

Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation

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Abstract

In southern Central America, 10 species of emballonurid bats occur, which are all aerial insectivores: some hunt flying insects preferably away from vegetation in open space, others hunt in edge space near vegetation and one species forages mainly over water. We present a search call design of each species and link signal structure to foraging habitat. All emballonurid bats use a similar type of echolocation call that consists of a central, narrowband component and one or two short, frequency-modulated sweeps. All calls are multi-harmonic, generally with most energy concentrated in the second harmonic. The design of search calls is closely related to habitat type, in particular to distance of clutter. Emballonurid bats foraging in edge space near vegetation and over water used higher frequencies, shorter call durations and shorter pulse intervals compared with species mostly hunting in open, uncluttered habitats. Peak frequency correlated negatively with body size. Regular frequency alternation between subsequent calls was typical in the search sequences of four out of 10 species. We discuss several hypotheses regarding the possible role of this frequency alternation, including species identification and partitioning of acoustic channels. Furthermore, we propose a model of how frequency alternation could increase the maximum detection distance of obstacles by marking search calls with different frequencies.

Introduction

Emballonuridae (sheath-tailed bats or sac-winged bats) are pan-tropical. Currently, 19 species are recognized for the Neotropics (Simmons, 2005), of which 10 occur in southern Central America (Reid, 1997). Emballonurid bats are all aerial insectivores, with some species hunting close to vegetation at forest edges and in forest gaps and others above the canopy and over open landscapes (Kalko, 1995). One species, *Rhynchonycteris naso*, forages mainly over water (Kalko, 1995; O'Farrell & Miller, 1997; Nogueira & Pol, 1998; Fenton *et al.*, 1999). Emballonurid bats produce shallow-modulated and multi-harmonic echolocation calls with most energy concentrated in the second harmonic. Although overall call structure is rather similar within the family, there are species-specific differences in call parameters, namely peak frequency, call duration, pulse interval, direction of call modulation, and presence or absence of short, frequency-modulated (fm) components (Barclay, 1983; Kalko, 1995; O'Farrell & Miller, 1997; Fenton *et al.*, 1999; Ochoa, O'Farrell & Miller, 2000; Ibáñez *et al.*, 2002, 2004).

The design of search signals in bats is to a large extent influenced by habitat (Neuweiler, 1989; Fenton, Portfors & Rautenbach, 1998; Schnitzler & Kalko, 1998, 2001; Jones,

1999; Neuweiler, 2003; Schnitzler, Moss & Denzinger, 2003). For any bat foraging in open space, the main echolocation requirement is long-range detection (Neuweiler, 1990). Compared with bats that fly in confined areas, bats in open space emit longer and shallow-modulated calls, where most energy is focused in a narrow frequency band to increase the likelihood of prey detection by perception of acoustic glints (Kober & Schnitzler, 1990; Kalko, 1995). Additionally, calls are lower in frequency, thus benefiting from less atmospheric attenuation (Griffin, 1971; Lawrence & Simmons, 1982; Barclay, 1983; Houston, Boonman & Jones, 2003). Furthermore, longer pulse intervals reduce or eliminate the possibility of receiving an echo after the emission of a subsequent call, which might lead to erroneous echo assignment.

In contrast, bats foraging in edge space have to avoid collision with the surrounding vegetation while searching for food and need to discriminate potential prey against the cluttered background (e.g. Schnitzler & Kalko, 1998, 2001). These bats benefit from higher frequencies and distinct fm-components that provide more precise information about distance, direction and texture of objects (Neuweiler, 1990; Schnitzler & Kalko, 1998). In addition to the correlation of main foraging habitat with call structure, the call frequency of echolocating bats also varies with body size (Pye, 1979;

Aldridge & Rautenbach, 1987; Weid & von Helversen, 1987; Heller & von Helversen, 1989; Jones, 1994, 1999), with smaller species generally emitting higher calls.

Four out of the 10 emballonurid bat species known from southern Central America regularly alternate peak frequencies between subsequent calls during search flight (Pye, 1973; Barclay, 1983; Kalko, 1995), as it is known for a range of fast and high flying, aerial hawking bats such as the European noctule *Nyctalus noctula* with its characteristic 'plip-plop' search calls (Watson, 1970; Pye, 1973; Ahlén, 1981; Miller & Degn, 1981), other aerial insectivorous vespertilionid bats (Ahlén, 1981; Weid & von Helversen, 1987; Denzinger *et al.*, 2001) and free-tailed bats (Molossidae; Heller, 1995; Fenton *et al.*, 1998; Kössl, Mora & Vater, 1999; Kingston *et al.*, 2003; Mora *et al.*, 2004).

The significance of this behaviour remains controversial (Kingston *et al.*, 2003). Possible scenarios include (1) jamming avoidance to discriminate own echoes from conspecifics foraging in the same area (Habersetzer, 1981), (2) increase in bandwidth by integrating information over several calls (Heller, 1995), (3) facilitation of species recognition between species with similar signal design and calling frequencies (Heller & von Helversen, 1989; Kalko, 1998; Schnitzler & Kalko, 2001) and (4) increase of maximum detection range (Weid & von Helversen, 1987; Fenton *et al.*, 1998; Denzinger *et al.*, 2001; Kingston *et al.*, 2003; Mora *et al.*, 2004) by marking calls to discriminate between echoes of successive calls. The four explanations are not mutually exclusive.

The purpose of this study was to assess, compare and interpret the echolocation calls of 10 potentially co-existing emballonurid bat species from southern Central America. We focus on the interspecific variation of search calls with regard to species identification and summarize general trends, in particular habitat type and body size, that influence signal design. Furthermore, we take data from four species to explore the possible functional significance of call frequency alternation. We discuss several hypotheses and extend a model calculation proposed by Holderied & von Helversen (2003), focusing on maximum detection distance and the potential role of call alternation by marking subsequent calls with different peak frequencies.

Materials and methods

Study sites

We recorded the echolocation calls of emballonurid bats at several field sites in the lowlands of Costa Rica and Panama from 1996 to 2004. Most recordings and observations in Costa Rica were made in the evergreen lowland rainforest at La Selva Biological Station (Organisation of Tropical Studies; see McDade *et al.*, 1994) and in the deciduous dry forest at Santa Rosa (Area Conservation Guanacaste). Recordings in Panama were taken in the semi-deciduous, moist tropical lowland forest on Barro Colorado Island (see Leigh, 1999), a field station of the Smithsonian Tropical Research Institute, and in Soberania National Park.

Species identification and habitat classification

We followed the nomenclature of Simmons (2005) and regard *Centronycteris centralis* as a species different from its South American congener *Centronycteris maximiliani* (Simmons & Handley, 1998; Woodman, 2003). We positively identified species specificity of echolocation calls for 10 emballonurid bat species with reference recordings, thereby clarifying the misidentification of two species in Kalko (1995) that had been erroneously assigned to *Cormura brevirostris* (correct species: *Centronycteris centralis*) and *Peropteryx* spec. (correct species: *Cormura brevirostris*). Reference recordings were obtained from individuals that had been captured at their roosts or in the field with mist nets and were subsequently released into open space or very large forest gaps. Foraging *Diclidurus albus* permitted unambiguous initial identification in the field because of the white fur and transparent wings. Captured bats were identified, weighed and measured (e.g. reproductive status, forearm length). We recorded most bats at dawn; this permitted visual observation of their flight behaviour and prevented possible confusion with other species flying near the recording area.

In addition to the reference recordings, we recorded all 10 emballonurid species while foraging either within the forest, in gaps, at forest edges, or in open areas above the canopy, water or the ground to assess the general structure of their search calls. During the recording periods we observed the bats' flight behaviour with night vision goggles or under favourable conditions against the night sky and/or we listened to their calls with a stereo-headset. We commented on their behaviour simultaneously with the sound recordings and estimated their position in space, namely their distance to vegetation. On the basis of our comments on the bats' flight behaviour and referring to habitat classifications given in other studies (for a review, see Schnitzler & Kalko, 2001; Schnitzler *et al.*, 2003), we assigned each species to one of three main foraging habitats: (1) edge space (estimated average distance of bat to vegetation: 2–5 m), (2) open space (estimated average distance of bat to vegetation: >5 m) and (3) space over water. We pooled all of our observations and finally assigned a specific habitat type to each of the bat species when an estimated 80% or more of all observations of the respective bat species originated from this habitat. Within habitats, we ranked species along a continuous axis in relation to the estimated distance to vegetation (clutter).

Sound recordings

We obtained most recordings with a real-time recorder Ultrasoundgate (Benedict v. Laar) at a sampling rate of 500 kHz and a resolution of 16 bits (AKG microphone, frequency response between 12 and 120 kHz) and with a custom-made real-time recorder (PC-Tape, Animal Physiology, University of Tuebingen, Tuebingen, Germany) at a sampling rate of 480 kHz and a resolution of 16 bits

[microphone: flat frequency response (± 3 dB) between 30 and 120 kHz; drop in sensitivity of ± 6 dB for frequencies below 15 and above 160 kHz]. In both cases, the digital recordings were stored on a hard disk of a laptop. Some earlier recordings were made with an Ultrasonic Laar Bridge Box detector [AKG microphone (AKG Acoustics, Heilbronn, Germany), flat frequency response between 12 and 120 kHz] with a sampling rate of 400 kHz, a resolution of 8 bits and a data memory of 6 s. The time-expanded recordings (10 times) were stored on a Sony TCD-D7 DAT-Recorder (Sony, Cologne, Germany). Initial recordings of *D. albus* were gathered with the Delay-line, a custom-made bat detector (Animal Physiology, University of Tuebingen) with a sampling rate of 312.5 kHz [microphone: flat frequency response (± 3 dB) between 30 and 120 kHz; drop in sensitivity of 0.2 dB kHz^{-1} for frequencies below 15 and above 200 kHz]. These recordings were read into a buffer (3.3 s real time), slowed down 15 times and then read out onto a Sony Walkman professional WM-D6C.

Sound analysis

Sound sequences were analysed with AVISOFT SASLAB PRO software, versions 3.95 and 4.34 (Raimund Specht, Berlin). Faint calls or calls with loud echoes were excluded from analysis. To generate spectrograms, we used a Flat Top window with a 1024 fast fourier transformation (FFT), a frame of 100% and an overlap of 93.75%. This resulted in a maximum frequency resolution of 488 Hz and a time resolution of 0.12 ms. We discriminated two call components: steep, fm-components (sweep rate $>400 \text{ Hz ms}^{-1}$) and narrowband, quasi-constant frequency (qcf) components (sweep rate $<400 \text{ Hz ms}^{-1}$; Fig. 1) following Schnitzler & Kalko (1998). Measurements were taken from the spectrogram with the 'bound cursor' (bound to the frequency with maximum intensity) on the screen. We limited our measurements to the second harmonic as it concentrated, with very few exceptions, most of the energy. The start and end of a call were set at the point where the amplitude of the oscillogram began to consistently rise or decrease above background noise. Call duration was measured by taking the time of sound emission at the start and end of the whole signal including fm-components. We used the automatic parameter measurements in Avisoft to extract the peak frequency of the qcf-component (frequency of maximum amplitude of the spectrum). The pulse interval between two calls was defined as the time between the start of one call and the start of the subsequent call. Pulse interval was assigned to the previous call. We calculated bandwidth of the individual fm-components as the frequency difference between the start of the initial fm-component and the qcf-part, and between the end of the qcf-component and the terminal fm-component, respectively (Fig. 1).

Statistics

Multivariate analysis of variance (MANOVA) was used to test for variation in call parameters (peak frequency, call

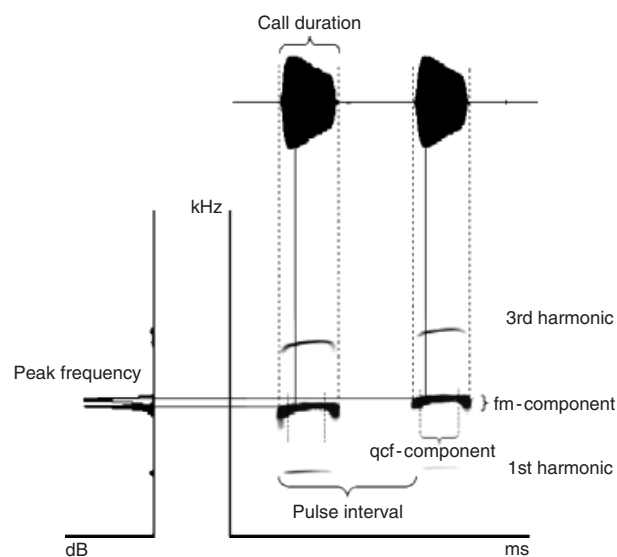


Figure 1 Echolocation calls of *Saccopteryx bilineata* (oscillogram, spectrogram and power spectrum) to illustrate the characteristic structure of emballonurid echolocation signals during search flight and our measurement points. We discriminate between steep broadband frequency-modulated (fm) components and narrowband, quasi-constant frequency (qcf) components. Pulse interval is measured from the start of the first call to the start of the second call. Measurements were taken from the second harmonic only, in which most of the energy is concentrated.

duration, pulse interval, direction of modulation of qcf-component, and bandwidth of initial and terminal fm-component) and interaction between call frequency type classified as low, middle and high in relation to the peak frequencies of the calls. Individuals were nested within each species to minimize pseudoreplication. We conducted a univariate *F*-test [analysis of variance (ANOVA)] for each parameter included in the MANOVA and a multivariate unequal *n* honestly significant difference (HSD) *post hoc* test for significance of single parameters between individual species and call frequency types.

We used a MANOVA with call frequency types nested within species including an interaction with habitat to test whether species flying in different habitats also differ in call parameters. We conducted a univariate *F*-test (ANOVA) for each parameter and a multivariate unequal *n* HSD *post hoc* test for significant differences of call parameters between habitats. For each species that regularly alternated call frequency during search flight, we used a MANOVA, with individuals nested within call type, to assess differences between calls emitted at different frequencies. We conducted an ANOVA for each call parameter and used an unequal *n* HSD *post hoc* test to reveal significant differences between the call types.

In our analysis we focus on interspecific differences in call structure and therefore selected these sequences for analysis from recordings where the bats foraged in their main habitat, and where the recordings originated from different localities and nights to minimize pseudoreplication by recording the same individual repeatedly. For each species,

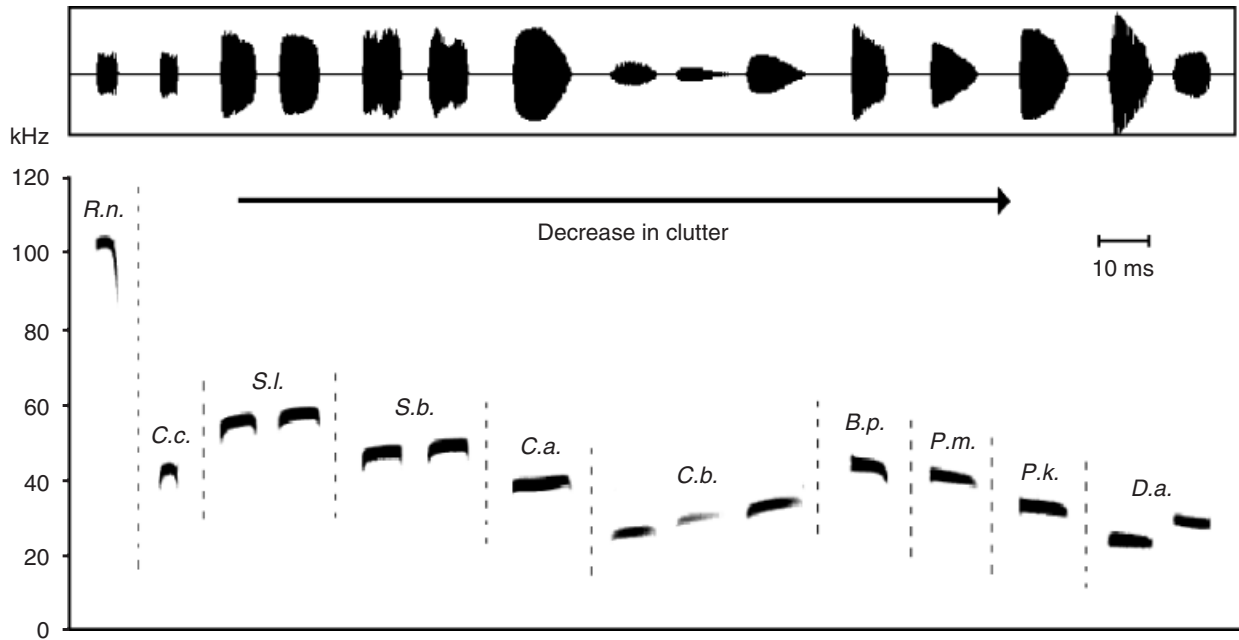


Figure 2 Spectrograms and oscillograms of echolocation calls emitted during search flight in 10 emballonurid species in southern Central America in relation to their preferred foraging habitat including (1) open space, (2) close to vegetation (clutter) or (3) above water. Pulse intervals are not scaled. *R. n.*, *Rhynchonycteris naso*; *C. c.*, *Centronycteris centralis*; *S. l.*, *Saccopteryx leptura*; *S. b.*, *Saccopteryx bilineata*; *C. a.*, *Cyttarops alecto*; *C. b.*, *Cormura brevirostris*; *B. p.*, *Balantiopteryx plicata*; *P. m.*, *Peropteryx macrotis*; *P. k.*, *Peropteryx kappleri*; *D. a.*, *Diclidurus albus*.

except *Peropteryx kappleri* where our sample size was low ($n = 9$ sequences), we included 12 sequences with approximately the same number of echolocation pulses per sequence. For the presented tables and the correlation analysis (habitat vs. call parameters and frequency vs. body mass and forearm), we first averaged measurements of call parameters over each sequence (pass of one individual over the microphone) and then calculated mean \pm standard deviation for each species (mean of means).

We used a Spearman rank order correlation to assess a possible relationship between frequency and body mass, as well as frequency and forearm length. Furthermore, we applied a Spearman rank order correlation to test for an association of different call parameters and distance of foraging bats to vegetation. All statistical analyses were conducted in STATISTICA, version 7.0.

Results

General design of search flight calls

The echolocation calls of 10 species of emballonurids all consisted of a rather uniform signal type. The main energy was concentrated in a central, shallow modulated narrowband (qcf) part, accompanied by one or two short fm-sweeps. Calls were multi-harmonic, generally with most energy concentrated in the second harmonic. Although the overall signal structure was similar across species, the search call design differed significantly between species (Figs 2 and 3; Table 1) [MANOVA Wilks $\lambda = 0.02$, $F_{(12,37)} = 618$, $P < 0.0001$]. The

univariate results for each dependent variable revealed significant differences for each parameter tested (Table 1).

Foraging habitat and call design

Five species foraged predominantly in edge space (*Ce. centralis*, *Saccopteryx leptura*, *Saccopteryx bilineata*, *Co. brevirostris* and *Cyttarops alecto*) and four species hunted mainly in open space (*Peropteryx macrotis*, *P. kappleri*, *Balantiopteryx plicata* and *D. albus*). One species, *R. naso*, mostly foraged over water. Between these three groups defined by preferred habitat type, search call parameters differed significantly [Wilks $\lambda = 0.01950$, $F_{(42,7362.7)} = 230.52$, $P < 0.0001$] in peak frequency [$F_{(14,1574)} = 8482.58$, $P < 0.0001$], call duration [$F_{(14,1574)} = 46.09$, $P < 0.0001$] and pulse interval [$F_{(14,1574)} = 163.18$, $P < 0.0001$]. In addition, we found significant differences in bandwidth, including modulation of the qcf-component [$F_{(14,1574)} = 232.60$, $P < 0.0001$] as well as the initial [$F_{(14,1574)} = 140.76$, $P < 0.0001$] and terminal fm-component [$F_{(14,1574)} = 146.49$, $P < 0.0001$].

Within two habitats, edge and open space, we observed a species-specific trend with respect to preferred distance to vegetation. This trend ranged in edge space from *Ce. centralis*, which we found almost always hunting in small openings within dense forest, to *Co. brevirostris* and *Cy. alecto*, which preferably foraged in larger gaps and semi-open space above small rivers or larger forest clearings. In open space, the trend ranged from *B. plicata*, which mostly foraged above open, savannah-like areas or pastures, to

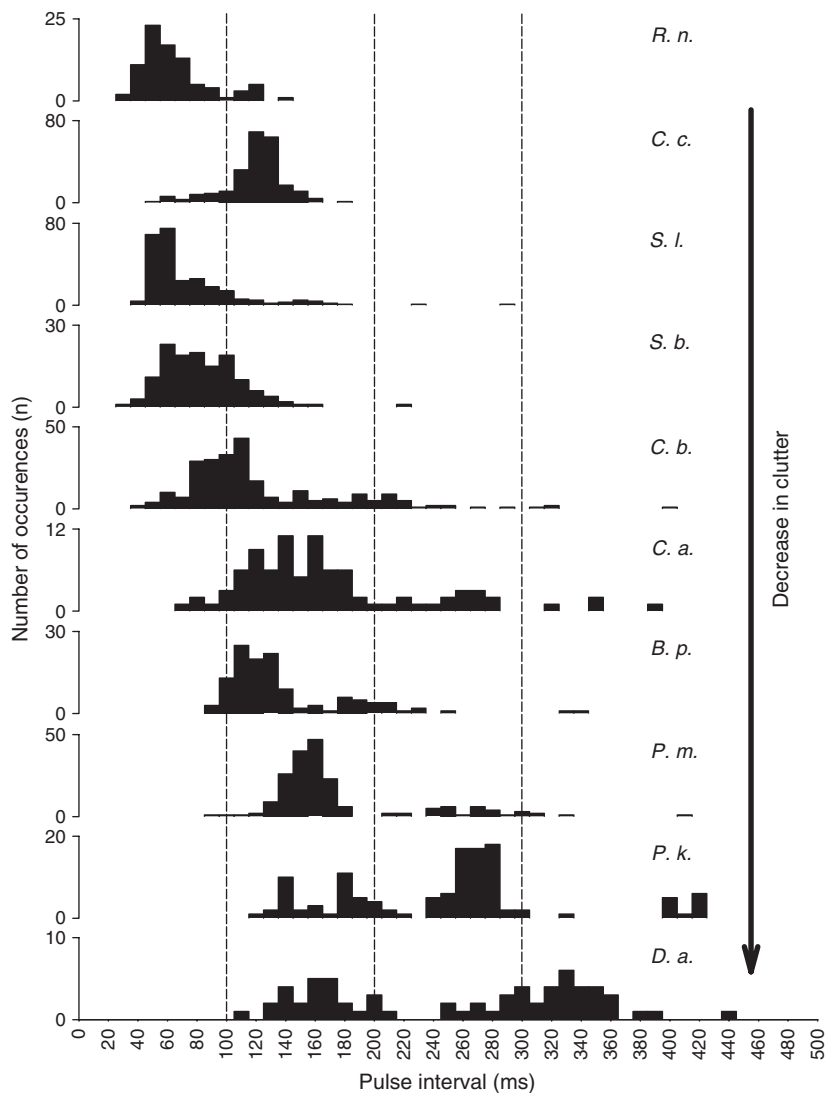


Figure 3 Histograms of pulse interval during search flight in 10 emballonurid species of southern Central America. Class width is 10 ms. Dotted lines mark 100 ms, 200 ms and 300 ms pulse interval length. *R. n.*, *Rhynchonycteris naso*; *C. c.*, *Centronycteris centralis*; *S. l.*, *Saccopteryx leptura*; *S. b.*, *Saccopteryx bilineata*; *C. a.*, *Cyttarops alecto*; *C. b.*, *Cormura brevirostris*; *B. p.*, *Balantiopteryx plicata*; *P. m.*, *Peropteryx macrotis*; *P. k.*, *Peropteryx kappleri*; *D. a.*, *Diclidurus albus*.

D. albus, which mainly hunted high above the canopy and the ground. Call parameters, in particular peak frequency ($r_s = -0.76$, $P < 0.05$), call duration ($r_s = 0.79$, $P < 0.05$) and pulse interval ($r_s = 0.86$, $P < 0.05$), of the species correlated with this ecological trend (Figs 2 and 3). Overall, bats in edge space broadcasted echolocation calls at higher frequencies with shorter pulse intervals and call durations than bats hunting in open space (Figs 2 and 3, Table 1). Call duration correlated positively with pulse interval ($r_s = 0.89$, $P < 0.05$), but both these parameters correlated negatively with frequency (call duration: $r_s = -0.78$, $P < 0.05$; pulse interval: $r_s = -0.80$, $P < 0.05$).

Correlation of call frequency with body size

Within the 10 species, the peak frequency of search calls correlated negatively with body size (Fig. 4; peak frequency vs. body mass, $r_s = -0.79$, $P < 0.05$; peak frequency vs. forearm length, $r_s = -0.85$, $P < 0.05$). Smaller species such

as *R. naso* [4 g, forearm (FA) = 37 mm] and *S. leptura* (4.5 g, FA = 41 mm) used higher frequencies (96 and 53/56 kHz, respectively), while larger bats such as *Co. brevirostris* (10 g, FA = 48.5 mm), *P. kappleri* (7.5 g, FA = 46 mm) and *D. albus* (20 g, FA = 66 mm; Reid, 1997) produced search calls at lower frequencies (25/28/32, 32 and 23/27 kHz, respectively).

Call frequency alternation

The search signals of four species, *S. leptura*, *S. bilineata*, *D. albus* and *Co. brevirostris*, were characterized by regular alternation of call frequencies, two frequency types in the first three species and three in *Co. brevirostris*. Echolocation parameters between call frequency types differed significantly in all four species, *S. bilineata* [Wilks $\lambda = 0.25$, $F_{(6,22)} = 107$, $P < 0.0001$], *S. leptura* [Wilks $\lambda = 0.18$, $F_{(6,23)} = 168.149$, $P < 0.0001$], *D. albus* [Wilks $\lambda = 0.14$, $F_{(8,84)} = 85.89$, $P < 0.0001$] and *Co. brevirostris* [Wilks

Table 1 Search flight call parameters of 10 emballonurid species from southern Central America (mean \pm sd; results of the univariate *F*-test)

Species	Call type	Peak frequency of qcf-component (kHz)	Call duration (ms)	Pulse J: interval (ms)	Modulation of qcf-component	Bandwidth of qcf-component (kHz)	Bandwidth of initial fm-component (kHz)	Bandwidth of terminal fm-component (kHz)	Number of calls of (n)	Number of individuals (n)
<i>Rhynchonycteris naso</i>		98.2 \pm 2.3 ^a	4.8 \pm 0.9 ^a	58 \pm 12 ^{a,h}	Straight/Up	0.9 \pm 0.8 ^a	0.5 \pm 0.6 ^a	7.3 \pm 3.7 ^a	153	12
<i>Centronycteris centralis</i>		41.3 \pm 0.3 ^b	5.9 \pm 1.4 ^b	119 \pm 10 ^b	Straight	0.7 \pm 0.3 ^b	2.9 \pm 0.9 ^b	1.6 \pm 0.3 ^b	156	12
<i>Saccopteryx leptura</i>	Low	51.3 \pm 1.8 ^c	7.2 \pm 1.5 ^c	68 \pm 24 ^h	Up	1.6 \pm 0.8 ^c	0.5 \pm 0.6 ^c	0.4 \pm 0.5 ^{b,c}	132	12
	Middle	54.6 \pm 1.8 ^d	6.8 \pm 1.2 ^c	90 \pm 28 ^g	Up	1.4 \pm 1.2 ^d	0.4 \pm 0.6 ^c	0.6 \pm 0.7 ^{b,c}	132	12
<i>Saccopteryx bilineata</i>	Low	44.5 \pm 1.3 ^e	7.5 \pm 1.5 ^c	73 \pm 17 ^h	Up	0.8 \pm 0.4 ^b	1.4 \pm 1.1 ^c	0.7 \pm 0.7 ^{b,c}	120	12
	Middle	46.8 \pm 1.1 ^f	7.6 \pm 1.3 ^c	105 \pm 25 ^{b,g}	Up	0.6 \pm 0.3 ^e	1.0 \pm 1.1 ^c	0.7 \pm 0.7 ^{b,c}	120	12
<i>Cyttarops alecto</i>		35.9 \pm 0.4 ^g	9.8 \pm 1.6 ^d	154 \pm 22 ^c	Up	1.5 \pm 0.6 ^f	1.1 \pm 0.4 ^a	0.8 \pm 0.5 ^c	123	12
				265 \pm 68 ^d						
<i>Cormura brevirostris</i>	Low	25.2 \pm 1.5 ^h	8.2 \pm 2.0 ^f	119 \pm 45 ^{b,g}	Up	1.5 \pm 1.3 ^{d,f}	1.0 \pm 1.0 ^{a,c}	0.6 \pm 0.6 ^{c,d}	76	12
	Middle	28.1 \pm 0.6 ⁱ	8.2 \pm 1.8 ^f	100 \pm 21 ^b	Up	1.2 \pm 0.5 ^f	0.8 \pm 0.4 ^a	0.4 \pm 0.3 ^c	105	12
	High	31.4 \pm 0.4 ^j	8.6 \pm 1.6 ^f	107 \pm 38 ^{b,g}	Up	1.6 \pm 0.9 ^f	0.8 \pm 0.5 ^a	0.4 \pm 0.4 ^c	102	12
<i>Balaniopteryx plicata</i>		42.6 \pm 0.8 ^k	8.1 \pm 1.8 ^f	136 \pm 27 ^b	Straight	1.0 \pm 0.6 ^g	0.5 \pm 0.6 ^d	1.6 \pm 1.3 ^{b,c}	144	12
<i>Peropteryx macrootis</i>		38.9 \pm 0.9 ^l	9.3 \pm 1.0 ^{a,e,f}	139 \pm 14 ^c	Straight	0.7 \pm 0.2 ^g	0.3 \pm 0.2 ^{d,e}	1.9 \pm 0.5 ^{b,c}	163	12
				215 \pm 34 ^d					140	9
<i>Peropteryx kappleri</i>		31.6 \pm 1.6 ^j	9.6 \pm 2.2 ^{e,f}	170 \pm 34 ^e	Straight	1.1 \pm 0.4 ^g	0.4 \pm 0.3 ^{d,e}	1.3 \pm 0.2 ^{b,c}	62	12
				280 \pm 31 ^f					36	12
<i>Diclidurus albus</i>	Low	23.5 \pm 0.3 ^m	9.4 \pm 4.7 ^{d,e,f}	317 \pm 43 ^f	Straight	0.7 \pm 0.2 ^g	0.2 \pm 0.1 ^e	0.1 \pm 0.2 ^d	62	12
	Low	23.5 \pm 0.3 ^m	9.6 \pm 5.7 ^{d,e,f}	162 \pm 28 ^{c,e}	Straight	0.7 \pm 0.2 ^g	0.2 \pm 0.1 ^e	0.1 \pm 0.2 ^d	36	12
	Middle	25.8 \pm 1.3 ^h	9.7 \pm 5.0 ^{d,e}	249 \pm 54 ^d	Straight	1.0 \pm 0.7 ^g	0.2 \pm 0.3 ^d	0.2 \pm 0.1 ^{c,d}	34	12
Univariate results $F_{(117,1471)} =$		1426.01	48.69	28.93		58.67	41.30	40.61		
		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$		

Letters indicate the results of the unequal *n* post hoc test. Different letters indicate significant differences within the call parameter and between species. qcf, quasi-constant frequency; fm, frequency-modulated.

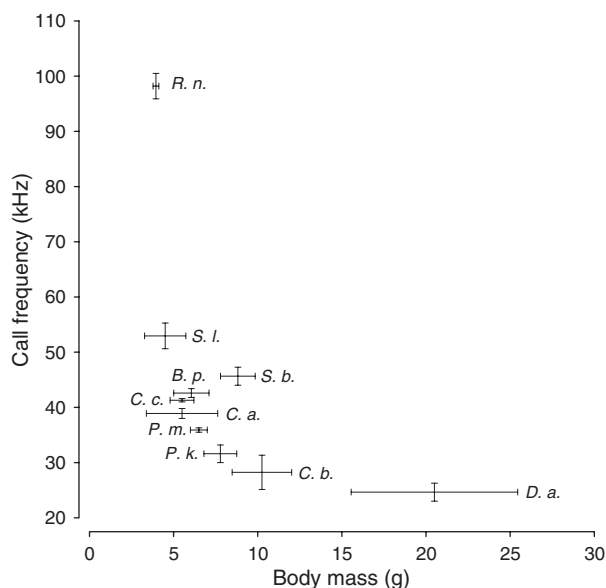


Figure 4 Relationship between call frequency and body mass in 10 emballonurid species of southern Central America. Data for *Cyttarops alecto* and *Diclidurus albus* were taken from Reid (1997). Crosses and bars indicate the mean \pm standard deviation of frequency and body mass measurements. *R. n.*, *Rhynchonycteris naso*; *C. c.*, *Centronycteris centralis*; *S. l.*, *Saccopteryx leptura*; *S. b.*, *Saccopteryx bilineata*; *C. a.*, *Cyttarops alecto*; *C. b.*, *Cormura brevirostris*; *B. p.*, *Balantiopteryx plicata*; *P. m.*, *Peropteryx macrotis*; *P. k.*, *Peropteryx kappleri*; *D. a.*, *Diclidurus albus*.

$\lambda = 0.24$, $F_{(12,46)} = 39.48$, $P < 0.0001$]. In both *Saccopteryx* species, the two call types formed characteristic duplets as the pulse interval between low and high calls was significantly shorter than that between high and low calls [*S. bilineata*: $F_{(23,226)} = 9.39$, $P < 0.0001$; *S. leptura*: $F_{(23,238)} = 6.29$, $P < 0.0001$; Table 1]. The univariate F -test showed that the two call types also differed significantly in call duration [*S. bilineata*: $F_{(23,226)} = 18.96$, $P < 0.0001$; *S. leptura*: $F_{(23,238)} = 23.46$, $P < 0.0001$] and bandwidth of the qcf-component [*S. bilineata*: $F_{(23,226)} = 13.62$, $P < 0.0001$; *S. leptura*: $F_{(23,238)} = 21.83$, $P < 0.0001$].

In *Co. brevirostris*, call duration [$F_{(34,236)} = 8.94$, $P < 0.0001$], pulse interval [$F_{(34,236)} = 6.60$, $P < 0.0001$] and bandwidth of the qcf-component [$F_{(34,236)} = 2.82$, $P < 0.0002$] differed significantly between the three call types, but the *post hoc* test revealed that the highest call did not differ significantly in any of the three parameters from the other two call types. *Diclidurus albus* hunting above the canopy usually used only low calls with very long pulse intervals (Fig. 3). When it switched to frequency alternation at lower flight altitudes, the pulse interval between low and high calls became significantly shorter [$F_{(30,89)} = 2.65$, $P < 0.0002$], forming duplets as in both *Saccopteryx* species. Call types also differed in call duration [$F_{(30,89)} = 11.39$, $P < 0.0001$] and bandwidth of the qcf-component [$F_{(30,89)} = 4.24$, $P < 0.0001$].

Although frequency alternation was prominent in the four species, the bats occasionally dropped one frequency within a sequence. The two *Saccopteryx* species occasionally emitted regularly spaced search calls at only one frequency after they had captured insects and ate them in flight, or when they were flying near their roost. *Cormura brevirostris* sometimes omitted the lower call within a sequence and switched to duplets alternating between middle and high calls probably when approaching vegetation. *Diclidurus albus* used one call frequency with very long pulse intervals when flying high in uncluttered space and started call alternation when approaching either prey or obstacles.

Discussion

General echolocation call design and species identification

The search calls of emballonurid bats studied in the Old and New World tropics are remarkably similar in some structural features. They all consist of a prominent qcf-component, thus gathering much energy in a narrow frequency band. This is likely to be associated with an increase in hearing sensitivity and is mostly seen as an adaptation to hunt flying insects on the wing (Bradbury & Vehrenkamp, 1976; Kalko, 1995; Schnitzler & Kalko, 1998, 2001). The prominent qcf-component may not only increase detection distance, but also facilitate detection of weak echoes from small insects, the preferred prey of most emballonurid species, by enhancing the perception of acoustic glints created by the beating wings of insects even when the echolocation calls are rather short (Sum & Menne, 1988).

Although the general structure of search calls is very similar in the 10 emballonurid species from southern Central America, we also found distinct, species-specific differences in peak frequency, direction of modulation of the qcf- and fm-components, call duration, pulse interval and bandwidth of the initial and terminal fm-components which allow unambiguous identification of all species by their echolocation calls (Table 1). This makes them ideal candidates for acoustic monitoring programmes aimed at assessing of species diversity and habitat use of aerial insectivores that are otherwise mostly underrepresented in inventories based on mist netting (Kalko, 1998).

Overall, our data add and expand on search call characteristics of emballonurid bats in a comparative approach including *Cy. alecto*, a species that to our knowledge has not been described before. Furthermore, our data corroborate the general findings of other studies on search calls of neotropical emballonurid bats (Barclay, 1983; Kalko, 1995; O'Farrell & Miller, 1997; Fenton *et al.*, 1999; O'Farrell *et al.*, 1999; Ochoa *et al.*, 2000; Ibáñez *et al.*, 2002; Rydell *et al.*, 2002; Bayefsky-Anand, 2006) except for Biscardi *et al.* (2004) who recorded *P. macrotis* calling at 42 kHz in Brazil, which is at least 3 kHz higher than our recordings and those of Rydell *et al.* (2002) from Central America. This may hint towards geographic variation, differences in body size or the involvement of two species instead of one.

In addition to the 10 emballonurid species currently known from southern Central America, search calls of four more emballonurid species have been described for the Neotropics that also resemble the other emballonurids in general call structure: *Balantiopteryx io* with peak frequencies around 49 kHz, *Balantiopteryx infusca* with peak frequencies around 56 kHz (Ibáñez *et al.*, 2002) and *Saccopteryx canescens* with peak frequencies around 53 kHz (Ochoa *et al.*, 2000; E. K. V. Kalko, unpubl. data). Interestingly, *S. canescens* does not alter call frequency in contrast to its congeners *S. bilineata* and *S. leptura*. A further, up to now unidentified emballonurid species with a peak frequency of about 59 kHz was recorded in Para, Brazil by Biscardi *et al.* (2004).

Correlation of species-specific call design and foraging habitat

Signal variation between species reflects acoustic parameters of foraging style and preferred foraging habitat and prey type (Neuweiler, 1989; Heller, 1995; Kalko, 1995; Fenton *et al.*, 1998, 1999; Neuweiler, 2003; Schnitzler & Kalko, 2001; Schnitzler *et al.*, 2003). As expected, call parameters of species correlated strongly with the estimated average distance of bats to vegetation. Emballonurid bats hunting in open space emitted calls with rather long duration and long pulse intervals at lower frequencies, probably to increase the likelihood of prey detection and to benefit from reduced atmospheric attenuation. The general structure of search calls resembles that of aerial hawking molossid (Kingston *et al.*, 2003) and vespertilionid bats (Kalko & Schnitzler, 1993) flying in open space. However, energy distribution differs strongly as the main energy of search calls in emballonurid bats mostly resides in the second or higher harmonics, in contrast to molossid and vespertilionid bats where it is concentrated in the first harmonic. This pattern may in part reflect phylogenetic relationships as emballonurid bats represent the basic group of extant bats whereas vespertilionid and molossid bats form a sister group (Teeling *et al.*, 2005).

In contrast to open space bats, foragers in edge space near vegetation broadcast calls at higher frequencies with distinct fm-components, shorter call duration, and shorter pulse interval, which is also in accordance with our initial predictions. A shorter call duration reduces the possibility of receiving echoes from clutter during sound emission and an overlap of clutter echoes with prey echoes (Schnitzler & Kalko, 2001). A shorter pulse interval reduces echoes arriving after the emission of a preceding call, which could lead to wrong echo assignation. Interestingly, the bandwidth of search calls in emballonurid bats flying in edge space remains narrow (<10 kHz) compared with molossid and vespertilionid bats where bandwidth may encompass 30–50 kHz or more (e.g. Schnitzler & Kalko, 2001; Siemers, Kalko & Schnitzler, 2001). Perhaps emballonurid bats integrate information over several harmonics, thus achieving a higher overall bandwidth.

Correlation of call frequency with body size

Another factor influencing search signals, namely frequency, is body size. In the 10 species, call frequency was negatively correlated with both body mass and forearm length. A similar trend has already been established for other families of bats (e.g. Pye, 1979; Aldridge & Rautenbach, 1987; Weid & von Helversen, 1987; Heller & von Helversen, 1989; Bogdanowicz, Fenton & Daleszczyk, 1999; Jones, 1994, 1999). A probable cause may be the physical rule that larger structures associated with sound production, such as drum membranes and strings, produce lower-frequency sounds than smaller structures and vice versa (Pye, 1979; Jones, 1999). Additionally, adaptations for detecting smaller prey by using smaller wavelengths may also play a role (Pye, 1979; Jones, 1999; Houston *et al.*, 2003). For example, the small *R. naso* has a call frequency much higher (95 kHz) than the almost similar-sized *S. leptura* (54/57 kHz), which might be influenced by the very small size of soft insect prey that *R. naso* catches above water surfaces (E. K. V. Kalko, pers. obs.).

Call frequency alternation

Four emballonurid species alternated call frequencies during search flight. Call frequencies of these species fell into distinct, non-overlapping groups, either two (duplets) as in both species of *Saccopteryx* and in *D. albus* or three (triplets) as in *Co. brevirostris* (see Table 1). The significance of this call frequency alternation remains unclear. Kingston *et al.* (2003) discussed several propositions in detail.

As in observations of call alternation in molossid bats, an anti-jamming role (Habersetzer, 1981) seems to be unlikely for emballonurid bats, as frequency alternation was not dependent on the presence or absence of conspecifics (Kössl *et al.*, 1999; Kingston *et al.*, 2003). Heller (1995) argued that call frequency alternation may serve to increase overall bandwidth, thereby improving classification and localization abilities, assuming that bats integrate information over several calls, which they are clearly able to do (Moss & Surlykke, 2001). However, it remains doubtful as to how important this may be when only two narrow frequency bands that are rather close together are used.

Potentially, call alternation could facilitate species recognition and permit the partitioning of acoustic channels in a given habitat (Heller & von Helversen, 1989; Kalko, 1998; Schnitzler & Kalko, 2001). For instance, while *S. bilineata* alternates calling frequency, *Ce. centralis* that forages in similar habitats does not, which – at least to the human observer – is the easiest parameter to distinguish between these two species. Also, *S. bilineata* and *S. leptura* locally co-occur in South America with a third species, *S. canescens*, which does not alter the peak frequency of its search calls.

The idea of increasing maximum detection range by ‘marking’ search calls by different frequencies, which permits discrimination between echoes of succeeding calls (Weid & von Helversen, 1987; Heller, 1995; Fenton *et al.*, 1998), remains one of the most probable explanations for

Table 2 Maximum detection distance calculated for different dynamic ranges and sound spreading (point source and acoustic mirror)

Species	Call type	Blind window (m)	Call-to-call window (m)	Maximum detection distance (m)				
				Acoustic mirror: dynamic range 90 (dB)	Point source: dynamic range (dB)			
					130	110	90	70
<i>Rhynchonycteris naso</i>		0.8	9	6	6	5	3	2
<i>Centronycteris centralis</i>		1.0	20	18	18	12	7	4
<i>Saccopteryx leptura</i>	Low–middle	1.2	11	13 ▶	13 ▶	9	6	3
	Middle–low	1.2	15	12	12	9	6	3
<i>Saccopteryx bilineata</i>	Low–middle	1.3	11	17 ▶	17 ▶	12 ▶	7	4
	Middle–low	1.2	17	16	16	11	7	3
<i>Cyttarops alecto</i>		1.7	25	23	22	14	8	4
		Double PI	44					
<i>Cormura brevirostris</i>	Low–middle	1.4	19	39 ▶	34 ▶	21 ▶	11	5
	Middle–high	1.4	15	33 ▶	30 ▶	18 ▶	10	4
	High–low	1.5	17	28 ▶	26 ▶	17 ▶	9	4
<i>Balantiopteryx plicata</i>		1.4	22	18	18	12	7	4
<i>Peropteryx macrotis</i>		1.6	23	20	20	13	8	4
		Double PI	36					
<i>Peropteryx kappleri</i>		1.7	28	28	26	16	9	4
		Double PI	47					
<i>Diclidurus albus</i>	Low	1.7	54	43	36	21	11	5
	Low–middle	1.6	27	43 ▶	36 ▶	21	11	5
	Middle–low	1.6	42	37	32	20	10	4

The blind window is the distance of an object whose echo returns during the emission of the call. The call-to-call window, which represents the maximum distance of an object whose echo returns before the emission of the next call, was calculated from the mean pulse interval minus mean call duration. The black arrowheads indicate cases in which the maximum detection distance exceeds the call-to-call window. Double PI, double pulse interval typical of bats flying in open space.

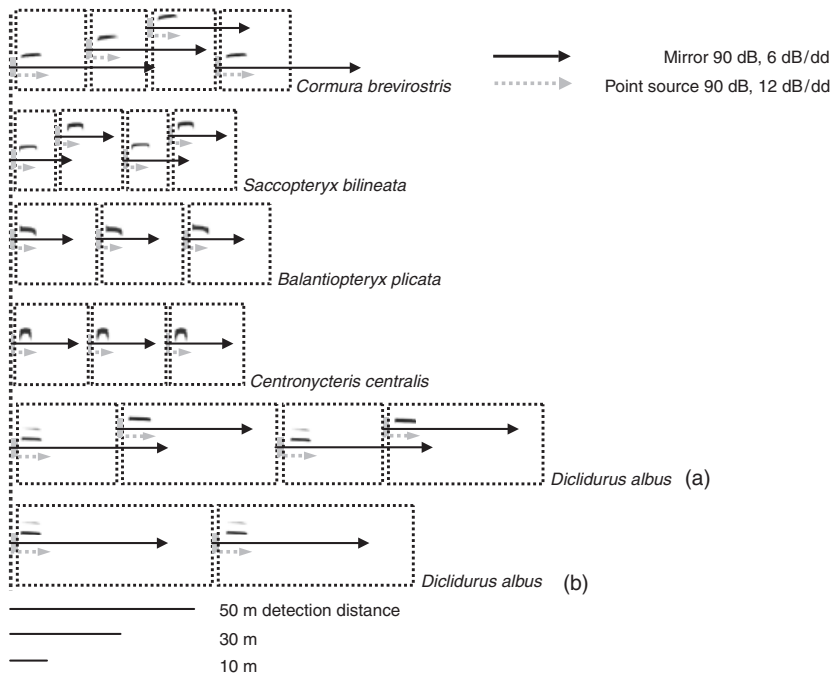


Figure 5 Comparison of ‘call-to-call window’ and maximum detection distance calculated for different-sized targets. Sound velocity and attenuation were determined for 28 °C and 75% humidity. We considered (a) a planar background target (solid arrow) acting as an acoustic mirror reflecting the echo (6 dB per doubling distance) and (b) a smaller, prey-sized target acting as a point source (grey arrow) with spherical spreading (12 dB per doubling distance). For both we assumed a dynamic range of 90 dB between echo and call. The dotted line at the left indicates the start of the echolocation sequence. Large blank boxes represent the call-to-call window in metres. Smaller grey boxes represent the blind window in metres. Yard sticks for 50, 30 and 10 m are given below the visualization of the echolocation sequence. Frequency and pulse interval of the sonograms are not scaled and sonograms are given only for a better visualization of the model.

call alternation. Holderied & von Helversen (2003) proposed that the maximum distance at which a bat with one calling frequency can perceive echoes from a search call is

limited to the ‘wing beat window’ or better to the ‘call-to-call window’. This means that only those echoes that arrive after the end of a call, but not later than the beginning of the

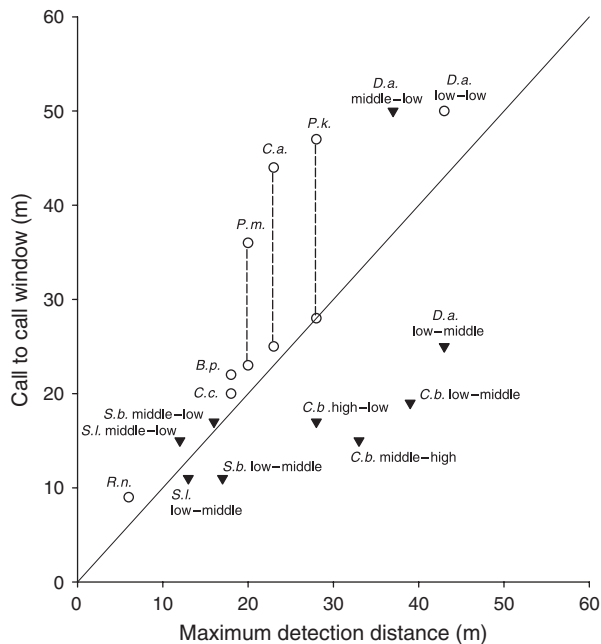


Figure 6 Relation between call-to-call window and maximum detection distance calculated for a dynamic range of 90 dB and a large planar background. ▼, species with call frequency alternation; ○, species without call frequency alternation. The straight line indicates a perfect match between call-to-call window and maximum detection distance. Below the line maximum detection distance exceeds the call-to-call window, which indicates that echoes could still be perceived after the emission of the next call. We included two measurement points for *C. a.*, *P. m.* and *P. k.* since those three species skip calls frequently, thereby doubling their pulse interval and their call-to-call window. *R. n.*, *Rhynchonycteris naso*, *C. c.*, *Centronycteris centralis*, *S. l.*, *Saccopteryx leptura*, *S. b.*, *Saccopteryx bilineata*, *C. a.*, *Cyttarops alecto*, *C. b.*, *Cormura brevirostris*, *B. p.*, *Balantiopteryx plicata*, *P. m.*, *Peropteryx macrotis*, *P. k.*, *Peropteryx kappleri*, *D. a.*, *Diclidurus albus*.

next call, can be processed. We assumed that emballonurid bats, similarly to vespertilionid bats, do not perceive sound while emitting a call, and denote this time hereafter as 'blind window'. In the following, we extend the model calculation of Holderied & von Helversen (2003) for call frequency alternation in emballonurid bats.

A weak echo arriving just after a call, but stemming from the penultimate call, must be an extremely irritating incident for a bat as it may be unable to decide whether the weak early echo originates from a distant obstacle, or from an overseen nearby object that may necessitate a sudden flight manoeuvre. This situation is most probable when a bat flies in the vicinity of large objects such as structures that reflect echoes not as a point source but like a mirror and thus produce far-reaching echoes. This may happen in the neighbourhood of larger planar objects like a wall or rock face, a steep bank of a river, the edge of a forest or even the ground below. In contrast to bats using distinct broadband fm-components in their call such as vespertilionid and molossid bats flying in edge space, bats with narrowband

qcf-signals and very short fm-components such as emballonurid bats will probably not be able to classify the echoes of more distant objects in greater detail based on their spectral shift due to low-pass filter characteristics of atmospheric attenuation (Griffin, 1971; Lawrence & Simmons, 1982; Houston *et al.*, 2003). How does one assign an echo correctly to the call from which it originated? Obviously, frequency is a possibility to mark a call and thus its echo(es).

To investigate whether potentially confusing situations in which echoes from a call still arrive at the bat's ear after it has already emitted the next call, we calculated maximum detection distance (D_{\max}) for all 10 emballonurid species: those without call alternation (*R. naso*, *Ce. centralis*, *Cy. alecto*, *B. plicata*, *P. macrotis* and *P. kappleri*), those with call alternation (*S. leptura*, *S. bilineata* and *Co. brevirostris*) and one species with both strategies, with and without call alternation (*D. albus*) (Table 2), using the following equation (Möhl, 1988):

$$DT = SL + TLA + TLS + TS$$

DT is the detection threshold. Although the functional hearing threshold of a flying bat is not very well known, we estimated it to be between 0 and +30 dB SPL (sound pressure level). SL (source level) is call intensity, which in many aerial insectivorous bats is around 130 dB (Holderied & von Helversen, 2003). TLA is transmission loss owing to absorption and TLS is transmission loss owing to spherical spreading. TS is target strength ($D_{\text{ref}} = 0.1$ m) of an object, which is around -40 dB for a very small insect and -20 dB for a moth (Kober & Schnitzler, 1990; Waters, Rydell & Jones, 1995). A TS around 0 dB might refer to a middle-sized bird (Holderied & von Helversen, 2003). We combined the three terms SL, TS and DT into one term, 'dynamic range', measured in dB SPL [dynamic range = (SL + TS) - DT]. We calculated maximum detection distances for a set of dynamic ranges between 70 and 130 dB (Table 2). We also discriminated between two target types, a point source (small objects including prey items, conspecifics or predators) and an acoustic mirror (large objects including rock faces, riverbanks and ground) (Holderied & von Helversen, 2003; Holderied *et al.*, 2005). The total spreading loss (call and echo) for a target point source that re-radiates incident sound and reflects spherical waves at distance D from the bat is

$$2 \times 20 \log(D_{\text{ref}}/D)$$

It differs from the spreading loss for a large planar object that reflects all sound energy:

$$20 \log(D_{\text{ref}}/2D)$$

Atmospheric attenuation is $2\alpha D$. α and sound velocity (348 m s^{-1}) were taken from Bazley (1976) for temperature and relative humidity under tropical conditions (28 °C and 75% relative humidity).

Our model shows that the maximum detection distance for targets that produce spherical spreading (e.g. point sources such as insect prey) calculated for a dynamic range of 70–90 dB will not be problematic whether bats alternate call frequency or not, as echoes will always return within the call-to-call window (Table 2; Fig. 5). This means that call

alternation does not improve the detection range for prey. However, we found two situations in which call alternation in bats can lead to the perception of echoes that return after the next call (Figs 5 and 6; Table 2): (1) A target that reflects all sound energy as a point source (target strength of 0 dB) corresponding, for example, to a ball with a radius of 10 cm (Holderied & von Helversen, 2003) at a dynamic range between 110 and 130 dB. In nature, this may be a bat falcon in front, perhaps a rare but risky situation. (2) A larger planar structure such as the edge of a forest or a rocky wall that reflects echoes as a mirror. In this case, a dynamic range of 90 dB will suffice for a bat with call alternation to perceive echoes from an object after it has emitted the next call. Such a situation occurs when the bat emits calls at an SPL of 130 dB, even if one takes into account a loss of about 40 dB resulting from some absorption by leaves and/or by a less sensitive hearing threshold. A bat foraging in edge space may often get unexpected echoes of this type in the field when flying around a tree or when entering another tree fall gap after having passed the branches of trees. In this situation, a bat can react in two ways. Either it can prolong its calling interval to overcome the problem of correct call assignment, but with the disadvantage of getting less information per unit time, or it can combine rather short calling intervals with frequency alternation, as we have documented for *S. leptura*, *S. bilineata* and *Co. brevirostris*.

Whereas bats foraging in edge space, including both *Saccopteryx* and *Co. brevirostris*, use alternating call frequencies probably to allow high calling rates in habitats with many obstacles, *D. albus* foraging in open space appears to follow a different strategy as it switches between sequences with call alternation and sequences with only one frequency, which is emitted at very long pulse intervals (up to 317 ms). Most likely, the use of modes depends on the height over ground and the distance of the bat to far-away obstacles. Call frequency alternation is likely to be mostly used when bats fly somewhat lower and/or closer to vegetation (E. K. V. Kalko, unpubl. data). *Diclidurus albus* thus resembles, in foraging habitat and hunting style, bats from other families such as members of the genus *Nyctalus* and *Lasiurus* (Vespertilionidae) and molossid bats, which are all likely to sample information about large objects from a distance during fast flight using call alternation (Holderied & von Helversen, 2003).

Overall, we conclude that call alternation does not provide an advantage for the detection of small targets, in particular prey insects, as echoes from prey all fall within the 'call-to-call window' of bats (Table 2). However, call alternation might provide an advantage to the bat regarding perception of large, distant targets combined with a higher calling rate than bats foraging in similar habitats at lower calling rates and 'monotonous' calling frequencies.

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