RESEARCH ARTICLE

The sonar beam of *Macrophyllum macrophyllum* implies ecological adaptation under phylogenetic constraint

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ABSTRACT

All animals are adapted to their ecology within the bounds of their evolutionary heritage. Echolocating bats clearly show such adaptations and boundaries through their biosonar call design. Adaptations include not only the overall time-frequency structure, but also the shape of the emitted echolocation beam. *Macrophyllum macrophyllum* is unique within the phyllostomid family, being the only species to predominantly hunt for insects in the open, on or above water, and as such it presents an interesting case for comparing the impact of phylogeny and ecology as it originates from a family of low-intensity, high-directionality gleaning bats, but occupies a niche dominated by very loud and substantially less-directional bats. Here, we examined the sonar beam pattern of *M. macrophyllum* in the field and in a flight room and compared it to closely related species with very different feeding ecology and to that of the niche-sharing but distantly related *Myotis daubentonii*. Our results show that *M. macrophyllum* uses higher source levels and emits less-directional calls than other phyllostomids. In the field, its call directionality is comparable to *M. daubentonii*, but in the flight room, *M. macrophyllum* is substantially more directional. Hence our results indicate that ecology influences the emitted call, pushing the bats to emit a louder and broader beam than other phyllostomids, but that phylogeny does limit the emitted intensity and flexibility of the overall beam pattern.

KEY WORDS: Echolocation, Ecological adaptation, Sonar beam, Source level

INTRODUCTION

All living organisms explore and expand to new habitats. In doing so, animals evolve morphological, physiological and behavioural traits adapted to these new niches. The evolution of such traits is, however, likely limited by phylogenetic inertia, i.e. an animal's evolutionary pathway is constrained by previous adaptations (Blomberg and Garland, 2002). Bats (*Chiroptera*) are no exception to this and they have evolved to successfully colonize most of the world with around 1350 species specialized to thrive in many different habitats and niches (Burgin et al., 2018). Bats are the only true flying mammals, and the majority of species use echolocation, which presumably are the major reasons for their great evolutionary success. Echolocation is an active sensing system, and combined with powered flight, it allows bats to hunt and navigate at night in complete darkness, by emitting high frequency

sound pulses and localizing and identifying objects from the returning echoes (Griffin, 1986).

Bats will dynamically alter features of their emitted calls in response to the context at hand, such that echolocation calls emitted by bats flying in dense vegetation or in close proximity to prey are often profoundly different from calls emitted by the same bats flying out in the open sky. When resolving target echoes in densely vegetated habitats (cluttered habitats) or identifying and accurately localizing prey, bats usually emit short, relatively low intensity, broad-banded pulses to decrease clutter load and to increase localization accuracy and resolution. On the other hand, when searching for prey in open habitats, bats emit long duration, high intensity, low frequency pulses as these greatly improve detection distance (Jensen and Miller, 1999; Kalko and Schnitzler, 1993; Neuweiler, 1990; Schnitzler and Kalko, 2001; Surlykke and Moss, 2000). In spite of the great intraspecies variability in echolocation calls, there are still clear differences between echolocation calls emitted by bats from different niches, e.g. gleaning bats catching non-airborne prey, emit more broad-band calls than aerial hawkers when flying in the same environment (Siemers and Schnitzler, 2004).

The emitted calls are also directional, that is, most sound is emitted in the forward direction and the sound pressure drops progressively as the off-axis angle increases (Hartley and Suthers, 1987; Hartley and Suthers, 1989; Schnitzler and Grinnell, 1977; Shimozawa et al., 1974; Simmons, 1969). Recent studies suggest that directionality is as important for navigation by echolocation as the temporal and spectral structures of the calls because it contributes greatly to the bats' active space, i.e. the volume in space where they can perceive objects. Directionality is adapted to context on par with other call parameters (Jakobsen et al., 2015; Jakobsen and Surlykke, 2010; Kounitsky et al., 2015; Matsuta et al., 2013; Motoi et al., 2017; Surlykke et al., 2009) and closely related bat species navigating the same closed environment converge on the same beam pattern (Jakobsen et al., 2013). Call directionality is a product of the emitted call frequency and the emitter size/shape. Modifications to either will change directionality such that a smaller emitter or lower frequency will broaden the beam. For mouth emitting bats, the emitter size is presumably defined by the size of the open mouth. While most bats emit sound through the mouth, roughly 30% emit sound through the nostrils (Eick et al., 2005; Pedersen, 1993) and the vast majority of these have elaborate structures (nose-leaves) associated with the nostrils to facilitate a directional sound emission (Hartley and Suthers, 1987; Schnitzler and Grinnell, 1977).

The biggest family of nose emitting bats are the New World leaf-nosed bats or Phyllostomidae. This family consists of more than 200 species of which the vast majority forage in highly cluttered habitats using a gleaning strategy where stationary food is taken from surfaces (Burgin et al., 2018; Denzinger et al., 2017; Simmons, 2005). Phyllostomid echolocation is very conserved across species,

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and consists of short multi-harmonic calls with most energy in the 2nd to 4th harmonic (Brinkløv et al., 2009). Although recent studies have shown that phyllostomid bats can emit fairly high source levels, they are still relatively quiet compared with other echolocating species (Brinkløv et al., 2009; Brinkløv et al., 2010; Surlykke et al., 2013). Call directionality has been measured for two phyllostomid species, *Trachops cirrhosus* and *Carollia perspicillata*, freely navigating a flight room and both show significantly higher directionality than other bats measured to date. The high directionality may be an adaptation to gleaning prey in dense vegetation because the highly directional beam reduces the clutter load significantly when flying in such habitats, and it focuses the beam on a very small area, increasing the likelihood of detecting inconspicuous objects (Brinkløv et al., 2011; Dukas, 2004; Surlykke et al., 2013).

The long-legged bat, *Macrophyllum macrophyllum*, is a unique exception within the phyllostomids as it is the only trawling member of the family, hunting insects on or directly above water (Meyer et al., 2005). *Macrophyllum macrophyllum* emits calls with a time-frequency structure like other phyllostomids, but of higher intensities (Brinkløv et al., 2010). It is one of few phyllostomid bats known to use a distinct search, approach and buzz pattern in its echolocation emission during prey capture, as otherwise observed in the majority of aerial hawking and trawling bats (Brinkløv et al., 2009; Gessinger et al., 2019; Weinbeer and Kalko, 2007). These specific adaptations show that *M. macrophyllum* has adapted its echolocation to the hunting niche, but it is still a nose-emitting bat originating from a family dominated by gleaners. The obvious questions are therefore whether *M. macrophyllum* has also adapted its call directionality to the hunting niche and if it shows the same flexibility in the emitted beam pattern as other bats foraging in the same niche. To answer these questions, we measured source levels and the sonar beam pattern of *M. macrophyllum* both in the open habitat in the field and in the confined space of a flight room. We compare our results to measurements from other phyllostomid bats (*C. perspicillata* and *T. cirrhosus*) and to data from *Myotis daubentonii*, a similar-sized trawling vespertilionid bat that shows high flexibility in emitted echolocation beam, emitting a narrower beam in the field compared with the lab (Surlykke et al., 2009).

MATERIALS AND METHODS

We recorded echolocation calls from long-legged bats *Macrophyllum macrophyllum* (Shinz 1821) in the field flying on Lake Gatún in the Panama Canal and in a 2.5 m×4 m flight room at the Smithsonian Tropical Research Institute (STRI) on Barro Colorado Island (BCI), using a 12-microphone array. The array consisted of 12 G.R.A.S. ¼ inch 40 BF microphones amplified by 30 dB using Avisoft amplifiers with a 15 kHz high-pass filter and further 27 dB amplified and digitized by an Avisoft USGH 1216. The sampling rate was 300 kHz per channel and the data were stored on a laptop. We recorded 5 s files, with a 3 s pre-trigger and a 2 s post-trigger and calibrated the microphones after each recording session with a G.R.A.S. 42 AB sound calibrator. Temperature and humidity were measured and noted both before and after the recordings.

In the field, the setup was attached to a raft positioned close to the bats' roost in an old shipwreck in the laboratory cove at BCI and the bats were recorded as they left the roost flying out over open water towards the array. The array was arranged with 10 horizontal microphones 0.3 m apart and 1 microphone above (0.5 m) and 1 below (0.3 m) the fourth horizontal microphone. The 10 horizontally placed microphones were 0.5 m above the water surface. In the flight room we used a cross configuration with 6

horizontal microphones approximately 0.3 m apart and 3 microphones above and 3 below the third horizontal microphone 0.2 m apart. We recorded 3 bats (2 females and 1 male) in the flight room, all caught from their roost on the same day as the recordings took place. The bats were released into the flight room individually and were recorded when approaching the array on their own accords. All experiments were licensed and approved by STRI (IACUC permit: 20100816–1012–16).

We localized the bats at each sound emission by triangulation from the difference in arrival time on each of the 12 microphones. We only used call sequences where the bats flew directly towards the array for further analysis and for the field recordings only search calls, defined as a pulse interval (PI) of >30 ms between strobe groups consisting of a maximum of 3 calls, and calls localized to further than 3 m from the array to avoid any approach behaviour (Brinkløv et al., 2010). We compensated each call for transmission loss and microphone directionality and calculated source-levels and call directionality as described in Jakobsen et al. (2012). We further computed the average beam shape by pooling the relative sound-pressures into 1 deg bins and smoothing the resulting curve using a standard running average. From the average beam shape, we calculated the directivity index (DI) which is the increase in sound pressure emitted in the forward direction by a directional source compared to an omnidirectional source radiating the same acoustic power (see Surlykke et al., 2013 for details). We also measured the RMS pressure in the 2nd, 3rd and 4th harmonic by filtering the compensated call using a third-octave band-pass filter centred at the approximate peak frequency of the relevant harmonic and computing the 95% energy content of the filtered signal. Finally, we measured the centroid frequency (between 40 kHz and 110 kHz) using the spectralCentroid command in Matlab.

Acoustic recordings of bats flying over water may be significantly impacted by interference between the directly transmitted signal and reflections from the water surface (see Surlykke et al., 2009). To investigate the impact of these reflections on our measurements of the sonar beam shape, we performed a playback experiment, measuring the directionality of an Avisoft ScanSpeak emitting sound over an artificial pond (3 m×5 m). We played a 5 ms linear FM sweep (50 kHz to 12.5 kHz) at two different elevations above the pond (0.1 and 0.5 m) and nine distances to our recording setup: 1.25–5.25 m at 0.5 m intervals. We measured directionality with the same microphone array used for bat recordings but with 11 microphones on a horizontal line 0.3 m apart and 1 microphone above the 6th horizontal microphone. The 11 microphones were level with the speaker for both elevations and the speaker was oriented directly towards the centre microphone. We also conducted a trial with the speaker 0.1 m above the water surface and the microphones placed 0.5 m above the surface at all nine distances to test the impact of animals flying below the array. As a control comparison, we measured speaker directionality at 0.5 m elevation at the same distances without the pond and with acoustic foam covering the floor to minimize potential reflections on the recordings (melamin 50/50 pyramid panels from IAC Nordik, Hvidovre, Denmark). We recorded 12 sound pulses at each distance for all recording setups. From the test experiment, it is clear that in spite of the reflection from the water surface, the overall beam pattern is conserved (Fig. 1A); there is a slight change in directionality when recording at 0.5 m above water apparent at 45 deg with a resultant lowering of estimated directivity index (DI) value of 1.3 dB (DI without water=18.4 dB, DI at 0.1 m=18.1 dB and DI at 0.5 m=17.1 dB). It is also clear that measuring above the beam aim introduces significant errors to the measurements at close

distances, i.e. the measured beam pattern becomes substantially broader than the actual beam pattern at greater off-axis angles, but this has little or no effect at distances greater than 3 m which corresponds with our selection criteria for the field recordings (Fig. 1B). Source level estimates are also affected by reflections from the water surface, but to a lesser extent than the worst-case scenario predicted by Surlykke et al. (2009). When the sound source and microphones are in the same horizontal plane, source level measurements differ by 2 dB or less between the non-reflection and the water reflection scenario (Fig. 1C). When the speaker is placed below the microphones the estimated source levels are underestimated at distances below two meters and overestimated at distances above 4 m with a maximum difference of +3.3 dB at the distances within our selection criteria.

RESULTS

In the field we made 75 recordings from a minimum of five different individuals. During our recording sessions we observed up to five different bats at the same time, and most bats flew in the same direction, likely commuting from the roost to their hunting grounds

(Weinbeer et al., 2006). Of the 75 recordings, 18 met our criteria, resulting in a total of 42 calls for directionality measurements. In the flight room we obtained 110 recordings from the three individuals, of these, 21 fulfilled our criteria, with 80 useable calls in total for directionality measurements: 61 calls from bat A, 6 from bat B and 13 from bat C.
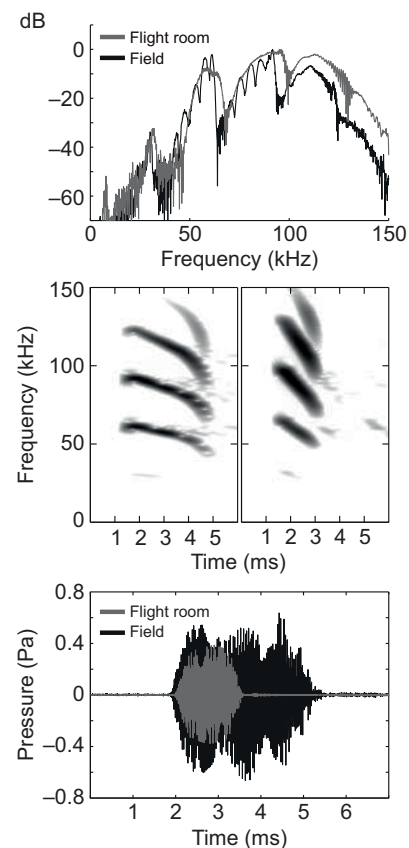
In the field, *M. macrophyllum* emitted calls of significantly higher mean source level (116 versus 104 dB RMS re. 20 µPa at 0.1 m), longer duration (2.5 ms versus 1.2 ms) and lower centroid frequency (87 kHz versus 89 kHz) than in the flight room (Fig. 2, Table 1). The bats also emitted slightly more directional calls in the field than in the flight room, DI=16 dB versus 14.5 dB in the flight room (half-amplitude angle, i.e. the angle where pressure has dropped by 6 dB relative to the frontal sound pressure, of 19 deg in the field versus 26 deg in the lab; Table 2 and Fig. 3). Because *M. macrophyllum* flies so close to the water surface in the field, it is not possible to get microphones low enough to adequately estimate the vertical directionality, and directivity estimates from the field assume that the beam pattern is radially symmetrical. The flight room recordings indicate that this is not true (Fig. 4). Rather, the beam is asymmetrical in the vertical plane, but the difference in computed DI using only the horizontal measurements and using both horizontal and vertical is only 0.5 dB (Table 1).

DISCUSSION

Our results show that *M. macrophyllum* emits a broader beam than other free-flying phyllostomids measured to date, DI of the overall
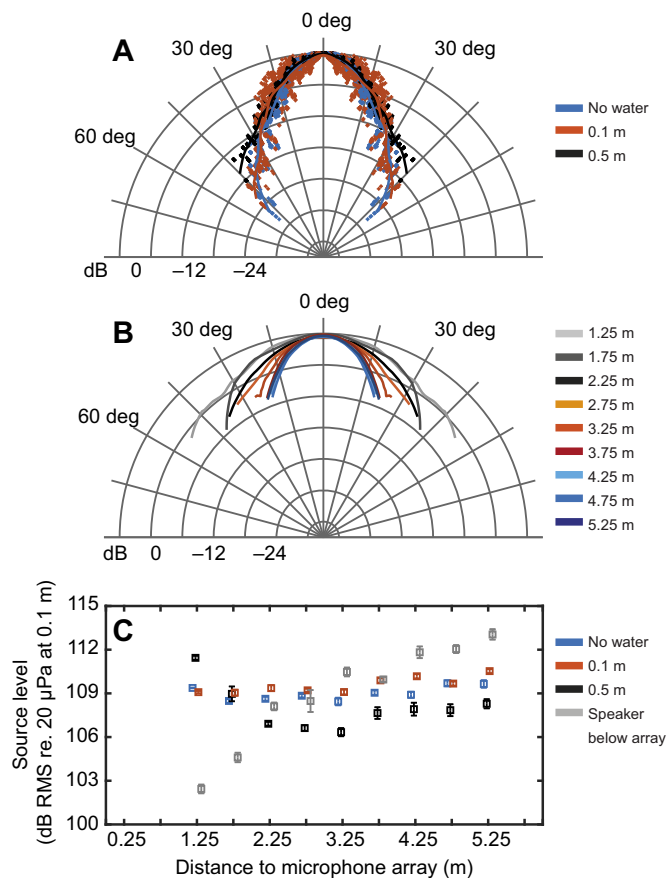
Fig. 1. Measured directionality and source level from an Avisoft ScanSpeak emitting a 5 ms sweep (50 kHz to 12.5 kHz). (A) Measurements with the microphone array and speaker without water, at 0.1 m and at 0.5 m above water, data are pooled for distances from 5.25 m to 1.25 m, lines are averages from 1 deg bins smoothed with a standard running average. (B) Measurements with the microphone array at 0.5 m above water and the speaker at 0.1 m above water also at distances from 5.25 m to 1.25 m. (C) Source-level measurements ±s.d. for all four configurations at each distance. Measurement distances are identical for all configurations, but the points are separated slightly for ease of presentation.

Fig. 2. Spectrum, spectrograms and oscillograms of typical calls emitted by the long-legged bat *Macrophyllum macrophyllum* in the field and in the flight room.

Table 1. Source level, duration and frequency for calls in the field and flight room

	Field	Flight room
Source level (dB RMS re. 20 µPa at 0.1 m)		
Entire call	116±2.5	104±3.5*
2nd harmonic	104±3.5	92±2.5*
3rd harmonic	104±3.0	96±3.5*
4th harmonic	100±3.5	97±3.0*
Duration (ms)	2.5±0.4	1.2±0.2*
Frequency (kHz)		
Centroid	87±2.0	89±3.0*
2nd harmonic peak	59±2.5	58±1.5*
3rd harmonic peak	89±3.5	88±3.0
4th harmonic peak	105±7.0	107±5.0

Source levels are given for both the entire call and at the 2nd, 3rd and 4th harmonic using third-octave filters centred at the measured peak frequency of the respective harmonic. Values are means±s.d. of N=42 calls from the field and N=80 calls from the flight room. *P<0.05 between the field and flight room (ANOVA analysis).

call is 3 dB lower for *M. macrophyllum* than for both *C. perspicillata* and *T. cirrhosus* flying in a flight room (DI=17 dB; Brinkløv et al., 2011; Surlykke et al., 2013), the corresponding half-amplitude angles were ~8 deg larger horizontally (26 deg for *M. macrophyllum* versus 16 deg and 18 deg for *C. perspicillata* and *T. cirrhosis*, respectively) and 16 deg larger vertically for *M. macrophyllum* (~30 deg for *M. macrophyllum* versus ~14 deg for both *C. perspicillata* and *T. cirrhosus* in flight). The emitted beam is also narrower in the field compared with the flight room, but not by much. Interestingly, size of the nose-leaf does not appear to dictate directionality in *M. macrophyllum* when compared with *C. perspicillata* and *T. cirrhosus*, all three bats emit calls with similar frequency content (Brinkløv et al., 2011; Surlykke et al., 2013) but *M. macrophyllum* has a larger nose-leaf (longer lancet and broader base) than both *C. perspicillata* and *T. cirrhosus* (Arita, 1990). Intuitively, the larger nose-leaf should yield a narrower beam for *M. macrophyllum*, but the opposite is true. As shown by Hartley and Suthers (1987), position of the nose-leaf has significant impact on the emitted beam pattern and *M. macrophyllum* may utilize a different nose-leaf configuration in flight than *C. perspicillata* and *T. cirrhosus* to achieve the broader beam (i.e. different bend and curvature of the leaf and different nostril separation).

Similarly to previous studies, we find a slight increase in the frequency content of the calls emitted in the flight room compared

Table 2. Directivity index (DI) and half-amplitude angle based on entire calls and for the 2nd, 3rd and 4th harmonic, calculated in both the field and flight room
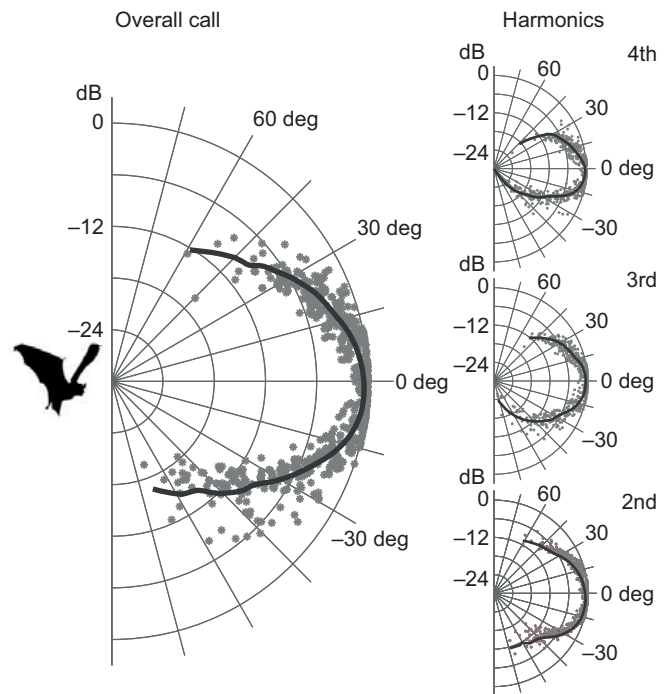
		Flight room	
Directivity index	Field	Horizontal	Horizontal+vertical
Entire call	16 dB	14.5 dB	14 dB
2nd harmonic	14 dB	10 dB	11.5 dB
3rd harmonic	18 dB	14 dB	14 dB
4th harmonic	19 dB	17 dB	16.5 dB
Half-amplitude angle		Horizontal	Vertical (upper/lower)
Entire call	19 deg	26 deg	31 deg/27 deg
2nd harmonic	29 deg	42 deg	35 deg/32 deg
3rd harmonic	17 deg	27 deg	32 deg/27 deg
4th harmonic	15 deg	20 deg	23 deg/21 deg

DI in the flight room is computed using the horizontal measurements alone or using both the horizontal and vertical. Vertical half-amplitude angles are given for the upper and lower part of the beam.
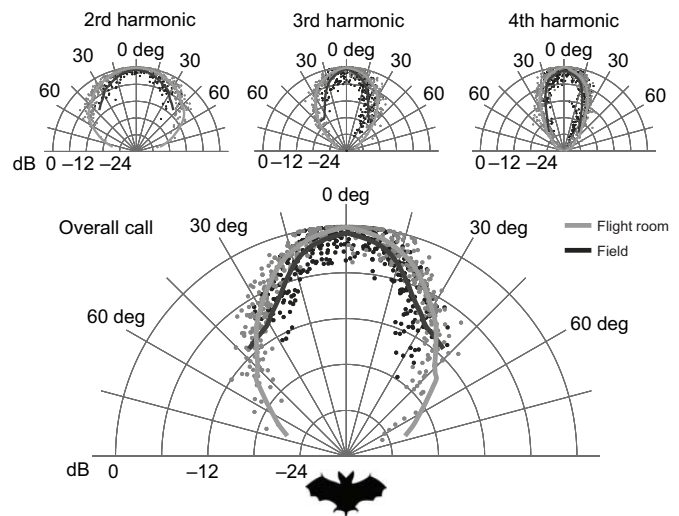
Fig. 3. Horizontal sound beam directionality of all *M. macrophyllum* calls from the field (black) and the flight room (grey, *n*=3). The plot shows the beam pattern for both the overall call and the 2nd, 3rd and 4th harmonic alone. Lines are averages from 1 deg bins smoothed with a standard running average.

with the field (Brinkløv et al., 2010). The rise in frequency by itself should increase call directionality, but interestingly, it is accompanied here by a lower DI (decreased call directionality), indicating a parallel change in the emitter characteristics. The change in emitted beam pattern is, however, minute, and substantially lower than what has previously been measured for *M. daubentonii*. In the field, both species emit a similar beam pattern with DI=16 dB, but in the flight room, *M. macrophyllum* emits a much narrower beam than *M. daubentonii* (DI=14 dB for

Fig. 4. Vertical sound beam directionality of all *M. macrophyllum* calls in the flight room (*n*=3). Directionality is plotted for the entire call and the 2nd, 3rd and 4th harmonic alone. Lines are averages from 1 deg bins smoothed with a standard running average.

M. macrophyllum versus 11 dB for *M. daubentonii*; Jakobsen et al., 2013). For *M. daubentonii*, the difference in emitted beam pattern between the field and the flight room is likely produced by reducing the mouth gape. While it is likely that phyllostomids can steer and adjust the echolocation beam by modifying the nose-leaf and/or nostril size and separation (Surlykke et al., 2013; Weinbeer and Kalko, 2007), the flexibility in changing emitter size may be substantially less than for mouth-emitting bats. Reduced emitter-size flexibility may explain the relatively small variation in beam pattern between field and flight room for *M. macrophyllum*. Conversely, it may also represent a difference in echolocation strategy. *Trachops cirrhosus* and *C. perspicillata*, both gleaners, emit very narrow echolocation beams whereas the brown long-eared bat (*Plecotus auritus*), a vespertilionid gleaner, and *Megaderma lyra*, a megadermatid gleaner, emit comparably broader beams (DI=~13 dB; Jakobsen et al., 2018; Möhres and Neuweiler, 1966). Both *P. auritus* and *M. lyra* emit sound through the nostrils, which means that the narrow beam is not inherent to gleaning nasal emitters. Gleaning phyllostomid bats in general may utilize a narrow beam in confined spaces whereas vespertilionids and megadermatids utilize a broader beam.

Our study, in agreement with previous studies (Brinkløv et al., 2009, 2010), reports the highest source level measured for any phyllostomid even when considering potential overestimations caused by reflections from the water. The high source level will yield a substantially larger detection volume for prey compared with that of other phyllostomids but still considerably smaller than the ecologically similar *M. daubentonii*, which emits higher source levels and lower frequency calls. Differences in receiver characteristics may reduce the gap in detection distance between *M. macrophyllum* and *M. daubentonii*, e.g. the much larger outer ears of *M. macrophyllum* should provide substantial acoustic gain, but they also provide a more directional receptive field, such that while frontal detection range increases, peripheral echoes are more strongly attenuated.

High source levels confer a longer detection range, which is presumably advantageous when hunting flying insects. However, there are several vespertilionid bats that emit as low or lower source levels than *M. macrophyllum* when catching flying insects (Corcoran and Conner, 2017; Goerlitz et al., 2010; Lewanzik and Goerlitz, 2018). These quiet vespertilionid bats presumably avoid detection by eared prey, and the inconspicuousness granted by the lower source levels outweigh the disadvantage of the lower detection distance. Whether a similar adaptive significance is conferred to phyllostomids is unknown, but it could be elucidated by examination of the type of insect prey exploited by *M. macrophyllum*. Conversely, the relatively low intensities emitted by *M. macrophyllum* compared with most trawling and aerial-hawking bats could be a product of the sound emission mode, such that the physiology behind phyllostomid nasal sound emission limits the emitted sound pressures and *M. macrophyllum* is emitting sound pressures as high as its physiology allows. High intensity echolocation is not limited to oral-emitting bats, as is evident from rhinolophids (Schuchmann and Siemers, 2010) but it is also clear that, in addition to the large inherent differences between the high-duty cycle echolocation of rhinolophids and the low-duty cycle echolocation of phyllostomids, nose-leaf morphology and cranial morphology is dramatically different between the two (Pedersen, 1998; Pedersen and Müller, 2013). On the basis of these differences, it has been hypothesized by Pedersen (1998) that rhinolophids have sacrificed olfaction for higher call intensity while phyllostomids have not and it is therefore likely that *M. macrophyllum* is indeed calling at peak intensity.

As proposed by Weinbeer and Kalko (2007), we believe that the unique combination of phylogeny and ecological niche is what dictates the echolocation behaviour of *M. macrophyllum*. The time-frequency structure of the calls is typical for phyllostomids, but *M. macrophyllum* emits higher source levels and less-directional calls than other phyllostomids. *Macrophyllum macrophyllum* is, however, still substantially quieter than the similar sized trawling vespertilionid, *M. daubentonii*, and shows less flexibility in the emitted beam pattern. Whether the observed differences between these two species represent a different approach to similar perceptual tasks, or phylogenetic inertia (i.e. *M. macrophyllum* cannot produce higher source levels in the field and a broader beam in the flight room) remains to be seen, but it is clear that *M. macrophyllum* is ensonifying its surroundings in a way that facilitates a wider receptive field and greater detection distance than phyllostomid gleaners, but still less so than a niche-sharing vespertilionid bat.

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