



ECHOLOCATION OF THREE SPECIES OF SAC-WINGED BATS (*BALANTIOPTERYX*)

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We describe and compare field recordings of echolocation calls of the neotropical emballonurid sac-winged bats *Balantiopteryx plicata*, *B. io*, and *B. infusca*. These 3 species have search-phase calls with principal energy in the 2nd harmonic, characterized by a long narrowband component followed by a short broadband component. Variation in call parameters follows only partially the scaling pattern with body size generally found in bats. Based on characteristics of their echolocation calls, we hypothesize that *B. io* and *B. infusca* forage in more cluttered habitats than does the congeneric *B. plicata*, which typically hunts in open areas.

Key words: *Balantiopteryx*, bats, body size, echolocation, Emballonuridae, habitat

Bats use a wide array of foraging strategies that are coupled with an equally high diversity in structure of their echolocation calls (Fenton 1990; Neuweiler 1989; Schnitzler and Kalko 1998). Two components can be distinguished in a bat call: a descending or ascending, short, broadband frequency segment and a short-to-long narrowband segment. Differences in bat echolocation calls result from variation in these components and their different combinations.

A sequence of bat echolocation calls can be described in terms of search, approach, and terminal phases. These phases correspond to commuting and searching for prey, detection and location of prey, and final prey capture (*sensu* Griffin et al. 1960). Echolocation characteristics of bats are constrained by habitat conditions, acoustic

laws, and ability of the bat to produce sound and to process echoes. In aerial insectivorous bats with no Doppler shift compensation, calls show a more prominent narrowband component, a lower frequency, and a lower bandwidth (small broadband component) in uncluttered than in cluttered habitats. Pulse durations and pulse intervals are longer in cluttered habitats (Schnitzler and Kalko 1998). Echolocation parameters are influenced by body size of bats as well, in such a way that larger species of bats tend to use low-frequency calls, long pulses, and large pulse intervals (Jones 1999).

In this context, echolocation of emballonurids has been only marginally examined in relation to habitat use (Kalko 1995) and body size (Jones 1996, 1999). Within this family, the 3 species of sac-winged bats (*Balantiopteryx*) show differences in size and general habitat preferences. The gray sac-winged bat, *B. plicata*, is fairly com-

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mon across arid areas from Mexico to Costa Rica (Arroyo-Cabrales and Jones 1988a). In contrast, Thomas's sac-winged bat, *B. io*, and the Ecuadorian sac-winged bat, *B. infusca*, are restricted in distribution to areas originally covered by rain forest (Arroyo-Cabrales and Jones 1988b). *B. io* is found in limited areas from southern Mexico to Belize and Guatemala, and *B. infusca* is known only from northwestern Ecuador and southwestern Colombia (Arroyo-Cabrales and Jones 1988b; McCarthy et al. 2000).

We analyzed interspecific variation in aspects of echolocation in these 3 species. Our 1st objective was to describe in detail for the 1st time the echolocation calls of *B. plicata*, *B. io*, and *B. infusca* during search, approach, and terminal phases. Our 2nd objective was to compare parameters of echolocation calls among the 3 species in relation to qualitative differences in body size and foraging habitat.

MATERIALS AND METHODS

The echolocation calls of the 3 species of *Balantiopteryx* were recorded in different localities and in their natural habitats. *B. plicata* was studied in September 1997 and May 1998 in Maruata, Michoacán, Mexico (18°17'N, 103°23'W, elevation 0 m) and in Los Ortices, Colima, Mexico (19°07'N, 103°44'W, elevation 280 m). Both localities are characterized by deciduous and thorn forests. Colonies were found in caves and culverts and consisted of 200–300 individuals. We recorded echolocation calls in areas of sparse trees and coconut palms (about 30 m apart) and in open grass pastures. During the recordings, *B. plicata* was hunting 3–15 m above ground level and at least 3–4 m away from vegetation. *B. io* was studied in May 1998 in Teapa, Tabasco, Mexico (17°33'N, 92°57'W, elevation 100 m) in a limestone massif with abundant cavities. Recordings of echolocation calls were obtained around Coconá Cave in a garden area with sparse trees at least 10–20 m apart. The colony had 300 individuals. *B. infusca* was studied in December 1999 in Lita, Imbabura, Ecuador (0°52'N, 78°28'W, elevation 500 m) near its roost in an abandoned railway tunnel in an area of premontane rain forest. The

recordings were obtained in open corridors carved in a forested steep slope. Colonies had about 40 individuals (McCarthy et al. 2000). The 3 species were recorded in relatively open areas, with obstacles at least 5 m away from the bats. For all the species, only sequences from solitary individuals were selected for this study to avoid possible variation in the calls due to conspecifics (jamming avoidance).

Field identification of echolocation calls was based on previous recordings of at least 10 hand-released individuals (except for *B. infusca*, for which recordings were made at the entrance of the roost). Age and sex were determined and forearm length measured on the individuals. A 2-way analysis of variance (ANOVA) was used to test for differences in forearm length (body size estimate) by sex and species.

Echolocation calls were sampled (3 s/sample) with ultrasound bat detectors D-980 (Pettersson Elektronik, Uppsala, Sweden) in time-expanded mode (10×) and recorded on metal-XR Sony tapes with a Sony Walkman DC6 cassette recorder (Sony Company, Tokyo, Japan). Recordings were analyzed with a Kay DSP 5500 Sonagraph (Kay Elemetrics Corporation, Pine Brook, New Jersey). Duration and pulse interval were measured with a resolution of 0.3 ms on sonograms. Frequency and amplitude parameters were measured in a power spectrum built with 512-point fast-Fourier transform of each complete pulse. Peak frequency was defined as the frequency with the most energy. To minimize effects of atmospheric attenuation, bandwidth was measured (when possible) as the difference between the -20-dB high-frequency (initial frequency) and the -20-dB low-frequency (final frequency) cutoffs with regard to peak frequency. Harmonics (fundamental, 2nd, or 3rd) corresponding to each peak in the power spectrum were also recorded. For all call features, mean $\pm 1 SE$ was calculated from mean value of each sequence (i.e., average of all pulses in the sequence). For pulse interval (time from beginning of the measured pulse to beginning of the previous one), we also calculated mean $\pm SE$ using all pulses from all sequences because the distribution of this variable may be obscured when means are averaged. Duty cycle ($100 \times \text{duration/interval}$) was also calculated from individual pulses. The risk of pseudoreplication was considered negligible given the large size of the colonies and that recordings

TABLE 1.—Forearm length as a measure of body size in 3 species of *Balantiopteryx*.

	Males				Females			
	<i>n</i>	\bar{X}	<i>SE</i>	Range	<i>n</i>	\bar{X}	<i>SE</i>	Range
<i>B. io</i>	6	38.0	0.34	36.6–38.8	17	39.4	0.19	38.3–41.4
<i>B. infusca</i>	5	38.7	0.22	38.0–39.4	11	40.0	0.39	37.9–42.4
<i>B. plicata</i>	13	42.1	0.28	39.8–43.8	11	43.1	0.36	40.9–45.9

were obtained simultaneously in 2 different points and during different days for each locality. Pulse interval and duty cycle in the 3 species and pulse duration for *B. io* and *B. infusca* showed significant departure from normality (Shapiro–Wilks' test). Consequently, non-parametric statistics (Kruskal–Wallis test) were used to compare differences among means of call parameters for the 3 species. All statistical analyses were performed with Statistica 5.5 (StatSoft 1999).

RESULTS

Body size.—Forearm length was larger in *B. plicata* and in females within each species (Table 1). The 2-way ANOVA showed that differences between species were highly significant ($F = 94.7$, $P < 0.0001$), as well as those between sexes ($F = 20.5$, $P < 0.0001$), but not the interaction factor between them ($F = 0.1$, $P = 0.90$). A posteriori tests showed that *B. plicata* was significantly larger than *B. io* and *B. infusca* for both sexes (Tukey's Honest Significant Difference [HSD], $P < 0.001$), but difference

in size between *B. io* and *B. infusca* was not significant (Tukey's HSD, $P > 0.1$).

Search phase.—Principal energy is located in the 2nd harmonic in search-phase calls of all 3 species. In *B. plicata*, there is usually a 1st harmonic, which is 10–25 dB lower than the 2nd harmonic. Third or 4th harmonics appear less often and always are weaker than the 2nd harmonic. In the other 2 species, the 1st harmonic is only occasionally present 20–25 dB below the 2nd, and the 3rd is only rarely noticeable (Figs. 1–5).

In each of the 3 species, the calls consist mainly of a narrowband component, which drops slightly by 1–1.5 kHz. The calls of *B. infusca* start with a short, steep, upward broadband component (Fig. 5). The equivalent segment is weaker in *B. io* and is generally missing in *B. plicata*. Calls always end with a short, steep, downward broadband component, and neither frequency nor time parameters show differences among consecutive pulses. Call parameters are significantly different among species. Frequency variables are lowest, and time parameters are longest in *B. plicata*, whereas these values are highest in *B. infusca* and intermediate in *B. io* (Table 2). The distribution of pulse intervals (Fig. 6) is skewed in the 3 species (Shapiro–Wilks' $W = 0.760$, $P < 0.0001$). Distribution of pulse intervals is most skewed in calls of *B. plicata* and less skewed in calls of *B. io* ($W = 0.850$, $P < 0.0001$) and *B. infusca* ($W = 0.844$, $P < 0.0001$). Modal values are 115 ms for *B. plicata* and 95 ms for *B. io* and *B. infusca* (Fig. 6). In *B. plicata*, amplitude of the 2nd harmonic sometimes alternates between

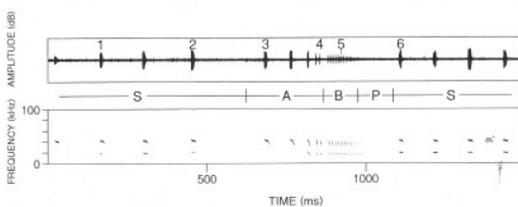


FIG. 1.—Echolocation calls of *Balantiopteryx plicata*. Sonogram and oscillogram for call sequence, showing frequency and amplitude of calls during a capture attempt. Calls include search phase (S), approach phase (A), buzz or terminal phase (B), and pause (P) before the next search call. (Numbers indicate pulses shown in greater detail in Fig. 2.)

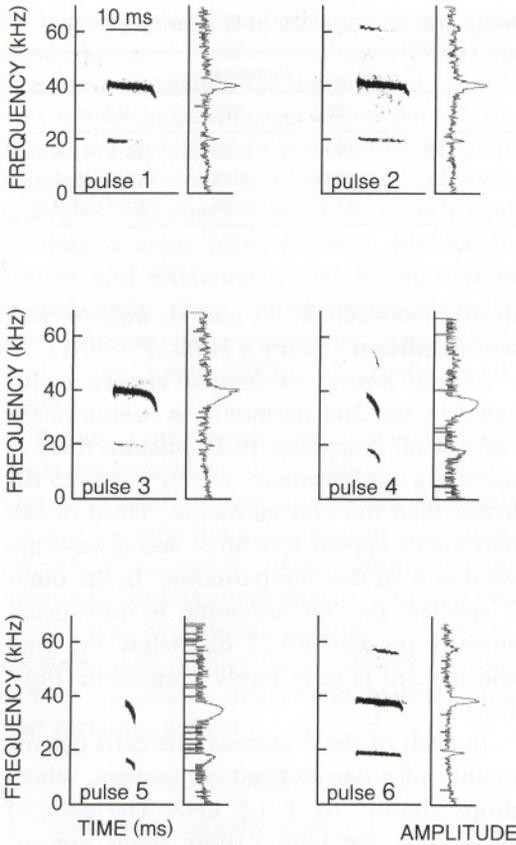


FIG. 2.—Sonograms and spectrograms of selected pulses from phases in sequence shown in Fig. 1.

stronger and weaker (5- to 10-dB difference) consecutive calls.

Approach and terminal phases.—Approach and terminal phases were sufficiently documented only for *B. plicata*. In this species, the 1st pulse of the approach phase is distinguished from that of the search phase by a shortened narrowband segment and more clearly by a broadband component with a downward sweep (Figs. 1 and 2). Bandwidth increases from 2.9 ± 0.8 kHz in the last pulse of the search phase to 6.6 ± 2.1 kHz ($n = 8$) in the 1st pulse of the approach phase. Total number of pulses is 9.9 ± 5.9 in the approach phase and 19.1 ± 3.8 ($n = 17$) in the terminal phase. Total duration is 686.8 ± 485.2 ms for the approach phase and 133.9 ± 28.8 ms ($n =$

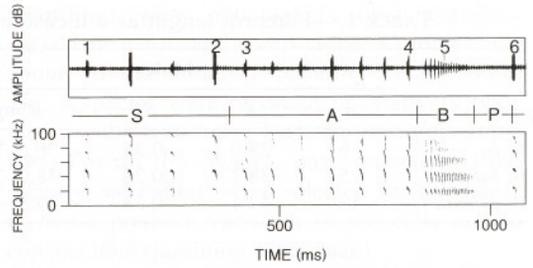


FIG. 3.—Echolocation calls of *Balantiopteryx io*. Sonogram and oscillogram for call sequence in a capture attempt, including search phase (S), approach phase (A), buzz or terminal phase (B), and pause (P) before the next search call.

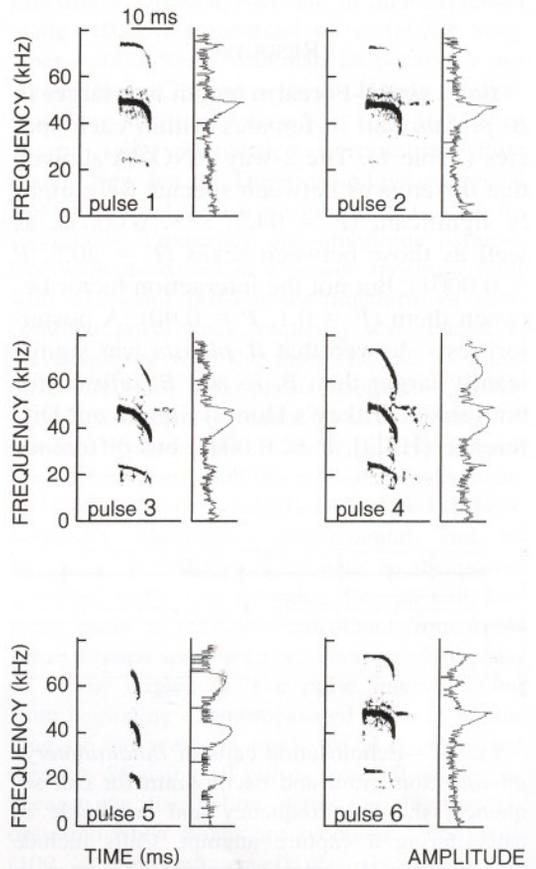


FIG. 4.—Sonograms and spectrograms of selected pulses from phases in sequence shown in Fig. 3.

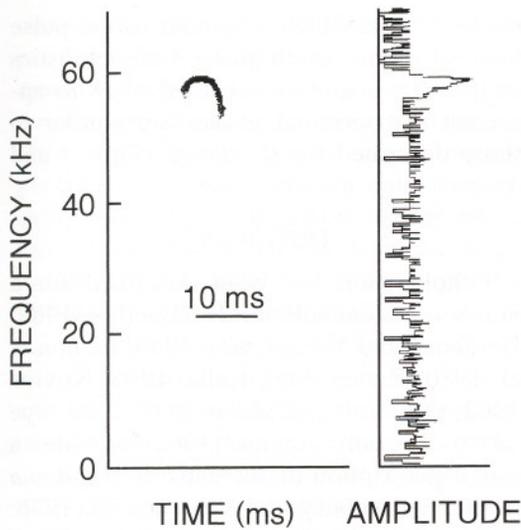


FIG. 5.—Echolocation calls of *Balantiopteryx infusca*. Sonogram and spectrogram from a selected pulse in search phase.

17) for the terminal phase. Pulse duration and pulse interval are gradually reduced during the approach phase, changing from a duration of 11.4 ± 2.0 ms and an interval of 102.7 ± 22.9 ms ($n = 15$) in the 1st pulse to 4.9 ± 1.2 ms and 21.9 ± 11.3 ms

($n = 17$) in the last pulse, respectively. In most sequences ($n = 12$), the approach phase is separated by a longer interval from the terminal phase. The terminal phase starts with a sharp shortening of the pulse interval. In this phase, the pulse duration and pulse interval decrease from 3.5 ± 0.4 ms and 9.5 ± 0.9 ms in the initial part of the sequence to 2.4 ± 0.3 and 5.7 ± 0.6 ms in the final part. Peak frequency diminishes in the approach phase and is 2.6 ± 1.5 kHz ($n = 11$) lower than that in the last pulse of the search phase. Peak frequency in the terminal phase decreases from 36.7 ± 0.3 kHz in the initial part to 35.9 ± 1.1 kHz in the final part ($n = 6$). Peak frequency was normally located on the 1st half of the pulse, although sometimes another peak could be detected at lower frequency. Bandwidth increases during approach phase, averaging 8.4 ± 1.7 kHz ($n = 9$), and shortens slightly in the terminal phase to 7.2 ± 0.9 kHz ($n = 6$). Duty cycle increases from $11.6 \pm 3.2\%$ in the 1st pulse of the approach phase to $27.2 \pm 8.7\%$ ($n = 17$) in the last pulse, and from $36.7 \pm 4.9\%$ in the initial part of the terminal phase to $43.7 \pm$

TABLE 2.—Parameters of search-phase echolocation calls of 3 species of *Balantiopteryx*. All differences among species were statistically significant (Kruskal–Wallis H , $P < 0.001$).

	Pulse (ms)		Duty cycle	Sound frequency (kHz)			
	Duration	Interval		Initial	Final	Peak	Bandwidth
<i>B. plicata</i>							
n	46	658	620	27	27	47	27
\bar{X}	12.1	136.4	9.7	42.1	39.4	41.2	2.8
SE	0.2	1.8	0.1	0.2	0.2	0.2	0.1
Range	8.8–14.2	71.2–355.0	2.8–16.1	40.2–43.7	37.9–41.3	38.6–43.9	1.6–3.7
<i>B. io</i>							
n	46	611	607	18	19	46	18
\bar{X}	7.8	92.9	8.6	50.2	45.9	49.1	4.3
SE	0.2	0.8	0.1	0.2	0.2	0.1	0.2
Range	5.4–11.5	43.7–202.5	3.4–17.2	47.9–51.6	44.1–48.1	46.5–51.2	3.1–6.0
<i>B. infusca</i>							
n	14	106	104	12	12	14	12
\bar{X}	6.7	119.5	5.6	57.0	51.1	55.7	5.9
SE	0.2	4.1	0.1	0.5	0.9	0.5	0.5
Range	5.8–11.5	53.1–307.8	2.6–11.5	55.0–60.2	47.6–57.1	53.1–59.2	3.0–8.6
H	77.44	636.62	226.58	47.78	48.54	88.37	37.45

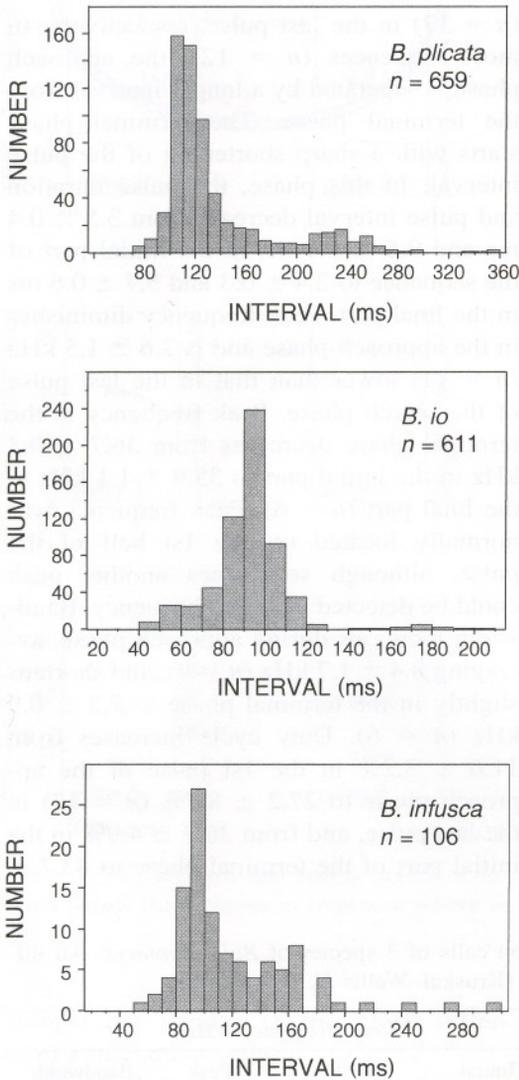


FIG. 6.—Distributions of pulse intervals (time between pulses) for all calls recorded in search phase from *Balantiopteryx plicata*, *B. io*, and *B. infusca*.

7.0% in the final segment (Figs. 1 and 2). Maximum amplitude occurs in the 2nd harmonic, although the 1st harmonic is often present, reaching almost the same amplitude as that of the 2nd harmonic, particularly at the end of the buzz (Figs. 1 and 2). Occasionally, higher harmonics (mainly the 3rd) are noticeable. The interval between the last pulse of the buzz and the 1st call of the next search phase is 118.9 ± 11.84

ms ($n = 14$), which is similar to the pulse interval in the search phase. Characteristics of the only sequence recorded of *B. io* approach and terminal phases are similar to those described for *B. plicata* (Figs. 3 and 4).

DISCUSSION

Echolocation has been described for a number of emballonurids (Barclay 1983; Bradbury and Vehrencamp 1976; Fenton et al. 1980; Heller 1989; Kalko 1995; Novick 1962; O'Farrell and Miller 1997, 1999; Pye 1980), but only Novick (1962) provides a rough description of the calls of *B. plicata* in flight. Bradbury and Vehrencamp (1976: 341) point out that pulses of *B. plicata* show "considerable energy at 20–40 kHz." The calls of *B. io* are only known from 1 Anabat-II sonogram from Belize (O'Farrell and Miller 1999), which shows them to be similar to calls we have described. *B. infusca* has been rediscovered only recently (McCarthy et al. 2000), and its echolocation is described here for the 1st time. Calls of the 3 species are similar to other emballonurids in that they include a long narrowband component and maximum amplitude on the 2nd harmonic. The final broadband component distinguishes them from emballonurids that fly in open areas like *Diclidurus*, *Taphozous*, or *Saccolaimus* (Fenton et al. 1980; Heller 1989; Kalko 1995; Pye 1980). Calls of *Balantiopteryx* are more similar to calls of bats that forage close to vegetation or over water surfaces (e.g., *Rhynchonycteris*, *Cormura*, and *Saccopteryx*—Barclay 1983; Kalko 1995; O'Farrell and Miller 1997). But calls of *B. plicata* and *B. io* lack the initial broadband segment and show a slightly downward narrowband component, which turns upward in other forest emballonurids.

During the search phase, the 3 species of *Balantiopteryx* show similar structure in echolocation calls but different values in call parameters. Peak frequency, pulse duration, and pulse interval change with body size due to morphological and functional

constraints (Jones 1999). Larger species produce lower-frequency calls because structures related to sound production produce lower sounds as linear size increases (Pye 1979). Larger species also show longer pulse intervals between calls because call production is linked to wingbeat, which has a lower rate as bat size increases (Fenton et al. 1998; Jones 1994). Pulse interval follows this general rule in *Balantiopteryx*, being greatest in the largest species (*B. plicata*) and least in the smallest (*B. infusca* and *B. io*). Nevertheless, differences between species of *Balantiopteryx* in peak frequency and pulse duration only agree partially with the general pattern in relation to body size. As expected, *B. plicata*, the largest species, shows the lowest peak frequency and pulse duration, but this relationship does not hold between *B. io* and *B. infusca*. Although similar in size, *B. io* shows notably lower peak frequency and larger pulse duration than does *B. infusca*.

Species of bats that hunt in cluttered habitats with no Doppler-shift compensation show particular echolocation characteristics. The calls typically have a large broadband component because this segment provides precise information about location of the target as well as detailed information about the structure of the habitat (Schnitzler and Kalko 1998; Simmons and Stein 1980). In these cluttered habitats, bats do not need a large effective detection range and, therefore, can shift their frequency up to high values, despite atmospheric attenuation (Griffin 1971; Lawrence and Simmons 1982). Minimum detection distance (with no overlap between returning echoes and outgoing pulses) is shorter in bats in cluttered spaces and is constrained by pulse duration (Kalko and Schnitzler 1993; Schnitzler et al. 1987). Maximum detection distance (with no overlap between an echo and the next pulse) is lower in bat calls in cluttered habitat because this distance is constrained by pulse interval (Fenton 1990).

B. plicata in Costa Rica forages in open areas 10–25 m above the ground or above

the canopy (Bradbury and Vehrencamp 1976). Habitat characteristics of hunting grounds of *B. io* and *B. infusca* are still unknown, and it is possible that they may forage above the forest canopy. But echolocation calls of *B. io* and *B. infusca* show larger peak frequency, lower pulse duration (shorter minimum detection distance), and lower pulse interval (shorter maximum detection distance) than do calls of *B. plicata*. These call characteristics suggest that *B. io* and *B. infusca* hunt within the rainforest and use more cluttered environments than does *B. plicata*. But the observed differences could also be affected by the relation of these call variables to size. Nevertheless, the fact that calls of *B. io* and *B. infusca* have larger bandwidths supports a hypothesis of differential habitat use because this characteristic is associated with cluttered habitats and is not affected by size (Jones 1999).

The skewness in distribution of pulse interval is associated with high frequency of wingbeats without call emission, a typical feature of aerial insectivorous bats that use uncluttered habitats (Schnitzler and Kalko 1998). Similarly, *Myotis nigricans* shows alternating amplitudes in consecutive pulses only when it hunts in open spaces (Siemers et al. 2001). We have found this behavior only in *B. plicata*, the only 1 of the 3 species that is well known to forage in open areas. Nevertheless, no neurophysiological mechanisms have been shown to cause this behavior.

During approach and terminal phases, *B. plicata* and *B. io* show changes in calls known to be associated with obtaining accurate target information once a potential prey has been detected (Kalko and Schnitzler 1998). A narrowband segment that is typical of the terminal phase of calls of other neotropical emballonurids, such as *S. bilineata*, *S. leptura*, and *C. brevirostris* (Barclay 1983; Kalko 1995), is missing in the 2 species of *Balantiopteryx* we recorded. The terminal phase is continuous in both species, and it cannot be divided into 2 parts

(Buzz I and Buzz II) as in vespertilionids (Kalko and Schnitzler 1998). Unfortunately, the paucity of information in the literature about the approach and final phases of other species hampers further comparisons.

RESUMEN

Describimos y comparamos las señales de ecolocación de los murciélagos emballonúridos neotropicales *Balantiopteryx plicata*, *B. io*, y *B. infusca* a partir de registros en libertad. Durante la fase de búsqueda las 3 especies tienen señales con más energía en el segundo armónico. Estas señales se caracterizan por un componente inicial largo de banda estrecha seguido por un componente corto de banda ancha. Los parámetros de las señales siguen parcialmente los patrones de variación respecto al tamaño corporal encontrados generalmente en murciélagos. En base a las características de los pulsos de ecolocación, hipotetizamos que *B. io* y *B. infusca* buscan el alimento en hábitats con más obstáculos que *B. plicata*, que caza en espacios abiertos.

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LITERATURE CITED

- ARROYO-CABRALES, J., AND J. K. JONES, JR. 1988a. *Balantiopteryx plicata*. Mammalian Species 301:1-4.
- ARROYO-CABRALES, J., AND J. K. JONES, JR. 1988b. *Balantiopteryx io* and *Balantiopteryx infusca*. Mammalian Species 313:1-3.
- BARCLAY, R. M. R. 1983. Echolocation calls of emballonurid bats from Panama. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 151:515-520.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1976. Social studies and foraging in emballonurid bats. I. Field studies. Behavioral Ecology and Sociobiology 1: 337-381.
- FENTON, M. B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology 68:411-422.
- FENTON, M. B., G. P. BELL, AND D. W. THOMAS. 1980. Echolocation and feeding behaviour of *Taphozous mauritanus* (Chiroptera: Emballonuridae). Canadian Journal of Zoology 58:1774-1777.
- FENTON, M. B., C. V. PORTFORS, I. L. RAUTENBACH, AND J. M. WATERMAN. 1998. Compromises: sound frequencies used in echolocation by aerial-feeding bats. Canadian Journal of Zoology 76:1174-1182.
- GRIFFIN, D. R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). Animal Behaviour 19:55-61.
- GRIFFIN, D. R., F. A. WEBSTER, AND C. R. MICHAEL. 1960. The echolocation of flying insects by bats. Animal Behaviour 8:141-154.
- HELLER, K. G. 1989. Echolocation calls of Malaysian bats. Zeitschrift für Säugetierkunde 54:1-8.
- JONES, G. 1994. Scaling of wingbeat and echolocation pulse emission rates in bats: why are aerial insectivorous bats small? Functional Ecology 8:450-457.
- JONES, G. 1996. Does echolocation constrain the evolution of body size in bats? Symposia of the Zoological Society of London 69:11-128.
- JONES, G. 1999. Scaling of echolocation call parameters in bats. Journal of Experimental Biology 202: 3359-3367.
- KALKO, E. K. V. 1995. Echolocation signal design, foraging habitats and guild structure in six neotropical sheath-tailed bats (Emballonuridae). Symposia of the Zoological Society of London 67:259-273.
- KALKO, E. K. V., AND H.-U. SCHNITZLER. 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. Behavioral Ecology and Sociobiology 33:415-428.
- KALKO, E. K. V., AND H.-U. SCHNITZLER. 1998. How echolocating bats approach and acquire food. Pp. 197-204 in Bat biology and conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- LAWRENCE, B. D., AND J. A. SIMMONS. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. Journal of the Acoustical Society of America 71:585-590.
- MCCARTHY, T. J., L. ALBUJA, AND I. MANZANO. 2000. Rediscovery of the brown sac-wing bat, *Balantiopteryx infusca* (Thomas, 1897), in Ecuador. Journal of Mammalogy 81:958-961.
- NEUWEILER, G. 1989. Foraging ecology and audition in echolocating bats. Trends in Ecology & Evolution 4:160-166.
- NOVICK, A. 1962. Orientation in Neotropical bats. I. Natalidae and Emballonuridae. Journal of Mammalogy 43:449-455.
- O'FARRELL, M. J., AND B. W. MILLER. 1997. A new examination of echolocation calls of some neotrop-

- ical 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.
- PYE, D. 1979. Why ultrasound? *Endeavour* 3:57–62.
- PYE, D. 1980. Adaptiveness of echolocation signals in bats. *Trends in Neuroscience* 3:232–235.
- SCHNITZLER, H.-U., AND E. K. V. KALKO. 1998. How echolocating bats search and find food. Pp. 183–196 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.
- SIEMERS, B. M., E. K. V. KALKO, AND H.-U. SCHNITZLER. 2001. Echolocation behavior and signal plasticity in the neotropical bat *Myotis nigricans* (Schinz, 1821) (Vespertilionidae): a convergent case with European species of *Pipistrellus*? *Behavioral Ecology and Sociobiology* 50:317–328.
- 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. 1999. *Statistica for Windows*. StatSoft, Inc., Tulsa, Oklahoma.

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