

Intense echolocation calls from two ‘whispering’ bats, *Artibeus jamaicensis* and *Macrophyllum macrophyllum* (Phyllostomidae)

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SUMMARY

Bats use echolocation to exploit a variety of habitats and food types. Much research has documented how frequency–time features of echolocation calls are adapted to acoustic constraints imposed by habitat and prey but emitted sound intensities have received little attention. Bats from the family of Phyllostomidae have been categorised as low intensity (whispering) gleaners, assumed to emit echolocation calls with low source levels (approximately 70 dB SPL measured 10 cm from the bat’s mouth). We used a multi-microphone array to determine intensities emitted from two phyllostomid bats from Panamá with entirely different foraging strategies. *Macrophyllum macrophyllum* hunts insects on the wing and gaffs them with its tail membrane and feet from or above water surfaces whereas *Artibeus jamaicensis* picks fruit from vegetation with its mouth. Recordings were made from bats foraging on the wing in a flight room. Both species emitted surprisingly intense signals with maximum source levels of 105 dB SPL r.m.s. for *M. macrophyllum* and 110 dB SPL r.m.s. for *A. jamaicensis*, hence much louder than a ‘whisper’. *M. macrophyllum* was consistently loud (mean source level 101 dB SPL) whereas *A. jamaicensis* showed a much more variable output, including many faint calls and a mean source level of 96 dB SPL. Our results support increasing evidence that echolocating bats in general are much louder than previously thought. We discuss the importance of loud calls and large output flexibility for both species in an ecological context.

Key words: bats, echolocation, field recordings, intensity, phyllostomids, source levels.

INTRODUCTION

Echolocating bats actively probe their environment with echolocation or biosonar, emitting short, high frequency (typically >20 kHz) calls and use the returning echoes to orientate and detect food in the dark. There are more than 1100 extant bat species (Simmons, 2005) of which approximately 950 echolocate, exploiting a broad spectrum of food, habitats and foraging strategies. Echolocation call parameters such as frequency, duration and intervals between pulses are adapted to the acoustic constraints of food type and foraging environment (e.g. Jones and Holderied, 2007; Jones and Teeling, 2006; Schnitzler and Kalko, 2001). Emitted intensity of echolocation signals is equally critical for the function of echolocation but call intensity has received relatively little attention after the pioneering studies by Griffin (Griffin, 1958), who provided the first quantitative data on intensity of bat echolocation calls. Based primarily on recordings from handheld bats, Griffin classified bats into two broad groups: (1) loud aerial insectivores emitting source levels (sound pressure measured 10 cm from the bat’s mouth) of up to 110 dB SPL and (2) whispering bats foraging within or from vegetation or other surfaces and emitting source levels of roughly 70 dB SPL.

Improvements in acoustic and filming techniques have made it easier to quantify the bat’s distance and position relative to the recording microphone and thus to determine the emitted call intensity of flying bats. Recent results from field studies have documented considerably higher source levels than predicted by Griffin in a number of aerial hawking species (Holderied and von Helversen, 2003; Holderied et al., 2005; Jensen and Miller, 1999;

Surlykke and Kalko, 2008; Surlykke et al., 1993). However, source levels from Phyllostomidae and other ‘whispering’ bats have not been revisited quantitatively in more natural situations such as foraging on the wing. Consequently, Griffin’s original estimates and classification are still generally accepted. Low intensity signals would well reflect the foraging behaviour of the endemic family of New World leaf-nosed bats (Phyllostomidae) as they typically forage within vegetation where increased intensity produces more clutter echoes. The presumed low call intensity is supported by low sound levels recorded in the lab from handheld or sitting bats or ‘guestimates’ from bat detector recordings in the field (e.g. Griffin, 1958; Hartley and Suthers, 1987; Heffner et al., 2003; Korine and Kalko, 2005; Novick, 1977; Thies et al., 1998). Interestingly, a recent study suggests that certain phyllostomids such as the Cuban flower bat, *Phyllonycteris poeyi*, may sometimes call at rather high intensities in the field (Mora and Macias, 2007) but again based on detection range with a bat detector and not calculations of the output level. Hence, the aim of this study was to measure emitted intensities from phyllostomid bats while engaged in natural behaviour, in this case, searching and approaching food on the wing.

Generally, phyllostomid bats are highly diverse, with more than 165 species (Simmons, 2005) feeding on a wide variety of food resources, including fruit, nectar, pollen, insects, small vertebrates and blood (Findley, 1993). Despite the variety of food, most phyllostomid bats use fairly similar feeding strategies, typically picking food items from vegetation in highly cluttered environments (Kalko et al., 1996a; Kalko et al., 1996b). All phyllostomid species recorded so far share the same general echolocation call structure.

Calls are broadband, frequency-modulated (FM), multi-harmonic and usually of short duration (<3 ms) (Jennings et al., 2004; Kalko, 2004; Kalko and Condon, 1998; Korine and Kalko, 2005; Thies et al., 1998; Weinbeer and Kalko, 2007).

We determined source levels of echolocation calls from the fruit-eating bat *Artibeus jamaicensis* (Leach 1821) and the insectivorous trawling bat, *Macrophyllum macrophyllum* (Schinz 1821). The two species are sympatric and both belong to the family Phyllostomidae but they have completely different diets and foraging behaviours. *A. jamaicensis* is a relatively large (40–55 g), typical phyllostomid frugivore. At the study site it feeds mainly on different types of figs (Jennings et al., 2004; Kalko et al., 1996a; Kalko et al., 1996b), which are usually nestled in leaf axils on the outer branches and difficult to detect by echolocation alone (Korine and Kalko, 2005). Thus, *A. jamaicensis* depends on multiple sensory cues, particularly scent, for foraging. For orientation, it emits broadband, multi-harmonic echolocation calls with signal durations of 1.0–3.9 ms measured during hand-release in background-cluttered space (Jennings et al., 2004). In contrast to aerial insectivores, *A. jamaicensis* and other plant-visiting phyllostomid bats do not produce a terminal phase or buzz characterised by very short pulse interval (~5 ms) and call duration (<1 ms) as they approach food. However, echolocation calls are emitted continuously during foraging, even as bats land to pick up fruit (Korine and Kalko, 2005; Schnitzler and Kalko, 2001; Thies et al., 1998).

M. macrophyllum (6–9 g) (Harrison 1975) is much smaller than *A. jamaicensis* and unique among phyllostomids because it forages either by trawling and gaffing insects from the water surface with its large feet and tail membrane or by hawking aerial prey within 50 cm of the water surface (Weinbeer and Kalko, 2007). This behaviour contrasts strongly with all other phyllostomid bats that have been studied so far as they pick food with their mouth. *M. macrophyllum* is the only known phyllostomid bat emitting distinct search and approach phase calls of decreasing duration and pulse intervals followed by a pronounced terminal buzz phase, where call repetition rate increases up to 160 Hz (Weinbeer and Kalko, 2007). Hence, the echolocation behaviour of *M. macrophyllum* shows a temporal call pattern similar to that of non-phyllostomid insectivorous bats capturing insects on the wing (Schnitzler and Kalko, 2001) whereas the short (1.9–3.6 ms) and multi-harmonic structure of the individual search calls is similar to that of other more typical phyllostomid bats (Weinbeer and Kalko, 2007).

Thus, although *A. jamaicensis* and *M. macrophyllum* belong to the same family, they clearly differ in foraging strategy and the sensory tasks they have to solve, which is reflected in their different echolocation call patterns but not in the calls themselves. We hypothesised that the emitted intensity would also reflect these differences. We predicted that *A. jamaicensis* would emit rather faint echolocation calls, given the highly cluttered surroundings, where the challenge is to discriminate between food (fruit) and background (vegetation). Trawling bats also hunt close to background, i.e. the water; however, a calm water surface acts as an acoustic mirror reflecting almost all signal energy away from the bat (Schnitzler et al., 2003; Siemers et al., 2001). Hence, this habitat is probably acoustically closer to open space than to background cluttered space, which may explain why the loudest echolocation calls to date, source levels up to 137 dB SPL, have been determined for two trawling bats, *Noctilio leporinus* and *Noctilio albiventris* (Surlykke and Kalko, 2008). Thus, in spite of its smaller size, we expected the insectivorous trawling bat *M. macrophyllum* to emit much louder calls than *A. jamaicensis*, comparable with those of trawling bats from other families.

MATERIALS AND METHODS

Study site

We conducted our study during the wet season (mean temperature at night, 27°C; relative humidity, 100%) in August 2005 in Panamá on Barro Colorado Island (BCI) (9 deg. 10' N, 79 deg. 50' W), a field station of the Smithsonian Tropical Research Institute (STRI) in Lake Gatún, near the Panamá Canal. We recorded the echolocation behaviour of *M. macrophyllum* and *A. jamaicensis* in a flight room (4.4×4.5 m, 2 m high) in the rainforest near the main buildings of the BCI research station. The flight room had a concrete floor and side walls and ceiling of metal netting, padded on the inside with fine-meshed plastic netting. Temperature, humidity and noise level in the room matched ambient levels.

Bats

We caught *M. macrophyllum* (five adult males; 7–9 g) with a handheld mist net from a colony near the laboratory clearing on BCI. Age, weight, sex and reproductive status of the individuals were noted and pregnant or juvenile bats were released. The bats were handfed with mealworms after capture. Recording sessions started at approximately 20:00 h on the evening of capture and continued for two subsequent nights. In the first session, three bats were recorded while flying together. During all following sessions, the bats were recorded individually.

A. jamaicensis (five adult males; 46–55 g) were caught with mist nets on Bohio peninsula (mainland) across the Panamá Canal from BCI. Bats were weighed and handfed with slices of banana before being released in the flight room. *A. jamaicensis* were recorded over three nights following capture. All five bats were present simultaneously in the flight cage but during recordings only one bat flew at a time.

All bats were released at the point of capture after the final recording session.

Flight room setup

For the recordings of *M. macrophyllum*, we placed mealworms on the water surface of a plastic pool (diameter, 125 cm; height, 22 cm; water level, 20 cm). *A. jamaicensis* were offered slices of ripe banana from a plastic feeding platform (20×24 cm) on a tripod. A custom-built T-shaped array with four 1/4" condenser microphones (G.R.A.S. type 40B, G.R.A.S. Sound and Vibration A/S, Holte, Denmark and/or B&K type 4135, Brüel & Kjær, Nærum, Denmark) was used for the sound recordings. The frequency response of both microphone types without grid is flat (±2 dB) from 4–100 kHz. The array was built from thin metal rods and mounted on a camera tripod. Three microphones were positioned horizontally, equally spaced at 30 cm and one microphone was vertically displaced 30 cm above the centre microphone of the linear array (Fig. 1A).

Signals were pre-amplified (G.R.A.S., type 26AL), amplified 40 dB (G.R.A.S., type 12AA) and high pass filtered with custom-built 13.5 kHz filters. A/D conversion and data acquisition were done with an IOtech Wavebook 512 (IOtech, Cleveland, OH, USA) sampling at 250 kHz per channel. Data were stored in the circulating buffer of the Wavebook with pre- and post-trigger times of 1 s and transferred to an IBM ThinkPad Laptop computer (type T30 or type X40, IBM Danmark A/S, Kgs. Lyngby, Denmark). The 1 s pre-trigger time allowed sufficient time to register the response on a bat detector (type D240, Pettersson Elektronik AB, Uppsala, Sweden) and visually inspect flight paths before triggering the 2 s data file recordings. Flight behaviour was recorded with a Sony Handycam with night shot (DCR-H C39E PAL, Sony Corporation, Tokyo, Japan) synchronised in time with the computer for later

control of the flight paths calculated from the sound recordings. A Dictaphone (Olympus DM 20, Olympus Denmark A/S, Ballerup, Denmark) recorded voice notes. Microphones were calibrated (B&K sound calibrator type 4231) prior to and following all recording sessions.

Sound analysis

Initial screening and further processing of recordings were done using a custom made program, SigPro (Simon Boel Petersen, Copenhagen, Denmark). Sound files were chosen for further analysis based on good signal-to-noise ratios ($S/N > +10$ dB for signal energy relative to energy of the noise immediately before the signal).

Signal duration, pulse interval (time between the start of consecutive calls) and repetition rate was measured from oscillograms. Peak frequency and bandwidth ($BW_{-20\text{dB}}$), was measured from power spectra. $BW_{-20\text{dB}}$ was measured as the width of the spectrum at -20 dB relative to the spectrum peak for the harmonic that was usually most prominent, i.e. the second harmonic for *M. macrophyllum* and the third harmonic for *A. jamaicensis*.

The time-of-arrival differences between recordings of the same signal at each of the four microphones were found by cross-correlation using the channel with highest signal amplitude as a model (Fig. 1B). Using the time delays combined with the speed of sound (348 ms^{-1} at an ambient temperature of 27°C), we determined consecutive 3-D positions of the bat relative to the array at the moment of each call emission (custom made software, SoundMapper, v. 7, Christian Brandt, University of Southern Denmark, Odense, Denmark). Flight paths and thus the flight direction of the bats relative to the array were then estimated and verified by the IR video recordings and voice comments. To get the on-axis sound level, we only estimated intensities of calls emitted from bats approaching the microphones head on, assuming that the bat emits its signal in the direction of the flight path.

We estimated source levels (i.e. the emitted sound pressure referenced to a standard distance of 10 cm from the bat's mouth) by adding transmission loss (spherical spreading and atmospheric attenuation) to the r.m.s. sound levels recorded at the microphone. We used the standard attenuation of -6 dB per doubling of distance for spherical spreading. Atmospheric absorption was calculated using the peak frequency of each echolocation call and absorption values in dB m^{-1} at 100% relative humidity and 27°C (ANSI, 1978). All sound pressures are given in dB SPL, i.e. re. 20 Pa r.m.s. Note for comparison with other data that many sound pressures in the literature are peak values, thus numerically higher than r.m.s. values.

Echolocation detection ranges

The estimated source levels were used to estimate approximate sonar detection ranges for *M. macrophyllum* and *A. jamaicensis* using a simplified version of the sonar equation (Urick, 1983):

$$DT = SL - 2TL + TS, \quad (1)$$

where DT is the detection threshold, SL is the estimated source level, $2TL$ is the two-way transmission loss including both spherical spreading and atmospheric attenuation, and TS is the target strength of the food item.

Statistics

We recorded a total of 460 sound files. Out of 250 files recorded from *A. jamaicensis*, only 45 files fulfilled the $+10$ dB signal-to-noise criterion whereas this criterion was fulfilled by 156 of the 210 files recorded from *M. macrophyllum*. 50 files (31 from *M. macrophyllum* and 19 from *A. jamaicensis*) gave useful flight paths,

where bats approached the array directly. Acoustic positioning was based on a minimum of five reliable positions (calls) and checked against the IR video recordings and/or voice comments. We calculated source levels of all search calls emitted towards the array from these flight paths. Data for *M. macrophyllum* were separated according to whether more bats flew simultaneously (in a group) or individually and, therefore, the database consisted of three experimental categories: (1) *M. macrophyllum*_{group} (10 files); (2) *M. macrophyllum*_{ind} (21 files); and (3) *A. jamaicensis* (19 files). We used a one-way analysis of variance (ANOVA) followed by a Bonferroni adjusted Fisher's Least Significant Difference to evaluate differences between the three categories for the following parameters: signal duration, pulse interval, repetition rate, peak frequency and bandwidth of the most intense harmonic. Data for signal duration, pulse interval and bandwidth were transformed [$X' = \log_e(X+1)$] to obtain normality and homogeneity of variances (Zar, 1984).

M. macrophyllum calls had most energy in either the second or third harmonic. The distribution of the dominant harmonic was compared between *M. macrophyllum*_{group} and *M. macrophyllum*_{ind} using a 3×2 contingency table of counts for calls with either second or third harmonic as dominant, followed by Bonferroni adjusted pairwise comparisons by χ^2 -tests with Yates' correction for continuity (Zar, 1984).

Statistical analysis was performed using SAS (v. 9.1 for Windows, SAS Institute, Cary, NC, USA). For all statistical tests, a significance level of $\alpha=0.05$ applies.

RESULTS

Flight behaviour

After being released into the flight room, all of the bats stayed on the wing for some time (up to 20 min) in exploratory flight. After adjusting to the surroundings of the room, the bats either settled on a perch in the corner opposite the microphone array or hung from the ceiling. During recording sessions, all of the bats promptly went for the food, either mealworms offered on the water surface or bananas on the feeding platform, without further training or encouragement.

Echolocation calls were rarely recorded while bats were stationary but calls were always recorded when the bats took flight. The insectivorous *M. macrophyllum* was on the wing almost continuously and often approached the pool and the mealworms on the water surface, quickly changing from search to approach behaviour. They also stayed on the wing while consuming prey and continued foraging as soon as more mealworms were deposited on the water surface. When *M. macrophyllum* were tested as a group (three bats together), all the bats were mostly in flight at the same time. They would sometimes take mealworms from the surface simultaneously, although two bats never went for the same prey item at once.

Apart from the initial exploratory flights upon release into the flight room, the frugivorous *A. jamaicensis* spent relatively more time hanging stationary from the ceiling than *M. macrophyllum*. *A. jamaicensis* seemed to take turns feeding, so that only one bat at a time would be on the wing. They also approached food differently from *M. macrophyllum*. Instead of going directly for the banana, *A. jamaicensis* would circle around the flight room for a while and only land on the platform after several exploratory passes where the tripod was approached without landing. After landing on the platform, the bats immediately took a piece of fruit and flew off with it to a perch or the ceiling, where they stayed and ate the banana while hanging.

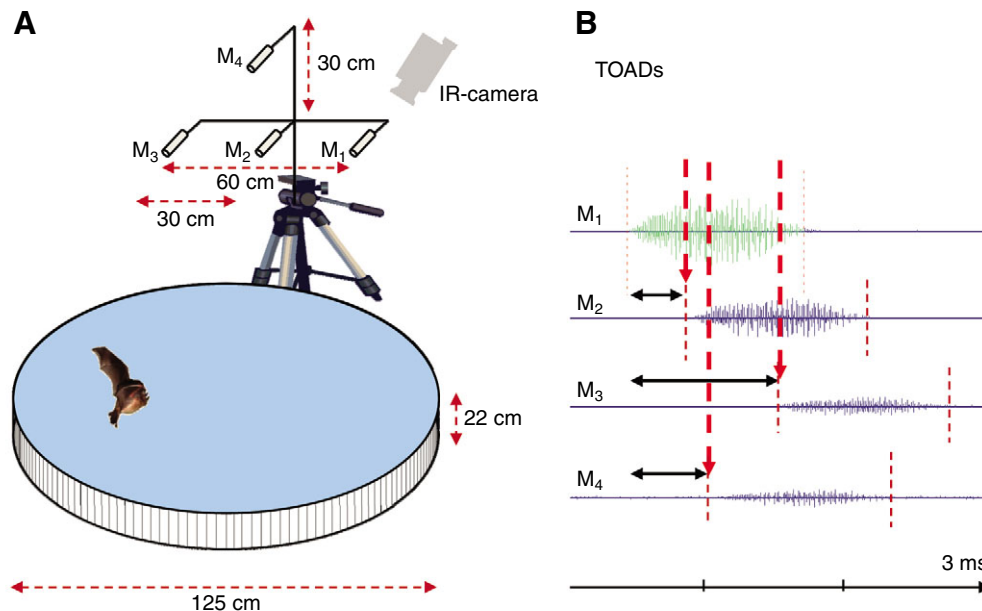


Fig. 1. (A) The flight room setup used to record *M. macrophyllum* while the bats flew over a pool, approaching and gaffing mealworms from the surface. Echolocation sounds were recorded with an array with four microphones (M_1 – M_4) and flight behaviour documented by an infrared (IR) video camera. (B) A four-channel recording with Time-Of-Arrival-Differences (TOADs, thick broken red lines) due to the distance between the microphones. TOADs were determined by cross-correlating the four channel recordings of a signal using the one with highest amplitude (green) as the model. Thin broken red lines mark the start and end of signals on each channel.

Echolocation behaviour

M. macrophyllum and *A. jamaicensis* were both continuously echolocating during flight and food acquisition. They emitted short (<3 ms) multi-harmonic echolocation signals with similar basic time–frequency structure (Fig. 2; Table 1) as previously reported (e.g. Jennings et al., 2004; Korine and Kalko, 2005; Weinbeer and Kalko, 2007).

Calls were often emitted in a regular pattern but both *M. macrophyllum* and *A. jamaicensis* also emitted search phase calls

in groups of two or three and very rarely groups of four or five calls. Grouping of search calls did not appear to be related to obvious changes in flight behaviour. By contrast, predictable grouping of calls was seen when *M. macrophyllum* started approaching prey, emitting groups of 4–5 calls of decreasing duration and pulse interval as previously reported (Weinbeer and Kalko, 2007). Just before gaffing prey from the water surface, a single terminal buzz was emitted with repetition rate increasing up to 160 calls s^{-1} whereas pulse interval dropped to 5–6 ms and pulse duration to 0.5 ms. In

Table 1. Means (\pm s.e.m.) of call parameters for the three experimental categories: *M. macrophyllum*_{ind}, *M. macrophyllum*_{group} and *A. jamaicensis*

Experimental group	Duration (ms)	Pulse interval (ms)	Repetition rate (calls s ⁻¹)	Peak frequency (kHz)			Lower frequency (kHz)	Upper frequency (kHz)	Mean SL (dB SPL)	Max. SL (dB SPL)
				2 nd Harmonic	3 rd Harmonic	BW _{-20dB} (kHz)				
<i>M. macrophyllum</i> individual	1.3 ^A (± 0.0) <i>n</i> =183 <i>N</i> =21	37.8 ^A (± 1.7) <i>n</i> =160 <i>N</i> =20	26.0 ^A (± 1.4) <i>N</i> =20	56.6 ^A (± 0.3) <i>n</i> =18 <i>N</i> =21	82.1 ^C (± 0.3) <i>n</i> =165 <i>N</i> =21	17.3 ^A (± 0.4) <i>n</i> =38 <i>N</i> =19	45.8 (± 0.4) <i>n</i> =38 <i>N</i> =19	63.1 (± 0.3) <i>n</i> =38 <i>N</i> =19	101 ^A (± 0.9) <i>n</i> =125 <i>N</i> =15	105
<i>M. macrophyllum</i> group	1.4 ^A (± 0.1) <i>n</i> =72 <i>N</i> =10	32.3 ^A (± 4.0) <i>n</i> =69 <i>N</i> =10	33.7 ^B (± 1.9) <i>N</i> =10	54.2 ^B (± 0.2) <i>n</i> =59 <i>N</i> =10	80.6 ^C (± 1.4) <i>n</i> =13 <i>N</i> =10	17.4 ^A (± 0.4) <i>n</i> =20 <i>N</i> =10	43.7 (± 0.4) <i>n</i> =20 <i>N</i> =10	61.0 (± 0.4) <i>n</i> =20 <i>N</i> =10	95 ^B (± 1.2) <i>n</i> =52 <i>N</i> =6	100
<i>A. jamaicensis</i>	0.9 ^B (± 0.1) <i>n</i> =116 <i>N</i> =19	62.5 ^B (± 6.4) <i>n</i> =97 <i>N</i> =17	18.6 ^C (± 1.9) <i>N</i> =19		78.8 (± 1.0) <i>n</i> =116 <i>N</i> =19	24.4 ^B (± 1.0) <i>n</i> =30 <i>N</i> =17	66.0 (± 0.7) <i>n</i> =30 <i>N</i> =17	90.4 (± 0.7) <i>n</i> =30 <i>N</i> =17	96 ^B (± 1.7) <i>n</i> =116 <i>N</i> =18	110

Source levels (SL) are from bats >2 m away from the microphones. Mean and maximum source levels are given. Numbers with different superscript letters are significantly different. For both *M. macrophyllum*_{ind} and *M. macrophyllum*_{group}, bandwidth (BW_{-20dB}) is given for the second harmonic, for *A. jamaicensis* it is for the third harmonic. *N* is the number of flight sequences and *n* the number of calls analysed.

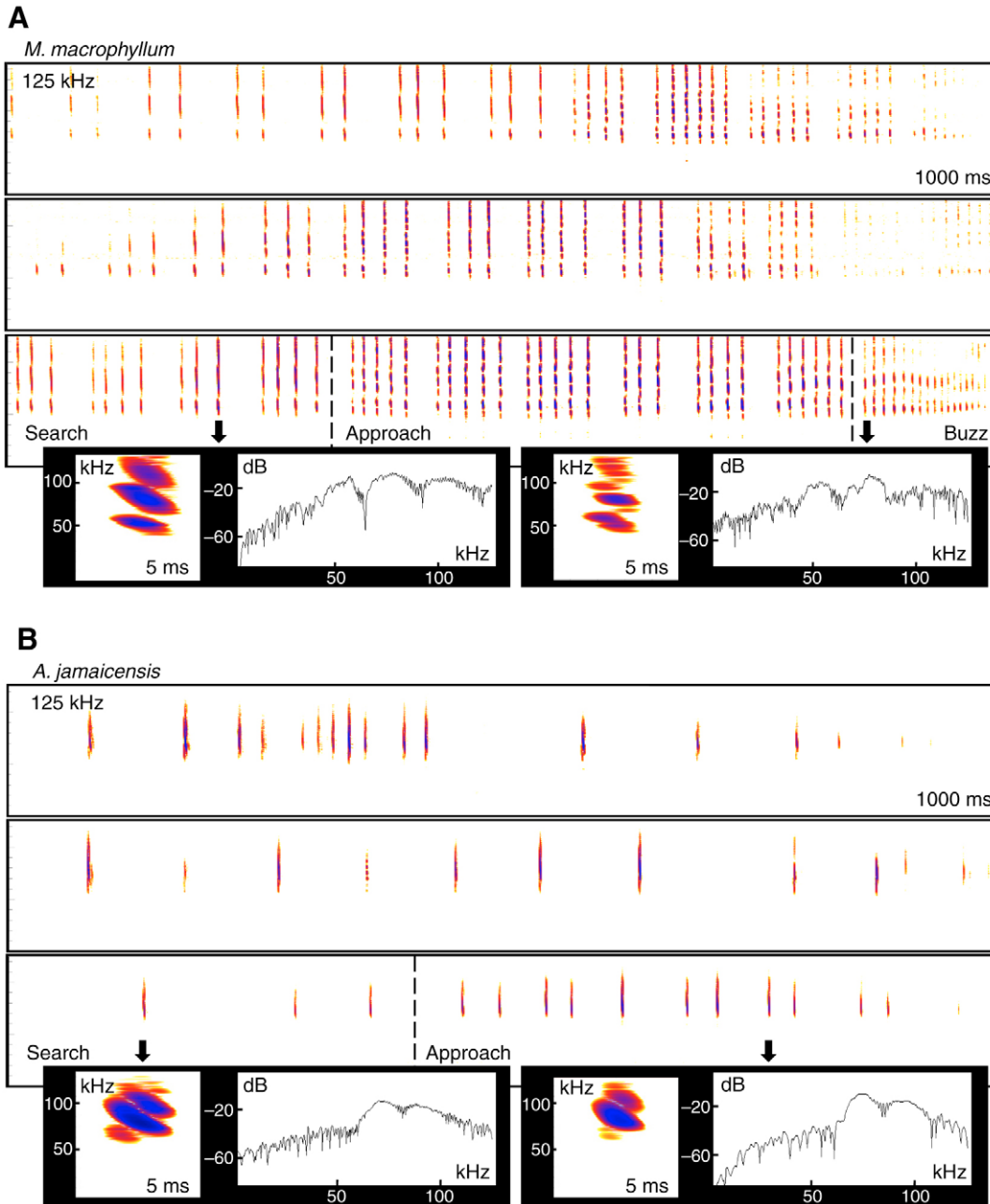


Fig. 2. Spectrograms and power spectra from *M. macrophyllum*_{ind} (A) and *A. jamaicensis* (B). The spectrograms (FFT size 512, Hanning window, complete duration 1000 ms) show echolocation sequences recorded from bats approaching food on the wing. For each of the two species selected signals are shown below in expanded spectrograms (total duration 5 ms) and as power spectra (FFT size 1024). *M. macrophyllum* has distinct search, approach and terminal buzz phases where repetition rate increases from 42 calls s⁻¹ to 132 calls s⁻¹ whereas pulse duration decreases from 1.7 ms (A left black box) to 0.8 ms (A right black box). *A. jamaicensis* calls change from single emissions to grouping of calls with repetition rates up to 20 calls s⁻¹. Pulse duration is 1.7 ms (B left black box) and 1.2 ms (B right black box). Bandwidth does not change considerably for either species.

contrast to *M. macrophyllum*, *A. jamaicensis* did not decrease call duration or pulse interval in a systematic way when approaching food and no call sequences included a terminal buzz, although calls were emitted in groups of 2–3 when the bats were approaching the tripod. Even within groups of calls, pulse intervals were always above 20 ms and repetition rates were consistently below 50 calls s⁻¹ (Fig. 2).

We found significant differences in call duration between the three experimental categories (one-way ANOVA, $F_{2,47}=12.52$, $P<0.0001$; LSM *post hoc* tests) with *A. jamaicensis* emitting significantly shorter calls (0.9 ms) than both *M. macrophyllum*_{group} and *M. macrophyllum*_{ind} (Table 1). There was no significant difference in duration between the two *M. macrophyllum* categories (1.3 ms for *M. macrophyllum*_{ind} and 1.4 ms for *M. macrophyllum*_{group}).

Repetition rates were also significantly different (one-way ANOVA, $F_{2,46}=15.51$, $P<0.0001$; LSM *post hoc* tests) between the

three experimental categories (Table 1). *A. jamaicensis* emitted calls with significantly lower repetition rates (19 calls s⁻¹) than both *M. macrophyllum*_{group} and *M. macrophyllum*_{ind}, and the two *M. macrophyllum* categories also differed significantly: the repetition rate of 26 calls s⁻¹ for individual bats (*M. macrophyllum*_{ind}) was significantly lower ($P=0.0202$; LSM *post hoc* test) than for *M. macrophyllum*_{group}, with mean search call repetition rates of 34 calls s⁻¹. The higher repetition rate when several individuals flew simultaneously was not due to methodological difficulties, as our multi-microphone recordings allowed for unequivocal assigning of calls to individual bats. Hence, all analysed call sequences were from flight paths of individual bats not only when bats were flying alone but also when more bats were on the wing simultaneously.

None of the bats changed the bandwidth of their calls according to the behavioural situation. Even when *M. macrophyllum* took prey from the water surface overall call bandwidth (bandwidth for the

full signal, including all harmonics above a -20 dB threshold) was the same throughout the pursuit sequence. *A. jamaicensis* calls had energy in the second, third and fourth harmonic, while the first harmonic was usually not above noise in our recordings. Most energy was consistently concentrated in the third harmonic around 79 kHz (Fig. 2). Bandwidth ($BW_{-20\text{dB}}$) of the third harmonic was *ca.* 29 kHz (Table 1). *M. macrophyllum* search calls had up to four harmonics. The first harmonic had little energy and was often below the noise in our recordings. Main energy was concentrated in the second and third harmonic at approximately 55 and 82 kHz. The fourth harmonic was less powerful, usually 10–15 dB below the third harmonic. The energy of the second and third harmonic was almost equal, differing by 0–10 dB but when sorting calls according to most prominent harmonic, each call was scored as belonging to only one harmonic group, either second or third, irrespective of how small the energy difference was. When *M. macrophyllum* were flying in a group, the majority of their calls (82%) had most energy in the second harmonic whereas nearly all calls (90%) emitted by bats flying individually had most energy in the third harmonic. Bandwidth ($BW_{-20\text{dB}}$) of the second harmonic was the same (17 kHz) for both *M. macrophyllum* test categories (two-sample *t*-test, $P=0.8638$) (Table 1).

Distance compensation

When the bats flew close to the array they decreased their source levels. To get an estimate of how far from the array this zone of compensation ended, each flight path (Fig. 3) was tested for linear relation between source levels and distance to the array using linear regression analysis, gradually including source levels starting from the shortest distance until a plateau was reached.

Source levels as a function of distance to the array were fitted to a linear model for 10 flights for *M. macrophyllum*_{ind}, five flight sequences for *M. macrophyllum*_{group} and five flight sequences for *A. jamaicensis*. Each flight included ≥ 4 data points covering a distance of at least 0.5 m within 0–2 m distance of the array. The distance compensation was only seen when the bats flew individually whereas *M. macrophyllum*_{group} showed no relation between distance to the array and source level (Fig. 4).

A. jamaicensis and *M. macrophyllum*_{ind} showed distance compensation up to an approximate distance of 2 m from the array. Beyond this distance a plateau was reached where source levels were independent of distance (Fig. 4). Subsequently, a distance of 2 m was used as a cut-off value for all experimental categories, including *M. macrophyllum*_{group}, to ensure that the source level estimates were based on calls emitted outside the compensation zone.

The relationship between source levels and distance up to 2 m from the array was described well by linear regression analysis for both *A. jamaicensis* and for *M. macrophyllum*_{ind}. No statistical difference was found between the mean slopes of the two test categories, which were both 18 dB m^{-1} (two-sample *t*-test, $P=0.9791$). Previous experiments have fitted the slope of compensation with a logarithmic model (Boonman and Jones, 2002; Hartley, 1992; Hiryu et al., 2007; Holderied et al., 2005; Surlykke and Kalko, 2008) but we fitted data points to a linear model because the main purpose was to distinguish between the compensation zone (0–2 m distance from the array) and the plateau (>2 m from the array)

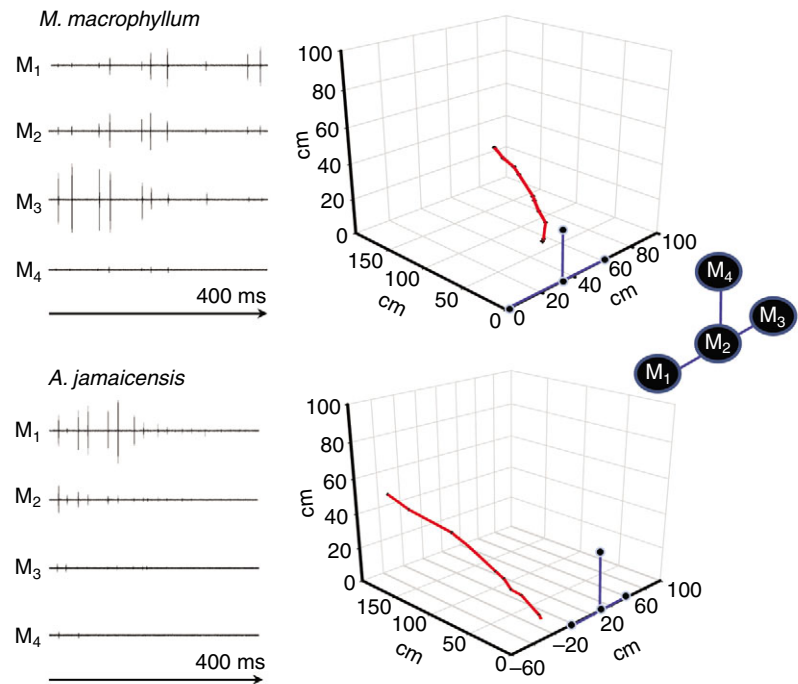


Fig. 3. Four-channel recordings of search signals and corresponding 3-D flight paths for *M. macrophyllum*_{ind} and *A. jamaicensis*. The configuration of the array is shown as closed circles connected with blue lines in the correct position relative to the flight paths as well as enlarged between the two graphs.

where source levels were independent of distance. We had relatively few data points for each flight within the compensation zone and a linear model therefore gave the better fit.

Source levels

Both species emitted source levels much louder than the *ca.* 70 dB SPL, which has been generally assumed to be characteristic for phyllostomid bats (Fig. 4; Table 1).

Source levels differed significantly between test categories (one-way ANOVA, $F_{2,36}=4.48$, $P=0.0183$; LSM *post hoc* tests). Mean source level of calls from individual *M. macrophyllum* (101 dB SPL) was higher than for *M. macrophyllum*_{group} (95 dB SPL). We also estimated a highest maximum source level for individually flying *M. macrophyllum* of 105 dB SPL whereas for *M. macrophyllum*_{group} the maximum was 100 dB SPL. *A. jamaicensis* calls had a mean source level of 96 dB SPL but variation was much greater than for *M. macrophyllum*. Our database included many low amplitude calls in addition to several calls with maximum source levels of around 110 dB SPL. Thus, although the mean source level from *A. jamaicensis* was lower than for *M. macrophyllum*_{ind}, the highest maximum source levels estimated in this study were for *A. jamaicensis*.

The positioning of the bats was based on time-of-arrival-differences between all four microphones in the array but each source level estimate was based only on one recording of a call, i.e. from the recording channel with maximum amplitude (Fig. 1), as this microphone was closest to the acoustic axis. Some recordings of *A. jamaicensis* showed large differences between signal amplitudes of the same signal on the four channels despite the short distance between the microphones in the array, in contrast to *M.*

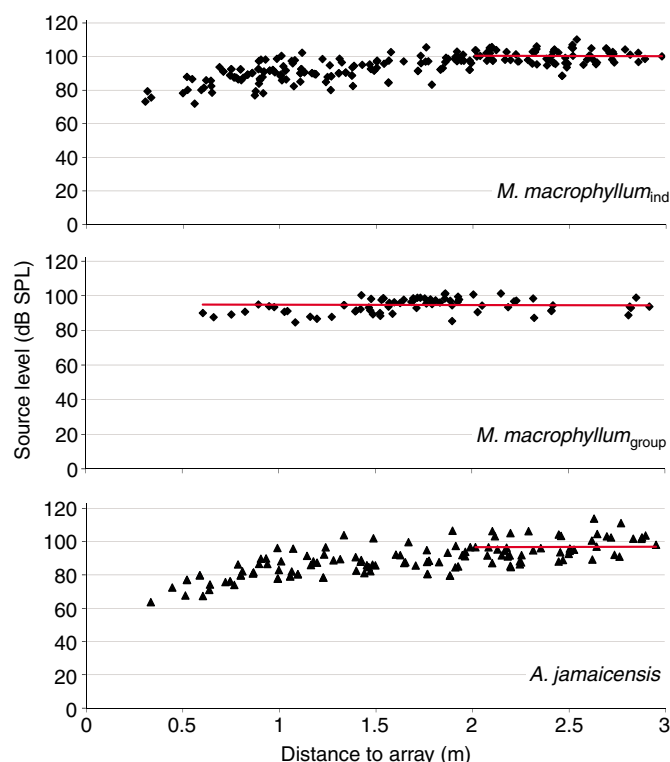


Fig. 4. Scatter plots of source levels from *M. macrophyllum*_{ind}, *M. macrophyllum*_{group} and *A. jamaicensis* as a function of distance to the array. For *M. macrophyllum*_{ind} and *A. jamaicensis*, mean source levels increased the further away the bats were from the array up to 2 m. Beyond 2 m, source levels were independent of distance and mean values are indicated by the horizontal trend lines. There was no correlation between distance and source level for *M. macrophyllum*_{group}.

macrophyllum recordings, which generally showed high signal amplitudes on all channels (Fig. 3). As the same microphone array was used to record both species, this indicates that *A. jamaicensis* emits a more directional narrow echolocation beam than *M. macrophyllum* but the data did not allow us to examine this further.

DISCUSSION

How loud are ‘whispering’ bats? To pursue this question and reveal possible influence of hunting strategy and food type on signal level, for the first time we determined the emitted intensities from two flying phyllostomid bats with very different foraging strategies; the trawling bat, *M. macrophyllum*, taking insects from or near water surfaces and *A. jamaicensis*, which feeds on fruit mostly in the cluttered forest interior. Our results show that these supposedly quiet bats can emit surprisingly loud echolocation calls, with estimated mean source levels of 101 and 96 dB SPL, respectively, far louder than the ‘whispers’ (ca. 70 dB SPL), previously ascribed to phyllostomids (Griffin, 1958). Indeed, both species would have been characterised as high intensity bats according to Griffin’s original classification. Contrary to our expectations, the measurements revealed louder maximum source levels for the frugivorous *A. jamaicensis* (110 dB SPL) than for the insectivorous *M. macrophyllum* (105 dB SPL).

Although the source levels of both species proved to be much higher than expected, it is unlikely that we have overestimated the emitted intensities. We took care only to include calls from flights towards the microphones (Fig. 3) but if the bats turned their

heads during flight we may have included some off-axis calls. However, such an error could only produce too low source level estimates. Positive interference from sound reflection from the water may result in source level estimates that are up to 6 dB too high but it is unlikely to be a problem here for *M. macrophyllum* because calls were short and the distance from microphone to bat was short compared with the distance from the microphone to the water, which delayed the reflected signal sufficiently to distinguish it from the directly transmitted signal. Also, we did not see notches in the spectra of search calls from *M. macrophyllum* (Fig. 2) in contrast to approach and buzz phase calls as well as, for example, in recordings of the longer calls from sympatric trawling noctilionid bats.

Finally, our estimates may be conservative because they are from the confined space of a flight room. Phyllostomid bats may turn out to be even louder in the field, in particular the trawling *M. macrophyllum*, because it flies in open space over the water and faces fewer or no immediate obstacles. Other insectivorous bats have been shown to produce much higher sound pressures in the field than in the lab (Holderied et al., 2005; Jensen and Miller, 1999; Surlykke and Kalko, 2008). By contrast, the source levels estimated for *A. jamaicensis* in the cluttered flight room may well correspond to their natural output when foraging in highly cluttered space.

M. macrophyllum: source levels and foraging ecology

M. macrophyllum is an edge and gap space forager following the definition of Schnitzler and Kalko (Schnitzler and Kalko, 2001) and Schnitzler and colleagues (Schnitzler et al., 2003). Source levels ranging from 103 to 137 dB SPL have been estimated in the field from trawling and aerial insectivorous bats of different sizes and from a number of families (Boonman and Jones, 2002; Holderied and Helversen, 2003; Holderied et al., 2005; Jensen and Miller, 1999; Rydell et al., 1999; Surlykke and Kalko, 2008; Surlykke et al., 1993). The mean source level of 101 dB SPL determined in the present study for *M. macrophyllum*_{ind} is just below this range and it is not unlikely that the source level emitted from this so-called ‘whispering’ bat in the field over open water is even higher.

Radio-tracking data support the notion that *M. macrophyllum* forages exclusively over water using larger home ranges than other small phyllostomids with a mean size of 24 ha (max. 151 ha) (Meyer et al., 2005; Weinbeer and Kalko, 2007). The particular foraging strategy of *M. macrophyllum* is further reflected by morphological adaptations including a long and broad tail membrane lined at the inside with sensory hairs and covered with protruding dermatics. The tail membrane is stabilised in flight with a pair of extra-long calcars and additionally by the very large feet with laterally compressed claws. Prior to a capture attempt, *M. macrophyllum* slides its tail membrane over the water surface. Usually, prey is then caught and immediately transferred to the mouth with a joint action of the tail membrane and large feet (Weinbeer and Kalko, 2007).

The foraging strategy of *M. macrophyllum* strongly resembles that of other trawling bats, in particular vespertilionids such as *Myotis daubentonii* (Jones and Rayner, 1988; Kalko and Schnitzler, 1989) and both noctilionids, *Noctilio leporinus* and *N. albiventris* (Kalko et al., 1998). The adaptations for foraging in open space are also reflected in the high output intensity of its echolocation calls, and the distinct temporal call pattern throughout a pursuit, including terminal buzzes, which resembles most other aerial insectivores from other families but is exceptional for a phyllostomid (Weinbeer and Kalko, 2007).

When *M. macrophyllum* were recorded flying in a group, they emitted signals with significantly lower source levels (mean source level of 95 dB SPL) than bats flying alone (mean source level of 101 dB SPL) and there was no correlation between source level and distance to the microphone array. They also had significantly higher call repetition rate and most calls had main energy in the second harmonic compared with bats flying individually, where the majority of calls had most energy in the third harmonic (Table 1). These results indicate that the interactions between bats flying simultaneously in a restricted space create a more complex acoustic scene, where reactions to other bats drown out or mask reactions to the array.

A. jamaicensis: source levels and foraging ecology

Like most other phyllostomid bats, the frugivorous *A. jamaicensis* is mainly a narrow space gleaner forager. *A. jamaicensis* is often difficult to detect on a bat detector, supposedly because it is very quiet. Consequently, our results, which show that this bat can emit intense calls with mean source levels of 96 dB SPL and maximum levels of 110 dB SPL, are surprising. The maximum levels exceeded even those recorded for the insectivorous *M. macrophyllum*. It is perhaps not so surprising that *A. jamaicensis* can produce higher intensities than *M. macrophyllum* considering the large difference in size between the two species. *A. jamaicensis* (40–55 g) is approximately six times larger than *M. macrophyllum* (6–9 g). Yet high source levels disagree with common difficulties in detecting and recording phyllostomids. However, our experimental design focused on determining the highest source levels. Hence, the mean source levels that we report here for *A. jamaicensis* may represent the upper range of its normal output intensity: a conclusion that is supported by our data screening. We restricted our analyses to recordings with a S/N ratio of +10 dB or better to permit accurate acoustic positioning. Only 45 out of 250 files recorded from *A. jamaicensis* fulfilled this criterion, in contrast to more than 50% of the files recorded from *M. macrophyllum*. The majority of discarded files from *A. jamaicensis* were not empty but contained echolocation calls below criterion, indicating that most of the time they emitted quiet calls. Predominantly quiet echolocation calls agree well with the gleaner behaviour of a frugivore at close range, when the bat has already detected fruit at longer range by smell and then approaches the fruit in dense vegetation. In addition, the large difference in recorded amplitude on the four microphones in the array suggested that *A. jamaicensis* may emit a narrow echolocation beam, adding to the difficulties in detecting this species acoustically. Beam width might relate to the difference in capture technique between the two species. *M. macrophyllum* uses the feet and tail membrane to capture moving insects and a broader beam reduces the risk of losing the insect whereas *A. jamaicensis* picks stationary fruit with its mouth and may therefore benefit from the more precise localisation of a narrow beam.

The large difference of 14 dB between the mean and maximum source level documented that *A. jamaicensis* can vary the output intensity over a large dynamic range. Flexible adjustment to a wide range of behavioural situations might be particularly important for large frugivorous bats like *A. jamaicensis* that often perform long-distance flights of several kilometres per night during which they cross open space or fly above the canopy (Handley et al., 1991; Kalko et al., 1996a). Higher output intensities translate into longer echolocation detection ranges useful for general orientation in open space, which may complement other sensory cues, particularly olfaction and vision. Echolocation behaviour is likely to differ between commuting and feeding. For example, because fig trees fruit irregularly throughout the season, bats often need to commute

long-distance to search for and harvest specific trees. As fig trees occur in a variety of locations in the forest as well as along shorelines and in forest patches, the bats face a range of spaces to deal with in its search for ripe figs, ranging from highly cluttered within the forest to almost open spaces above the canopy or along the shoreline, where intensity might be even higher than the maximum levels we determined in the flight cage.

Detecting the food

Hearing sensitivity has been measured for several phyllostomid species. Behavioural audiograms show fairly similar thresholds at the most prominent echolocation frequencies: *A. jamaicensis* (13 dB SPL at 56 kHz), *Phyllostomus hastatus* (9 dB SPL at 50 kHz) and *Carollia perspicillata* (16.5 dB SPL at 71 kHz) (Heffner et al., 2003; Koay et al., 2002; Koay et al., 2003). Recently, Hoffmann and colleagues reported a threshold below 0 dB at echolocation frequencies for *Phyllostomus discolor* (Hoffmann et al., 2008). All these thresholds were obtained in echo-reduced chambers. To take into account noise from wind and background for a bat flying in its natural habitat, we assumed a detection threshold of 15 dB for both species in order to estimate detection distances. We used target strengths of –20 dB for a small moth (Surlykke et al., 1999) for *M. macrophyllum* and –10 dB for a single fig in free air (*Ficus obtusifolia*, S.B., E.K.V.K. and A.S., unpublished observations) for *A. jamaicensis*. For *M. macrophyllum*, we estimated sonar detection ranges of 3 m using the maximum source level of 105 dB SPL and 2.7 m based on mean source level of 101 dB SPL. These detection ranges are at the lower end of the ranges estimated for sympatric aerial insectivorous and trawling bats from other families (Jung et al., 2007; Surlykke and Kalko, 2008), corresponding to the estimate of output intensity for *M. macrophyllum* being in the low end of the range for behaviourally comparable bats, much lower than for example the sympatric trawling bats *N. leporinus* (60–70 g) and *N. albiventris* (30–40 g). The reason *M. macrophyllum* is not as loud as the sympatric Noctilionidae may be phylogenetic but size may also play a role. Being 6–9 g, *M. macrophyllum* is much smaller than the two noctilionid species. Other data also suggest a correlation between body size and emitted intensity, e.g. the fairly quiet output of the open air forager *Molossus molossus* (5 g) (Surlykke and Kalko, 2008).

For *A. jamaicensis* the estimated detection ranges for *F. obtusifolia* were 5 and 3 m based on the maximum (110 dB SPL) and mean (96 dB SPL) source level, respectively. However, it is unlikely that *A. jamaicensis* detects figs by echolocation at long range as figs are often nestled among leaves. Scent is likely to be the primary cue for long-range detection and classification of ripe fruit (Kalko and Condon, 1998; Korine and Kalko, 2005; Thies et al., 1998) but scent cues are not precise markers for close-range localisation of a single fruit. Because our results confirmed that *A. jamaicensis* and other frugivorous phyllostomids continuously echolocate (Korine and Kalko, 2005; Thies et al., 1998), it is likely that echolocation also plays some role in this final stage, guiding bats to the exact position of food items. Nectar-feeding bats such as *Glossophaga* spp. use echolocation to find particular morphological features of the flower *Muconia holtonii* that guide the bats to the corolla (von Helversen and von Helversen, 1999; von Helversen and von Helversen, 2003) and also *Leptonycteris curasoae* echolocate in the final phases when feeding on the nectar and pollen of cacti (E.K.V.K., unpublished observations).

Influence of phylogeny and foraging ecology on call design

Ecological constraints inferred by the habitat and foraging area shape the foraging behaviour and, hence, the design of bat

echolocation. In many families of bats, e.g. Vespertilionidae and Emballonuridae, spectral and temporal features of echolocation calls clearly reflect the foraging behaviour of the species, such that open air foragers are characterised by long, narrowband signals that decrease in duration and increase in bandwidth when the bat approaches the ground or background vegetation (Fenton, 1990; Neuweiler, 1989; Schnitzler and Kalko, 2001; Schnitzler et al., 2003). However, such obvious correlation has not been shown within the Phyllostomidae, where all species studied so far emit rather similar multi-harmonic, short, steep FM calls, irrespective of their diverse feeding behaviours and habitats. This is corroborated by our results as well as those of Weinbeer and Kalko (Weinbeer and Kalko, 2007), which show that despite the unique foraging strategy of *M. macrophyllum*, its basic signal structure closely resembles that of other phyllostomids as represented by *A. jamaicensis*. The echolocation modifications in *M. macrophyllum* for a lifestyle very different from that of other phyllostomid bats mainly concern duration and intensity but not frequency and bandwidth of the calls. It may be that trawling can be accomplished with a variety of echolocation signals, as signal structure is highly diverse in trawling bats, ranging from very intense, long duration signals with a long constant frequency component in *N. leporinus* and *N. albiventris* (Kalko et al., 1998; Schnitzler et al., 1994; Surlykke and Kalko, 2008), over intermediate duration, steep broadband FM signals with most signal energy in the first harmonic recorded from *M. daubentonii* (Kalko and Schnitzler, 1989), to even shorter FM sweeps with signal energy concentrated in the second or third harmonic (*M. macrophyllum*).

If the large range in output intensity shown by *A. jamaicensis* indicates that phyllostomids in general are capable of emitting rather intense echolocation calls, this could in theory provide them access to a wide range of acoustic niches without requiring further adaptations of the echolocation calls. However, other limitations such as wing morphology are also important factors restricting the availability of niches.

Our results indicate that the 'generic' phyllostomid signal is flexible enough to serve echolocation purposes in a number of different habitats. However, recent observations of the Cuban flower bat *Phyllonycteris poeyi* and the Lesser Long-nosed bat *Leptonycteris curasoae* (Phyllostomidae) suggest that completely open space may require substantial adaptations of this signal type to cope with sensory demands. Both species emit long (up to 7.2 ms for *P. poeyi*) and apparently rather intense calls when flying in wide open space, but decrease call intensity and duration when approaching a cave entrance (E.K.V.K., unpublished observations) (Mora and Macías, 2007). Recordings of both *L. curasoae* and *P. poeyi* even showed how calls emitted in the open had most energy in the first harmonic, while bats flying in a cave emitted multi-harmonic calls, resembling those of other phyllostomid bats.

Concluding remarks

We have demonstrated that two species of phyllostomid bats, *M. macrophyllum* and *A. jamaicensis*, emit echolocation signals with intensities greatly exceeding previous estimates. The unique trawling behaviour of *M. macrophyllum* already suggested that it might be loud but it was surprising that *A. jamaicensis* could emit such intense calls. The results further showed that *A. jamaicensis* can adjust source level over a large range, and we predict that future studies of phyllostomid bats in their natural habitat will reveal that this family has a great level of flexibility in adapting sonar call intensity to acoustic constraints of habitat and feeding ecology. Perhaps such

studies will reveal other loud members of the speciose Phyllostomidae just waiting to be heard.

LIST OF ABBREVIATIONS

dB SPL r.m.s.	sound pressure level in decibel referenced to 20 μ Pa root mean square
S/N	signal-to-noise ratio
FM	frequency-modulated
BW _{-20dB}	bandwidth of the spectrum at -20 dB relative to the spectrum peak

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REFERENCES

- ANSI (1978). American National Standard. Method for the calibration of the absorption of sound by the atmosphere. ANSI S1 26-1978. Standards Secretariat. Acoustical Society of America. 335 East 45th Street, New York, NY 10017, USA. American Institute of Physics for the Acoustical Society of America.
- Boonman, A. and Jones, G. (2002). Intensity control during target approach in echolocating bats; stereotypical sensori-motor behaviour in Daubenton's bats, *Myotis daubentonii*. *J. Exp. Biol.* **205**, 2865-2874.
- Fenton, M. B. (1990). The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* **68**, 411-422.
- Findley, J. S. (1993). *Bats: A Community Perspective*. Cambridge: Cambridge University Press.
- Griffin, D. R. (1958). *Listening in the Dark*. New Haven: Yale University Press.
- Handley, C. O., Jr, Gardner, A. L. and Wilson, D. E. (1991). Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. *Smiths. Contrib. Zool.* No. 511 Smithsonian Inst. Press, Washington, D.C.
- Harrison, D. L. (1975). *Macrophyllum macrophyllum*. *Mamm. species* **62**, 1-3.
- Hartley, D. J. (1992). Stabilization of perceived echo amplitudes in echolocating bats 1. Echo detection and automatic gain-control in the big brown bat, *Eptesicus fuscus*, and the fishing bat, *Noctilio leporinus*. *J. Acoust. Soc. Am.* **91**, 1120-1132.
- Hartley, D. J. and Suthers, R. A. (1987). The sound emission pattern and the acoustical role of the noseleaf in the echolocating bat, *Carollia perspicillata*. *J. Acoust. Soc. Am.* **82**, 1892-1900.
- Heffner, R. S., Koay, G. and Heffner, H. E. (2003). Hearing in American leaf-nosed bats. III: *Artibeus jamaicensis*. *Hear. Res.* **184**, 113-122.
- Hiryu, S., Hagino, T., Riquimaroux, H. and Watanabe, Y. (2007). Echo-intensity compensation in echolocating bats (*Pipistrellus abramus*) during flight measured by a telemetry microphone. *J. Acoust. Soc. Am.* **121**, 1749-1757.
- Hoffmann, S., Baier, L., Borina, F., Schuller, G., Wiegrebbe, L. and Firzlauff, U. (2008). Psychophysical and neurophysiological hearing thresholds in the bat *Phyllostomus discolor*. *J. Comp. Physiol.* **A 194**, 39-47.
- Holderied, M. W. and von Helversen, O. (2003). Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. Lond. B, Biol. Sci.* **270**, 2293-2299.
- Holderied, M. W., Korine, C., Fenton, M. B., Parsons, S., Robson, S. and Jones, G. (2005). Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. *J. Exp. Biol.* **208**, 1321-1327.
- Jennings, N. V., Parsons, S., Barlow, K. E. and Gannon, M. R. (2004). Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropt.* **6**, 75-90.
- Jensen, M. E. and Miller, L. A. (1999). Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. *Behav. Ecol. Sociobiol.* **47**, 60-69.
- Jones, G. and Holderied, M. W. (2007). Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. Lond. B, Biol. Sci.* **274**, 905-912.
- Jones, G. and Rayner, J. M. V. (1988). Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera, Vespertilionidae). *J. Zool.* **215**, 113-132.
- Jones, G. and Teeling, E. C. (2006). The evolution of echolocation in bats. *Trends Ecol. Evol.* **21**, 149-156.
- Jung, K., Kalko, E. K. V. and von Helversen, O. (2007). Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J. Zool.* **272**, 125-137.
- Kalko, E. K. V. (2004). Neotropical leaf-nosed bats (Phyllostomidae): 'whispering' bats as candidates for acoustic surveys? In *Bat Echolocation Research, Tools, Techniques and Analysis* (ed. R. M. Brigham, E. K. V. Kalko, G. Jones, S. Parsons and H. J. G. A. Limpens), pp. 63-69. Austin, TX: Bat Conservation International.
- Kalko, E. K. V. and Condon, M. A. (1998). Echolocation, olfaction and fruit display: how bats find fruit of flagelliferous cucurbits. *Funct. Ecol.* **12**, 364-372.
- Kalko, E. K. V. and Schnitzler, H. U. (1989). The echolocation and hunting behaviour of Daubenton's, *Myotis daubentoni*. *Behav. Ecol. Sociobiol.* **24**, 225-238.
- Kalko, E. K. V., Handley, C. O., Jr and Handley, D. (1996a). Organization, diversity, and long-term dynamics of a Neotropical bat community. In *Long-term Studies in Vertebrate Communities* (ed. M. Cody and J. Smallwood), pp. 503-553. Los Angeles, CA: Academic Press.

- Kalko, E. K. V., Herre, E. A. and Handley, C. O., Jr** (1996b). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *J. Biogeogr.* **23**, 565-576.
- Kalko, E. K. V., Schnitzler, H. U., Kaipf, I. and Grinnell, A. D.** (1998). Echolocation and foraging behavior of the lesser bulldog bat, *Noctilio albiventris*: preadaptations for piscivory? *Behav. Ecol. Sociobiol.* **42**, 305-319.
- Koay, G., Bitter, K. S., Heffner, H. E. and Heffner, R. S.** (2002). Hearing in American leaf-nosed bats. I: *Phyllostomus hastatus*. *Hear. Res.* **171**, 96-102.
- Koay, G., Heffner, R. S., Bitter, K. S. and Heffner, H. E.** (2003). Hearing in American leaf-nosed bats. II: *Carollia perspicillata*. *Hear. Res.* **178**, 27-34.
- Korine, C. and Kalko, E. K. V.** (2005). Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behav. Ecol. Sociobiol.* **59**, 12-23.
- Meyer, C. F. J., Weinbeer, M. and Kalko, E. K. V.** (2005). Home-range size and spacing patterns of *Macrophyllum macrophyllum* (Phyllostomidae) foraging over water. *J. Mammal.* **86**, 587-598.
- Mora, E. C. and Macias, S.** (2007). Echolocation of Poey's flower bat (*Phyllonycteris poeyi*) unlike those of other phyllostomids. *Naturwissenschaften* **94**, 380-383.
- Neuweiler, G.** (1989). Foraging ecology and audition in echolocating bats. *Trends Ecol. Evol.* **4**, 160-166.
- Novick, A.** (1977). Acoustic orientation. In *Biology of Bats*. Vol. 3 (ed. W. A. Wimsatt), pp. 74-289. New York: Academic Press.
- Rydell, J., Miller, L. A. and Jensen, M. E.** (1999). Echolocation constraints of Daubenton's Bat foraging over water. *Funct. Ecol.* **13**, 247-255.
- Schnitzler, H.-U. and Kalko, E. K. V.** (2001). Echolocation by insect-eating bats. *Bioscience* **51**, 557-569.
- Schnitzler, H. U., Kalko, E. K. V., Kaipf, I. and Grinnell, A. D.** (1994). Fishing and echolocation behavior of the greater bulldog bat, *Noctilio leporinus*, in the field. *Behav. Ecol. Sociobiol.* **35**, 327-345.
- Schnitzler, H.-U., Moss, C. F. and Denzinger, A.** (2003). From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**, 386-394.
- Siemers, B. M., Stitz, P. and Schnitzler, H.-U.** (2001). The acoustic advantage of hunting at low heights above water: behavioural experiments on the European 'trawling' bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*. *J. Exp. Biol.* **204**, 3843-3854.
- Simmons, N. B.** (2005). An eocene big bang for bats. *Science* **307**, 527-528.
- Surlykke, A. and Kalko, E. K. V.** (2008). Echolocating bats cry out loud to detect their prey. *PLoS ONE* **3**, e2036.
- Surlykke, A., Miller, L. A., Möhl, B., Andersen, B. B., Christensen-Dalsgaard, J. and Jørgensen, M. B.** (1993). Echolocation in two very small bats from Thailand: *Craseonycteris thonglongyai* and *Myotis siligorensis*. *Behav. Ecol. Sociobiol.* **33**, 1-12.
- Surlykke, A., Filskov, M., Fullard, J. H. and Forrest, E.** (1999). Auditory relationships to size in Noctuid moths: bigger is better. *Naturwissenschaften* **86**, 238-241.
- Thies, W., Kalko, E. K. V. and Schnitzler, H.-U.** (1998). The roles of echolocation and olfaction in two Neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*, feeding on Piper. *Behav. Ecol. Sociobiol.* **42**, 397-409.
- Urick, R. J.** (1983). *Principles of Underwater Sound*. New York: McGraw-Hill.
- Von Helversen, D. and von Helversen, O.** (1999). Acoustic guide in bat-pollinated flower. *Nature* **398**, 759-760.
- Von Helversen, D. and von Helversen, O.** (2003). Object recognition by echolocation: a nectar-feeding bat exploiting the flowers of a rain forest vine. *J. Comp. Physiol. A* **189**, 327-336.
- Weinbeer, M. and Kalko, E. K. V.** (2007). Ecological niche and phylogeny: the highly complex echolocation behavior of the trawling long-legged bat, *Macrophyllum macrophyllum*. *Behav. Ecol. Sociobiol.* **61**, 1337-1348.
- Zar, J. H.** (1984). *Biostatistical Analysis*. 2nd edn. Englewood Cliffs, NJ: Prentice-Hall.