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ACOUSTIC IDENTIFICATION OF MORMOOPID BATS: A SURVEY DURING THE EVENING EXODUS

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Echolocation calls emitted by the 4 species of Cuban mormoopid bats were compared to determine vocal signatures that enable identification of each species in the field during their evening exodus. Echolocation calls produced by *Mormoops blainvilli* are downward frequency-modulated (FM) signals in the range of 68.4–52.5 kHz. Echolocation calls emitted by *Pteronotus macleayii* and *P. quadridens* have a similar design consisting of a short constant-frequency (CF) segment followed by a downward FM segment. The CF segment was at 70.0 kHz in calls from *P. macleayii*, and at 83.3 kHz in calls from *P. quadridens*. Echolocation calls from *P. parnellii* consist of a long CF segment, which is preceded by a short initial upward sweep and followed by a downward FM terminal sweep. The CF value of the 2nd harmonic was a good parameter for species identification. The features of the echolocation calls of each of the species were used to identify them during the evening exodus from 2 Cuban caves.

Key words: echolocation, evening exodus, identification, mormoopid bats

Effective monitoring of echolocation calls is vital in many studies of the ecology and conservation of bats (Fenton 1997). Ultrasonic microphones, "bat detectors," have been developed to allow investigators to hear, "visualize," or both, the ultrasonic echolocation calls of bats (Hayes 1997; O'Farrell and Miller 1999; Sherwin et al. 2000). The use of acoustic detection has been shown to be a powerful supplement to standard capture methods to identify many insectivorous bats that are generally underrepresented in field inventories (O'Farrell and Miller 1999; O'Farrell et al. 1999).

It is argued that most bats could be identified by the frequency–time structure of their echolocation calls, with the exception of a number of species known to use low-intensity, short-duration calls that seem to differ little among species (e.g., phyllostomids—Griffin 1958; Hayes 2000; Jones et al. 2000; Kalko et al. 1996). Some authors have criticized the qualitative approach for acoustic identification of species of bats because of intraspecific variation resulting from geography, habitat, and species-assemblage factors (Barclay 1999; Barclay et al. 1999; Guillén et al. 2000). However, the low within-species variability in the echolocation calls of some families, such as Mormoopidae, should make it possible to use acoustic methods for species identification (Ibañez et al. 1999; Macías and Mora 2003; Mora et al. 2002; O'Farrell and Miller 1997; Schnitzler et al. 1987, in litt.).

Echolocation signals of mormoopid bats can readily be distinguished from calls of members of other families (Fenton 1994; Ibañez et al. 1999, 2000; Koessl et al. 1999; Macías and Mora 2003; O'Farrell and Miller 1999). However, interspecific identification of sympatric mormoopids has not been well studied.

Here, we describe the echolocation calls produced by the 4 species of Cuban mormoopids: *Pteronotus quadridens*, *P. macleayii*, *P. parnellii*, and *Mormoops blainvillei* in an enclosed space, showing that calls of these species are reliably identifiable. The usefulness of acoustic identification of Cuban species of this family was proved in an acoustic survey conducted during the evening exodus from their diurnal roost.

Materials and Methods

Echolocation calls from single individuals.—We captured 8 *M. blainvillei*, 4 *P. macleayii*, 5 *P. parnellii*, and 14 *P. quadridens* to characterize their echolocation calls while they were flying in cluttered space. Bats were captured using mist nets. After capture, each bat was released from the hand and allowed to fly in circles until several passes of echolocation calls were recorded in a bat-free, enclosed sector of a cave, measuring 4 × 3 × 3 m. Species identification was based on a key of external characters given by Silva (1979).

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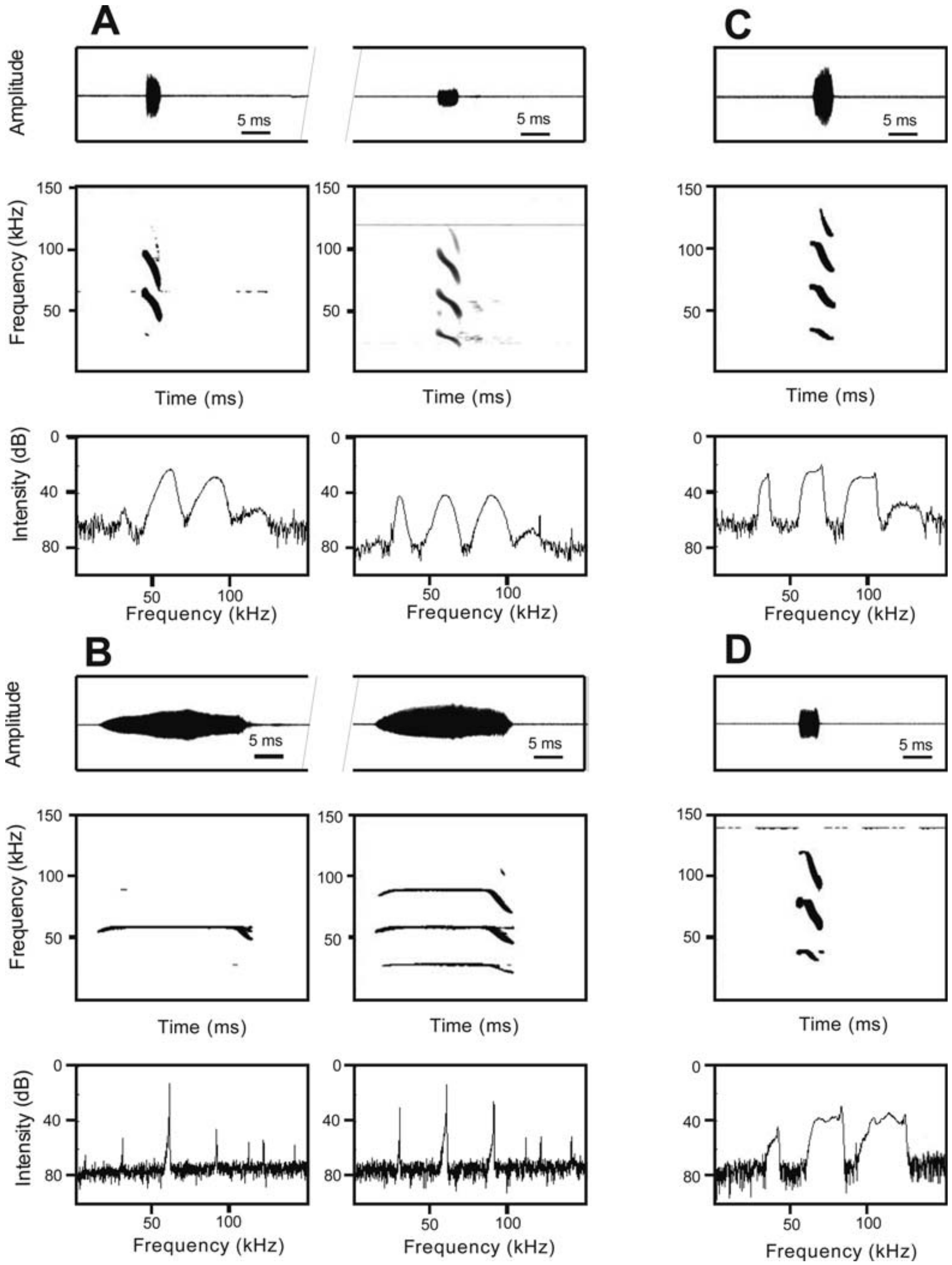

Fig. 1.—Representative oscillograms (above), spectrograms (middle), and power spectra (below) of the echolocation calls emitted by each of the 4 species of Cuban mormoopid bats while flying in a confined space. A) *Mormoops blainvillei*, B) *Pteronotus macleayii*, C) *P. parnellii*, and D) *P. quadridens*. *M. blainvillei* emits frequency-modulated signals, whereas *P. macleayii*, *P. quadridens*, and *P. parnellii* produce constant-frequency–frequency-modulated signals. Sonograms of *P. macleayii* and *P. quadridens* always show 3 harmonics, whereas *M. blainvillei* and *P. parnellii* vary their harmonic composition and sonograms show 2 or 3, or 1 or 3, harmonics, respectively.

Recording equipment and sound analysis.—Echolocation calls were recorded using an ultrasonic detector (U30 Ultra Sound Advice, London, United Kingdom) with flat sensitivity (± 2 dB) between 20 and 200 kHz. The detector's high-frequency output was fed to an analog–digital input port of a digital signal-processing board (model PCM-DAS 16S/330, Plug-In Electronic, Eichenau, Germany). The board was controlled with the commercial software BatSound 2.1 (Pettersson Elektronik AB, Uppsala, Sweden). Sampling frequency was set at 312 kHz. Echolocation calls were displayed simultaneously as spectrograms and temporal digitized recordings (oscillograms) with BatSound 2.1. Spectrograms were made of consecutive fast-Fourier transforms with a 99% overlap. Usually, a 512-point fast-Fourier transform was chosen to get a good compromise between frequency and time resolution. On oscillograms and spectrograms, time resolution was 0.1 ms. On spectrograms the frequency resolution was 610 Hz. To obtain power spectra, fast-Fourier transforms were calculated with 256–2,048 data points. Spectrograms and power spectra were made using a Hanning window. The length of the fast-Fourier

TABLE 1.—Mean values ± *SD* of acoustic parameters measured in the echolocation calls emitted by each of the studied mormoopid species (*Mormoops blainvillei*, *Pteronotus parnellii*, *P. macleayii*, and *P. quadridens*) while flying in a confined space. A comparison of the species calls was done with an analysis of variance for each of the parameters. *n* is the number of individuals. *P* shows very significant differences ($P < 0.01$) among the species. Lowercase letters represent the results of a Student–Newman–Keuls test ($P < 0.05$) applied to each parameter (a different from b; b different from c; c different from d). 1st, 2nd, and 3rd refer to 1st, 2nd, and 3rd harmonics of a call. Acoustic parameters are defined in the text.

	M. blainvillei ($n = 8$)	*P. parnellii* ($n = 5$)	*P. macleayii* ($n = 4$)	*P. quadridens* ($n = 14$)	*P*
DUR (ms)	2.42 ± 0.17 c 1.8[a]	21.23 ± 0.87 a 25–27[a] 30.4[b]	4.03 ± 0.07 b 2.9[a]	3.79 ± 0.14 b 3.1[a]	<0.01
CF 1st (kHz)		29.90 ± 0.46 c	35.51 ± 0.36 b	41.71 ± 0.37 a	<0.01
CF 2nd (kHz)		60.60 ± 0.08 c 61.3[a]	70.69 ± 0.43 b 71.2[a]	83.40 ± 0.36 a 77–83[a]	<0.01
DurCF 2nd (ms)		16.19 ± 0.11 a	1.22 ± 0.09 b 1[a]	1.24 ± 0.08 b 1.2[a]	<0.01
CF 3rd (kHz)		90.26 ± 0.15 c	105.18 ± 0.69 b	124.00 ± 0.60 a	<0.01
IF 1st (kHz)	33.33 ± 0.16 c	29.90 ± 0.46 d	35.51 ± 0.36 b	41.90 ± 0.22 a	<0.01
FF 1st (kHz)	25.76 ± 0.84 c	24.40 ± 0.53 c	28.17 ± 0.18 b	31.49 ± 0.19 a	<0.01
IF 2nd (kHz)	67.05 ± 0.45 c	60.60 ± 0.08 d	70.69 ± 0.43 b	83.40 ± 0.36 a	<0.01
FF 2nd (kHz)	48.14 ± 0.74 c	48.05 ± 0.61 c	54.94 ± 0.97 b	61.22 ± 0.38 a	<0.01
IF 3rd (kHz)	98.67 ± 0.42 c	90.26 ± 0.15 d	105.11 ± 0.74 b	124.00 ± 0.06 a	<0.01
FF 3rd (kHz)	78.45 ± 1.45 c	73.28 ± 1.07 d	83.73 ± 0.92 b	93.83 ± 0.47 a	<0.01
PF 1st (kHz)	30.94 ± 0.22 c	30.00 ± 0.08 c	34.92 ± 0.26 b	41.00 ± 0.19 a	<0.01
MINF 1st (kHz)	27.20 ± 0.26 c	29.73 ± 0.08 b	29.41 ± 0.04 b	30.15 ± 0.21 a	<0.01
MAXF 1st (kHz)	34.24 ± 0.18 c	30.21 ± 0.07 d	36.11 ± 0.29 b	42.05 ± 0.20 a	<0.01
BW 1st (kHz)	7.16 ± 0.30 ab	0.48 ± 0.03 c	6.66 ± 0.31 b	7.91 ± 0.22 a	<0.01
PF 2nd (kHz)	61.03 ± 0.44 c	60.00 ± 0.17 c	69.02 ± 0.55 b	80.92 ± 0.59 a	<0.01
MINF 2nd (kHz)	51.59 ± 1.07 c 49[a]	59.61 ± 0.16 b 54.5[b]	58.69 ± 0.65 b 55.2[a]	69.97 ± 0.59 a	<0.01
MAXF 2nd (kHz)	67.26 ± 0.51 c 68[a]	60.23 ± 0.16 d 63.5[b]	71.07 ± 0.44 b	83.21 ± 0.39 a	<0.01
BW 2nd (kHz)	15.67 ± 1.23 a	0.62 ± 0.05 b	12.37 ± 0.38 a	15.24 ± 0.51 a	<0.01
PF 3rd (kHz)	90.46 ± 0.78 c	90.01 ± 0.25 c	100.62 ± 1.25 b	113.24 ± 1.62 a	<0.01
MINF 3rd (kHz)	78.20 ± 0.76 c	89.57 ± 0.25 b	88.03 ± 2.37 b	100.42 ± 0.65 a	<0.01
MAXF 3rd (kHz)	99.00 ± 0.43 c	90.24 ± 0.25 d	106.21 ± 0.79 b	123.71 ± 0.57 a	<0.01
BW 3rd (kHz)	19.79 ± 0.63 b	0.67 ± 0.02 c	18.47 ± 1.55 b	23.28 ± 0.67 a	<0.01

[a] Schnitzler et al. 1990.

[b] O'Farrell and Miller 1997.

transforms to construct the power spectra was chosen according to the length of the signals.

The following parameters were measured or calculated in each echolocation call recorded with a maximum intensity of more than 20 dB above the ambient noise level: (1) duration of the signal (DUR), time between the start and the end of a pulse, measured in ms from the oscillogram; (2) initial frequency (IF) and (3) final frequency (FF), measured in the spectrogram in kHz; (4) value of the constant-frequency (CF) segment, measured in kHz from the spectrogram; (5) peak frequency (PF), frequency in kHz, corresponding with the maximum value in the power spectrum; (6) minimal frequency (MINF) and (7) maximal frequency (MAXF), lowest and highest values, respectively, of frequency measured 20 dB below maximum intensity in the power spectrum; (8) bandwidth (BW), calculated as the difference between maximal and minimal frequencies; (9) slope of frequency modulation of the frequency-modulated (FM) segment of the 2nd harmonic (SFM2nd), calculated by the ratio difference in kHz between the initial and final frequency of the segment to the duration of the segment; and (10) duration of the CF segment (DurCF) of the 2nd harmonic, measured in ms in the spectrogram. Metrics 2 through 8 were measured in each of the harmonics of the calls.

Statistical procedures.—For each species, descriptive statistics (mean ± *SD* and ranges) were calculated. Univariate inferential procedures, analysis of variance (ANOVA), and Student–Newman–Keuls test were used to test for differences between species. All tests were performed with STATISTICA for Windows version 6.0 (StatSoft, Inc. 2001). In all tests, values of $P < 0.05$ were considered significant.

Acoustic survey.—We sampled the echolocation calls emitted by mormoopid bats while they were leaving their diurnal roost during the evening exodus at 2 caves located in Havana Province, Cuba. Acoustic surveys were done at Indio Cave (30.3 km southeast from Havana City) during 30 June and 2 and 3 July 2001 and at Numancia Cave (57.6 km southeast from Havana City) during 24 July and 29 and 2 August 2001.

At each cave, recording equipment was positioned at the main horizontal entrance. The bat detector was pointed directly at the entrance ensuring that in every recording, bats were flying toward the microphone. Every 5 min, recordings of 3-s duration were recorded. We began sampling at 2000 h and finished at 2200 h.

RESULTS

Description of echolocation calls by species.—We evaluated 689 echolocation calls from individuals of the 4 species of Cuban mormoopid bats flying in an enclosed space (179 calls of *M. blainvillei*, 165 of *P. parnellii*, 171 of *P. macleayii*, and

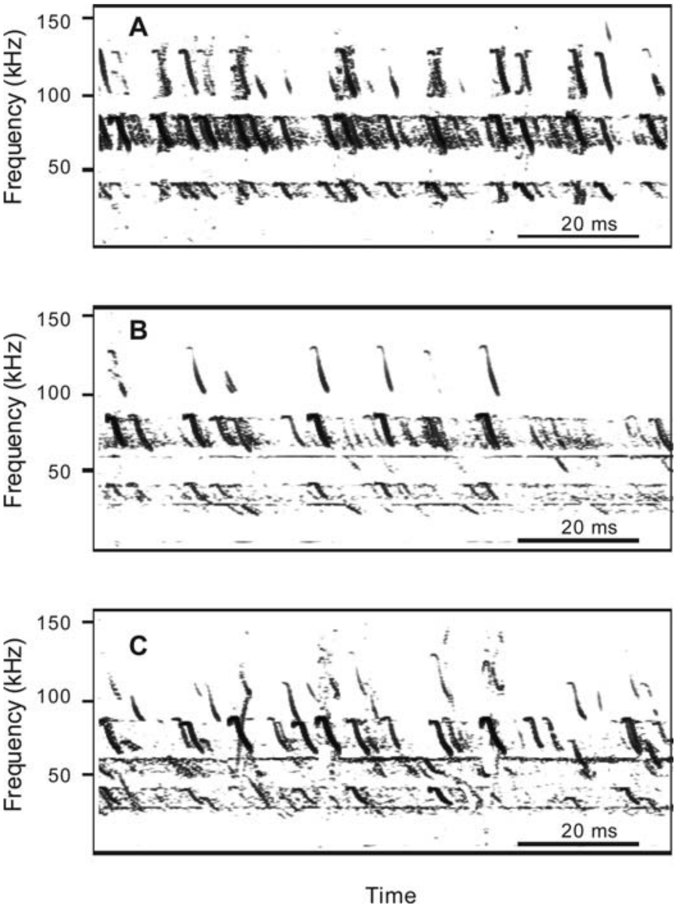

Fig. 2.—Representative spectrograms from recordings made during the evening exodus of mormoopid bats from Numancia cave. A) Time = 2020 h; showing only calls from *Pteronotus quadridens*. B) Time = 2030 h; showing calls from *P. quadridens* and *P. parnellii*. C) Time = 2050 h; showing calls from *P. quadridens*, *P. parnellii*, and *P. macleayii*. Values and lengths of the constant-frequency portion of each harmonic make it possible to differentiate between the 3 species. The 3 recordings shown were made in the same night.

174 of *P. quadridens*). From these recordings, we describe the characteristics of echolocation calls of each species and the variations we encountered.

Echolocation calls produced by *M. blainvillei* are FM signals. Generally, the signals contained 3 harmonics; the 2nd and 3rd harmonics were always detected, whereas the 1st and 4th harmonics were typically present but often detected at least 20 dB lower than the 2nd harmonic (Fig. 1A). The echolocation calls of *P. parnellii* consist of a rather long CF segment (at about 60 kHz in the 2nd harmonic), which is preceded by a short initial upward sweep and followed by a downward FM terminal sweep. The signals contain 3 harmonics with most energy in the 2nd harmonic. However, in 47 (28%) of the calls, the 2nd harmonic was detected at least 20 dB more than the 1st or 3rd harmonics (Fig. 1B).

Echolocation calls of *P. macleayii* (Fig. 1C) and *P. quadridens* (Fig. 1D) were similar. They produce signals of about 3.8 ms consisting of a short CF segment followed by a downward FM component. However, they can be differentiated by their spectral characteristics. The CF segment of the 2nd harmonic in calls emitted by *P. macleayii* is lower (67.5–73.4 kHz) than calls by *P. quadridens* (78.9–86.8 kHz), with no overlap of frequency of the CF segment in these 2 species. Echolocation signals of *P. macleayii* and *P. quadridens* always contain 3 harmonics, with most of the energy in the 2nd one. Results of the comparison of the acoustic parameters using ANOVA and the Student–Newman–Keuls test indicate statistically significant differences in all the measured parameters of the echolocation calls of the 4 species (Table 1).

Acoustic survey during the evening exodus.—An acoustic survey was done to identify each species during the evening exodus (Fig. 2). The 1st type of echolocation calls recorded at the entrance of the cave were CF-FM calls with CF values of the 3 harmonics at about 41, 83, and 124 kHz, respectively, thus corresponding to *P. quadridens* (Fig. 2A). About 5 min later there were, in addition, calls of 3 harmonics with an initial upward FM component followed by a long CF portion (at 61 kHz, 2nd harmonic) and a downward FM segment, characteristic of calls emitted by *P. parnellii* (Fig. 2B). Later, recordings show calls of *P. quadridens*, *P. parnellii*, and CF-FM calls with the CF value of the 3 harmonics at 34, 70, and 104 kHz, respectively, corresponding to *P. macleayii* (Fig. 2C). At none of the caves did we record echolocation calls of *M. blainvillei*.

In the sonograms recorded during the exodus, we measured CF value of the 2nd harmonic to validate if it is a good parameter for the acoustic identification of the 3 *Pteronotus* species. Although the CF mean value of the 2nd harmonic in the echolocation calls emitted during the evening exodus was slightly higher, these values were in the range of values of those calls emitted while bats were flying in the confined space (Fig. 3). Thus, the CF value of the 2nd harmonic appears to be a reliable variable for the accurate identification of these species. We calculated the difference between the CF values of calls emitted while bats were flying out of the cave and those of the calls emitted in the confined space and compared their mean values. The lowest mean value of shift is present in *P. parnellii* (Student–Newman–Keuls test, *P. macleayii*: 2.45 ± 1.36 kHz; *P. quadridens*: 1.93 ± 1.75 kHz; *P. parnellii*: 0.94 ± 0.68 kHz; $P < 0.001$).

DISCUSSION

Identification of mormoopids based on their echolocation calls.—Insectivorous bat species from the family Mormoopidae exhibit the lowest level of interspecific variation in design of their echolocation calls among insectivorous species thus far studied (Fenton 1994; Ibañez et al. 1999; Macías and Mora 2003; Vater 1978). The echolocation calls of mormoopids consist mainly of multiharmonic signals with a short CF component followed by an FM segment. This design is a general feature across the mormoopid species of the genus *Pteronotus* (Ibañez et al. 1999, 2000; O'Farrell and Miller 1997; Schnitzler and Kalko 1998). The design of the echolocation signals of the Cuban species of *Pteronotus* is similar to that described for other species of the same genus at other localities (Ibañez et al. 1999, 2000; O'Farrell and Miller

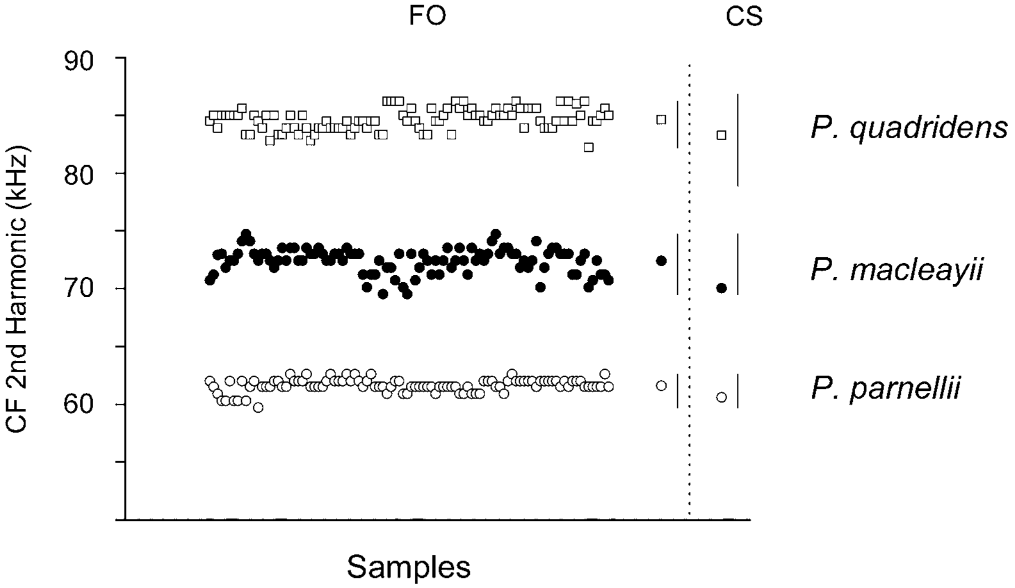

Fig. 3.—Constant-frequency values of the 2nd harmonics (CF 2nd harmonic) of 100 echolocation calls (samples) emitted by *Pteronotus quadridens*, *P. macleayii*, and *P. parnellii* while flying out (FO) of the cave. Also shown are mean values and ranges (vertical lines) of the 3 species flying out of the cave and while flying in a confined space (CS).

1997; Schnitzler and Kalko 1998; Schnitzler et al. 1990), as well as that from *Mormoops* (Rydell et al. 2002). The only differences are in the value of the parameters that characterize the calls, possibly due to body size (Jones 1999). The values of parameters of the calls of Cuban mormoopids are within the range of values described elsewhere (O'Farrell and Miller 1997; Schnitzler et al. 1990; Table 1).

The similarity between structure of calls between Cuban and mainland species could be explained by their origin, by the correspondence of foraging conditions, or both. Mormoopid bats have a wide continental distribution (Nowak 1994). Koopman (1989) pointed out that possibly *Pteronotus* and *M. blainvillei* have their origin in Central America. In addition, we cannot exclude the possibility that this latter species arrived in the Greater Antilles following the North Route, based on the relationships between populations from Cuba and Florida (Koopman 1989). On the other hand, it has been extensively demonstrated that the design of echolocation signals is partially determined by the structure of the areas used by bats for foraging (Schnitzler and Kalko 1998). Species of *Pteronotus* use echolocation calls to search for insects in areas of high structural clutter (Ibañez et al. 1999, 2000; O'Farrell and Miller 1997, 1999; Schnitzler and Kalko 1998; Schnitzler et al. 1990; Simmons and Stein 1980).

In contrast with some other bat species, such as *Tadarida brasiliensis* (Simmons et al. 1978) and *Molossus molossus* (Mora et al. 2004), which dramatically change the structure of their echolocation calls depending on their behavior, the structure of echolocation calls from Cuban *Pteronotus* flying in confined spaces is similar to that used when the bats are emerging from their diurnal roost or when hunting (Macías and Mora 2003; Schnitzler et al. 1987). Thus, the analysis of the echolocation calls of the Cuban *Pteronotus* showed that each species could be identified by the structure of its echolocation calls in at least 2 different behavioral contexts. Furthermore, even though species of *Pteronotus* share similar designs of their echolocation calls, the frequency of the CF segment, particularly in the 2nd harmonic, could be used for accurate identification of the species.

Doppler shift.—Doppler shifts are frequency changes brought about by the relative motion between a sound source and a sound detector. In echolocating bats, signals are Doppler-shifted in proportion to flight velocity or movement of an echoic surface (Gaioni et al. 1990; Keating et al. 1994). The CF values of the 2nd harmonic of the echolocation calls of the 3 species recorded in the evening exodus are slightly higher than those recorded from the bats flying in confined space (Fig. 3). This could be attributed to the differences in the recordings situations. In the confined space, we recorded the bats flying both toward and away from the microphone. Thus, frequencies of recorded echolocation calls are affected by positive and negative Doppler shift. In recordings made while bats were flying out of the caves, the microphone was pointed directly toward the entrance. Therefore, only positive changes in frequency due to Doppler shift would be expected. Consequently, the mean value of the CF of the 2nd harmonic is higher than that in calls recorded in the confined space.

It has been demonstrated that *P. parnellii* decreases the frequency of its emissions in such a way that the frequency of the returning echo is stabilized in a narrow band to which the ear is tuned (Schnitzler 1970). This Doppler-shift compensation process also has been highly perfected in horseshoe bats (Rhinolophidae) of the Old World (Keating et al. 1994; Schnitzler 1970; Vater et al. 2003). The lower shift found in *P. parnellii* could be explained by its Doppler-shift compensation, which may be not present in the other species, or by lower flight speed for *P. parnellii* (Henson 1970; Norberg and Rayner 1987; Silva 1979; Vater et al. 2003).

RESUMEN

Se compararon las llamadas de ecolocalización emitidas por las 4 especies de murciélagos cubanos pertenecientes a la familia Mormoopidae, para determinar firmas vocales que posibiliten la identificación de estas especies en el campo durante su éxodo nocturno. Al volar en espacios cerrados, cada especie emite típicamente llamadas de ecolocalzacion compuestas por 3 armónicos, difiriendo en sus características espectrales y temporales. *Mormoops blainvillei* emite llamadas de frecuencia modulada (FM) descendente en una gama de frecuencias entre 68.4–52.5 kHz. Las llamadas emitidas por *Pteronotus macleayii* y *P. quadridens* presentan un patrón similar que consiste en un segmento corto de frecuencia constante (FC) seguido de uno de frecuencia modulada descendente. El segmento de FC se encuentra en 70.0 kHz en las llamadas de *P. macleayii* y en 83.3 kHz en las llamadas de *P. quadridens*. Las llamadas de *Pteronotus parnellii* consisten en un segmento de FC de larga duración precedido por un componente de FM ascendente y seguido de un componente de FM descendente. Las llamadas de mayor duración son emitidas por *P. parnellii* (20.6 ms) y las llamadas más cortas son emitidas por *M. blainvillei* (2.4 ms), mientras las llamadas de *P. macleayii* y de *P. quadridens* presentan duraciones intermedias, entre 3.9 y 3.8 ms, respectivamente. Estas especies pueden ser identificadas por las características espectrales y temporales de sus llamadas de ecolocalización. El valor de frecuencia constante del segundo armónico es un buen parámetro para la identificación acùstica de cada especie.

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LITERATURE CITED

BARCLAY, R. M. R. 1999. Bats are not birds—a cautionary note on using echolocation calls to identify bats: a comment. Journal of Mammalogy 80:290–296.

BARCLAY, R. M. R., J. H. FULLARD, AND D. S. JACOBS. 1999. Variation in the echolocation calls of the hoary bats (*Lasiurus cinereus*): influence of body size, habitat structure, and geographic location. Canadian Journal of Zoology 77:530–534.

FENTON, M. B. 1994. Echolocation: its impact on the behaviour and ecology of bats. Ecoscience 1:21–30.

FENTON, M. B. 1997. Science and the conservation of bats. Journal of Mammalogy 78:1–14.

GAIONI, S. J., H. RIQUIMAROUX, AND N. SUGA. 1990. Biosonar behavior of mustached bats swung on a pendulum prior to cortical ablation. Journal of Neurophysiology 64:1801–1817.

GRIFFIN, D. R. 1958. Listening in the dark. Yale University Press, New Haven, Connecticut.

GUILLÉN, A., J. JUSTE, AND C. IBAÑEZ. 2000. Variation in the frequency of the echolocation of *Hipposideros rubber* in the Gulf of Guinea: an exploration of the adaptive meaning of the constant frequency value in rhinolophid CF bats. Journal of Evolutionary Biology 13:70–80.

HAYES, J. P. 1997. Temporal variation in activity of bats and the design of the echolocation-monitoring studies. Journal of Mammalogy 78:514–524.

HAYES, J. P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. Acta Chiropterologica 2:225–237.

HENSON, O. W. 1970. The ear and audition. Pp. 181–256 in Biology of bats (W. A. Wimsatt, ed.). Academic Press, New York.

IBAÑEZ, C., A. GUILLÉN, J. JUSTE AND J. L. PÉREZ-JORDÁ. 1999. Echolocation calls of *Pteronotus davyi* (Chiroptera: Mormoopidae) from Panama. Journal of Mammalogy 80:924–928.

IBAÑEZ, C., R. LÓPEZ-WILCHIS, J. JUSTE, AND M. LEÓN-GALVÁN. 2000. Echolocation calls and noteworthy record of *Pteronotus gymnonotus* (Chiroptera: Mormoopidae) from Tabasco, Mexico. Southwestern Naturalist 45:345–347.

JONES, G. 1999. Scaling of echolocation call parameters in bats. Journal of Experimental Biology 202:3359–3367.

JONES, G., N. VAUGHAN, AND S. PARSONS. 2000. Acoustic identification of bats from directly sampled and time expanded recording of vocalizations. Acta Chiropterologica 2:155–171.

KALKO, E. K. V., C. O. HANDLEY, JR., AND D. HANDLEY. 1996. Organization, diversity, and long term dynamics of a neotropical bat community. Pp. 503–553 in Long term studies of vertebrate communities (M. L. Cody and J. A. Smallwood, eds.). Academic Press, New York.

KEATING, A. W., O. W. HENSON, M. M. HENSON, W. C. LANCASTER, AND D. H. XIE. 1994. Doppler-shift compensation by the mustached bat: quantitative data. Journal of Experimental Biology 188: 115–129.

KOESSL, M., F. MAYER, G. FRANK, M. FAULSTICH, AND I. J. RUSSELL. 1999. Evolutionary adaptations of cochlear function in Jamaican mormoopid bats. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 185:217–228.

KOOPMAN, K. F. 1989. A review and analysis of the bats of the West Indies. Pp. 635–644 in Biogeography of the West Indies: past, present, and future (C. A. Woods, ed.). Sandhill Crane Press, Inc., Gainesville, Florida.

MACÍAS, S., AND E. C. MORA. 2003. Variation of echolocation calls of *Pteronotus quadridens* (Chiroptera: Mormoopidae) in Cuba. Journal of Mammalogy 84:1428–1436.

MORA, E., ET AL. 2002. Aplicación de métodos biocùaticos y convencionales en la caracterización de la comunidad de murciélagos de la Cueva del Indio, Tapaste, La Habana, Cuba. Biología 16:159–166.

MORA, E. C., S. MACÍAS, M. VATER, F. CORO, AND M. KOESSL. 2004. Specializations for aerial hawking in the echolocation system of *Molossus molossus* (Molossidae, Chiroptera). Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 190:561–574.

NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 316:337–419.

NOWAK, R. M. 1994. Walker's bats of the world. Johns Hopkins University Press, Baltimore, Maryland.

O'FARRELL, M. J., C. CORBEN, W. L. GANNON, AND B. W. MILLER. 1999. Confronting the dogma: a reply. Journal of Mammalogy 80: 297–302.

O'FARRELL, M. J., AND B. W. MILLER. 1997. A new examination of echolocation calls of some neotropical bats (Emballonuridae and Mormoopidae). Journal of Mammalogy 78:954–963.

O'Farrell, M. J., and B. W. Miller. 1999. Use of vocal signatures for the inventory of free-flying neotropical bats. Biotropica 31:507–516.

Rydell, J., H. T. Arita, M. Santos, and J. Granados. 2002. Acoustic identification of insectivorous bats (order Chiroptera) of Yucatán, Mexico. Journal of Zoology (London) 257:27–36.

Schnitzler, H.-U. 1970. Comparison of echolocation behavior in *Rhinolophus ferrum-equinum* and *Chilonycteris rubiginosa*. Bijdragen tot de Dierkunde 40:77–80.

Schnitzler, H.-U., and E. K. V. Kalko. 1998. How echolocating bats search and find food. Pp. 183–204 in Bat biology and conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.

Schnitzler, H.-U., E. K. V. Kalko, L. Miller, and A. Surlykke. 1987. The echolocation and hunting behavior of the bat, *Pipistrellus kuhli*. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 161:267–274.

Sherwin, R. W., W. Gannon, and S. Haymond. 2000. The efficacy of acoustic techniques to infer differential use of habitat by bats. Acta Chiropterologica 2:145–153.

Silva, G. 1979. *Los murciélagos de Cuba*. Editorial Academia, La Habana, Cuba.

Simmons, J. A., et al. 1978. Echolocation by free-tailed bats (*Tadarida*). Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 125:291–299.

Simmons, J. A., and R. A. Stein. 1980. Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 135:61–84.

StatSoft, Inc. 2001. Statistica (data analysis software system). Version 6. StatSoft, Inc., Tulsa, Oklahoma.

Vater, M. 1978. Narrow-band frequency analysis in bats. Pp. 200–225 in Recent advances in the study of bats (M. B. Fenton, P. Racey, and J. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

Vater, M., M. Kössl, E. Foeller, F. Coro, E. Mora, and I. J. Russell. 2003. Development of echolocation calls in the mustached bat, *Pteronotus parnellii*. Journal of Neurophysiology 90:2274–2290.

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