A NEW EXAMINATION OF ECHOLOCATION CALLS OF SOME NEOTROPICAL BATS (EMBALLONURIDAE AND MORMOOPIDAE)

Michael J. O'Farrell and Bruce W. Miller

O'Farrell Biological Consulting, 2912 North Jones Boulevard, Las Vegas, NV 89108 (MO'F)
Wildlife Conservation Society, Gallon Jug, Belize (BWM)

In northwestern Belize, two emballonurids (*Rhynchonycteris naso* and *Saccopteryx bilineata*) and three mormoopids (*Pteronotus parnellii*, *P. davyi*, and *P. personatus*) were examined acoustically with the Anabat II bat detector and associated analysis system. *R. naso* used calls consisting of a short constant frequency (CF) at 47 kHz and concave downward frequency modulated (FM) sweep to ca. 40 kHz with two strong harmonics. Echolocation sequences of *S. bilineata* revealed a paired cadence of calls. Both signals in a pair slowly increased in frequency, forming a quasi-CF (QCF) component and terminated with a short, downward FM sweep. The initial call of a pair ranged from 44.5 to 46.6 kHz and the second ranged from 46.6 to 48.7 kHz. *P. parnellii* used a long CF call at 63.5 kHz, with a terminal downward FM sweep to ca. 54.5 kHz. *P. davyi* produced calls with an initial short CF at 68.1 kHz, a downward FM sweep, and a terminal short CF at 58.0 kHz. *P. personatus* emitted calls similar in shape to *P. davyi*, with the initial CF at 83.0 kHz and the terminal CF at ca. 68.0 kHz. Previous descriptions of echolocation calls for these species compare favorably with those obtained in this study, but the Anabat equipment generally revealed more variation and detail than previously described. The echolocation calls described in this study provide precise vocal signatures for the accurate identification of free-flying individuals of the species studied.

Key words: *Pteronotus parnellii*, *Pteronotus davyi*, *Pteronotus personatus*, *Saccopteryx bilineata*, *Rhynchonycteris naso*, echolocation, Anabat II, vocal signatures

The recording and description of echolocation calls of some Neotropical bats began with the pioneering work of Griffin (1953) and Griffin and Novick (1955). Although data gathered were surprisingly good, technological limitations prevented recording under a variety of field conditions. Thus, much of the early descriptions of vocalizations were generated from captive bats. Bats of the families Emballonuridae and Mormoopidae tended to produce high-intensity sounds that were easier to detect and record than the low-intensity, highly directional sounds produced by bats in the Phyllostomidae. Subsequent examination of some of these species, using improved equipment, resulted in more definitive descriptions of echolocation calls (Novick, 1963; Pye, 1973), although the

ability to record individuals under field conditions was still limited.

Early studies of Neotropical species of emballonurids provided descriptions of sonar calls of free-flying individuals in Trinidad and Costa Rica, but the focus was on low-frequency communication calls (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976). Orientation calls were presented as oscilloscope tracings of sonogram envelopes or detailed verbal descriptions. Improved equipment yielded more detailed descriptions of design of echolocation signals for emballonurids in Panama and Costa Rica (Barclay, 1983; Kalko, 1995). The resolution of sonograms, however, make visual comparisons among the species difficult.

Patterns of frequency-time structure based on constant-frequency (CF) and fre-

quency-modulated (FM) components of echolocation calls have been described for some Microchiroptera (Simmons and Stein, 1980; Simmons et al., 1979). Variations in the frequency-time structure (e.g., frequency bandwidth, duration of calls) have proved useful in identification of species (Fenton and Bell, 1981) and assessment of intraspecific variation with respect to habitat and behavior (Kalko and Schnitzler, 1993; Obrist, 1995). Although the frequency-time structure has proved effective as a tool for identification of species, little standardized information exists for most species, particularly for Neotropical species.

The range of bat detectors available and the subsequent analysis and display of echolocation calls vary (Fenton, 1988). Cost of equipment and quality of output are equally variable and generally are prohibitive for many workers. The recent availability of the inexpensive and field-portable Anabat II bat detector and analysis system provides greater flexibility in obtaining recordings of echolocation calls of free-flying bats.

The purpose of the present paper is to provide a new examination of design of echolocation calls using the frequency-time structure display from the Anabat II system for some species of emballonurid and mormoopid bats that have been studied and described in other terms in the past. This information will assist in providing a baseline for establishing standardized vocal signatures for the identification of free-flying bats of the species examined.

MATERIALS AND METHODS

During 7–18 February 1995, we sampled the bat fauna in the region around Gallon Jug in the northwestern corner of Belize using conventional mist nets, a double-frame harp trap, and acoustic sampling with an Anabat II bat detector (Titley Electronics, Ballina, Australia). Northwestern Belize is comprised of Subtropical Moist Forests, following the Holdridge Life Zone System (Holdridge, 1967), and is similar to the broad-leaved forests of the Peten in northern Guatemala and much of Mexico's Yucatan

Peninsula (Hartshorn, 1984). Within a 53,000-ha tract of private property, a total of nine sites representing seven habitat types were sampled.

The general habitats being sampled by nets and trap were monitored acoustically to provide a library of vocalizations representative of the detectable bat fauna present. Emphasis was placed on monitoring the collecting devices in an attempt to provide recordings of bats just prior to capture. In such cases, initial echolocation calls could be linked directly to a known species. However, this was not always possible and provided only a small portion of the potential vocal repertoire of that species.

Several methods to obtain echolocation calls of known species were used after capture. For species that were abundant, individuals were released near the point of capture at times when activity of bats was absent. Some released bats circled the area and provided a series of vocalizations that appeared to be representative of normal flight. Some individuals of abundant species and all individuals of less-common species were released in a solid-ceiling, lathe-sided enclosure (12.50 by 6.75 m). Recordings were obtained for known individuals in unrestrained flight within the enclosure.

The detector output of all incoming vocalizations of bats was directed through the Anabat II ZCA Interface Module, processed with associated software, and displayed on a laptop computer. Thus, the frequency-time structure of signals could be examined as they were being produced. Vocal sequences were selected and saved directly on the hard drive for future examination. As described, this system allowed instantaneous monitoring of vocalizations of bats with equal ease in the field or laboratory setting and eliminated possible distortions of sound associated with use of tape recorders. Taxonomic nomenclature for all taxa follows Koopman (1993).

RESULTS

Emballonuridae.—Vocal signatures of two members of this family were positively identified. *Rhynchonycteris naso* was a common species associated with streams and the vegetated edges of various water sources. It was found roosting under a small wooden pier, supporting a water pump and delivery system, at the edge of Laguna Verde, a small natural lake and on the sides of
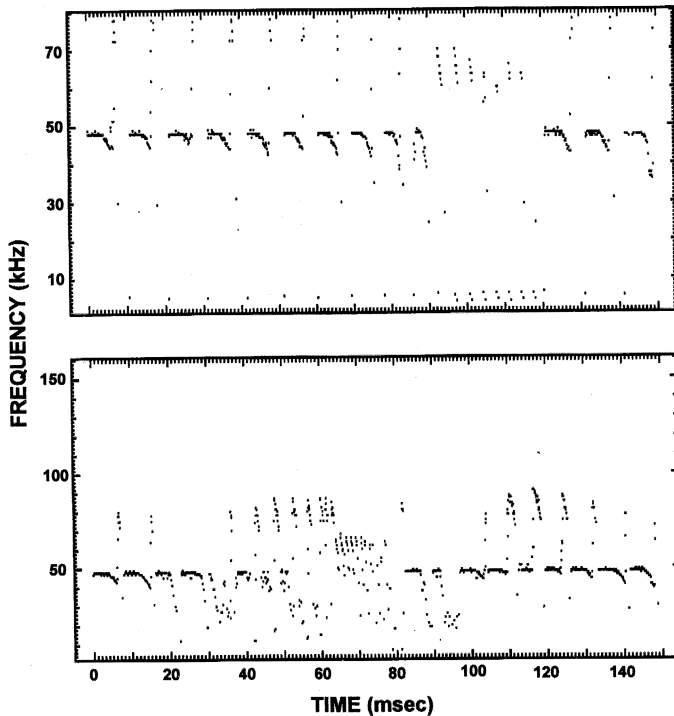
FIG. 1.—Frequency-time display of a vocal sequence produced by *Rhynchonycteris naso* from Belize. The bottom screen is the same vocal sequence, incorporating a feeding buzz, with an expanded frequency range to better illustrate the second harmonic. The time between calls on both screens is compressed to allow more calls per screen.

trees lining the edge of Chan Chich Creek. Because this species roosts in relatively well-lighted habitat and initiates flight before dark, positive visual identification was possible. Several evenings of monitoring concentrated foraging activity of *R. naso* revealed a consistent repertoire of signals (Fig. 1). Search and orientation calls demonstrated an initial short CF at 47 kHz followed by a concave FM sweep to ca. 40 kHz (Table 1). Sometimes the initial CF portion was preceded by a discernible, 1 kHz up sweep. Similarly, the terminal FM portion varied, occasionally extending down to ca. 35 kHz. The CF portion varied in length (4–6 msec) during search and orientation behavior and then decreased progressively through the pursuit phase.

The generally used frequency scale (0–80 kHz; top screen of Fig. 1) masked the presence of harmonic information, which

was revealed by changing the frequency scale (0–160 kHz; bottom screen of Fig. 1). The zero-crossings analysis used by the Anabat system forfeits harmonic information (C. Corben, pers. comm.). The signal displayed on the screen represents the dominant harmonic. If the strengths of two harmonics are about equal, the harmonic being displayed may alternate between the two values. Thus, the harmonic displayed depends on a variety of factors such as relative strength of emitted sounds, atmospheric attenuation, direction relative to the detector, and the frequency response of the detector. However, in the case of *R. naso*, the important fact for identification purposes is that a second harmonic will be apparent for most call sequences.

The CF at 47 kHz was constant during flight at feeding grounds. However, individuals startled at the roost generally flew

TABLE 1.—*Characteristics of calls of free-flying emballonurid bats from Belize;* n = *number of individual search-orientation calls, one standard error is given in parentheses.*

Species	n	Duration of call (msec)	Time between calls	Minimum frequency (kHz)	Maximum frequency (kHz)
Saccopteryx bilineata					
First call	40[a]	6.7	55.8	44.5	46.6
		(0.21)	(1.85)	(0.21)	(0.18)
	20[b]	5.9	58.7	42.1	45.5
		(0.83)	(5.20)	(0.61)	(0.37)
41, 41, 60[c], respectively		9.4	85.8		45.1
		(0.21)	(3.18)		(0.07)
Second call	40[a]	6.6	82.5	46.6	48.7
		(0.15)	(3.09)	(0.19)	(0.17)
	23[b]	5.4	92.5	44.8	47.6
		(0.58)	(16.00)	(0.46)	(0.22)
38, 38, 57[c], respectively		9.0	52.0		47.1
		(0.28)	(1.50)		(0.08)
Rhynchonycteris naso	41[a]	6.7	60.8	40.2	47.2
		(0.12)	(2.99)	(0.53)	(0.06)
90, 82, 70[c], respectively		5.0	53.5		102.5
		(0.08)	(2.20)		(0.11)
				80[d]	100

[a] This study.
[b] Barclay (1983); time between calls converted from intercall interval.
[c] Kalko (1995).
[d] Bradbury and Vehrencamp (1976).

away from the initial roosting site in a loop to a nearby spot. Recordings made during this behavior revealed an unusual sequence of calls. Repetitive sequences of 8–12 calls began with QCF–FM calls progressively increasing in frequency (e.g., 39–28, 41–29, 43–29, 45–34, 45–34, 45–34, 45–38, 48–39, 45–39 kHz). Although exact frequencies seemed to vary somewhat, the pattern was constant.

Saccopteryx bilineata was in all habitats sampled based on acoustic sampling and identification of vocal signatures. We captured this species in forest trails, which could be effectively blocked with nets or the harp trap. Initially, individuals released in the trails provided no reference calls. Subsequently, release in the enclosure revealed the use of highly distinctive vocalizations (Fig. 2). Design of pulses of search and orientation calls incorporated an increasing frequency over most of the call, terminating in a short down sweep. The ma-

jority of the call can be categorized as a quasi-CF (QCF) component (Kalko and Schnitzler, 1993).

Most echolocation sequences demonstrated an alternating cadence of paired calls (Fig. 2). The paired calls began with a signal ranging from ca. 43–45 kHz (low-frequency pulse; LF), and the next was ca. 46–48 kHz (high-frequency pulse; HF). As a vocal sequence progressed from search-orientation through pursuit, the signals decreased in duration and became horseshoe-shaped. The paired relationship of a lower- followed by higher-frequency call continued through entire sequences.

No difference was noted between duration of LF and HF calls of a pair (Table 1). The paired nature of LF and HF pulses was apparent based on time between calls. Time between calls (TBC) for the first call reflects the time between LF and HF pulses, and TBC for the second call is the time between HF and succeeding LF pulses. The
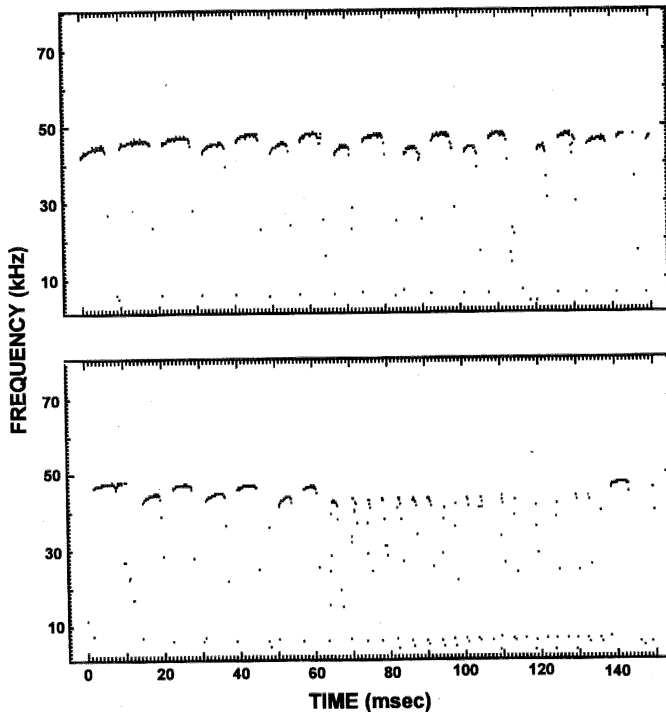
FIG. 2.—Frequency-time display of a vocal sequence produced by *Saccopteryx bilineata* from Belize. The top screen begins with orientation-search calls ranging into pursuit calls. The bottom screen is a continuation of the same sequence terminating in a feeding buzz. The time between calls on both screens is compressed to allow more calls per screen.

null hypothesis that TBC are equally spaced regardless of low- or high-frequency characteristics is rejected ($t = 8.65$; $d.f. = 39$; $P < 0.001$).

Mormoopidae.—Vocal signatures of three species were positively identified. *Pteronotus parnellii* was in all habitats sampled and was a common species captured. It produced a distinctive echolocation call comprised of an initial short FM up sweep, a long CF component at 63.5 kHz, and a long downward FM sweep to ca. 54.5 kHz (Fig. 3; Table 2). During vocal sequences, no feeding buzzes were detected, only a shortening of the call duration. Five sequences ($n = 48$ individual calls) of bats in apparent pursuit of prey yielded mean duration of 12.7 msec ($SE = 0.10$) and mean time between calls of 30.0 msec ($SE = 1.02$). Of all bats we have tested to date (M. J. O'Farrell, in litt.), including species

within the Vespertilionidae and Molossidae, *P. parnellii* was distinctive in that no other variation in calls was observed.

Pteronotus davyi also was in all habitats sampled. Recording sessions with this species in the enclosure were more successful than with other species, because it tended to fly consistent laps producing signals identical to those gathered in the field.

Design of echolocation calls consisted of a short CF at ca. 68 kHz, a downward FM sweep, and a terminal short CF component at ca. 58 kHz (Fig. 4; Table 2). Under controlled conditions, no variation was noted. Under field situations, some signals in a sequence appeared to contain only the FM and terminal CF components. This was probably an artifact of direction of signal and attenuation of higher frequencies rather than actual missing signal components. Recognition of these incomplete signals is
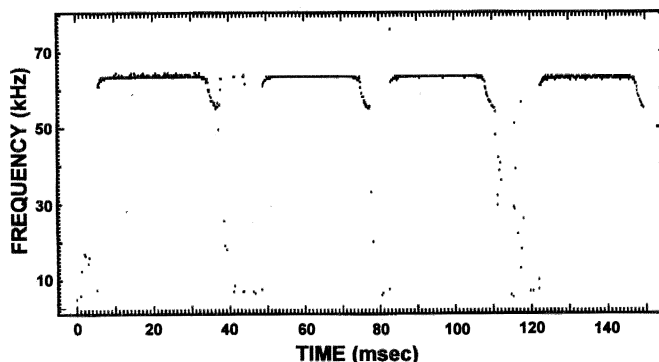
FIG. 3.—Frequency-time display of a vocal sequence produced by *Pteronotus parnellii* from Belize. The time between calls is compressed to allow more calls per screen.

important for identification purposes. Few terminal-pursuit sequences were observed; these showed rapid pulses composed only of the FM component.

Pteronotus personatus was associated with streams and was most abundant at the Rio Bravo. Design of echolocation calls was similar to that of *P. davyi*, consisting of a short CF at 83 kHz, a downward FM sweep, and a terminal short CF component at 68 kHz (Fig. 5; Table 2). However, the initial CF component was shorter, and the terminal CF element tended to be longer than signals of *P. davyi*. Under controlled conditions, calls were of shorter duration with little or no terminal CF component; lower harmonic elements were common.

Under field situations, some signals in a sequence appeared to contain only the FM and terminal CF components and, occasionally, a lower harmonic element.

DISCUSSION

Seven characteristic aspects of echolocation calls of bats have been described (Simmons and Stein, 1980); constant frequency, frequency modulation, sequence of components, duration, harmonics, amplitude, and adaptive variations. Frequency characteristics (CF, FM), duration, and the pattern of change in frequency over time appear to be important for identifying species of free-flying bats (Fenton and Bell, 1981). The presence of multiple harmonics

TABLE 2.—*Characteristics of calls of free-flying mormoopid bats from Belize; n = number of individual search-orientation calls, one standard error is given in parentheses.*

Species	n	Duration of call (msec)	Time between calls	Minimum frequency (kHz)	Maximum frequency (kHz)
Pteronotus davyi	35[a]	5.5	62.2	58.0	68.1
		(0.13)	(3.38)	(0.20)	(0.17)
		3.1[b]		63	78
Pteronotus personatus	25[a]	5.7	48.3	68.0	83.0
		(0.14)	(1.50)	(0)	(0.21)
		3.2[b]		76	106
Pteronotus parnellii	30[a]	30.4	61.9	54.5	63.5
		(0.50)	(2.69)	(0.17)	(0)
		25[b]		56	64

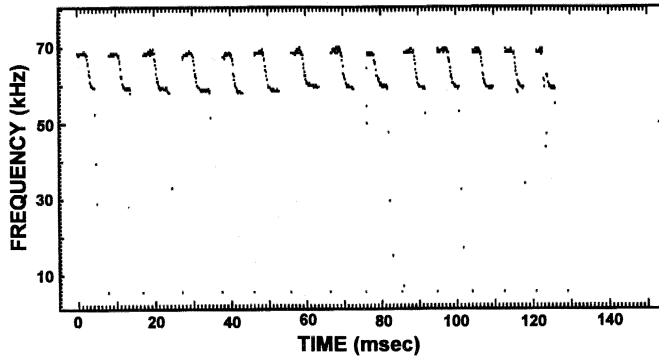[a] This study.
[b] Novick (1963).

FIG. 4.—Frequency-time display of a vocal sequence produced by *Pteronotus davyi* from Belize. The time between calls is compressed to allow more calls per screen.

has received much attention when displaying frequency-time characteristics (Fenton and Bell, 1981; MacDonald et al., 1994; Simmons and Stein, 1980; Simmons et al., 1979). Variations in echolocation calls occur at the individual level (i.e., progression in shape of call from orientation and search behavior through pursuit and capture of prey—Simmons et al., 1979) or between individuals (e.g., change in design of call with a shift in foraging strategy or use of microhabitat—Faure and Barclay, 1994; Simmons et al., 1978; Simmons and O'Farrell, 1977).
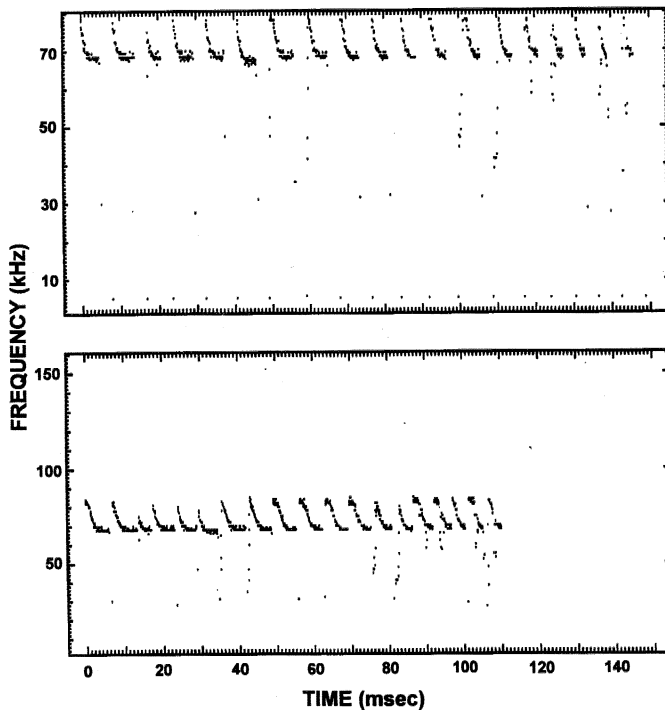

FIG. 5.—Frequency-time display of a vocal sequence produced by *Pteronotus personatus* from Belize. The bottom screen is the same vocal sequence with an expanded frequency range. The time between calls on both screens is compressed to allow more calls per screen.

Zero-crossing analysis allows examination of all aspects of echolocation calls except for amplitude and harmonic information. Although simultaneous examination of all harmonics present is not possible, some harmonic information is available if two strong harmonics exist and there is an alternation of energy between harmonics as for *R. naso* (Fig. 1). It has yet to be established that the loss of this information from echolocation calls is important with respect to identifying the species emitting the calls.

Of the species examined in the present study, *P. parnellii* has been the most extensively investigated, primarily due to abundance, relative ease in obtaining specimens, and the use of a long CF–FM, otherwise only known for bats in the Rhinolophidae. Novick (1963) provided a detailed description of design of pulses and noted that earlier equipment provided less than satisfactory results. His verbal description and that illustrated by Simmons and Stein (1980) are identical to that found in this study (Fig. 3), although two harmonics were described by Novick (1963) and three were illustrated by Simmons and Stein (1980). Novick's (1963) description of the second harmonic with the CF at ca. 64 kHz corresponds to our findings (Table 2). Duration of pulses compare generally with those given by Novick (1963). A more detailed examination of changes in duration of pulse during approach and pursuit noted an increase in the CF portion from 20 msec at 4 m from the target to 28–32 msec 1.5–2.5 m from the target and then a rapid decline to 16–8 msec within 0.5 m of the target (Novick and Vaisnys, 1964). We observed several pursuit phases with the CF portion of the signals ranging from 15 to 11 msec.

Echolocation calls of *Pteronotus personatus* have been examined from Mexico (Novick, 1963, 1965) and from Panama (Simmons et al., 1979). Calls from Mexican individuals showed two to four harmonics, shorter duration, and higher minimum and maximum frequencies than found in the present study (Table 2). Novick (1965) described a frequency pattern with a lazy Z shape incorporating a short CF and an FM sweep terminating in a short CF. Pye (1973) described a similar call that sometimes had the terminal CF of ca. 1 msec. Calls from Panamanian individuals demonstrated three harmonics with an initial short CF at ca. 75 kHz and a terminal FM component to ca. 60 kHz for the third harmonic, estimated from the graphic display. In our study, search and orientation calls of unenclosed individuals contained the initial short CF component plus a consistent terminal CF that was a major portion of each call (Fig. 5). Individuals within an enclosure produced calls of shorter duration, lacking the terminal CF, and the consistent presence of a lower harmonic. Bats recorded in the previous studies were apparently in enclosed situations, which may account for the generally missing terminal CF. However, the initial short CF was a minimum of 13 kHz lower than that found by Novick (1963) and ca. 8 kHz higher than that reported by Simmons et al. (1979; Table 2). Similarly, the terminal CF was a minimum of 4 kHz lower (Novick, 1963) and ca. 8 kHz higher (Simmons et al., 1979) than previously reported. The differential in frequency ranges may be due to a variety of factors including the type of equipment used in earlier studies, flight conditions, and geographic variation.

Novick (1963) described an initial short CF–FM call with two harmonics for *P. davyi* in Mexico. We found this species in Belize to use orientation-search calls that were a short-CF, FM, and short-CF. Both CF components were absent during the terminal pursuit phase. Some calls in a sequence lacked the initial CF component. The initial and terminal CF components were 9 and 4 kHz lower, respectively, than Novick's (1963) values (Table 2). As with the preceding species, differences may be due to equipment, flight conditions, and geographic variation.

Information on echolocation calls of *Saccopteryx* and *Rhynchonycteris* is more var-

ied. In Trinidad (Bradbury and Emmons, 1974), calls of *S. bilineata* primarily featured low-frequency communication components, but did show several orientation or search calls with an apparent upsweep to ca. 60 kHz. A more detailed verbal description for this species in Costa Rica described paired cruising pulses with the first pulse ranging from 47 to 50 kHz and the second from 50 to 53 kHz (Bradbury and Vehrencamp, 1976). This alternating pattern of pulses was first described by Pye (1973), but calls were characterized as CF in nature. There was also the indication that pulses from bats in Trinidad were ca. 5 kHz lower. The quantitative information from Panama and Costa Rica (Barclay, 1983; Kalko, 1995) agree well with that from the present study (Table 1).

Pye (1973) noted a frequency difference of 2.5–3 kHz between the alternating CF calls of *S. bilineata*. He hypothesized that the LF calls were used for discrimination of targets, and the HF calls were used for navigation based on the presence of only LF calls were found during interception of targets. We found continued alternation of calls during the approach phase (Fig. 2), but the feeding buzz appeared to be only LF calls. Similarly, only HF calls were found unpaired, suggesting use for orientation or search for distant targets and supporting the above hypothesis. However, calls we recorded were not CF, rather a QCF signal consisting of an extended up sweep and shorter down-sweep portion similar to those signals described by Barclay (1983). As signals shortened during pursuit, the signals became more horseshoe-shaped, but the paired nature of initial LF followed by an HF component remained for all but the terminal feeding buzz (Fig. 2).

Barclay (1983) presented a compelling argument that the paired QCF signals may provide a wider bandwidth, thus providing more detailed acoustic information allowing use of cluttered habitat types. Kalko (1995) concluded that the four emballonurids in her study used CF–QCF for detection of prey and an FM component for evaluating position in relation to clutter. However, her study failed to show the use of an FM component in calls of *Saccopteryx*, implying the same conclusion as Barclay (1983). We found no prominent FM component in the calls of this species (Fig. 2).

Past examinations of echolocation signals from *R. naso* contained a high-frequency CF component (Table 1; Bradbury and Vehrencamp, 1976; Kalko, 1995). The described CF component was followed by a concave downward FM sweep. Bradbury and Vehrencamp (1976) noted the presence of two harmonics with the greatest energy in the second. We found *R. naso*, in Belize, to have two strong harmonics, although the first appeared dominant (Fig. 1). Systems using zero-crossing analysis, such as Anabat II, perceives the first harmonic as containing the greatest energy. The discrepancy between past and present studies may reflect differences in sensitivity of equipment. The vocal sequences for disturbed roosting individuals, demonstrating a progressive increase in frequency, has not been described before.

It is clear that the Anabat II bat detector provides detailed structural information of echolocation calls and that the calls of the species examined allow for accurate identification of free-flying individuals. The zero-crossings analysis provides an output that has more detail and clarity than sound spectrograms obtained with other equipment (e.g., Fenton and Bell, 1981; MacDonald et al., 1994). Harmonic and amplitude information are lost with this analytic approach, but neither has been proven to be important for use in identification of species. In fact, harmonic displays may add too much detail and obscure differences that would allow identification.

Establishment of such vocal signatures will aid in the ability to perform rapid and accurate inventories, establish activity patterns, use of habitat, and other aspects of the behavioral ecology of bat communities (Kalko, 1995). However, it is imperative to

establish the range of variation inherent in the vocal repertoire of each species. Geographic variation, temporal shifts in foraging strategies, and intraspecific and interspecific influences in patterns of calls need to be addressed. It also is important to establish the limitations of the equipment and the manner in which acoustic sampling is conducted. Properly performed, standardized, acoustic sampling will yield significant information for free-flying bats. Anabat appears to be a powerful tool for accomplishing such work.

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