

Dynamics of the echolocation beam during prey pursuit in aerial hawking bats

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In the evolutionary arms race between prey and predator, measures and countermeasures continuously evolve to increase survival on both sides. Bats and moths are prime examples. When exposed to intense ultrasound, eared moths perform dramatic escape behaviors. Vespertilionid and rhinolophid bats broaden their echolocation beam in the final stage of pursuit, presumably as a countermeasure to keep evading moths within their “acoustic field of view.” In this study, we investigated if dynamic beam broadening is a general property of echolocation when catching moving prey. We recorded three species of emballonurid bats, *Saccopteryx bilineata*, *Saccopteryx leptura*, and *Rhynchonycteris naso*, catching airborne insects in the field. The study shows that *S. bilineata* and *S. leptura* maintain a constant beam shape during the entire prey pursuit, whereas *R. naso* broadens the beam by lowering the peak call frequency from 100 kHz during search and approach to 67 kHz in the buzz. Surprisingly, both *Saccopteryx* bats emit calls with very high energy throughout the pursuit, up to 60 times more than *R. naso* and *Myotis daubentonii* (a similar sized vespertilionid), providing them with as much, or more, peripheral “vision” than the vespertilionids, but ensonifying objects far ahead suggesting more clutter. Thus, beam broadening is not a fundamental property of the echolocation system. However, based on the results, we hypothesize that increased peripheral detection is crucial to all aerial hawking bats in the final stages of prey pursuit and speculate that beam broadening is a feature characterizing more advanced echolocation.

directionality | bat | echolocation | perception | buzz

The evolutionary arms race between echolocating bats and their insect prey provides a textbook example of continuous evolution of measures and countermeasures to either acquire prey or escape capture (1). Bats can navigate and forage in complete darkness using echolocation, emitting short ultrasonic sound pulses and locating objects and prey in their surroundings from the returning echoes (2). In response, moths and other nocturnal insects have evolved ultrasound-sensitive ears that enable them to avoid foraging echolocating bats (negative phototaxis) and to initiate dramatic escape responses when in close proximity to them (3). As a possible countermeasure, some species of bats have evolved echolocation calls with low intensities [*Barbastellus barbastella* (4)] and/or frequencies [*Eudermamaculatum* (5)] outside the moths’ hearing range, enabling them to sneak up undetected, or at least without eliciting escape maneuvers from the prey.

Another potential countermeasure is the sudden broadening of the beam observed in the very last phases of prey pursuit in aerial hawking vespertilionid bats (6) and rhinolophid bats (7). When searching for, and approaching, prey, both vespertilionids and rhinolophids emit a fairly directional sound beam with higher sound pressure in the acoustic axis right in front of the bat and decreasing steeply as the off-axis angle increases (8, 9). Although the directional emissions provide the bats with a number of advantages over an omnidirectional emission (6), the downside is a decreased acoustic “field of view” that would enable prey to escape the bat’s sonar space, especially at close range. Presumably to counteract this effect, vespertilionids and rhinolophids broaden their echolocation beam when closing in on prey (6, 7). Vespertilionids do so by lowering the frequency of their

calls by almost an octave. The width of a sound beam depends on the wavelength emitted relative to the size of the emitter. Hence, increasing the wavelength by lowering the frequency by an octave will substantially increase the width of the beam for a constant mouth opening (6). The mechanism is still unknown for rhinolophids, but manipulating the fine structure of their nose-leaf could account for the change in beam directionality (10). By broadening the beam during the final stage of prey pursuit (the buzz), the bats counteract the prey’s evasive maneuvers, keeping larger off-axis angles within their acoustic field of view compared with the approach phase. The ubiquitous nature of this aspect of predator–prey interaction in echolocators is emphasized by recent findings showing that harbor porpoises (*Phocena phocena*) also broaden their beam during the buzz phase when catching fish (11).

Whereas the Vespertilionidae and Rhinolophidae are considered advanced echolocators, the Emballonuridae are thought to emit calls closely resembling those calls emitted by the first echolocating bats (12, 13). Like most vespertilionids, emballonurids hunt airborne insects. They emit sounds through their mouth. Their calls are short, multiharmonic, and of an almost constant frequency, with a suppressed first harmonic and most energy in the second harmonic (14) (Fig. 1). They go through the three standard hunting phases, search, approach, and buzz, when catching airborne prey (Fig. 1), but they do not change the call frequency during the buzz phase. Thus, emballonurids can only broaden their echolocation beam during the buzz by reducing their effective emitter size (e.g., by reducing their gape size). Investigating whether emballonurids broaden their beam during prey pursuit will throw light on whether the beam broadening is a fundamental property of the echolocation system in all aerial hawking bats, or possibly a more advanced trait that has only evolved in some families/species. Hence, the main purpose of this study is to investigate if emballonurids are broadening their beam during the terminal buzz. The only known exception to the

Significance

Many insects have evolved ultrasonic ears to detect and evade hunting bats, performing dramatic escape maneuvers in response to intense ultrasound. Presumably as a response, some bats broaden their echolocation beam in close proximity to insects to keep track of them at large off-axis angles. Here, we investigated if beam broadening is a general property of echolocation when hunting moving prey. The results show that emballonurid bats ensonify a wide area during pursuit, not by broadening the beam but by emitting high-intensity calls throughout pursuit. Thus, beam broadening is not a general property of echolocation, but we hypothesize that maintaining a broad acoustic field of view is crucial for all echolocators hunting moving prey.

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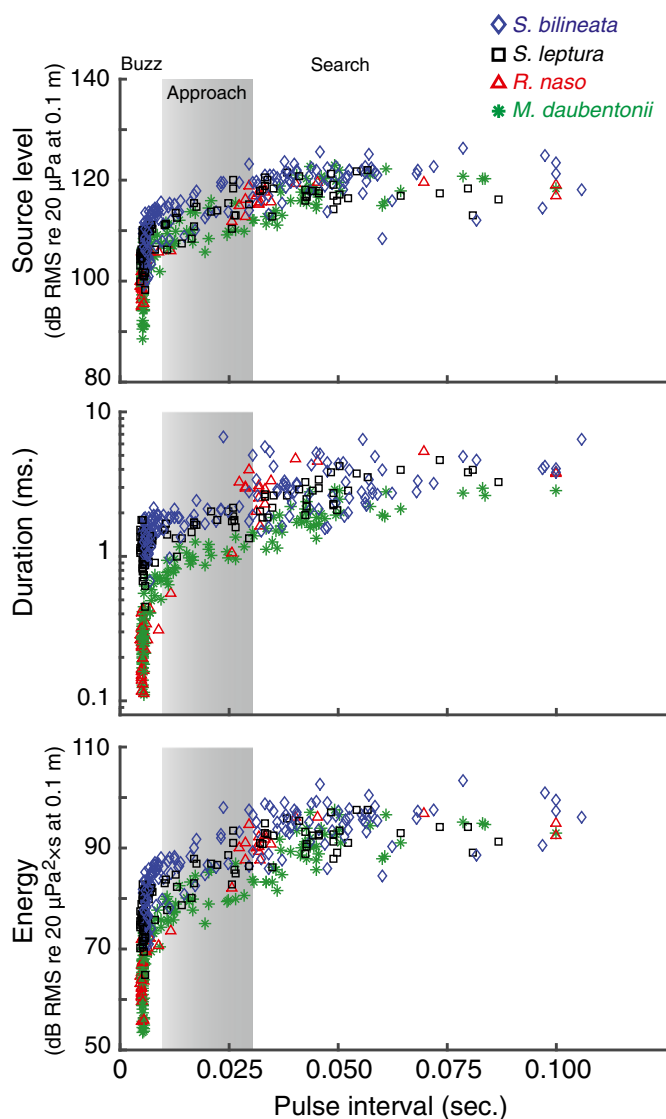


Fig. 2. Call parameters during prey capture. Measured SL, duration, and energy as a function of PI (time from call onset to call onset), with indication of the search, approach, and buzz phases for all species in the study.

significant difference in both the approach and buzz phases [0.7 dB ($P = 0.03$) and 0.4 dB ($P = 0.01$), respectively, which is biologically insignificant]. *R. naso*, however, clearly broadens the beam in the buzz phase ($P < 0.001$ compared with both approach and search). Because the directionality at 100 kHz remained the same ($P \gg 0.05$ for all comparisons at 100 kHz), mouth gape remained

constant, and the change in directionality is thus achieved solely by lowering the frequency of the call by approximately half an octave.

Discussion

The study shows that there is no change in emitted directionality during prey pursuit for *S. bilineata* and *S. leptura*. They change neither the emitted frequency nor the emitter size (mouth opening) during the pursuit sequence. In contrast, the results show a clear broadening of the beam during the buzz for *R. naso*, which emits frequencies that are roughly half an octave below those frequencies emitted during the search and approach. By lowering the frequency in the buzz while maintaining the same emitter size, *R. naso* increases the ratio of the wavelength relative to the emitter size to broaden the echolocation beam. Hence, *R. naso* uses the same strategy as vespertilionid bats (6).

Surprisingly, the study also shows that both *Saccopteryx* species are emitting very high SLs through the entire pursuit. The quietest calls from both species are around 100 dB (RMS re. 20 μ Pa at 0.1 m), substantially more than the output pressure of both *R. naso* and *M. daubentonii* at around 95 dB and 92 dB (RMS re. 20 μ Pa at 0.1 m), respectively. The *Saccopteryx* calls are also much longer in the last phase, which, combined with the amplitude differences, translates to 13 to 60 times more energy (energy difference $\Delta E = 11$ –18 dB) in *Saccopteryx* buzz calls than buzz calls from *R. naso* and *M. daubentonii* (Fig. 3 and Table 1). By emitting so much energy, the two *Saccopteryx* bats are ensonifying a much larger volume in space during the buzz. Fig. 6 illustrates the sound field around the bats in the search and buzz phases, comparing the two *Saccopteryx* bats (left-hand areas) with *M. daubentonii* (right-hand areas). In the search phase, the ensonified space is quite similar (Fig. 6, Left), but in the buzz phase, *S. bilineata* and *S. leptura* are still ensonifying a large volume, much larger than *M. daubentonii*, due to their high SLs and long call durations (Fig. 6, Middle). The difference is most pronounced in the forward direction, whereas the difference decreases with off-axis angle (Fig. 6, Right), because the beam broadening in vespertilionids causes more of the (reduced) energy to spread to the side. The figure suggests that the two *Saccopteryx* species achieve a broad acoustic field of view in the terminal phase by “brute force.” They ensonify their periphery with as much, or more, energy than the vespertilionids, which is likely to give the same detection probability for prey at off-axis angles as for vespertilionids, but at the expense of using much more energy.

Using more energy to achieve the same peripheral “vision” is not the only cost of the *Saccopteryx* strategy. It may also increase clutter load. Achieving a broad peripheral acoustic field of “view” by intensifying energy output will ensonify a much larger volume, and thus generate stronger echoes (Fig. 7), also from objects behind the prey, potentially masking prey echoes. The vespertilionid strategy to lower the energy but simultaneously ensonifying off-axis objects by broadening the beam, maintains their peripheral “view” but reduces echoes from further along the range axis, suggesting that they obtain a much clearer echo

Table 1. Call parameters during prey capture

Call parameters	Phase	<i>S. bilineata</i>	<i>S. leptura</i>	<i>R. naso</i>	<i>M. daubentonii</i>
SL, dB re. 20 μ Pa @ 0.1 m	Search	124 (1.5) ^A	122 (0.5) ^B	120 (0.5) ^B	122 (0.5) ^B
	Buzz	102 (1.5) ^A	100 (1.5) ^A	95 (0.5) ^B	92 (2.0) ^C
Duration, ms	Search	5.5 (0.6) ^A	4.3 (0.4) ^B	5.0 (0.4) ^{A,B}	2.9 (0.1) ^C
	Buzz	1.0 (0.1) ^A	0.6 (0.1) ^B	0.1 (0.01) ^C	0.1 (0.02) ^C
Energy, dB re. 20 μ Pa ² ·s @ 0.1 m	Search	101 (1.5) ^A	97 (0.5) ^A	96 (0.5) ^{A,B}	97 (0.5) ^B
	Buzz	73 (1.5) ^A	69 (2.5) ^B	57 (2.0) ^C	55 (1.0) ^C

Measurements are the average of the 10% highest values during the search phase and the 10% lowest values during the buzz to illustrate the extremes. SDs are given in parentheses, and the letters are comparisons between the species, where different letters (A, B, and C) represent significant differences. Test and P values are given in Table S1.

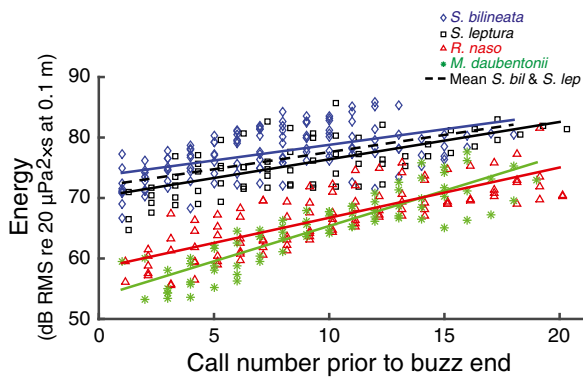


Fig. 3. Emitted call energy during buzz. Measured call energy as a function of call number before the end of the buzz. The lines are linear fits to the data points, and the dashed line represents the average for the two *Saccopteryx* bats.

scene closer to clutter than *S. bilineata* and *S. leptura* (Fig. 7). Tag studies from echolocating toothed whales (directly recording the echoes returning to the whale) clearly demonstrate how lowering the energy attenuates clutter and provides a clear “picture” of the prey echo (16). The relatively long buzz-call durations of the two *Saccopteryx* bats also indicate a large clutter load, because their clutter overlap zone (i.e., the distance between an object and clutter, in which the returning echo will overlap with the outgoing call) is 10–17 cm, whereas it is around 2 cm for *M. daubentonii* (and *R. naso*).

R. naso appears unique among the emballonurids, not only because it lowers the frequency and intensity in the buzz but also because its search calls are of unusually high frequency (14). However, compared with the two big *Noctilio* species [*Noctilio leporinus* at 55 kHz and *Noctilio albiventris* at 70 kHz (17)] that also hunt while flying very close to the water surface, the frequency that *R. naso* emits is less extreme and may suggest a general adaptation to the trawling strategy. The water surface reflects most energy away from the bats, particularly when searching for prey with a narrow sonar beam (18). High frequencies increase directionality and spatial resolution (i.e., higher frequencies reflect more efficiently off smaller objects), which may explain why the calls of all trawling bats contain high energy at high frequencies. However, in the final phase, where the bats are directing their beam toward both prey and the reflective water surface, it may be necessary for them to broaden the beam and lower their output substantially to maintain peripheral awareness while

discriminating between prey and the background. Thus, hunting strategy might explain why *R. naso*, but not the two *Saccopteryx* species, lowers the frequency and emits very short and low-intensity calls during the terminal phase.

Alternatively, the explanation for the high-energy output and constant beam shape of the two *Saccopteryx* species could be that their prey does not perform escape maneuvers and the open space does not require them to lower the output. Rhinolophid bats only broaden the beam when the target is moving (7), showing a much more specialized response to prey evasive maneuvers than vespertilionids. However, it seems unlikely that none of the prey insects in the many capture sequences we analyzed moved to the periphery of the sound beam (on purpose or inadvertently). Alternatively, the two *Saccopteryx* bats may be maintaining high-energy output to keep track of prey items further ahead in case the current prey item escapes. However, it would involve splitting attention between multiple targets, which is likely to reduce the chance of capturing any one prey item quite drastically (19). Thus, the results suggest that the two *Saccopteryx* bats simply cannot adjust their beam to encompass a broad but short field. Compared with vespertilionids, this lack of sophistication may result in prey sometimes escaping by being masked in clutter.

Although alternative hypotheses should be considered, we find it most likely that the high-energy output throughout the terminal phase serves to maintain the peripheral acoustic view. Thus, the results point to the critical importance of a broad acoustical field of view in the final stage of pursuit and corroborate previous findings from the very distantly related vespertilionids and rhinolophids. It is likely that further studies will confirm its ubiquitous nature in hawking and trawling bats (i.e., nongleaners, taking flying insects). So far, the results show different strategies to attain a broad acoustic field of view: a fairly simple mechanism in most emballonurids (high-energy output), a more elegant and probably more advanced approach in vespertilionids and *R. naso* (lowering the frequency), and an unknown method in the rhinolophids. Horseshoe bats and other constant-frequency bats may, due to their “acoustic fovea” with a disproportionately large part of the basilar membrane and sensory cells dedicated to a specific frequency (20), not have the freedom to adjust frequency sufficiently to broaden the beam. Because data show that they do, in fact, broaden the beam (7), whatever the mechanism, it points to the critical importance of a broad acoustic field of view in the final phase of insect capture.

It will be interesting to study more bat families to reveal if there are other mechanisms to keep the periphery within acoustic view right before capture. Like vespertilionids, many molossid bats lower the frequency in the buzz (21–23), which may be an example of convergent evolution. Beam width has never been determined

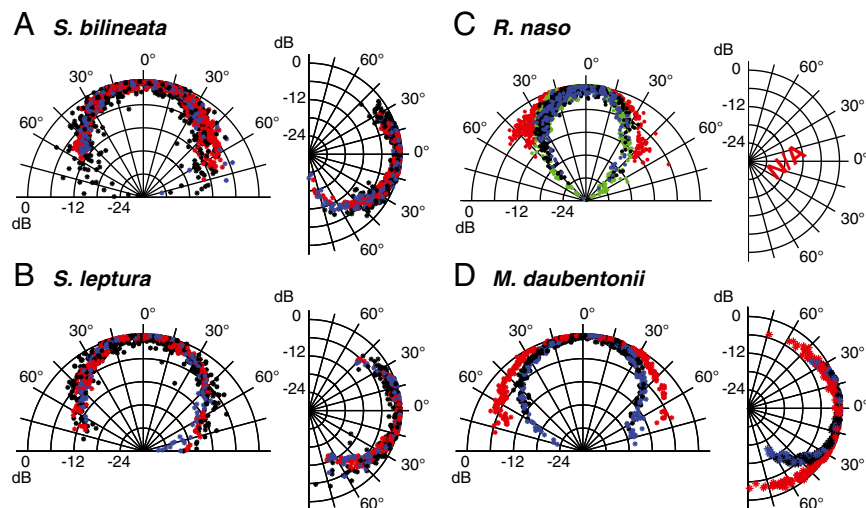


Fig. 4. Measured horizontal and vertical directionality. Measured beam patterns are color-coded by phase: search (black), approach (blue), and buzz (red) phases. (A) *S. bilineata* measured at 44 kHz. (B) *S. leptura* measured at 52 kHz. (C) *R. naso* measured at 100 kHz in search and approach, at 67 kHz in the buzz, and additionally at 100 kHz in the buzz (green). (D) *M. daubentonii* measured at 55 kHz in the search and approach and at 27.5 kHz in the buzz.

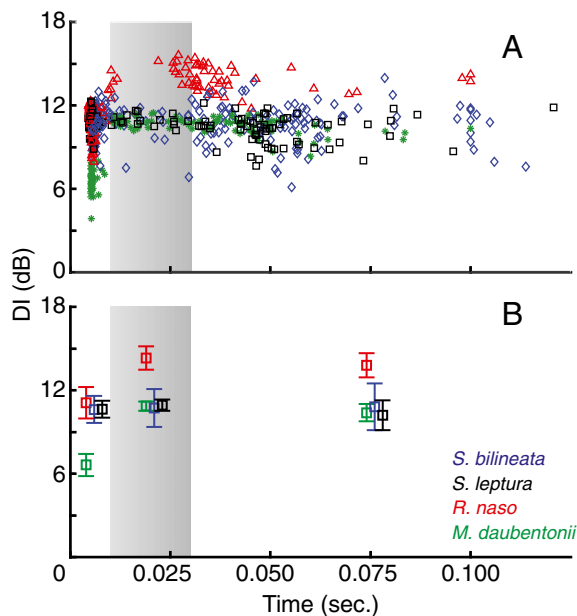


Fig. 5. Directivity index for pursuit sequences. (A) Calculated directivity index for each recorded call. (B) Average directivity index of each phase for each species with SDs. Measurements are taken at 44 kHz for *S. bilineata*, 52 kHz for *S. leptura*, 100 kHz (search/approach) and 67 kHz (buzz) for *R. naso*, and 55 (search/approach) and 27.5 kHz (buzz) for *M. daubentonii*. Calculations are based on a piston model fit using least squares. The directivity index compares the on-axis sound pressure with the sound pressure of an omnidirectional sound source.

in molossids, but physics dictate that a drop in frequency broadens the beam if gape size is unchanged. Nothing is known about beam width adjustments during pursuit in other nose and mouth emitters, which do not lower the frequency [e.g., the trawling insectivorous species *M. macrophyllum* (Phyllostomidae) and *N. leporinus* and *N. albiventris* (Noctilionidae)]. Conversely, it is equally interesting that a few vespertilionid species studied by Schmieder et al. (24) do not decrease the frequency during the buzz. It may be related to their feeding ecology, because all of the species studied are gleaners (25). To understand the evolutionary constraints for developing the ability to broaden the echolocation beam, it is of critical importance to get more field recordings of various bat species catching prey in their natural habitat, even though it is a challenge to record the echolocation beam shape of bats moving freely in three dimensions at the correct distance, direction, and behavioral context.

Broadening the beam during the terminal phase may be a newly acquired trait in the evolutionary arms race between insects and bats, enabling bats to decrease their output enough to hunt closer to clutter, while affording them the necessary peripheral view to keep track of off-axis prey at the same time. The global radiation of vespertilionids, near-global radiation of molossid bats, and wide distribution of horseshoe bats from the southern tip of Africa to northern Europe and far eastern Asia speak for the great evolutionary success of these three families, a success that might partly rely on a more advanced echolocation system encompassing the ability to broaden the beam in the final stage of prey pursuit.

Materials and Methods

We recorded the echolocation signals from *S. bilineata* and *S. leptura* flying in the field at three different sites at the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama, in March 2012. We counted the number of individuals by visual observations while it was still light enough, by checking our sound recordings, and by continuous acoustic monitoring using a Pettersson D240X bat detector throughout the session. Where multiple individuals are reported, these bats were always observed at the same time either visually or acoustically. The setup consisted of 12 40BF GRAS

¼-inch microphones [flat frequency response from 4 Hz to 100 kHz (± 2 dB); www.gras.dk] placed in a cross-shaped array, seven on a horizontal line and three above and two below the center microphone, forming a six-microphone vertical line, all placed 0.5 m apart. In November 2013, we recorded *R. naso* hunting above the waters off the coast around Barro Colorado Island, Panama. Here, the 12-microphone setup was placed with 10 microphones on a horizontal line 0.3 m apart and one microphone placed 0.5 m above and one microphone 0.3 m below the fourth microphone. Microphones were amplified by Avisoft power modules, and the sound was digitized by an Avisoft USGH 1216 sampling at 250 kHz and stored on a laptop computer. We recorded 3-s files, 2 s pretrigger and 1 s posttrigger, triggering the recording when a feeding buzz was heard on a D240X Pettersson bat detector. The microphones were calibrated before and after each recording session with a GRAS 42 AB sound calibrator.

We localized the bats at each sound emission by triangulating the difference in arrival time on each of the 12 microphones (26). Each call on each microphone was compensated for transmission loss [atmospheric attenuation and spherical spreading loss (27)] and microphone directionality (28) by computing the impulse response of the combined loss (from 0.1–110 kHz) and filtering the recorded call by it (details are provided in ref. 29). We then calculated the RMS sound pressure using the 95% energy content of an appropriately sized time window containing the call. The window size varied according to the change in call duration: 12 ms in the search phase, 8 ms in the approach, and 4 ms in the terminal phase. The emitted energy is the intensity over time; hence, we calculated the emitted energy as follows: $SL_{RMS} + 10 \times \log_{10}$ (call duration). We calculated the beam aim of the bats by fitting a second-order polynomial to each call recorded by the microphones in the horizontal plane and the vertical plane. The peak of the polynomial was used as a proxy for beam aim, and we subsequently computed the angle at which each microphone recorded the call relative to the beam aim. Thus, we obtained a horizontal angle and a vertical angle for the beam aim. Only capture sequences where the bats approached the array within a distance of 5 m and aiming their beam within 10° of the center microphone were used for analysis. Although we could not resolve the vertical beam pattern for *R. naso*, the microphones above and below the horizontal array still allowed us to select calls where the vertical beam aim was on the array, and the same criteria were used for these recordings as for the *Saccopteryx* recordings.

We divided calls into search, approach, and buzz phases based on pulse interval (PI). Calls with a PI greater than 30 ms were classified as search, calls with a PI between 30 and 10 ms were classified as approach, and calls with a PI below 10 ms were classified as buzz. Maximum SL was calculated as the mean of the 10% loudest calls from the search phase, and minimum SL was calculated as the mean of the 10% quietest calls from the buzz phase. Energy measurements were classified and calculated likewise. The minimum and maximum values for SL, duration, and energy were compared using a Tukey–Kramer honest significant difference (HSD) test. We use the 10% highest search calls and 10% lowest buzz calls as extremes to avoid overestimations or underestimations caused by measurement uncertainties.

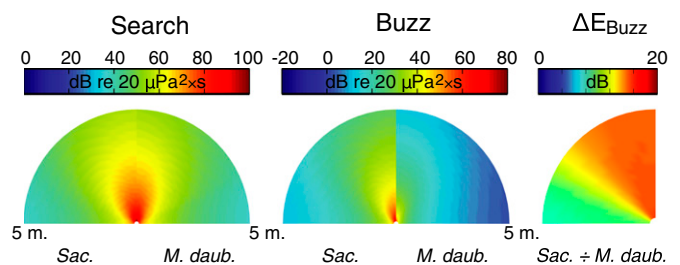


Fig. 6. Estimated sound field. Estimated sound field around a *Saccopteryx* (*Sac.*) bat (left-hand sides) and *M. daubentonii* (*M. daub.*) bat (right-hand sides) (i.e., the energy level around the bats when emitting search and buzz calls). The figure uses extremes of the measured values to compare the calls (Table 1). *Saccopteryx* is an average of the two species (i.e., 99 dB re. $20 \mu\text{Pa}^2\cdot\text{s}$ at 0.1 m in the search, 71 dB re. $20 \mu\text{Pa}^2\cdot\text{s}$ at 0.1 m in the buzz). (Left) In the search phase, the sound fields are quite similar. (Middle) In the buzz, *Saccopteryx* emits much more energy. Due to the lowering of the frequency and consequent broadening of the beam in *M. daubentonii*, the energy difference (ΔE_{buzz}) is much larger (16–18 dB) in the forward direction than off to the side (8–10 dB) (Right).

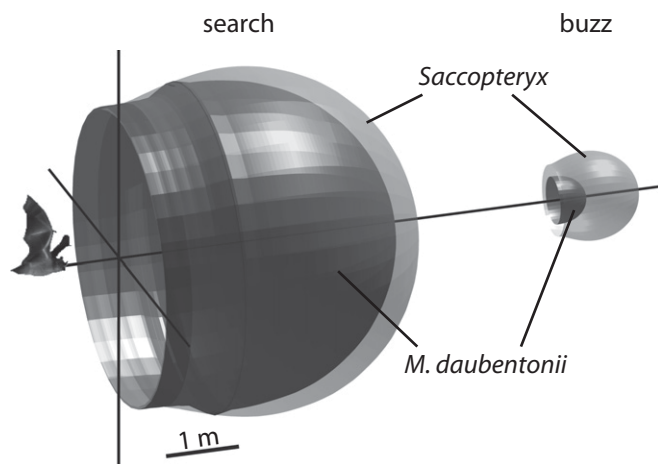


Fig. 7. Estimated prey detection area for *Saccopteryx* and *Myotis*. Estimated area in which a prey item with a target strength of -20 dB can be detected at a hearing threshold of 0 dB using the calls emitted by a hypothetical *Saccopteryx* bat (average measurements for *S. bilineata* and *S. leptura*) and by *M. daubentonii*. The search call area is a representation using the energy in the entire calls and represents the maximum detection area. The buzz call is based on the energy of the lowest frequency component (i.e., the second harmonic for *Saccopteryx*, 27 kHz for *M. daubentonii*) and represents the broadest component of calls. Both calculations are based on extreme values (i.e., average energy in the 10% loudest calls for search, average energy in the 10% quietest calls for buzz).

Directionality measurements at specific frequencies were performed by filtering the compensated calls using a third octave band-pass filter centered at the specific frequency and then measuring the RMS pressure of the 95% energy content as described previously. To quantify the directionality in each call, we fitted the piston model to the measured beam pattern of each

individual call using the angle at which each microphone recorded the call (relative to the beam aim) and the normalized compensated pressure (normalized to the highest pressure recorded for each call) by least squares (i.e., we obtained the $k \times a$ product for each recorded call). We then calculated the directivity index of a piston radiating sound with the same directionality:

$$\text{Piston model: } R_p(\theta) = \left| \frac{2 \times J_1(k \times a \times \sin(\theta))}{k \times a \times \sin(\theta)} \right|$$

$$DI_{\text{Piston model}} = 20 \times \log_{10}(k \times a),$$

where $R_p(\theta)$ is the ratio between the on-axis pressure and the pressure at a given angle θ , J_1 is a first-order Bessel function of the first kind, $k = 2\pi/\lambda$, λ is the wavelength and a is the sound emitter radius. Directionality was compared between phases (search, approach and buzz) using a Tukey–Kramer HSD test.

The sound field estimation for Fig. 6 was done by first compensating an on-axis call by filtering it with the impulse response of its transmission loss and microphone directionality. Next, we filtered the compensated call by the frequency response at intervals of 1° using measured directionality values at individual frequencies (44 kHz, 66 kHz, and 88 kHz for *S. bilineata*; from 27.5 – 110 kHz in one-third octave steps for *M. daubentonii*). We interpolated the measured directionality in 1 -kHz steps using the piston model and accounted for the change in relative piston size with frequency by interpolating fitted piston sizes at the before-mentioned frequencies using cubic interpolation. Finally, we applied the transmission loss out to 5 m in 0.1 -m steps. We used extremes of the measured values to compare the calls (i.e., maximum and minimum energy in the search and buzz, respectively, for each species). The value used for *Saccopteryx* was an average of the two species (i.e., 99 dB re. $20 \mu\text{Pa}^2\cdot\text{s}$ at 0.1 m in the search, 71 dB re. $20 \mu\text{Pa}^2\cdot\text{s}$ at 0.1 m in the buzz).

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