The Echolocation Repertoire of *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in Cuba

Annia Rodríguez and Emanuel C. Mora*

Department of Animal and Human Biology, Faculty of Biology, Havana University
calle 25 No. 455 entre J e I, Vedado, CP. 10 400, Ciudad de La Habana, Cuba
*Corresponding author: emanuel_mora@yahoo.com

ABSTRACT.—The echolocation behavior of *Eptesicus fuscus* was studied in the field in western Cuba. Bats leaving their roost produce short calls of around 2.3 ms showing two harmonics with a downward frequency modulation between 75 and 33 kHz in the first harmonic. During hunting, search calls typically show a single harmonic with a downward frequency modulation at the beginning of the signal, followed by a quasi-constant frequency component. Search calls are characterized by durations shorter than 8 ms and bandwidths of approximately 16 kHz. The minimal frequency is maintained rather constant around 33 kHz. Transitions from the search to the approach and terminal phases are characterized by an increase in duty cycle as a consequence of the increase in pulse repetition rate and the decrease in duration. Calls emitted in the laboratory are similar to those emitted in the wild. Compared with the echolocation repertoire of *E. fuscus* in North America, shorter calls with constant minimal frequencies are characteristic of this species in Cuba.

KEYWORDS.—bats, echolocation, *Eptesicus fuscus*

INTRODUCTION

Echolocation is tightly linked to the biology of microchiropteran bats and assists them to navigate the air and to find food (Griffin 1958). Variations described in the echolocation repertoire of several bat species were explained as adaptations of call designs to solve different perceptual tasks (Simmons and Stein 1980; Mora et al. 2004), as geographic variations (Thomas et al. 1987; Barclay et al. 1999), and as changes devoted to transmit information to other conspecifics (Fenton et al. 2004; Pearl and Fenton 1996).

The echolocation system of the big brown bat, *Eptesicus fuscus*, has been extensively studied in laboratory experiments (Covey and Casseday 1995; Simmons 1973; Simmons et al. 1995; Hartley and Suthers 1989). However, data on its echolocation call repertoire in the field are limited to Griffin’s work (1958), scarce detector recordings (Bett 1998) and cursory data in reviews and papers focusing on other aspects of echolocation (Simmons et al. 1979; Masters et al. 1995; Obrist 1995). Only recently, Surlykke and Moss (2000) presented an extensive description of the echolocation call repertoire of the North American *E. fuscus* both in the wild and in the laboratory.

Geographic variations in the echolocation repertoire of *E. fuscus* are known of populations from the East and West coast of the United States of America (Fenton 1995). However, the wide distribution of *E. fuscus* in North and South America, as well as in Bahamas and the Greater Antilles, predicts the existence of a higher degree of geographic variations in the echolocation behavior of this species.

In this paper we describe the echolocation behavior of *Eptesicus fuscus* in Cuba. Bats were studied under different flying conditions: 1) during their hunting behavior in the wild; 2) flying out of their natural roost; and 3) flying in the laboratory. We then discuss the differences between the echolocation behavior of *E. fuscus* in Cuba and in North America.
MATERIALS AND METHODS

Species identification and field locations

We studied the echolocation behavior of *Eptesicus fuscus* (Chiroptera: Vespertilionidae) at three different localities of Havana Province, western Cuba, between November, 2001 and September, 2003. In each locality bats were observed living in caves, with colonies of animals in cracks and narrow fissures of the cave ceiling. Species identification follows Silva (1979). Each animal was released immediately after identification, except for 10 of them that we used for laboratory recordings. Recordings of the bat's hunting behavior were made within 1 km around colonies. In each case the bats were hunting for insects while flying at heights up to 5 m above ground level in an area with scarce bushed vegetation. Recordings from bats flying out of the roost were made during their evening exodus. The study was conducted between 18:00 to 22:00 hours, a period corresponding to the first peak of *E. fuscus*’ nocturnal activity.

Sound recordings

We recorded the echolocation calls using an U30 Ultrasound Advice ultrasonic detector (London, UK) with a flat response characteristic (± 2 dB) between 20 and 200 kHz. During the recording sessions the heterodyne output was tuned to 35 kHz, thus allowing the acoustic monitoring of individuals. The high frequency output of the bat detector was fed into an analog–digital input port of a digital signal–processing board (model PCM-DAS 16S/330) which was controlled with the commercial software BatSound 2.1 (Pettersson Elektronik). Calls were recorded at a sampling frequency of 312 kHz. We analyzed recordings sequences with at least 5 pulses of good signal noise ratio (peak intensity with more than 20 dB above noise level measured in the power spectra). A database with 4 h of recordings (from which 34 sequences and 475 calls were finally selected) was available for the analysis of echolocation.

As they usually fly in small circles of less than 10 m in diameter, each *E. fuscus* was visually followed during the recordings. The microphone was always directed to solitary bats and care was taken to record only bats approaching the microphone. In the same area we recorded different bats one after the other to be confident about the source of the echolocation passes.

Recordings in an enclosed space were made from 10 bats, which were liberated individually in a laboratory room (6 m x 6 m x 3 m). For recording bats flying out of their roost the microphone was placed at the entrance of their roosting cave.

Sound analysis

Sequences of echolocation calls were displayed simultaneously as spectrograms, and temporal digitized recordings (oscillograms) using BatSound 2.1. Spectrograms were made of consecutive fast Fourier transforms (FFT’s) with a 99% overlap. Time was measured manually on the screen. On oscillograms time resolution was 0.1 ms. To obtain power spectra, FFT’s were calculated using 1024-2048 data points.

From each call that registered a maximal intensity of more than 20 dB above noise level we measured the following parameters: (1) duration (time between start and end of a call, measured in ms in the oscillogram); (2) peak frequency (frequency in kHz corresponding with maximal intensity in the power spectrum); (3) minimal and (4) maximal frequency, respectively, lower and higher values of frequency measured 20 dB below maximal intensity in the power spectrum; (5) bandwidth (calculated as difference between maximal frequency and minimal frequency); (6) \( Q_{10-dB} \) (calculated as peak frequency divided by bandwidth measured 10 dB below maximal intensity); (7) slope of frequency modulation (calculated by the following ratio: difference in kHz between the initial and final frequency of the call divided by the duration of the call). The variables included in parameter 7 were measured in the spectrogram. In each call sequence we measured interpulse interval from the beginning of a call to the start of next call.
Since our sample included more than one recording from the same individual, to minimize pseudoreplication, the parameters of each pass of a bat were averaged and treated as a single measurement before further analysis. All the values of the acoustic parameters are given as mean ± 1 SD. Since the data sets were not normally distributed (Kolmogorov-Smirnov test), we used nonparametric statistics (Kruskal-Wallis ANOVA). Statistical differences between several mean values were analyzed with a nonparametric Dunn’s post-hoc test (identical letters mean no statistically significant difference between the means). Correlation analysis (Spearman’s coefficient) was used to explore the strength of relationship between acoustic parameters. All analyses were made using the mean values for each pass and the level of significance was $\alpha = 0.05$.

A multivariate discriminant function analysis (DFA) was performed. The parameters used in this analysis were: duration, maximal frequency, minimal frequency, slope, peak frequency, and $Q_{10\text{-}dB}$. The cases were each of the situations and conditions of the recordings (e.g., flying from the roost, flying in the room, search, approach, and terminal phases of the hunting behavior). The DFA was employed to observe if cases could be separated in independent groups. The statistical $\lambda_{\text{partial}}$ was used to determine the contribution of each parameter to the classification of each case.

**RESULTS**

*Bats flying out of the roost*

Bats leaving their roost during the beginning of their evening foraging activity produced short calls ($2.3 \pm 0.5$ ms; $N = 8$ passes, 71 calls) with two harmonics overlapped in frequency when measured in the power spectra 20 dB below peak intensity. Each call is a downward frequency modulated sweep with the first most prominent harmonic between 75 and 33 kHz (Fig. 1A, Table 1). Calls were emitted during the first second of flight with an average interval of $63.0 \pm 24.9$ ms.

Bats leaving the roost emitted calls that increased in duration as the animals flew further away from the colony entrance and decrease in frequency slope modulation. The minimal frequency, however, remained constant at about 33 kHz (Fig. 1B).

*Fig. 1*. A. Oscillogram (above) and spectrogram (below) of the echolocation calls emitted by *Eptesicus fuscus* when leaving the roost during the beginning of their evening foraging activity. B. Above: Acoustic parameters characteristics of the calls shown in (A).

*Bats hunting in the field*

*Eptesicus fuscus*, hunting in the wild in Cuba, emitted search calls of a single harmonic above which occasionally appeared a very faint (more than 20 dB difference in intensity) second harmonic (Fig. 2). At the beginning of the signal, the calls show a downward frequency modulation, followed by a quasi-constant frequency component (Fig. 2). Search calls are characterized by durations shorter than 8 ms and bandwidths of approximately 16 kHz. As evidenced by a variation coefficient of 2.5, the smallest among the acoustic parameters, the minimal frequency is maintained rather constant around 33 kHz. Search calls are emitted at intervals of $87.7 \pm 19.2$ ms.

Calls emitted during the approach phase
show a similar design to search calls (Fig. 2B). The start of the approach phase was defined as the first signal in the sequence with a monotonic change in the parameter duty cycle that increased as a consequence of the increase in pulse repetition rate (inverse of PI) and a decrease in duration; this indicated a bat reacting to a potential prey (Fig. 3). Of four approaching sequences which grouped 53 calls, the shortest contained 6 and the longest 17 approach calls.

In the terminal phase (N = 42 calls distributed in 3 sequences), E. fuscus emitted steep downward modulated frequency signals (Fig. 2). The beginning of the final buzz is characterized by an abrupt increase in pulse repetition rate and a decrease in call duration (Fig. 3).

While hunting, E. fuscus operates at duty cycles below 20%. In addition, it keeps the minimal frequency of its calls relatively constant at around 33 kHz during the search and approach phases and only during the terminal phase drops below 25 kHz (Fig. 3; Table 2). As a consequence, changes in bandwidth are correlated (R = 0.98; N = 42 passes) with the maximal frequency (Fig. 4), which implies that broader signals are achieved by increasing this parameter.

Call duration is also correlated with bandwidth and thus with maximal frequency (R = -0.68) but not with minimal frequency (R = -0.09; N = 42; p = 0.55). In addition, call duration is correlated with the interpulse interval. The minimum values of interpulse intervals correspond to

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**TABLE 1.** Results of Kruskal-Wallis test used in the comparison of the echolocation calls emitted by *Eptesicus fuscus* when leaving the roost, during the foraging activity (represented by the search calls) and flying in an enclosed space. Number of calls analyzed in each behavioral situation is in parenthesis. The values of H show significant differences (p < 0.05, one asterisk) and very significant differences (p < 0.01, two asterisks). The letters in minuscule represent the results of the SNK test.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Leaving the roost (N = 8 passes; 71 calls)</th>
<th>Foraging (N = 11 passes; 138 calls)</th>
<th>Enclosed space (N = 15 passes; 166 calls)</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration (ms)</td>
<td>2.3 ± 0.3 c</td>
<td>4.6 ± 1.0 a</td>
<td>3.0 ± 0.7 b</td>
<td>22.80**</td>
</tr>
<tr>
<td>Slope (kHz/ms)</td>
<td>15.7 ± 1.8 a</td>
<td>5.9 ± 2.2 c</td>
<td>11.1 ± 1.5 b</td>
<td>28.97**</td>
</tr>
<tr>
<td>Peak frequency (kHz)</td>
<td>46.6 ± 3.6 a</td>
<td>36.5 ± 2.0 c</td>
<td>41.9 ± 2.6 b</td>
<td>26.55**</td>
</tr>
<tr>
<td>Minimal frequency (kHz)</td>
<td>33.2 ± 1.1</td>
<td>32.8 ± 0.8</td>
<td>33.0 ± 1.1</td>
<td>1.23 n.s.</td>
</tr>
<tr>
<td>Maximal frequency (kHz)</td>
<td>67.1 ± 3.1 a</td>
<td>47.3 ± 2.8 c</td>
<td>61.9 ± 4.4 b</td>
<td>29.10**</td>
</tr>
<tr>
<td>Q_{10-dB}</td>
<td>2.2 ± 0.5 c</td>
<td>3.7 ± 1.0 a</td>
<td>2.3 ± 0.8 c</td>
<td>25.49**</td>
</tr>
<tr>
<td>Bandwidth (kHz)</td>
<td>33.3 ± 4.6 a</td>
<td>16.4 ± 6.1 c</td>
<td>29.3 ± 6.9 b</td>
<td>28.76**</td>
</tr>
</tbody>
</table>

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**Fig. 2.** A. Oscillograms (above) and spectrograms (below) of the echolocation calls emitted by *Eptesicus fuscus* during their foraging behavior. The three panels correspond to a unique and continuous sequence in which the three phases of the foraging behavior can be recognized: search (s), approach (a) and final buzz (b). B. Above: Enlarged spectrograms of echolocation calls or groups of them, representative of each foraging phase, marked with an asterisk in (A). Below: Power spectra. The power spectrum of the final buzz call corresponds with the marked call with asterisk.
the shortest calls (R = 0.89; N = 22 passes; p = 0.00).

**Bats flying in enclosed space**

*Eptesicus fuscus* flying in an enclosed space emitted short calls (<4 ms; N = 15 passes, 166 calls) with two overlapping harmonics. The design is similar to those emitted by the animals in the surroundings of their roost or during the approach phase of the foraging behavior. The bandwidth, slope and call duration show intermediate values with regard to the rest of the calls in the echolocation call repertoire (Table 1). However, the minimal frequency remained around 33 kHz, showing no statistical differences with the other call types.

**Overall variability**

Each type of call in the echolocation repertoire of *E. fuscus* was included in a discriminant function analysis to look for similarities in their spectral and temporal design. A MANOVA showed that the model was significant (Wilks’ λ = 0.00367; F = 13.769; p < 0.01). The first two discriminant functions accounted for 95.88% of the variation in the data. The values of λ partial illustrated the following increasing discrimination power for the six parameters used: peak frequency > Q₁₀ > minimal frequency > slope > duration > maximal frequency. Calls emitted during the final buzz were 100% of the time correctly identified and grouped separately of the rest of the calls (Fig. 5; Table 3). However, other types of calls evidenced overlapping characteristics in their design thus difficult to determine their true group/nature.

**DISCUSSION**

**Call design**

In Cuba, the echolocation calls emitted by *E. fuscus* show the downward frequency

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Search (N = 11 passes; 138 calls)</th>
<th>Approach (N = 4 passes; 53 calls)</th>
<th>Buzz (N = 3 passes; 42 calls)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration (ms)</td>
<td>4.6 ± 1.0</td>
<td>2.8 ± 1.0</td>
<td>0.9 ± 0.1</td>
</tr>
<tr>
<td>Slope (kHz/ms)</td>
<td>5.9 ± 2.2</td>
<td>9.8 ± 5.1</td>
<td>10.2 ± 3.9</td>
</tr>
<tr>
<td>Peak frequency (kHz)</td>
<td>36.5 ± 2.0</td>
<td>36.3 ± 3.3</td>
<td>24.7 ± 4.2</td>
</tr>
<tr>
<td>Minimal frequency (kHz)</td>
<td>32.8 ± 0.8</td>
<td>29.4 ± 4.0</td>
<td>20.0 ± 0.4</td>
</tr>
<tr>
<td>Maximal frequency (kHz)</td>
<td>47.3 ± 2.8</td>
<td>50.8 ± 6.3</td>
<td>37.2 ± 4.2</td>
</tr>
<tr>
<td>Q₁₀-dB</td>
<td>3.7 ± 0.4</td>
<td>2.9 ± 0.8</td>
<td>2.4 ± 0.5</td>
</tr>
<tr>
<td>Bandwidth (kHz)</td>
<td>14.4 ± 2.2</td>
<td>21.3 ± 6.8</td>
<td>17.3 ± 4.0</td>
</tr>
</tbody>
</table>
modulated sweep design characteristic of vespertilionid bats (Fenton and Bell 1981; Kalko and Schnitzler 1993; O’Farrell et al. 1999; Parson and Jones 2000). The combination in the same signal of a frequency modulated (FM) and a quasi-constant frequency (QCF) component allows bats to modify independently both of them; this guarantees the adequate acoustic call characteristic to fulfill a specific task. For example, during the search phase insectivorous bats decrease the duration of the FM component and increase the QCF of the signal. As a consequence, the search calls are longer and narrower which causes the signal energy to concentrate in a narrow band of frequencies, thus facilitating the detection of distant prey (Simmons and Stein 1980; Schnitzler and Kalko 1998). On the other hand, the FM component is well suited for a precise localization and characterization of target (Simmons et al. 1979). When compared to the search calls, the approach and final buzz calls design in E. fuscus is dominated by the initial FM component that determines an increase in the bandwidth and a decrease in call duration. A wider bandwidth signal offers more information about the physical characteristic of the reflective surface (Schnitzler and Henson 1980; Simmons and Stein 1980). This change in call design is also characteristic of other vespertilionid bats and is present in the North American E. fuscus (Surlykke and Moss 2000). In addition, the high frequency repetition rate of the calls in the final buzz increase the quantity of information obtained per unit of time and allows the bat to prepare for the capture.

**Adaptation of echolocation calls to different flight conditions**

A change in the structure of echolocation calls to fit the requirements of each hunting phase (search, approach, and final buzz) is a common behavior in insectivorous bats, also found in E. fuscus (Griffin 1958; this study). Calls emitted under other circumstances are often intermediate in acoustic features to hunting calls. That is the case of calls emitted in the laboratory and leaving the roost in both, the North American and the Cuban E. fuscus (Surlykke and Moss 2000; this study).

FM bats adapt the characteristics of their calls to the degree of clutter present in their foraging areas (Simmons et al. 1979). The
adaptation of call duration to flight conditions, for example, is interpreted as a clutter rejection strategy (Kalko and Schnitzler 1993). According to this strategy, *E. fuscus* flying close to the roost and in enclosed spaces decreases the duration of its calls to avoid call-echo overlap.

**Geographical variations in echolocation calls of *E. fuscus***

The results gathered on the echolocation of *E. fuscus* in Cuba and North America show differences in acoustic parameters like call duration and minimal frequency. According to Surlykke and Moss (2000), *E. fuscus* in North America emits long signals (14-19 ms) while hunting in the field, similar to what is found in cruising bats after flying out of the roost. Likewise, these authors described a negative correlation between the minimal frequency and call duration for calls from *E. fuscus* in North America. Cuban *E. fuscus* appears to keep the minimal frequency constant during search and approach phases while hunting; furthermore, this frequency does not differ from the minimum frequency of echolocation calls recorded in the laboratory. This contrasts with a difference of almost 15 kHz among calls found in North American *E. fuscus* (see Fig. 3, Surlykke and Moss 2000). Part of this difference can be explained by the fact, that the sample from Cuban *E. fuscus* only included calls with durations up to 7 ms, whereas Surlykke and Moss (2000) report call durations up to 20 ms. Differences in call duration may well be explained by differences in hunting heights since *E. fuscus* in Cuba searches for prey flying close to ground and clutter, while in the continent it can search for insects more than 10 m above the ground (Surlykke and Moss 2000). In echolocating bats, the longest and lowest frequency calls are emitted by high flying bats (Jensen and Miller 1999). It is then, too soon, to propose the existence of fundamental differences in the acoustic behavior of *E. fuscus* in North American and the Caribbean. As demonstrated previously in Pipistrellus (Russo and Jones 2000; Mayer and von Helversen 2001): acoustic differences may point to the existence of sibling species; therefore new studies should further test this hypothesis.

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**Literature Cited**


