaughan, 1974; WL = 8.3 N/m^2, AR = 7.2) species was recorded in the large room (sequence 1–2), in the hotel room (sequence 3–5) and also inside a cave (sequence 6). We have been unable to obtain any good outdoor recordings of this species. In all our recordings it used short (3–4 ms) pulses of high intensity. The pulses are very characteristic of the species; they are curved down-sweeps, which

Table 1. *Peropteryx macrotis*. Characteristics (mean ± SD) of search pulses recorded from bats foraging alone at 5–10 m altitude around the canopy of trees (sequence 1–4), at 2 m along a trail in forest (sequence 5–6), and among other individuals in a city garden (sequence 7). Two sequences represent bats flying in non-foraging situations: exiting from a cave (sequence 8); and in a hotel room (sequence 9). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (2nd harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	CF	(ms)				
1	33.1 ± 1.4	38.6 ± 0.4	5.2 ± 0.5	**2**	6.7	3.5	5
2	35.9 ± 1.1	38.4 ± 0.0	6.3 ± 0.8	1,**2**,3	2.8–9.0	2.6	11
3	33.1 ± 0.9	38.6 ± 0.3	5.8 ± 0.3	1,**2**,3	7.0	4.1	11
4	33.3 ± 0.8	38.6 ± 0.2	5.6 ± 0.4	**2**	6.9	3.9	12
5	35.6 ± 0.9	38.5 ± 0.2	6.2 ± 0.4	**2**	9.1	5.6	6
6	36.7 ± 1.1	38.6 ± 0.2	7.1 ± 0.2	**2**	2.7	1.9	4
7	33.5 ± 2.8	36.0 ± 0.3	6.7 ± 0.2	1,**2**,3	19.0	12.7	3
8	36.5 ± 0.8	39.1 ± 0.1	7.6 ± 0.6	1,**2**,3	8.3	6.3	25
9	33.9 ± 1.2	38.4 ± 0.3	5.6 ± 1.0	1,**2**,3,4	4.6	2.6	14

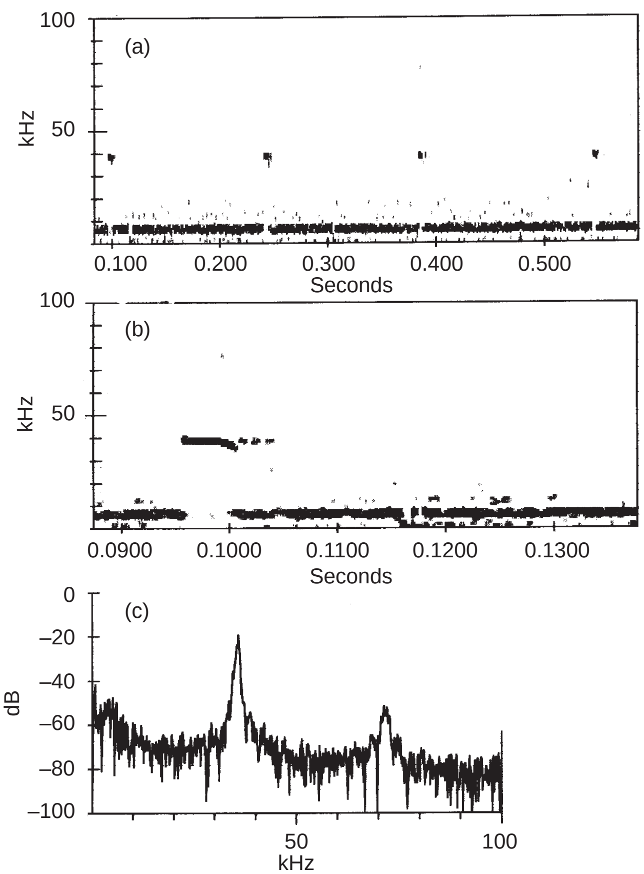

Fig. 1. *Peropteryx macrotis*: sonagram of (a) a typical pulse sequence and (b) a single pulse; (c) a power spectrum the same recording, which was obtained from a bat hunting in an open place (a garden).

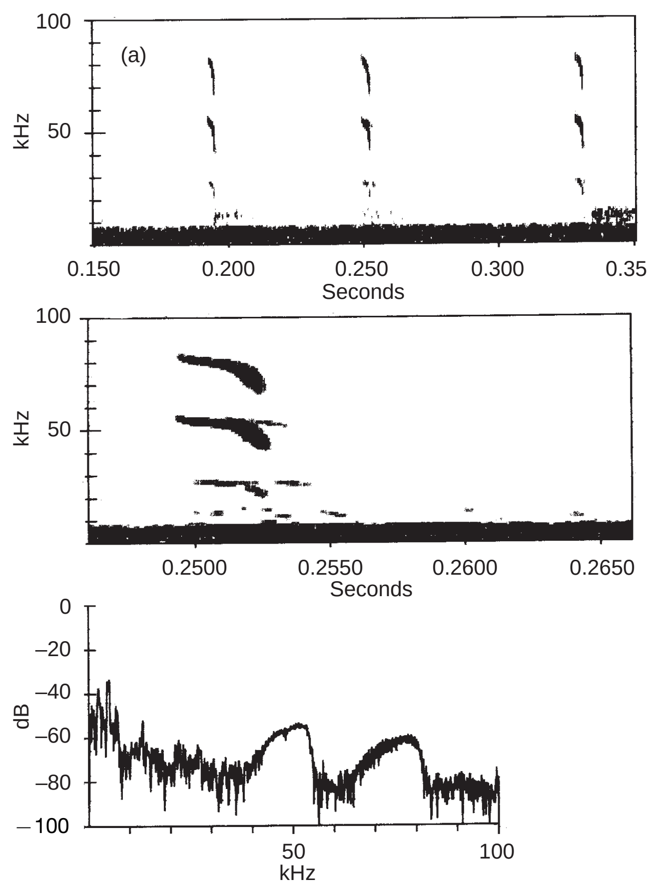

Fig. 2. *Mormoops megalophylla*: sonagram of (a) a search pulse sequence and (b) a single pulse; (c) a power spectrum from a recording inside the straw building.

are shallow at first and steepens towards the end. The pulses consist of three harmonics, the second and third are usually of high intensity while the fundamental is much weaker. Inside the cave, however, the fundamental was emphasized. The repetition rate is slow (*c.* 15 s^{-1}) and very regular in straight flight, but much faster when the bat approaches an obstacle (Table 2, Fig. 2).

Pteronotus davyi

This small species (FA = 43.3 mm, mass = 7.2 g, *n* = 10) typically forages in rapid flight (WL = 6.6 N/m^2, AR = 7.2) in open places 2–10 m above the ground, typically alone or together with one or two conspecifics. We have observed it feeding over ponds and cenotes, along forest trails and around streetlights. In search flight it uses short (6–8 ms), intense pulses, which

Table 2. *Mormoops megalophylla*. Characteristics (mean ± SD) of echolocation calls recorded inside the large straw building (sequences 1–2), in a hotel room (sequences 3–5) and inside a cave (sequence 6). Except in sequence 6, the frequencies of the second harmonic, which usually is the strongest, is given. In sequence 6 (inside a cave), the fundamental was the strongest harmonic. The third harmonic is sometimes also of high intensity (in sequences 1, 2 and 5), occasionally the strongest of the three. *n*, number of pulses in each sequence. Emphasized harmonics in bold

Sequence	Frequency (1st* or 2nd harmonic) (kHz) Max. ampl.	Pulse duration (ms)	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
1	48.9 ± 2.9	3.8 ± 0.3	1,**2**,**3**	15.4	5.9	14
2	54.1 ± 0.8	4.0 ± 0.8	1,**2**,3,4	16.0	6.4	32
3	54.0 ± 0.8	3.7 ± 0.5	**1**,**2**,3,4	18.3	6.7	55
4	49.1 ± 2.3	4.2 ± 0.4	1,**2**,3	30.1	13.9	13
5	52.6 ± 1.0	3.8 ± 0.6	1,**2**,**3**	19.4	7.4	11
6	25.3 ± 1.4*	3.5 ± 0.2	**1**,2	80.0	26.4	5

Table 3. *Pteronotus davyi*. Characteristics (mean ± SD) of search pulses recorded in forest openings or over cenotes at 2–5 m altitude (sequences 1–5) and indoors in a large straw house (sequence 6). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (2nd harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	CF1	CF2	(ms)				
1	60.3 ± 1.1	69.8 ± 0.7	8.2 ± 0.5	1,**2**,3	20.9	17.1	23
2	58.5 ± 0.6	69.5 ± 0.4	6.9 ± 0.7	1,**2**,3	9.7	6.7	29
3	60.1 ± 0.8	69.0 ± 0.6	8.3 ± 0.8	**1**,2	12.3	8.1	37
4	59.0 ± 1.4	68.9 ± 0.7	6.6 ± 0.5	1,**2**	12.6	8.3	38
5	60.1 ± 0.4	71.1 ± 0.4	6.7 ± 0.5	1,**2**,3	12.0	8.0	9
6	57.6 ± 1.2	67.7 ± 0.4	7.6 ± 0.8	1,**2**	7.3	5.5	22

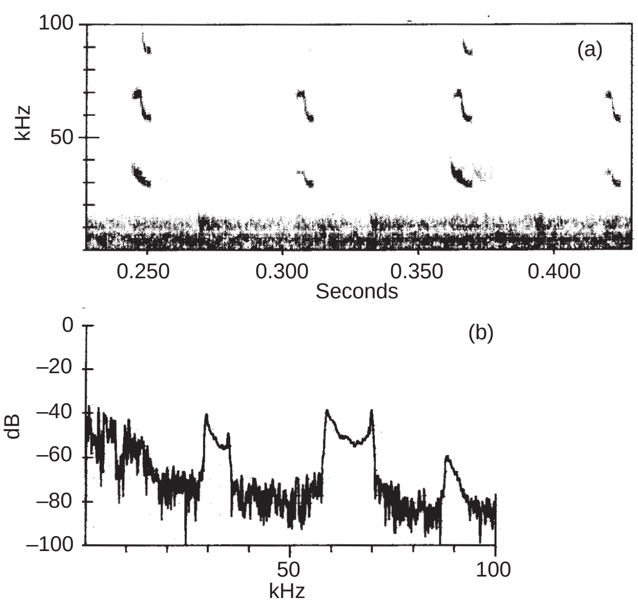

Fig. 3. *Pteronotus davyi*: (a) sonagram of a typical pulse sequence; (b) a power spectrum of a typical search pulse from a recording from a bat foraging over a pond.

usually are emitted at a regular rate of 12–17 s^{-1}. The second harmonic is emphasized, but the fundamental and the third harmonic are usually also evident, just as in many other mormoopids, and this could be confusing if frequency-dividing bat detectors are used. The pulses consist of two CF-components at 59–60 and 70–71 kHz, respectively. These components are of similar intensity and are joined by a down-sweep with somewhat less energy (Table 3, Fig. 3).

Pteronotus parnellii

This medium-sized (FA = 57.0 mm, mass = 14.7 g, $n = 5$) species is often seen feeding together with *P. davyi* and other smaller open air foragers, but it typically flies much closer to the ground (1m or less) or within the vegetation (WL = 7.9 N/m^2, AR = 6.7). It rarely ventures out in the open, and therefore is usually not so easy to see. The pulses are long (*c.* 25 ms) and consist of a CF-component that begins and ends with short sweeps. Most energy is always in the second harmonic at 65–66 kHz (Table 4, Fig. 4). This species is a flutter-detector, and therefore uses a much higher duty cycle (> 20%) than other species in the area considered here. It is easy to recognize with a bat detector.

Natalus stramineus

This small (FA = 36.8 mm, mass = 4.4 g, $n = 19$) bat can easily be distinguished from the other species of similar size (*Peropteryx*, *Myotis*, *Rhogeessa* and *Pteronotus davyi*) by its much slower and more manoeuvrable flight

Table 4. *Pteronotus parnellii*. Characteristics (mean ± SD) of search pulses recorded in small openings in forest (sequence 1–4), and indoors in a large straw house (sequence 5). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (2nd harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	CF	(ms)				
1	62.8 ± 2.4	67.1 ± 0.5	22.4 ± 2.1	1,**2**,3,4	18.0	40.3	18
2	65.0 ± 0.7	66.4 ± 0.3	23.6 ± 1.9	1,**2**,3,4	16.3	38.5	49
3	63.9 ± 1.4	66.1 ± 0.2	25.6 ± 2.1	1,**2**,3,4	15.7	40.2	47
4	63.1 ± 1.3	65.0 ± 1.2	25.0 ± 2.0	1,**2**,3,4	16.0	40.0	48
5	59.9 ± 1.4	64.9 ± 0.6	23.1 ± 1.6	1,**2**,3,4	19.6	45.3	47

Table 5. *Natalus stramineus*. Characteristics (mean ± SD) of search pulses recorded in the hotel room (sequences 1–2) and inside the large straw building (sequence 3). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (1st* or 2nd) harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	Max. ampl.	(ms)				
1	96.2 ± 0.5	106.5 ± 3.9	2.0 ± 0.3	1,**2**	41.7	8.3	4
2	104.1 ± 3.6	114.4 ± 0.9	1.6 ± 0.3	1,**2**	14.7–37.9	3.4	8
3	42.8 ± 1.5*	46.6 ± 1.3*	2.0 ± 0.0	**1**,2,3	18.2	3.6	40

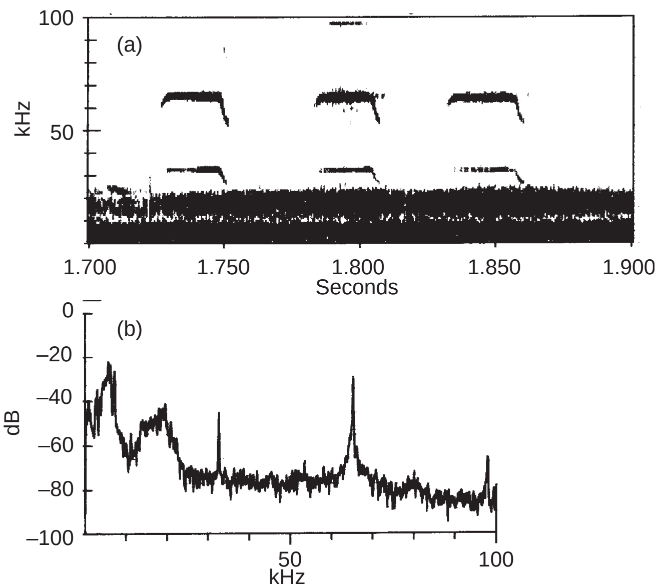

Fig. 4. *Pteronotus parnellii*: (a) sonagram of a typical search pulse sequence; (b) a power spectrum of a typical search pulse.

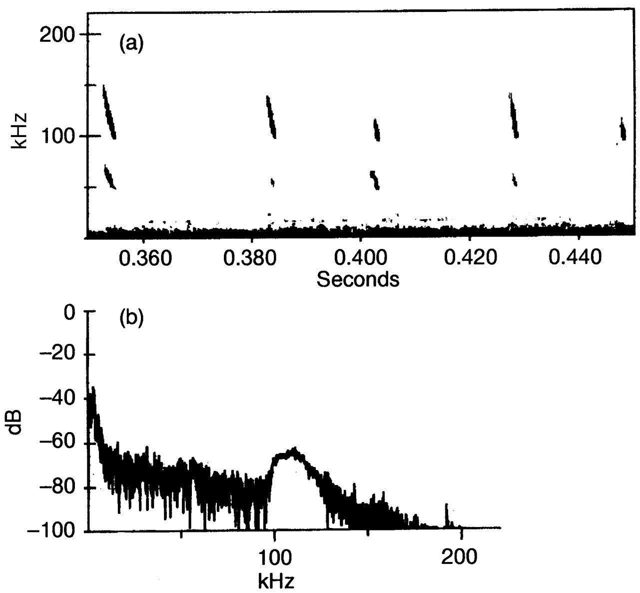

Fig. 5. *Natalus stramineus*: (a) sonagram of a pulse sequence emitted in the hotel room; (b) a power spectrum of a typical pulse.

(WL = 3. 9 N/m^2, AR = 5.6) and, most importantly, by its very weak echolocation calls that usually cannot be detected unless the bat is < 0.2–0.5 m from the microphone. This species typically flies near vegetation or the ground. The search calls consist of short (*c.* 2 ms) sweeps with most energy in the second harmonic at 100–130 kHz. Occasionally the fundamental frequency is emphasized (sequence 3). They are emitted at short but variable intervals and with low duty cycle (Table 5, Fig. 5). We were only able to record this species in the hotel room and inside a cave where it roosted.

Eptesicus furinalis

This small (FA = 38.8 mm, mass = 7.6 g, *n* = 3) *Eptesicus* species is usually seen feeding in open or semi-open places; in gaps in the forest, over cenotes, ponds and swimming-pools, along roads or near isolated trees on open land. It usually flies relatively fast (WL = 7.3, AR = 6.2) in regular circles or back and forth along tree-lines, typically 2–5 m above ground. The search calls consist of an initial down-sweep that ends in a narrow-band 'tail', that varies in extent with the proximity to obstacles or targets. Most energy is at 36–41 kHz. Search pulses are typically emitted regularly at a rate of 7–8 s^{-1} (Table 6, Fig. 6), although the intervals are shortened

Table 6. *Eptesicus furinalis*. Characteristics of search pulses recorded from bats foraging in open places at 2–5 m elevation (sequence 1–5) and over a swimming-pool before drinking (sequence 6). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (1st harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	Max. ampl.	(ms)				
1	33.1 ± 0.5	36.5 ± 0.4	9.4 ± 0.5	**1**	7.7	7.2	6
2	34.2 ± 0.3	35.8 ± 0.6	8.9 ± 0.2	**1**	7.5	6.7	5
3	35.1 ± 0.6	37.0 ± 0.7	8.7 ± 0.6	**1**,2	7.4–11.6	7.5	8
4	33.2 ± 0.8	36.7 ± 0.8	10.9 ± 0.7	**1**,2,3	9.2	10.0	30
5	37.1 ± 1.2	41.4 ± 1.2	7.7 ± 0.8	**1**	12.0	9.2	22
6	32.2 ± 1.8	36.7 ± 0.7	4.6 ± 0.6	**1**	13.5	6.2	4

Table 7. *Lasiurus intermedius.* Characteristics of search pulses of a bat flying in the opening above a water hole in forest. *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (1st harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	Max. ampl.	(ms)				
1	29.8 ± 1.0	32.6 ± 1.1	6.3 ± 1.2	**1**,2	13.1	8.3	8

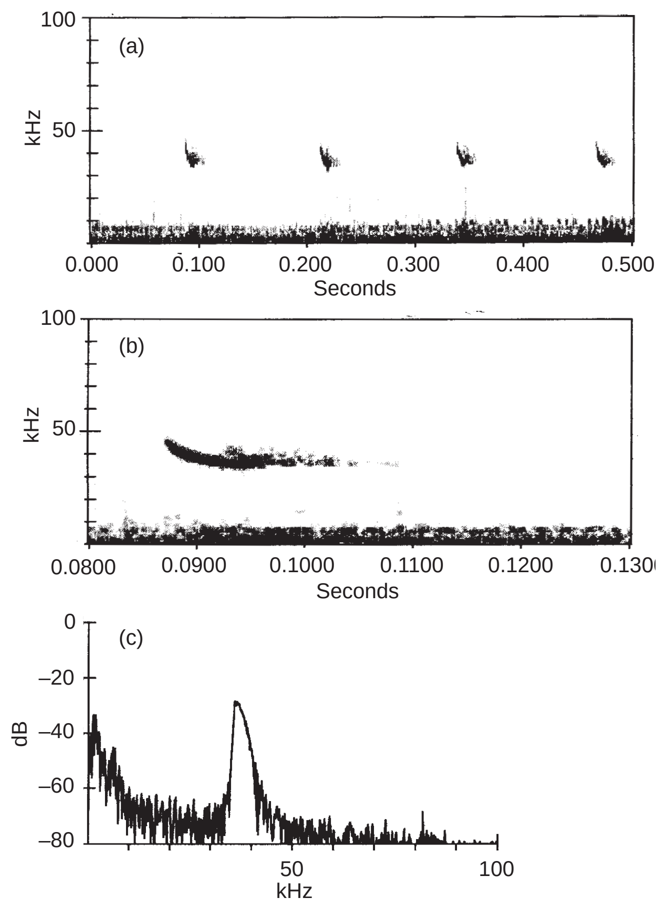

Fig. 6. *Eptesicus furinalis*: sonagram of (a) a typical search pulse sequence emitted in an open place and (b) a typical search pulse; (c) a power spectrum. The initial sweep is sometimes more extensive and the narrow band part may be shorter, particularly near clutter. Additional harmonics may also be present.

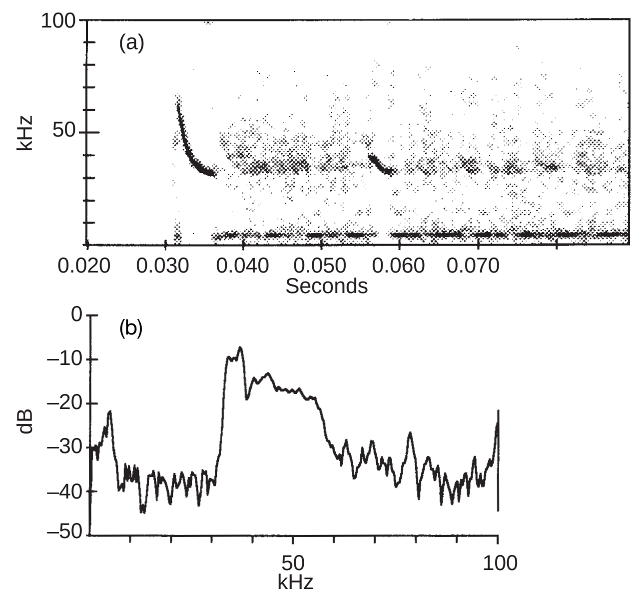

Fig. 7. *Lasiurus intermedius*: (a) sonagram of two sequential search pulses emitted as the bat descends toeards a water hole; (b) power spectrum of the first of these pulses.

when obstacles (or targets) are approached or when the bat flies in the vicinity of vegetation. Harmonics usually appear weak or attenuated when the bat flies in open areas, so that only the fundamental is evident.

Lasiurus intermedius

This relatively large (FA = 54.4 mm, mass = 20.2 g, *n* = 2), long-winged and hence fast-flying bat (WL = 10.8 N/m^2, AR = 7.7) was recorded flying at tree-top level (10–15 m) in a small opening in forest above a pond. In this situation it used *c.* 10 ms long

Table 8. *Lasiurus ega*. Characteristics (mean ± SD) of search phase pulses of bats foraging in openings in forest, at the height of the tree canopy (*c*. 10 m; sequences 1–4), and around a lamp post (sequence 5). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (1st harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	Max. ampl.	(ms)				
1	27.3 ± 2.5	31.3 ± 1.3	9.4 ± 1.2	**1**	8.0	7.1	8
2	26.6 ± 2.4	31.2 ± 1.4	10.2 ± 1.1	**1**,2,3	7.0	7.1	11
3	27.6 ± 1.4	30.7 ± 0.9	9.6 ± 0.7	**1**	6.7	6.4	16
4	27.6 ± 1.4	29.8 ± 1.3	10.8 ± 1.3	**1**	3.7	4.0	11
5	34.0 ± 2.2	38.0 ± 2.1	5.5 ± 1.2	**1**	12.3	6.8	26

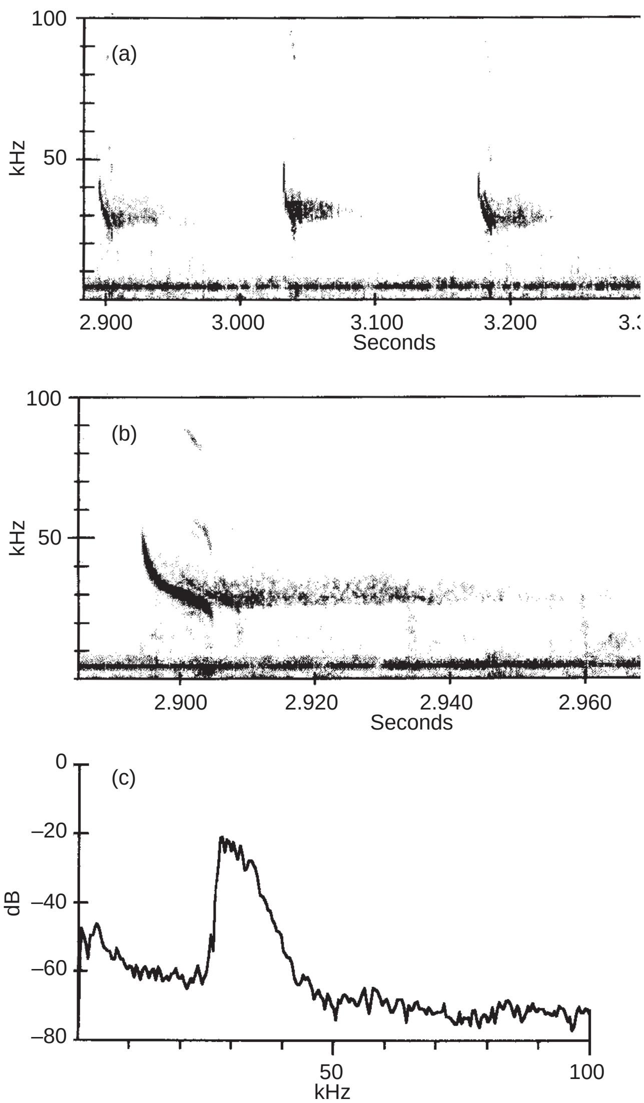

Fig. 8. *Lasiurus ega*: sonagram of (a) a typical search pulse sequence emitted in an open place and (b) a single pulse; (c) power spectrum.

down-sweeps with a narrow-band 'tail' at *c*. 28 kHz (Table 7, Fig. 7). In more open situations or at higher altitude the tail frequency is lower (*c*. 25 kHz), the pulses are longer and the repetition rate is lower. We, however, lack good recordings of this.

Lasiurus ega

This medium-sized (FA = 44.4 mm, mass = 10.7 g, *n* = 12), long-winged bat (WL = 7.2 N/m^2, AR = 7.6) was observed foraging in open places, near tree canopies and around streetlights, usually at about 10 m altitude. In the vicinity of obstacles it uses *c*. 10 ms long down-sweeps, that end in a short, narrow-band 'tail' and with most energy near 31 kHz. In open situations the 'tail', and hence the pulse, becomes longer, but we have no good illustration of this. The pulse repetition rate is typically about 0.7 s^{-1}, but occasionally lower in open situations, or higher in the vicinity of vegetation or other obstacles (Table 8, Fig. 8).

Myotis keaysi

This small (FA = 33.7 mm, mass = 3.8 g, *n* = 34; WL = 5.3 N/m^2, AR = 6.4) *Myotis* was recorded flying over cenotes and also inside the large straw building. In all cases the calls are short (*c*. 2.5 ms) but of high intensity and repeated at a high but variable rate (15–20 s^{-1}). The calls consist of steep down-sweeps that end in a narrow-band 'tail', which contains most of the energy at 59–63 kHz (Table 9, Fig. 9). The initial frequency is sometimes around 110 kHz (sequences 1 and 2) but it can also be much lower (about 80 kHz; sequence 3).

Rhogeessa aeneus

This very small (FA = 38.0 mm, mass = 3.5 g, *n* = 2) but fast-flying (WL = 5.3 N/m^2, AR = 6.1) vespertilionid is an open air forager. We have observed it circling around lights situated in woodland or near single trees, but also in larger openings in the forest or over cenotes, usually 2–10 m above the ground. The search calls are short (2–4 ms) but of high intensity (can be detected at least 10–20 m away) and are repeated regularly at either *c*. 13 or *c*. 25 s^{-1} (probably one or two calls per wingbeat). The pulses consist of a steep down-sweep, that ends in a short narrowband 'tail', which contains most of the energy at 48–54 kHz. Like in *Eptesicus* and *Myotis*, the fundamental is emphasized, but the second harmonic can sometimes be detected at *c*. 100 kHz

Table 9. *Myotis keasyi*. Characteristics (mean ± SD) of search pulses of three short sequences recorded above (2–5 m) a water hole (sequences 1–4) and inside the large straw building (5–7). *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (1st harmonic) (kHz)		Pulse duration	Harmonics evident	Repetition rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	Max. ampl.	(ms)				
1	58.1 ± 1.9	63.8 ± 1.4	3.0 ± 0.0	**1**	20.2	6.0	60
2	56.4 ± 0.9	61.2 ± 1.1	3.2 ± 0.5	**1**	24.0	7.7	29
3	56.9 ± 0.8	59.4 ± 0.4	3.0 ± 0.0	**1**	17.3	5.2	52
4	56.7 ± 1.4	58.6 ± 0.9	3.9 ± 0.4	**1**	21.4	8.3	30
5	58.4 ± 0.8	62.1 ± 1.0	2.6 ± 0.2	**1**,2	19.2	5.0	5
6	58.9 ± 1.4	63.0 ± 0.8	2.6 ± 0.4	**1**,2	19.0	4.9	9
7	59.2 ± 0.0	61.3 ± 0.5	2.5 ± 0.1	**1**	17.2	4.3	3

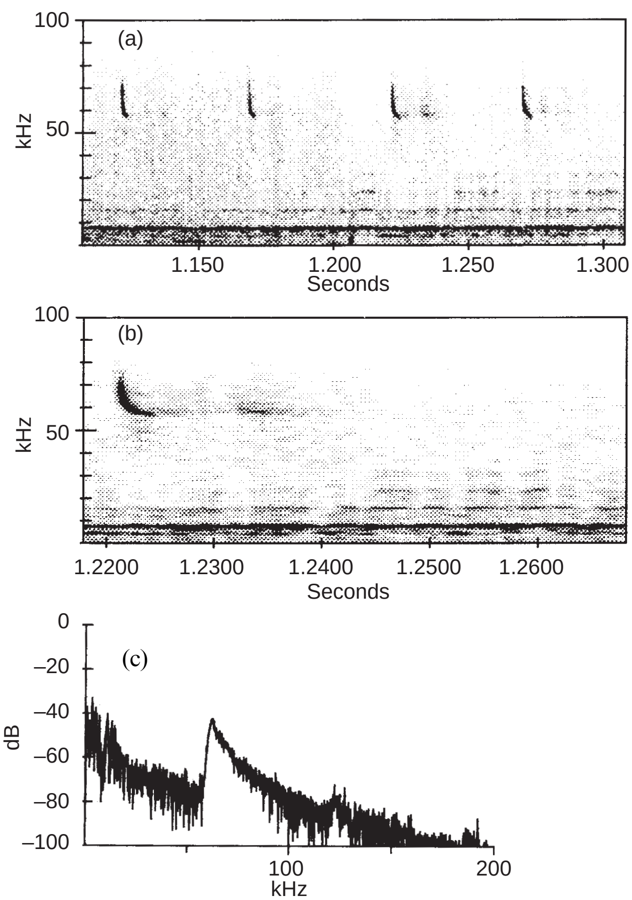

Fig. 9. *Myotis keasyi*: sonagram of (a) a search pulse sequence emitted inside the large straw building and (b) a single pulse from the same sequence; (c) a power spectrum.

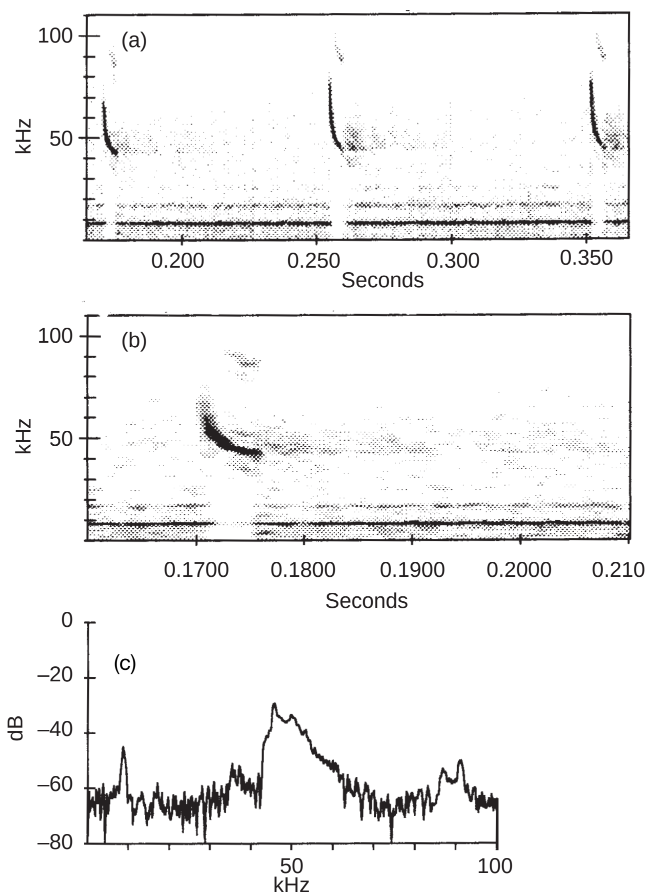

Fig. 10. *Rhogeessa aeneus*: sonagram of (a) a typical search pulse sequence emitted in an open place and (b) a single pulse from the same sequence; (c) a power spectrum.

(Table 10, Fig. 10). When released inside the small room, this species emitted short down-sweeps of lower intensity and with the frequency of the 'tail' at somewhat higher frequency (sequence 5); thus conforming with some of the calls emitted outdoors and with those described by Audet, Engstrom & Fenton (1993), recorded inside a small tent. Hence, as it moves from the open into a smaller air place, *Rhogeessa* changes from 4 ms calls of high intensity and low frequency 'tail' (*c*. 48 kHz) to 2 ms calls of lower intensity and higher 'tail' frequency (50–53 kHz). The initial frequency is also highly variable. Although the calls are similar to those of *Myotis keaysi,* the 'tail' frequency is always lower.

DISCUSSION

The Yucatan assemblage of aerial-feeding insectivorous bats is of relatively low species diversity by Neotropical standards. Excluding the molossids, it consists of 12

Table 10. *Rhogeessa aeneus*. Characteristics (mean ± SD) of search pulses recorded from one bat flying around a lamp post situated near a tree canopy (sequence 1–4) and indoors in a small room (6). The relatively long pulses, lower frequences and slow repetition rate in sequences 2 and 4 probably indicates that the bat was facing open air and as opposd to the tree canopy. *n*, number of pulses in each sequence. Emphasized harmonic in bold

Sequence	Frequency (1st harmonic) (kHz)		Pulse duration	Harmonics evident	Rep. rate (s^{-1})	Duty cycle (%)	*n*
	Lowest	Max. ampl.	(ms)				
1	49.6 ± 1.1	53.9 ± 0.6	2.0 ± 0.1	**1**	23.0	4.6	5
2	44.1 ± 1.8	50.7 ± 0.7	2.8 ± 0.2	**1**	13.1	3.7	3
4	48.8 ± 1.7	53.4 ± 1.3	2.2 ± 0.3	**1**,2	25.0	5.5	4
5	45.0 ± 2.5	48.2 ± 0.9	4.1 ± 0.6	**1**	15.7	6.4	6
6	45.3 ± 3.0	52.7 ± 1.5	2.6 ± 0.2	**1**,2	22.1	3.8	4

species (Arita, 1997). Of these the 10 species reported here are common while the remaining two (*Saccopteryx bilineata* and *Lasiurus blossevillii*) are very rare in Yucatan. In fact, both of the latter are known from the state on the basis of single reports, and in the case of *L. blossevillii* the record is based on a single skull found in a cave deposit (Arita, 1997).

The bats considered here are quite easy to identify acoustically in the field, with the aid of a high-quality bat detector. All species use echolocation calls with particular characteristics, which make them readily distinguishable. Useful interspecific differences are the pulse structure (CF, shallow FM or steep FM or various combinations of these), frequency, intensity and to some extent also the pulse repetition rate. Indeed, we found the bat species of Yucatan much easier to distinguish acoustically than the bats of northern Europe or North America, for example, where several congeneric species (i.e. of the genus *Myotis*) use similar echolocation calls, making a bat detector more demanding to use as a minitoring tool (Ahlén & Baagøe, 2000).

Echolocation calls of some of the species included here (*E. furinalis, L. ega*, *M. megalophylla*, *P. parnellii, P. davyi*, and *Rhogeessa* sp.) have previously been described by O'Farrell & Miller (1997, 1999) and O'Farrell, Corben *et al.* (1999) and O'Farrell, Miller & Gannon (1999). However, their descriptions are based on recordings from Belize, and their recordings were made through the Anabat ultrasound detector, which uses a divider system of sound processing. In contrast to the time expansion system used here, the Anabat does not retain all the information in a sound sequence. In particular, it provides no information about the harmonic content of the signal, but displays only the strongest one. Lack of information about the harmonic content could be a serious source of confusion in cases where bats 'switch' between harmonics, emphasizing different frequency bands in different situations, as for example emballonurids and mormoopids sometimes do (Fenton, Rydell *et al.*, 1999).

Kalko (1995) described the calls of '*Peropteryx* sp.' from Panama, but in this case the calls were clearly different from the *P. macrotis* we recorded in Yucatan. Therefore the calls described by Kalko was most likely not from *P. macrotis* but from another species, possibly *P. kappleri*. There is some confusion about the identity of the *Rhogeessa* on the Yucatan Peninsula; there may or may not be two separate species, *R. tumida* and *R. aeneus* (Audet *et al*., 1993). Audet *et al*. (1993) recorded *Rhogeessa* flying inside a small tent, a situation in which bats typically do not emit diagnostic pulses (Ahlén, 1981). The differences between the tent recordings of *Rhogeessa* and our recordings of *Rhogeessa* relate predominantly or entirely to differences in the echolocation situation. The differences cannot be used to argue that we recorded taxonomically different bats.

We stress that reliable identification of bats in flight often requires information of parameters besides the echolocation calls (Ahlén, 1981; Ahlén & Baagøe, 2000). One reason is that bat echolocation calls may vary considerably depending on the situation. For example, an aerial-hawking insectivore moving from an open area towards an obstacle or towards a place with more vegetation typically changes gradually from using relatively long, narrow-band pulses and long inter-pulse intervals to shorter, more broad-band pulses and shorter inter-pulse intervals (i.e. higher repetition rate). It may also emphasize higher frequencies near the vegetation (Kalko & Schnitzler, 1993). Another complicating factor is that many different bat species use similar calls under similar situations. For example, in obstacle avoidance or during the approach phase, most species use steep sweeps, and are therefore difficult to identify in such situations. It is therefore important that (1) the intraspecific variation is reasonably well known for each species that is included in the survey, (2) that the recording is related at least in rough terms to the situation in which the bat is flying and what it is doing, (3) that the identification is based not on one pulse or a short pulse sequence but on several sequences, hopefully including diagnostic ones, and (4) that the sound is interpreted in combination with as much additional information as possible, e.g. size, shape and behaviour. As a general rule, aerial-hawking bats (including *Lasiurus* spp., *Rhogeessa* sp. and *Myotis keaysi*) usually emit their most typical pulses when they fly in open places. Open situations are also those where it is least difficult to obtain supplementary information visually, and so are often preferable for identification attempts.

The technique described here allows rapid assessments of the species richness in various habitats on the Yucatan Peninsula, including forest, farmland and urban habitats (Hayes, 1997; Gaisler *et al.*, 1998). Monitoring using ultrasound detectors complements mist-netting, because the two methods are efficient for different suites of species. The aerial-hawking insectivores are relatively hard to catch but easy to find with a detector, while gleaning insectivores, frugivores, nectarivores and sanguivores are hard to find and to distinguish using a detector but relatively easy to catch. Nevertheless some species, such as *Natalus stramineus*, which is an aerial insectivores but nevertheless a low-intensity echolocator, could still easily be missed, even if both inventory methods are used simultaneously.

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