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Echolocation calls and wing morphology of bats from the West Indies

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Echolocation calls of 119 bats belonging to 12 species in three families from Antillean islands of Puerto Rico, Dominica, and St. Vincent were recorded by using time-expansion methods. Spectrograms of calls and descriptive statistics of five temporal and frequency variables measured from calls are presented. The echolocation calls of many of these species, particularly those in the family Phyllostomidae, have not been described previously. The wing morphology of each taxon is described and related to the structure of its echolocation calls and its foraging ecology. Of slow aerial-hawking insectivores, the Mormoopidae and Natalidae *Mormoops blainvillii*, *Pteronotus davyi davyi*, *P. quadridens fuliginosus*, and *Natalus stramineus stramineus* can forage with great manoeuvrability in background-cluttered space (close to vegetation), and are able to hover. *Pteronotus parnellii portoricensis* is able to fly and echolocate in highly-cluttered space (dense vegetation). Among frugivores, nectarivores and omnivores in the family Phyllostomidae, *Brachyphylla cavernarum intermedia* is adapted to foraging in the edges of vegetation in background-cluttered space, while *Erophylla bombifrons bombifrons*, *Glossophaga longirostris rostrata*, *Artibeus jamaicensis jamaicensis*, *A. jamaicensis schwartzi* and *Stenoderma rufum darioi* are adapted to foraging under canopies in highly-cluttered space and do not have speed or efficiency in commuting flight. In contrast, *Monophyllus plethodon luciae*, *Sturnira lilium angeli* and *S. lilium paulsoni* are adapted to fly in highly-cluttered space, but can also fly fast and efficiently in open areas.

Key words: Antilles, eco-morphology, flight, Neotropics, sonograms, time expansion, ultrasound

INTRODUCTION

Echolocation call structure can be expressed in terms of frequency and temporal parameters, several of which (e.g., duration, duty cycle, bandwidth, and intensity), vary among species. Components of calls have been categorised as constant frequency (CF: single tones which remain at one frequency for a time) or frequency modulated (FM: sweeping up or down in frequency). Calls can be made up of one or more of these components, and are consequently described as FM calls, CF/FM calls (with a CF component followed by an FM component), and so on (Vaughan *et al*., 1997; Schnitzler and Kalko, 1998; Fenton, 1999).

Interspecific variability in morphology of wings of bats is linked to differences in flight and hunting behaviour and to species' ecology (Norberg and Rayner, 1987), so that wing morphology can be used to predict flight behaviour. Interactions between aspect ratio, wing loading, and wing tip shape index affect flight (Norberg and Rayner, 1987). The aspect ratio describes the shape of the wings: at a simple level, high aspect ratio corresponds with long narrow wings and energy-efficient flight; a low aspect ratio with shorter wings and less efficient flight. The wing loading, a measure of the surface area of the wings compared to the body weight, is considered to be positively correlated with minimum speed and negatively correlated with manoeuvrability (ability to turn tightly) and agility (ability to turn quickly). The tip shape index quantifies the pointedness of the wing tips. Bats with short, rounded wing tips and high wing tip indices are able to hover (Norberg and Rayner, 1987). The tip shape index also describes the proportion that the chiropatagium on the one hand, and the plagiopatagium and propatagium on the other, contribute to total wing area: a high tip shape index indicates a relatively large chiropatagium (Aldridge and Rautenbach, 1987).

In combination, echolocation call structure and wing morphology are important indicators of the foraging ecology of bats, as they may constrain the foraging habitats bats can use, the types of food items that they can detect, and how those resources are perceived. These elements probably coevolved in bats, and certain combinations of flight behaviour and echolocation call structure are believed to be maladaptive (Aldridge and Rautenbach, 1987). Bats with long, narrow wings fly fast above vegetation, and hunt by aerial hawking. They use low frequency FM/CF calls for the echolocation of distant targets, and avoid high frequencies, which attenuate quickly (Schnitzler and Kalko, 1998). Bats with broad wings and low wing loading are adapted to slow, manoeuvrable flight in highly-cluttered space (dense vegetation). They hunt insects by slow aerial hawking or gleaning, or feed on fruit or flowers under the canopy. They use brief, broadband, low-intensity FM calls, to avoid overlap between their pulses and echoes of close targets, or longer calls with CF components which are suitable for the detection of the fluttering of insect wings, represented as acoustical glints in the echoes returning to the bats (Schnitzler and Kalko, 1998). Bats using long CF calls in highly-cluttered space distinguish between pulses and echoes by their frequency and not by their timing, so that pulses and echoes may overlap (Suga, 1990; Schnitzler and Kalko, 1998).

Little is known about many of the species of bats that are found in the West Indies. Data on wing morphology are often derived from small sample sizes, and measurements may be biased by the sole use of museum specimens (Norberg and Rayner, 1987; Bininda-Emonds and Russell, 1994). The low-intensity echolocation calls of many members of the family Phyllostomidae have not been recorded. The calls of some Phyllostomidae have source levels of approximately 70 dB sound pressure level (SPL) which makes them more difficult to record than those of many other bats, which have source levels of approximately 110 dB SPL (Surlykke, 1988). The aim of this study is to describe echolocation calls and wing morphology of bats from the West Indies and to relate these suites of characters to patterns of foraging.

Materials and Methods

Echolocation Calls and Wing Morphology

We caught bats in mist nets, harp traps, and hand nets in various habitats including rain forest, agricultural areas and day roosts in August and October 1995 on Puerto Rico (Greater Antilles, 18°N, 67°W), in July 1996 on Dominica (Lesser Antilles, 15°N, 61°W) and in January 1994, April 1995, and August 1996 on St. Vincent (Lesser Antilles, 13°N, 61°W). Voucher specimens were taken by MRG and placed in the Carnegie Museum, Pittsburgh, and in the Museum, Texas Tech University. Individuals were identified to species, or subspecies where appropriate (Baker *et al.*, 1984; Wilson and Reeder, 1993), sexed, and aged based on the degree of epiphyseal-diaphyseal fusion in wing phalanges (Anthony, 1988). Subspecies designations are used in this paper (Wilson and Reeder, 1993; Koopman, 1994) because two subspecies of *Artibeus jamaicensis* differ greatly in size and hence may differ in echolocation call frequency (Jones 1978, 1995).

We took morphological measurements and mass from adult males and non-pregnant adult females. Bats were weighed by using a spring balance (Pesola, Baar, Switzerland) to the nearest 0.5 g. We measured length of right forearm (FA) to the nearest 0.1 mm with dial callipers. We traced an outline of the right wing of each bat (Norberg and Rayner, 1987). Tracings were later digitised by using a magnetic tablet (SummaSketch III; Summagraphics, Seymour, Connecticut, USA) and software written by J. M. V. Rayner (Department of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom), so that the aspect ratio, wing loading, and tip shape index could be calculated (Norberg and Rayner, 1987). We categorised aspect ratio and wing loading as advocated by Bininda-Emonds and Russell (1994) based on descriptions by Norberg and Rayner (1987), as follows: aspect ratio: low $\leq$ 6.1, average = 6.1–7.3, high $\geq$ 7.3; wing loading: very low $\leq$ 6.45 N/m^2, low = 6.45–7.5 N/m^2, average = 7.5–10.3 N/m^2, high $\geq$ 10.3 N/m^2. For each species, we calculated values for second and third principal components of a principal-components analysis (PCA) carried out by Norberg and Rayner (1987) on data from 251 species. These components, which are independent of size (first component) and represent mainly aspect ratio and wing loading, allow bats to be placed into four broad groups (quadrants in a plot of the components) according to their wing morphology and predicted flight behaviour (Norberg and Rayner, 1987).

We released each bat from the hand in background-cluttered space (sensu Schnitzler and Kalko, 1998) close to site of capture, and recorded a sequence of its echolocation calls as it flew freely. The recorder was approximately 10 m from the releaser, so bats had flown on average 10 m before their calls were recorded. Calls from bats which flew away from the recorder could not be recorded. Echolocation calls recorded in this way may not be typical for bats which normally fly high above the ground in uncluttered space, as individual bats adjust their calls depending on their distance from objects (Schnitzler and Kalko, 1998), and high-flying bats do not normally encounter objects close to them. More typical calls are recorded from bats which normally fly in background-cluttered or highly-cluttered space close to vegetation (Parsons, 1997; Schnitzler and Kalko, 1998), such as the taxa included in this study. We used the microphone and high frequency output of a bat detector (S-25; Ultra Sound Advice, London, United Kingdom) to transfer calls to a digital capture device for time-expansion (Portable Ultrasound Processor; Ultra Sound Advice, London, United Kingdom). This digital capture device captured a 2.2 s sequence of echolocation calls, and replayed it to an audio cassette recorder (Walkman WM-D6C; Sony, Tokyo, Japan) at one tenth of the original speed. The bat-detector microphone had a frequency response of 20–120 kHz (± 3 dB), the digital capture device sampled at 448 kHz with 8-bit resolution, and the audio cassette recorder had a frequency response of 40 Hz–15 kHz (± 3 dB). Recordings were made onto 90-minute audio tapes (Metal XR; Sony, Tokyo).

Sound Analysis

Echolocation calls were digitised by a computer and analysed by using sound analysis software (BatSound v.3.3, Pettersson Elektronik AB, Uppsala, Sweden) at a sampling rate of 44.1 kHz, with 16-bit resolution. The effective bit-depth was 8 due to limitations of the digital capture device. To avoid pseudoreplication (Hurlbert, 1984) and to ensure the most accurate possible description was obtained, a single call from each individual was selected for analysis. The choice was based on subjective assessment of call quality: we selected one of the last echolocation calls in each sequence, which had a high signal to noise ratio, without being overloaded, and which was considered to be an orientation phase call (Thies *et al.*, 1998). We measured two temporal and three frequency variables from the harmonic containing most energy. These variables, described by Vaughan *et al.* (1997), were *duration* of the call (in ms), *interpulse interval* (in ms), *peak frequency* (most intense frequency or frequency of maximum energy; in kHz), *start frequency* (frequency at the beginning of the call; in kHz), and *end frequency* (frequency at the end of the call; in kHz). The duration of calls was measured from the oscillogram from the onset of the signal to its decay to the level of the background noise. Interpulse interval was measured from the beginning of the call being measured, to the beginning of the next call. The peak frequency was measured using a power spectrum created using an interpolated (95%) 1024-point FFT in conjunction with a Hamming window. Start and end frequencies of the harmonic with most energy were measured from a spectrogram also created using an interpolated 1024-point FFT in conjunction with a Hamming window. The frequency resolution for the FFTs was 488 Hz. The number of harmonics present within the frequency response of our recording equipment (maximum = 120 kHz) was also noted. Calls fell into three categories based on duty cycles, and are therefore described as having low (< 5%), intermediate (5–10%) or high (> 10%) duty cycles. After analysis, the recordings were re-recorded onto compact disc and deposited in the British Library National Sound Archive, London (http://www.bl.uk/catalogues/sound.html).

We took morphological measurements from 300 bats (see Table 2 and Fig. 5), but found sexual dimorphism in body mass of two subspecies. For these two taxa, data from males and females are shown separately in Table 2: *Monophyllus plethodon luciae* (males heavier than females, *t*-test, $t = 4.93$, $d.f. = 10$, $P < 0.001$) and *Artibeus jamaicensis schwartzi* (females heavier than males, *t*-test, $t = 3.32$, $d.f. = 83$, $P < 0.001$). None of the taxa measured in this study had high aspect ratio. We categorised our wing tip shape index data into arbitrary categories as follows: low (< 1.3), average (1.3–1.9; mean of the index for our taxa = 1.6), high (> 1.9). We calculated values for the aspect ratio and wing loading components for the PCA (Norberg and Rayner, 1987) from the mean of each taxon, but treated males and females separately for the two sexually dimorphic species, *M. plethodon luciae* and *A. jamaicensis schwartzi* (Fig. 6).

Results

We recorded and analysed echolocation calls produced by 119 bats of 12 species (14 taxa) in the families Mormoopidae, Phyllostomidae, and Natalidae (Table 1 and Figs. 1–4).

Mormoopidae

Four taxa from this family were examined: *Mormoops blainvillii* on Puerto Rico,

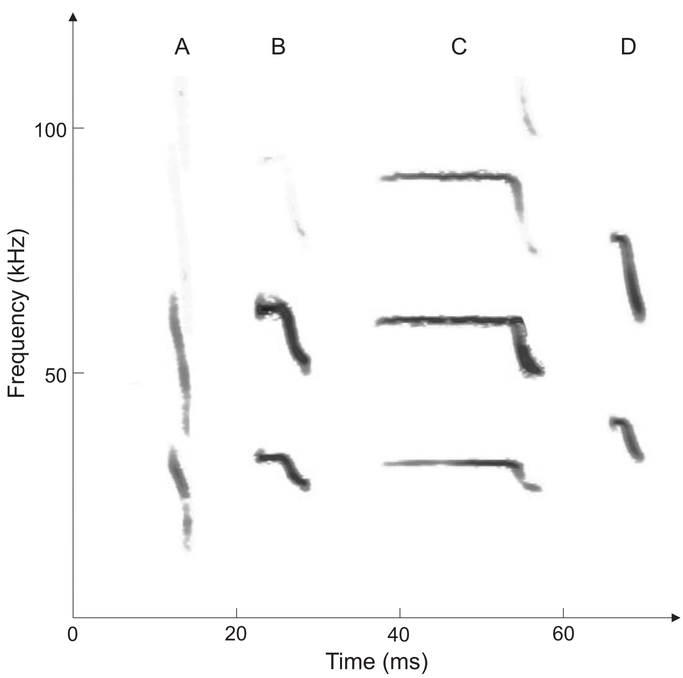

FIG. 1. Spectrograms of echolocation calls from bats of the family Mormoopidae. One echolocation call from each of *Mormoops blainvillii* (A), *Pteronotus davyi davyi* (B), *P. parnellii portoricensis* (C), and *P. quadridens fuliginosus* (D) is shown. The fundamental and second harmonic contained similar energy in calls of *P. davyi davyi* and *P. quadridens fuliginosus*. The second harmonic contained most energy in calls of *P. parnellii portoricensis*, the fundamental or second harmonic in calls of *M. blainvillii*

TABLE 1. Temporal and frequency variables of echolocation calls produced by 119 individual bats of 14 taxa (representing 12 species) caught and recorded on the islands of Puerto Rico, Dominica and St. Vincent, 1994–1996. For each variable, mean ± SD (minimum–maximum), or values separated by commas are shown, and one echolocation call per bat was analysed. Sample sizes shown are numbers of bats (*n* bats). The maximum number of harmonics (including the fundamental) produced by each species is shown. Harmonics with most energy are identified as f (fundamental), h2 (second harmonic), h3 (third harmonic), and h4 (fourth harmonic)

Taxon	Maximum number of harmonics	Harmonic with most energy	*n* bats	Duration (ms)	Interpulse interval (ms)	Frequency (kHz)		
						Peak	Start	End
M. blainvillii	4	f	2	3.2, 3.5	24, 78	27.2, 27.9	35.0, 32.0	10.0, 17.0
		h2	2	3.8, 2.0	26.1, 27	54.0, 54.5	61.0, 76.0	39.0, 40.0
P. davyi davyi	5	f	1	2.8	15	34.1	38.0	22.0
		h2	5	4.6 ± 1.5 (2.7–6.1)	41 ± 31 (13–85)	67.0 ± 2.2 (64.7–70.0)	70.3 ± 1.3 (69.0–72.0)	51.0 ± 4.4 (46.0–56.0)
P. parnellii portoricensis	4	f	1	14.5	38	31.2	28.0	23.0
		h2	9	22.0 ± 5.7 (15.2–32.0)	56 ± 20 (30–99)	61.3 ± 0.8 (60.0–62.3)	56.2 ± 3.9 (52.0–63.0)	46.8 ± 1.6 (44.0–49.0)
P. quadridens fuliginosus	3	f	4	4.8 ± 1.3 (3.6–6.2)	109 ± 79 (34–178)	40.4 ± 0.5 (39.9–40.8)	42.5 ± 1.3 (41.0–44.0)	30.3 ± 2.2 (28.0–33.0)
		h2	3	5.0 ± 0.6 (4.5–5.7)	82 ± 21 (61–103)	70.7 ± 7.1 (64.8–78.6)	82.0 ± 2.0 (80.0–84.0)	58.7 ± 2.9 (57.0–62.0)
B. cavernarum intermedia	4	f	2	4.8, 4.7	223, 230	33.4, 31.7	40.0, 39.0	17.0, 18.0
		h2	4	2.6 ± 0.5 (2.2–3.2)	76 ± 28 (46–108)	51.4 ± 2.8 (47.9–54.8)	66.8 ± 3.6 (64.0–72.0)	38.0 ± 2.3 (36.0–40.0)
E. bombifrons bombifrons	3	f	5	4.7 ± 1.0 (3.3–5.8)	107 ± 51 (67–197)	37.9 ± 4.3 (31.5–42.7)	54.2 ± 4.1 (50.0–59.0)	26.8 ± 1.9 (25.0–30.0)
G. longirostris rostrata	4	h3	8	1.6 ± 0.4 (1.2–2.3)	48 ± 22 (22–85)	90.8 ± 9.81 (81.4–110.8)	19.4 ± 20.2 (97.0–148.0)	72.5 ± 7.0 (64.0–82.0)
M. plethodon luciae	3	f	15	2.1 ± 1.0 (1.0–4.6)	70 ± 45 (18–164)	42.1 ± 6.6 (32.2–52.4)	61.5 ± 5.1 (55.0–72.0)	27.6 ± 4.2 (22.0–39.0)
		h2	10	1.3 ± 0.3 (0.9–1.6)	51 ± 27 (17–95)	85.6 ± 7.0 (78.0–99.0)	114.9 ± 10.7 (97.0–128.0)	58.5 ± 7.2 (44.0–68.0)
A. jamaicensis jamaicensis	5	h2	14	2.6 ± 0.8 (1.0–3.5)	73 ± 31 (33–133)	54.7 ± 3.6 (47.3–58.2)	72.5 ± 4.7 (64.0–83.0)	40.0 ± 2.6 (36.0–45.0)
		h3	6	1.8 ± 0.6 (1.1–2.6)	78 ± 81 (23–237)	72.2 ± 3.6 (68.2–77.6)	94.7 ± 6.4 (88.0–106.0)	56.7 ± 3.4 (51.0–60.0)

Table 1. Continued

Taxon	Maximum number of harmonics	Harmonic with most energy	*n* bats	Duration (ms)	Interpulse interval (ms)	Frequency (kHz) Peak	Start	End
A. jamaicensis schwartzi	5	h2	3	2.7 ± 1.0 (1.7–3.7)	97 ± 22 (73–116)	53.2 ± 7.0 (48.9–61.3)	74.0 ± 3.6 (71.0–78.0)	36.7 ± 4.9 (31.0–40.0)
		h3	7	2.9 ± 0.7 (1.6–3.9)	60 ± 57 (23–177)	65.7 ± 4.3 (59.3–73.4)	90.3 ± 8.5 (82.0–106.0)	45.6 ± 3.4 (43.0–53.0)
S. rufum darioi	3	f	1	3.1	76	67.6	95.0	26.0
S. lilium angeli	4	h2	5	2.7 ± 0.8 (1.3–3.3)	72 ± 23 (41–92)	73.1 ± 11.5 (55.3–85.1)	92.8 ± 8.8 (86.0–108.0)	46.2 ± 10.3 (36.0–59.0)
		h3	2	0.9, 1.0	16, 58	81.2, 79.4	108.0, 107.0	63.0, 64.0
		h4	1	1.0	58	79.4	107.0	64.0
S. lilium paulsoni	4	h2	2	1.7, 1.1	41, 42	56.0, 67.8	91.0, 75.0	36.0, 36.0
N. stramineus stramineus	3	f	2	2.8, 2.4	36, 35	44.6, 41.3	66.0, 74.0	30.0, 36.0
		h2	5	3.1 ± 0.8 (2.1–4.3)	32 ± 4 (28–38)	113.8 ± 5.1 (107.7–121.2)	152.8 ± 8.2 (143.0–162.0)	79.8 ± 5.5 (73.0–86.0)

Pteronotus davyi davyi on Dominica, and *P. parnellii portoricensis* and *P. quadridens fuliginosus* on Puerto Rico. They produced calls at intermediate (*M. blainvillii* and *P. quadridens fuliginosus*) and high (*P. davyi davyi* and *P. parnellii portoricensis*) duty cycles. The calls of *M. blainvillii* consisted of FM sweeps with up to four harmonics within the recording bandwidth of our equipment; the fundamental or second harmonic was the most intense (Fig. 1 and Table 1). *Pteronotus davyi davyi* and *P. quadridens fuliginosus* produced multiharmonic CF/FM echolocation calls (Fig. 1). *Pteronotus parnellii portoricensis* produced multiharmonic CF/FM calls in which the CF component was long (Fig. 1). The fundamental or second harmonic was the most intense in all three *Pteronotus* species (Table 1). All four mormoopids had average aspect ratio. *Pteronotus parnellii portoricensis* had low wing loading; the remaining three mormoopids had very low wing loading (Table 2 and Fig. 5). Wing tip shape index was low (indicating pointed wings) for *M. blainvillii*, and average to high (indicating more rounded wings) for three *Pteronotus* species. *Mormoops blainvillii*, *P. davyi davyi*, and *P. parnellii portoricensis* are heavier and larger than *P. quadridens fuliginosus* (Table 2), but all four taxa fall into quadrant 4 (Fig. 6): they are slow flyers which can hover. However, the hovering ability of *M. blainvillii* may be constrained by its low tip shape index.

Phyllostomidae

Brachyphylla cavernarum intermedia (subfamily Brachyphyllinae), caught on Puerto Rico, produced FM calls in which the steepness of the FM component varied (Fig. 2). Up to four harmonics were recorded, the fundamental or second harmonic being the most intense (Table 1). The duty cycle was low. *Brachyphylla*

TABLE 2. Morphological measurements of 300 adult non-gravid bats of 14 taxa (representing 12 species) caught on Puerto Rico, Dominica and St. Vincent, 1994–1996; FA: forearm length, A: aspect ratio, WL: wing loading, *I*: tip shape index (according to Norberg and Rayner, 1987). Mean ± SD are shown. Measurements of 147 bats included here, which were caught on St. Vincent in 1994 and 1995, are also given by Vaughan and Hill (1996)

Taxon	*n*	Mass (g)	FA (mm)	A	WL (Nm^{-2})	*I*
M. blainvillii	18	9.4 ± 0.8	47.3 ± 3.2	6.36 ± 0.29	5.60 ± 1.04	1.05 ± 0.26
P. davyi davyi	7	9.9 ± 0.8	48.3 ± 1.5	6.35 ± 0.17	6.33 ± 0.48	1.77 ± 0.36
P. parnellii portoricensis	6	11.3 ± 2.5	51.0 ± 0.9	6.68 ± 0.33	6.48 ± 1.04	1.93 ± 0.45
P. quadridens fuliginosus	16	5.7 ± 0.7	38.6 ± 1.1	6.92 ± 0.43	5.84 ± 0.88	1.75 ± 0.69
B. cavernarum intermedia	10	46.0 ± 3.9	66.3 ± 1.7	6.36 ± 0.27	13.6 ± 0.94	1.43 ± 0.35
E. bombifrons bombifrons	17	16.3 ± 2.6	48.2 ± 1.7	6.23 ± 0.38	9.57 ± 1.42	1.47 ± 0.39
G. longirostris rostrata	51	11.9 ± 1.1	38.5 ± 1.0	6.44 ± 0.57	9.34 ± 1.00	1.70 ± 0.84
M. plethodon luciae	8♂♂	16.7 ± 1.1	42.3 ± 0.6	6.55 ± 0.64	12.07 ± 0.76	1.59 ± 0.52
	21♀♀	14.6 ± 0.9	41.8 ± 1.1	6.40 ± 0.30	11.00 ± 0.66	1.72 ± 0.41
A. jamaicensis jamaicensis	17	45.5 ± 4.9	61.6 ± 2.2	6.05 ± 0.34	14.90 ± 1.63	1.57 ± 0.42
A. jamaicensis schwartzi	52♂♂	57.8 ± 6.5	66.2 ± 1.6	6.26 ± 0.34	16.18 ± 2.09	1.22 ± 0.42
	43♀♀	62.6 ± 7.5	66.5 ± 1.9	6.18 ± 0.48	17.31 ± 2.90	1.22 ± 0.38
S. rufum darioi	4	24.3 ± 3.4	49.0 ± 0.8	6.43 ± 0.27	11.56 ± 1.68	2.36 ± 0.23
S. lilium angeli	11	21.1 ± 0.9	44.3 ± 0.6	5.99 ± 0.24	11.60 ± 0.68	1.71 ± 0.40
S. lilium paulsoni	11	19.4 ± 2.7	42.7 ± 3.1	6.32 ± 0.59	11.59 ± 1.08	1.27 ± 0.36
N. stramineus stramineus	8	6.3 ± 0.8	41.3 ± 3.5	5.34 ± 0.29	4.34 ± 0.42	1.25 ± 0.56

cavernarum intermedia is a large, robust bat with average aspect ratio, high wing loading and average wing tip shape index (Table 2 and Fig. 5).

The low-intensity, low duty cycle, FM calls of *Erophylla bombifrons bombifrons* (subfamily Phyllonycterinae), recorded on Puerto Rico, consisted of two or three harmonics (Fig. 2), of which the fundamental was always the most intense (Table 1). *Erophylla bombifrons bombifrons* had average aspect ratio, wing loading, and wing tip shape index (Table 2 and Fig. 5). Both *B. cavernarum intermedia* and *E. bombifrons bombifrons* fall into quadrant 3 (Fig. 6): they fly well in clutter and are manoeuvrable and agile at low speeds.

Of the subfamily Glossophaginae, *Glossophaga longirostris rostrata* was caught on St. Vincent and *Monophyllus plethodon luciae* on Dominica and St. Vincent. Both taxa produced echolocation calls which were FM (Fig. 2) and had low duty cycles (Table 1). The calls of *G. longirostris rostrata* were of low intensity, and consisted of at least three harmonics (more may be present outside the recording bandwidth of the equipment). The fundamental was very faint and was often not visible in our spectral analysis. Most energy was in the third harmonic. Calls of *M. plethodon luciae* were extremely low-intensity and could only be recorded at very close range. Calls consisted of at least three harmonics and had most energy in the fundamental or second harmonic (Table 1). *Glossophaga longirostris rostrata* and *M. plethodon luciae* had average aspect ratio and average wing tip shape index; *G. longirostris rostrata* had average wing loading, while *M. plethodon luciae* had high wing loading (Table 2 and Fig. 5). Both males and females of *M. plethodon luciae* can achieve fast commuting flight and fly well in clutter (quadrant 2, Fig. 6), while *G. longirostris rostrata* is slightly more manoeuvrable and agile at very slow speeds (quadrant 3, Fig. 6).

Of the subfamily Stenodermatinae, *Artibeus jamaicensis jamaicensis* was caught on Puerto Rico and Dominica, *A. jamaicensis schwartzi* on St. Vincent, *Stenoderma rufum darioi* on Puerto Rico, *Sturnira lilium*

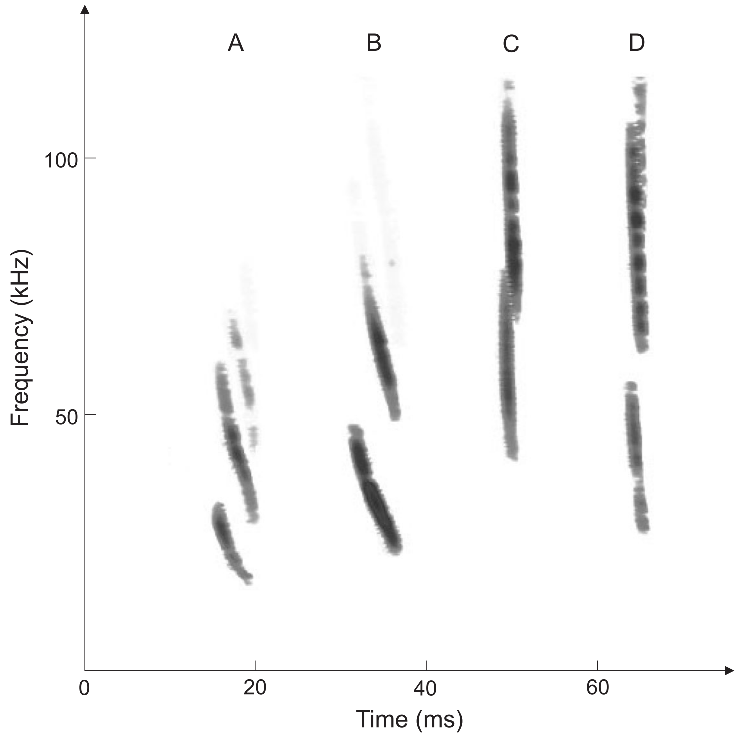

FIG. 2. Spectrograms of echolocation calls from bats of the phyllostomid subfamilies Brachyphyllinae, Phyllonycterinae and Glossophaginae. One echolocation call from each of *Brachyphylla cavernarum intermedia* (A; subfamily Brachyphyllinae), *Erophylla bombifrons bombifrons* (B; subfamily Phyllonycterinae), *Glossophaga longirostris rostrata* (C; subfamily Glossophaginae), and *Monophyllus plethodon luciae* (D; subfamily Glossophaginae) is shown. The fundamental of *G. longirostris rostrata* calls is very low intensity, and cannot be seen in the spectrogram. Some calls appear to be clipped at their maximum frequency, as higher frequencies were outside the bandwidth of the recording equipment

angeli on Dominica and *S. lilium paulsoni* on St. Vincent. All five taxa produced FM sweeps (Fig. 3) at low duty cycle (Table 1). The calls of *Artibeus jamaicensis jamaicensis* and *A. jamaicensis schwartzi* had up to five harmonics, of which the second or third was the most intense (Fig. 3). The calls of *A. jamaicensis jamaicensis* were very quiet and often not visible in spectrograms, but a comparison of second harmonics indicates that the calls of *A. jamaicensis schwartzi* are slightly lower in frequency than those produced by *A. jamaicensis jamaicensis*. Both subspecies of *A. jamaicensis* are robust bats with low to average aspect ratio and extremely high wing loading (Table 2). The heavier and bigger *A. jamaicensis schwartzi* had slightly higher wing loading and much more pointed wings (low wing tip shape index) than the lighter *A. jamaicensis jamaicensis* (average wing tip shape index, Table 2 and Fig. 5). Both subspecies are adapted to flight in clutter and have good turning performance (quadrants 2 and 3; Fig. 6).

The echolocation calls of *S. rufum darioi* were broadband FM sweeps (Fig. 3) produced at low duty cycle (Table 1). Calls consisted of fundamental, second, and third harmonics and most energy was found in the fundamental (Table 1). *Stenoderma rufum darioi* had average aspect ratio and high wing loading. The wing tips of *S. rufum darioi* were extremely rounded: the

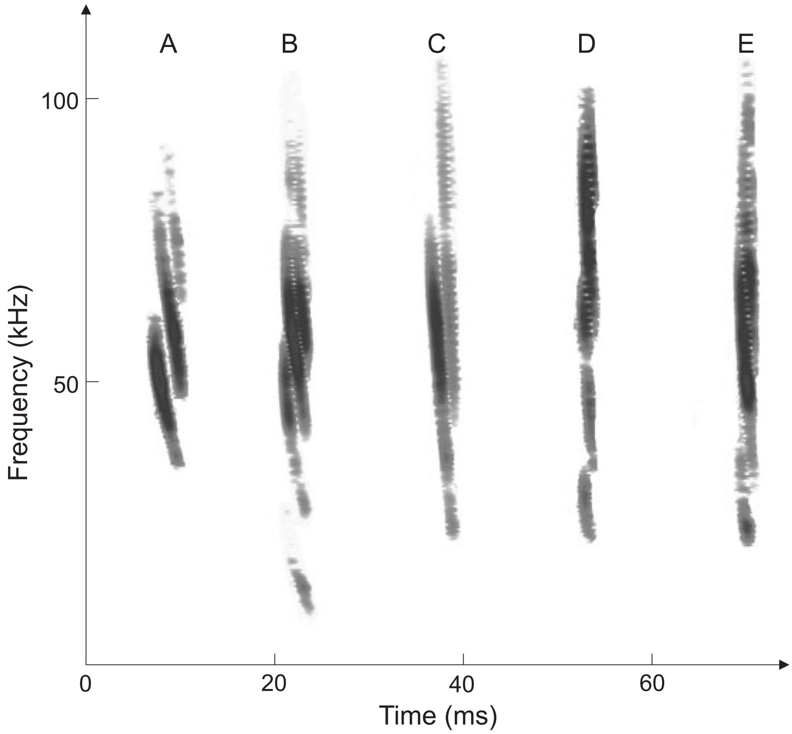

FIG. 3. Spectrograms of echolocation calls from bats of the phyllostomid subfamily Stenodermatinae. One echolocation call from each of *Artibeus jamaicensis jamaicensis* (fundamental not visible) (A), *A. jamaicensis schwartzi* (B), *Stenoderma rufum darioi* (C), *Sturnira lilium angeli* (D), and *S. lilium paulsoni* (E) is shown. The fundamental of *A. jamaicensis jamaicensis* calls is very low intensity, and cannot be seen in the spectrogram

tip shape index was much higher than that of any other species (Table 2 and Fig. 5). *Stenoderma rufum darioi* is adapted to slow flight in cluttered environments (quadrant 3; Fig. 6).

Sturnira lilium angeli and *S. lilium paulsoni* produced FM echolocation calls with low duty cycles (Fig. 3 and Table 1). Calls consisted of at least four harmonics, with most energy in the second harmonic of *S. lilium paulsoni* calls, and second, third, or fourth harmonic of *S. lilium angeli* calls (Table 1). *Sturnira lilium angeli* and *S. lilium paulsoni* had low to average aspect ratio and high wing loading. The wing tip shape index was average in *S. lilium angeli* and low in *S. lilium paulsoni* (Table 2 and Fig. 5). Both subspecies of *S. lilium* have good turning flight in clutter, but fall just inside quadrant 2 in Fig. 6, which shows that they can also fly fast when commuting.

Natalidae

Natalus stramineus stramineus was caught on Dominica and produced multiharmonic FM echolocation calls with most energy in the fundamental or second harmonic (Fig. 4). The duty cycle was intermediate. *Natalus stramineus stramineus* is a light bat with relatively long wing bones, which had the lowest aspect ratio (low) and by far the lowest wing loading (very low) of all taxa included here. Its wing tips are pointed (low wing tip shape index; Table 2 and Fig. 5). *Natalus stramineus stramineus* can fly very slowly in clutter and hunts by slow hawking and/or by gleaning (quadrant 3; Fig. 6).

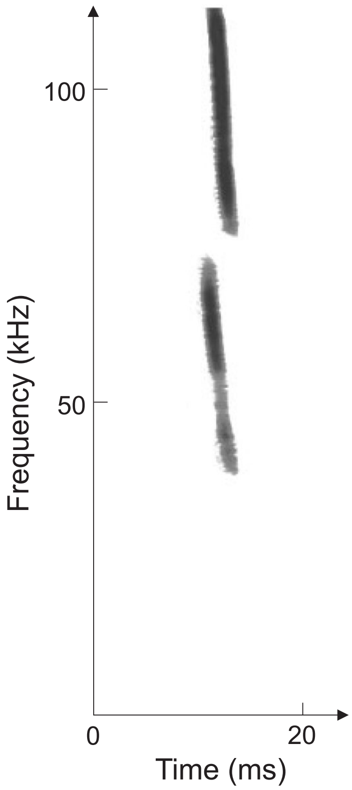

FIG. 4. Spectrogram of one echolocation call from *Natalus stramineus stramineus* (family Natalidae). The call appears to be clipped at its maximum frequency, as higher frequencies were outside the bandwidth of the recording equipment

DISCUSSION

Slow Aerial-Hawking Insectivores

Mormoopidae.—Echolocation calls of *M. blainvillii* have only previously been recorded in a flight cage (Schnitzler *et al*., 1991). Our recordings are broader in bandwidth (fundamental ca. 26 kHz; Fig. 1a) than recordings made in the flight cage (ca. 18 kHz; Schnitzler *et al*., 1991). Echolocation calls recorded on release may be more typical (i.e. similar to calls made during free flight) than those recorded in flight cages (Parsons, 1997). *Mormoops blainvillii* flies at greater heights and faster speeds than *Pteronotus* species (Goodwin, 1970) in background-cluttered space close to vegetation (Lancaster and Kalko, 1996). Its wing morphology is adapted for manoeuvrable flight and hovering, and it has a large uropatagium and pointed wing tips (Figs. 5 and 6). *Mormopterus blainvillii* feeds almost exclusively on Lepidoptera (Rodríguez-Durán and Lewis, 1987; Lancaster and Kalko, 1996).

In previous studies, most energy in calls of *P. davyi davyi* was in the second harmonic (Novick, 1963; Ibáñez *et al*., 1999) whereas in our study, most energy was in either the fundamental or the second harmonic (Fig. 1). However, the bat recorded by Novick (1963) produced calls that were several kHz higher in frequency than ours. The specimen studied by Novick (1963) was from Mexico, and probably belonged to the subspecies *Pteronotus davyi fulvus* (about 7 g; Adams, 1989) which is lighter and smaller than *P. davyi davyi* (approximately 10 g), and might therefore be expected to produce echolocation calls of higher frequency (Jones, 1995). Calls of *P. davyi fulvus*, analysed in a way which does not allow the description of harmonics or detailed call structure, were found to consist of a short CF portion at about 68 kHz, followed by an FM sweep, followed by another CF portion at about 58 kHz (duration 5.5 ms; interpulse interval about 68 ms; O'Farrell and Miller, 1997). Only one of our bats produced calls with the fundamental as the most intense harmonic. It is possible that the orientation of the bat producing that call and its distance to the microphone meant that the higher harmonics were sufficiently attenuated to make the fundamental appear to be the most intense. We find *P. davyi davyi* to have much more rounded wings, lower (though average) aspect ratio and lower wing loading than *P. davyi* as described by Norberg and Rayner (1987). Our data suggest that this subspecies is very manoeuvrable, and adept at very slow flight and

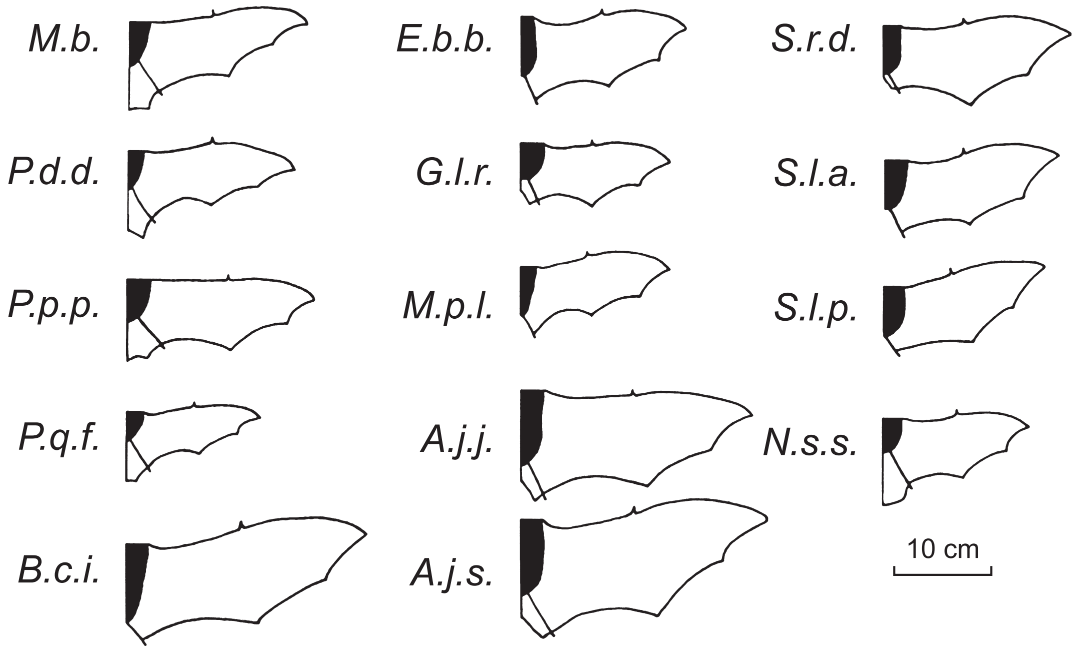

FIG. 5. Examples of wing tracings of the 14 taxa of bats caught on Puerto Rico, Dominica and St. Vincent. Abbreviations are as follows: *M. blainvillii* (*M.b.*), *P. davyi davyi* (*P.d.d.*), *P. parnellii portoricensis* (*P.p.p.*), *P. quadridens fuliginosus* (*P.q.f.*), *B. cavernarum intermedia* (*B.c.i.*), *E. bombifrons bombifrons* (*E.b.b.*), *G. longirostris rostrata* (*G..l.r.*), *M. plethodon luciae* (*M.p.l.*), *A. jamaicensis jamaicensis* (*A.j.j.*), *A. jamaicensis schwartzi* (*A.j.s.*), *S. rufum darioi* (*S.r.d.*), *S. lilium angeli* (*S.l.a.*), *S. lilium paulsoni* (*S.l.p.*) and *N. stramineus stramineus* (*N.s.s.*). In *P. davyi davyi*, the wing area (shown in white) extends over the body (shown in black)

hovering in background-cluttered space (Fig. 6).

In this study, *P. parnellii portoricensis* produced echolocation calls similar to those described in numerous previous studies of the echolocation of *P. parnellii* and suitable for the detection of fluttering prey movements in highly-cluttered space (Suga, 1990; Schnitzler and Kalko, 1998). Such echolocation calls are not suitable for the detection of non-fluttering prey, and are therefore not normally used by bats which glean (Schnitzler and Kalko, 1998). Our data suggest that this subspecies is very manoeuvrable and adept at very slow hawking flight and hovering in highly-cluttered space (Fig. 6). We find *P. parnellii portoricensis* to be much heavier and have more rounded wing tips than the *P. parnellii* described by Norberg and Rayner (1987). Observations show that *P. parnellii* flies close to the ground and to vegetation (Bonaccorso, 1979).

Echolocation calls and wing morphology of *P. quadridens* have not been described previously. Calls were similar in structure to those of *P. davyi davyi*, but *P. quadridens fuliginosus* produced echolocation calls of higher frequency, and is a smaller species. Its wing shape is similar to that of *P. parnellii portoricensis*, but it is expected to hunt in background-cluttered space.

All mormoopid species are said to be slow aerial-hawking insectivores, and three subspecies of *Pteronotus* considered here feed on Lepidoptera, Coleoptera, and Diptera (Bateman and Vaughan, 1974; Rodríguez-Durán and Lewis, 1987). According to Norberg and Rayner (1987) mormoopid wing shape is adapted to flight in relatively

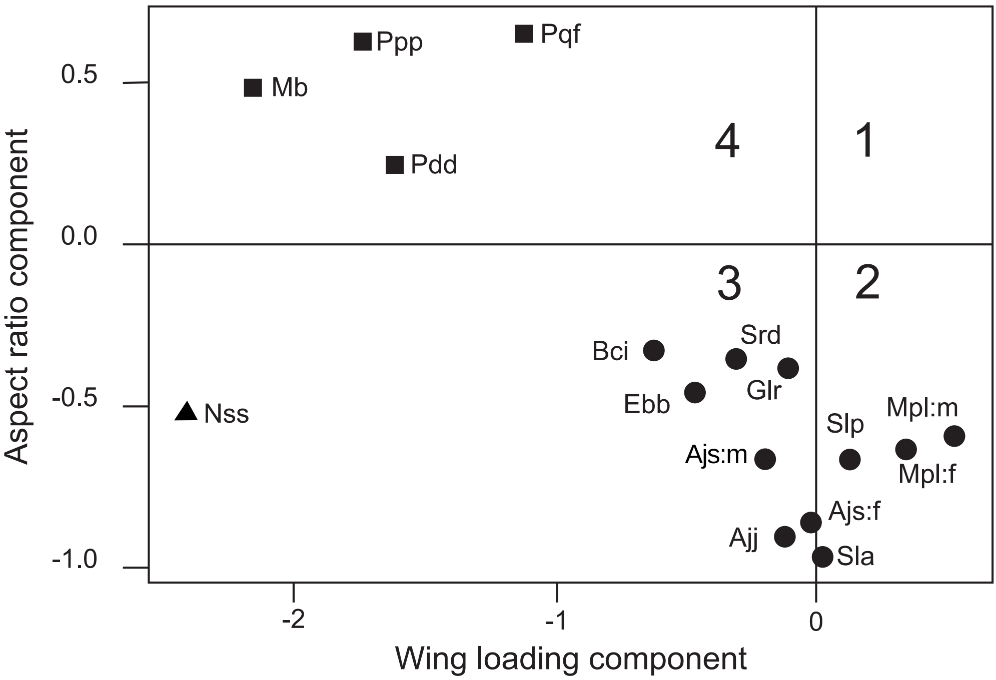

FIG. 6. Plot of size-independent components calculated for the bats in this study from a PCA conducted by Norberg and Rayner (1987) on 215 species. Abbreviations of taxa are as in Fig. 5, except for the sexually dimorphic taxa: *M. plethodon luciae* (Mpl:m for ♂♂ and Mpl:f for ♀♀) and *A. jamaicensis schwartzi* (Ajs:m for ♂♂ and Ajs:f for ♀♀); data points represent means for each taxon or gender. Different symbols represent the families: ■ = Mormoopidae, ● = Phyllostomidae, ▲ = Natalidae. Numbers represent quadrants, bats falling into each are broadly similar in their wing morphology and predicted flight behaviour. Bats in quadrant 1 fly fast and are agile, those in 2 are frugivores and nectarivores which can fly in clutter but also have high-speed commuting flight, those in 3 can hawk slowly and/or hover, those in 4 have good hovering performance (Norberg and Rayner 1987)

open areas at slow or average speeds with low manoeuvrability, possibly compensated for by wing musculature and anatomy which is adapted to fast, enduring and manoeuvrable flight (Vaughan and Bateman, 1970). Our wing morphology data show that the mormoopids described here are more manoeuvrable than suggested by Norberg and Rayner (1987), and we expect *P. parnelli portoricensis* to hunt in highly-cluttered space.

Natalidae. — Echolocation calls of the insectivore *N. stramineus stramineus* consisted of a short FM sweep, but intermediate duty cycle may mean that this species cannot easily fly in highly-cluttered space. The low aspect ratio, very low wing loading and the long wings (Smith and Starrett, 1979) of this species enable the slow, manoeuvrable flight (Norberg and Rayner, 1987) which has been observed in the field (Goodwin, 1970). However, Norberg and Rayner (1987) found that this species had extremely rounded wing tips, while we found very pointed ones (Fig. 5). *Natalus stramineus stramineus* probably feeds by slow aerial hawking in background-cluttered space around the edge of vegetation.

Frugivores, Nectarivores, and Omnivores

Phyllostomidae.—Multiharmonic FM echolocation calls of *B. cavernarum intermedia* have not been described previously.

It is a large species with high wing loading, which mainly forages opportunistically above the canopy on fruit, pollen and insects (Swanepoel and Genoways, 1983). It has short, wide wings, with average aspect ratio (Struhsaker, 1961; Fig. 5); this in combination with its brief echolocation calls means that it does not fly high above the canopy. We conclude that *B. cavernarum intermedia* feeds in and around edges of vegetation in background-cluttered space.

The echolocation calls of *E. bombifrons bombifrons*, not described previously, are suitable for use near vegetation. *Erophylla bombifrons bombifrons* eats fruit, pollen, nectar and insects (Gardner, 1977). The wing morphology of this species suggests that it is able to fly in clutter, but that its commuting flight is not fast or efficient (Fig. 6).

Echolocation calls of *G. longirostris rostrata* have not been described previously, and are suitable for use in highly-cluttered space. In Venezuela *G. longirostris* feeds on pollen and fruit (Soriano *et al*., 1991), and its wing morphology suggests that it can fly slowly in clutter (Fig. 6).

Echolocation calls of *M. plethodon luciae* were of similar duration and frequency to those of *G. longirostris rostrata* (Fig. 2), although sample sizes were small. Its wing morphology suggests that *M. plethodon luciae* is capable of fast flight away from clutter, which allows the use of longer duration calls without the problem of overlap between pulses and echoes from close targets (Fig. 6).

The echolocation calls of bats of the subfamily Glossophaginae are not well described in the literature. Their low-intensity FM calls are probably used only at close range (Griffin and Novick, 1955; Novick, 1963) and are suitable for use under the canopy in highly-cluttered space. The broad wings of glossophagine bats have relatively large chiropatagia, and are adapted for slow flight in clutter (Smith and Starrett, 1979; Norberg and Rayner, 1987; Figs. 5 and 6). Of the species included here, *M. plethodon luciae* is the most capable of fast flight in open space (Fig. 6).

The echolocation calls of *A. jamaicensis jamaicensis* and *A. jamaicensis schwartzi* were similar in structure to those of *A. jamaicensis richardsoni* from Panama (Griffin and Novick, 1955; Fullard and Belwood, 1988). *Artibeus jamaicensis schwartzi* produces echolocation calls of similar frequency to those of the smaller subspecies *A. jamaicensis jamaicensis* (Jones, 1995). *Artibeus jamaicensis* is primarily a frugivore, but also eats some insects, leaves, nectar and pollen (Heithaus *et al*., 1975; Bonaccorso, 1979; Rodríguez-Durán and Vázquez, 2001). Individuals of *A. jamaicensis richardsoni* can carry fruits weighing 20–40% of their body weight (Bonaccorso, 1979), so the wing morphology of this subspecies is expected to be adapted to load-carrying. Low wing loading is suitable for load-carrying (Norberg and Rayner, 1987), but the wing loading of this species is very high and is more suitable for turning flight at low speeds in clutter than for load-carrying (Lawlor, 1973; Fig. 6). *Artibeus jamaicensis* flies in the canopy and may hover while selecting fruit (Kalko *et al*., 1996; Stockwell, 2001)

The multiharmonic echolocation calls of *S. rufum darioi* have not been described previously. This rare species consumes a variety of fruits and is restricted to forest canopy in Puerto Rico (Willig and Gannon, 1996). Individuals of *S. rufum darioi* examined for this study had large chiropatagia, extremely rounded wing tips, high wing loading and average aspect ratio, and differ substantially from the three individuals described by Kopka (1973) as *Stenoderma* spp. and presented by Norberg and Rayner (1987) as *S. rufum*. Such a large difference in wing morphology is unlikely to be due to the effects of the preservation of Kopka's specimens (Bininda-Emonds and Russell, 1994), and we conclude that Kopka's bats do not belong to the species currently called *S. rufum*. Our data indicate that *S. rufum darioi* is able to fly slowly with great manoeuvrability in highly-cluttered space; its echolocation calls are suitable for this behaviour.

The echolocation calls of *Sturnira* species have not been previously described. The multiharmonic calls of *S. lilium angeli* and *S. lilium paulsoni* are similar in structure to those of *Artibeus* species and are useful for short-range detection. *Sturnira lilium* is a frugivore which forages under the canopy (Willig *et al*., 1993) and takes some nectar in the dry season (Heithaus *et al*., 1975). The wing morphology of *S. lilium* is suited to flight under the canopy in clutter (Lawlor, 1973; Fig. 5), but its commuting flight is relatively fast and efficient (Fig. 6).

Low-intensity, high frequency, multiharmonic broadband echolocation calls produced at low duty cycle are high-resolution calls characteristic of bats that forage close to vegetation in highly-cluttered space (Schnitzler and Kalko, 1998), as do the Phyllostomidae. All taxa included here are capable of flight and echolocation in clutter. *Monophyllus plethodon luciae* and *S. lilium* are most adapted to fast and efficient commuting flight. These species may be the most specialist feeders of the frugivores, nectarivores, and omnivores included here, and may therefore need to travel relatively long distances to find food.

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