ECHOLOCATION CALLS OF *PTERONOTUS DAVYI* (CHIROPTERA: MORMOOPIDAE) FROM PANAMA

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We studied echolocation signals broadcast by free-flying naked-backed bats (*Pteronotus davyi*) from Panama. Calls consisted of a segment of constant frequency, followed by a downward frequency modulated sweep, and ended with a short segment of quasi-constant frequency. Up to three harmonics were detectable. The second harmonic usually was more intense, and mean frequencies in the constant and quasi-constant segments were 68.0 and 58.0 kHz, respectively. Most pulses showed the highest intensity in the frequency corresponding to the constant segment of the second harmonic, but sometimes bats allocated most energy to the quasi-constant segment of that same harmonic or even to the constant or the quasi-constant segment of the fundamental harmonic. Pulses averaged 6.6 ms in duration and were repeated every 70.8 ms. The segment of constant frequency was always present, and its frequency changed little across extremely different behavioral situations.

Key words: *Pteronotus davyi*, naked-backed bat, echolocation, Panama, bats

The naked-backed bat (*Pteronotus davyi*) is a small mormoopid (forearm length, 41–50 mm; weight, 6.5–10 g) that is distributed from Mexico to Peru (Adams, 1989; Smith, 1972). However, little is known about its echolocation. Novick (1963*a*, 1963*b*) obtained a few recordings of one captive bat flying inside an enclosed space, and he described duration and rate of repetition of calls during search, approach, and terminal phases of echolocation (sensu Griffin et al., 1960). Pye (1980) also published a sonogram of *P. davyi* but provided no further information. More recently, O'Farrell and Miller (1997) described its echolocation calls in Belize but without presenting any information on harmonic structure. In this paper, we present a complete description of echolocation during the search phase in free-flying *P. davyi* in Panama and compare the structure of these pulses with calls emitted by a hand-held specimen. These data add to the comparative database on characteristics of echolocation systems, and provide a description of calls to aid in identification of the species using ultrasonic detectors. The usefulness of ultrasonic detection is illustrated with a survey of the species in the Coiba Archipelago, Panama.

MATERIALS AND METHODS

Recordings of *P. davyi* were obtained in January–February 1994 and March 1996 in Parque Nacional de Coiba, Panama, during a survey of bats (Ibáñez et al., 1997). The park comprised a group of islands off the Pacific coast of Panama, with Coiba the largest of these islands (ca. 7°30'N, 8°45'W). The survey included the islands of Coiba, Jicarón, Coibita o Ranchería, Canal de Afuera, Uva, and Brincanco. Vegetation on the islands was lowland rainforest (Pérez et al., 1996).

Flying bats were located by walking along paths for ca. 3 h after sunset while continuously scanning the ultrasonic spectrum from 10 to 150 kHz with an ultrasonic detector (model D-960—Pettersson Elektronik, Uppsala, Sweden) set to the heterodyne function. A second system consisting of an ultrasonic detector (model D-940—Pettersson Elektronik), ultrasonic microphone (model SM2—Ultrasound Advice, London, United Kingdom), preamplifier (model PS/2—Ultrasound Advice), and digital processor (model PUSP—Ultrasound Advice) also was used. When echolocation signals were detected, a sequence of ultrasounds (750 ms long with the D-960, and 2,230 ms long with the combined system) was captured with the expansion unit of the corresponding system. A sampling rate of 350 kHz with the D-960 or 448 kHz with the processor assured satisfactory recording of sounds ≤125 kHz. Stored sequences were played back 10 times slower and recorded onto metal audio tapes (model metal/XR—Sony, Tokyo, Japan) with a portable cassette recorder (model WM/D6C—Sony).

Sampling effort involved 5 nights on Coiba, 3 on Jicarón, 2 on Ranchería, 3 on Canal, 4 on Uva, and 1 on Brincanco. Before ultrasonic monitoring started, we set at least three mist nets (3 m high by 12 m long) under the canopy (lower end 1 m high). Nets were open and checked continuously while monitoring of sound occurred.

Characteristic signals of *P. davyi* were associated with the species after a male that was being monitored with an ultrasonic detector while flying was caught in a mist net. This specimen also was recorded later while being hand-held. Tapes were analyzed in the laboratory with a Kay DSP 5500 Sona-graph (Kay Elemetrics Corporation, Pine Brook, NJ). For each pulse, duration and period (time from beginning of the measured pulse to beginning of the previous one) were measured with 0.3 ms of resolution on a sonogram. An average power spectrum, built with 512 points fast-Fourier transforms with 30% overlap, was taken over each complete pulse, and frequency (in kHz) and amplitude (in dB with input levels held constant for all analyses) of each peak in the spectrum were recorded. The harmonic (fundamental, second, or third) and pulse segment (constant or quasi-constant) corresponding to each peak in the power spectrum also were recorded.

For all parameters, $\bar{X} \pm SD$ were calculated from mean values of each sequence (i.e., average of all pulses in the sequence). For period, we also calculated $\bar{X} \pm SD$ using all pulses from all sequences because distribution of this variable was obscured by averaging mean values. Duty cycle (100 × duration/period) also was calculated from individual pulses.

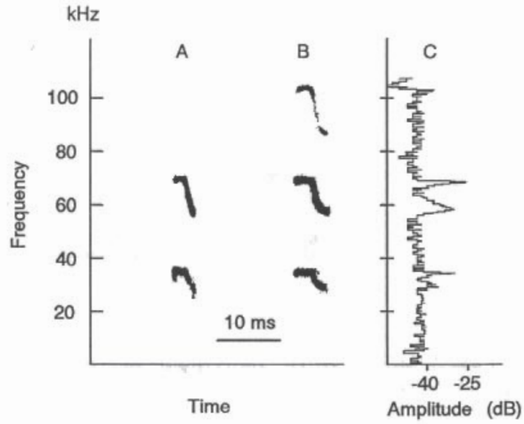

FIG. 1.—Sonogram of a pulse recorded from a) a hand-held *Pteronotus davyi* and b) under natural conditions. c) Power spectrum of call under natural conditions showing peaks of amplitude corresponding to the constant and quasi-constant components for the three harmonics.

RESULTS

Pteronotus davyi was found on Coiba (a netted male and seven sequences recorded at three sites) and the two islands closest to Coiba: Jicarón (five sequences at three sites) and Ranchería (18 sequences at two sites). The species was not detected on other islands. Four of 30 sequences that were recorded lacked pulses with enough intensity to be measured and were discarded. The remaining 26 sequences contained between one and 13 pulses (4.9 ± 3.3 pulses) suitable for analysis. All pulses likely represented search phases because sequences of approach or capture were never recorded.

Pulses showed up to three harmonics (Fig. 1b). The second harmonic was present in all calls (n = 127), the first harmonic was present in 77% of calls, and 23% showed the third harmonic. Pulses typically consisted of an initial segment of constant frequency, followed by a prominent, downward, frequency modulated sweep that ended in a short segment of quasi-constant frequency (Fig. 1b). Two conspicuous peaks

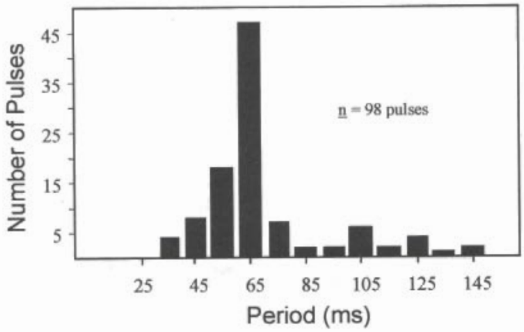

FIG. 2.—Period of individual echolocation pulses of *Pteronotus davyi.*

in amplitude appeared in each harmonic; one peak corresponded to the initial segment of constant frequency and the other to the terminal segment of quasi-constant frequency (Fig. 1c). Frequency with greatest intensity varied among and within harmonics. It usually corresponded to the segment of constant frequency in the second harmonic (61.4% of calls). However, frequency with maximum intensity was in the segment of quasi-constant frequency of the second harmonic in 26% of pulses, the segment of constant frequency of the first harmonic in 11%, and the segment of quasi-constant frequency of the first harmonic in 1.6%. Mean frequency of the constant segment was 68.0 ± 0.8 kHz, and frequency of the quasi-constant segment averaged 58.0 ± 0.9 kHz (n = 26 sequences, measured in the second harmonic). Calls had a duration of 6.6 ± 0.7 ms (n = 26 sequences). Pulse period averaged 70.8 ± 22.8 ms (n = 98 pulses) when measured across pulses and 76.6 ± 20.6 ms when measured across sequences (n = 21 sequences). Whether it was measured across pulses or sequences, distribution of that variable was highly skewed to the left, with a main peak at 65 ms (Fig. 2). Average duty cycle for 98 pulses was 10.1 ± 2.3%.

Calls from the hand-held male from Coiba (Fig. 1a) were clearly distinct from those recorded in the wild. Those from the hand-held bat never showed the third harmonic, and maximum intensity always was in the constant frequency segment of the first harmonic. They also lacked the quasi-constant segment, and consequently, they had only one peak of intensity, usually detectable only in the first harmonic. Frequency of the constant segment of the first harmonic averaged 34.3 ± 0.2 kHz, and mean duration of pulses was 3.9 ± 0.2 ms (n = 10 pulses).

DISCUSSION

In our survey, ultrasonic detectors were far more effective than netting in detecting *P. davyi.* In Coiba, Jicarón, and Ranchería, the species was found on 80% of the nights with ultrasonic detectors but captured in nets on only 10% of them. Presence of the species on two islands was detected only with the former method. Fenton et al. (1992) described mist-netting as a more appropriate method of sampling bats than acoustic detection in the Neotropics because of abundance of phyllostomids emitting faint echolocation calls. Nevertheless, ultrasonic monitoring shows a high effectiveness, relative to traditional netting, for the detection of some aerial insectivorous bats with distinctive echolocation calls, such as *P. davyi.*

Distribution of the pulse period of *P. davyi* (Fig. 2) is similar to that of other bats. In other species, the modal period matches the time of one wingbeat cycle (e.g., *Noctilio leporinus*—Schnitzler et al., 1994; European *Pipistrellus*—Kalko, 1994). Periods in the right tail of the distribution may be associated with short gliding flights without emission of sound, as they are in pipistrelles (Kalko, 1994). If *P. davyi* emits the search phase of echolocation at a rate of one pulse per wingbeat, as many other bats do (Jones, 1994), the highest peak of the pulse period at 65 ms would indicate a wingbeat rate of 15.4 Hz.

The frequency with the greatest intensity most commonly used by *P. davyi* (corresponding to the segment of constant frequency of the second harmonic) is above the range of frequencies heard by six species of moth from nearby Barro Colorado

Island (Fullard and Belwood, 1988). *P. davyi* feeds on Lepidoptera (Adams, 1989), and therefore, use of different harmonics in different instances could reflect a strategy to avoid detection by these potential prey, as predicted by the allotonic frequency hypothesis (Fenton and Fullard, 1979).

Novick (1963*a*, 1963*b*) described echolocation calls of *P. davyi* from a single captive individual from Mexico. Calls are similar in structure to those we obtained in Panama but ca. 3.5 ms shorter in duration, 10 kHz higher in frequency, and 5 kHz broader in bandwidth. The sonogram from *P. davyi* flying indoors published by Pye (1980) showed three harmonics. The second harmonic had a segment of constant frequency at ca. 70 kHz (Pye, 1980:234, fig. 3d). The recording system used by O'Farrell and Miller (1997) allowed detection of the dominant harmonic only. In their recordings from Belize, the dominant harmonic apparently was always the second. Frequencies of the constant and quasi-constant components (roughly corresponding to O'Farrell and Miller's minimum and maximum frequencies, respectively) were similar to our measures from Panama, but duration of calls from Belize was slightly shorter ($\bar{X}$ = 1.1 ms less). Differences in duration of calls between free-flying bats from Panama (this study) and Belize (O'Farrell and Miller, 1997) and a captive bat in Mexico (Novick, 1963*b*) are within the typical range of differences between calls broadcast in open versus indoor conditions (Griffin, 1986).

The large difference in frequency could be due to differences in equipment or behavioral settings (flying indoors versus in the open). However, data presented in our paper and by O'Farrell and Miller (1997) show that the frequency of echolocation calls of *P. davyi* are invariable across a range of behavioral settings. O'Farrel and Miller (1997) found that signals emitted by *P. davyi* flying inside an enclosure were similar to those emitted by free-flying individuals. We found that the constant frequency of the signals emitted by the hand-held bat from Panama was within the narrow range of variation in signals broadcast by free-flying conspecifics (Fig. 1). Calls in recent recordings of free-flying *P. davyi* from Michoacan and Colima, Mexico, have an average frequency of 72.5 kHz (range = 70.2–74.2 kHz) in the constant segment of the call (R. López-Wilchis, pers. comm.). It appears that at least some Mexican populations of *P. davyi* use pulses considerably higher in frequency than bats from Belize and Panama.

The frequency of the constant segment contained in the echolocation calls of *P. davyi* shows a narrow intrapopulational variation ($CV < 1.5\%$ in our recordings). Narrow intrapopulational variation and lack of behavioral plasticity in frequency are typically shown by bats with echolocation systems relying on narrow frequency analysis, such as paleotropical hipposiderids and rhinolophids or neotropical mormoopids (Fenton, 1994; Guillén, 1996; Vater, 1987). Presence of these patterns in *P. davyi* may indicate that this species also uses narrow frequency analysis.

Adaptation to environmental differences among sites is a hypothetical factor for explaining differences in frequency among populations of *P. davyi* that remains to be investigated. Bats recorded in Coiba and Belize live in tropical rainforest and subtropical moist forest, respectively. Recordings from Novick (1963*a*, 1963*b*) and R. López-Wilchis (pers. comm.) came from bats living in dry deciduous forest (Rzedowski, 1988). Heller and von Helversen (1989) noticed that species of horseshoe bats (genus *Rhinolophus*) living in wet environments used lower constant frequencies than those living in dry habitats. High frequencies are more severely attenuated in a humid atmosphere, and therefore, selection for lower frequencies may be expected under more humid conditions (Guillén, 1996; Heller and von Helversen, 1989).

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