

Convergent acoustic field of view in echolocating bats

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Most echolocating bats exhibit a strong correlation between body size and the frequency of maximum energy in their echolocation calls (peak frequency), with smaller species using signals of higher frequency than larger ones^{1,2}. Size–signal allometry or acoustic detection constraints imposed on wavelength by preferred prey size have been used to explain this relationship^{1,3}. Here we propose the hypothesis that smaller bats emit higher frequencies to achieve directional sonar beams, and that variable beam width is critical for bats. Shorter wavelengths relative to the size of the emitter translate into more directional sound beams⁴. Therefore, bats that emit their calls through their mouths should show a relationship between mouth size and wavelength, driving smaller bats to signals of higher frequency. We found that in a flight room mimicking a closed habitat, six aerial hawking vespertilionid species (ranging in size from 4 to 21 g, ref. 5) produced sonar beams of extraordinarily similar shape and volume. Each species had a directivity index of 11 ± 1 dB (a half-amplitude angle of approximately 37°) and an on-axis sound level of 108 ± 4 dB sound pressure level referenced to $20 \mu\text{Pa}$ root mean square at 10 cm. Thus all bats adapted their calls to achieve similar acoustic fields of view. We propose that the necessity for high directionality has been a key constraint on the evolution of echolocation, which explains the relationship between bat size and echolocation call frequency. Our results suggest that echolocation is a dynamic system that allows different species, regardless of their body size, to converge on optimal fields of view in response to habitat and task.

For echolocating bats, peak frequency in echolocation calls is negatively related to body size, a trend attributed to allometry^{1,2}. However, similarly sized birds, anurans and most mammals use much lower frequencies for communication^{6,7}, so allometry does not adequately explain why bats use such high frequencies for echolocation. Indeed, atmospheric attenuation⁸ increases rapidly with frequency, and echolocation range is much shorter than it would be at lower frequencies⁹. Thus, there must be some functional explanation why bats, especially smaller species, use such high-frequency sonar signals.

One hypothesis proposes that because small bats hunt small prey they use wavelengths short enough to be effectively reflected from their smallest quarry. However, this does not adequately explain bats' high-frequency calls, as it presumes that strong echoes will only be reflected from objects with diameters equal to or greater than the wavelength, which is not true. To reflect sound efficiently, the radius, a , of an object relative to the wavelength, λ , of the impinging sound has to fulfil $2\pi a/\lambda > 1$. Thus the effective diameter of the object only has to be greater than approximately $\lambda/3$ (ref. 10). Consequently, a 6-mm-diameter insect will reflect echoes efficiently at 20 kHz, which agrees well with data showing that even small insects (4–5 mm) reflect strong echoes down to 20 kHz¹¹. Diet analysis also reveals that many bats take prey with wing lengths much shorter than the wavelength of their sonar calls³.

We propose a new hypothesis to explain bat size–signal allometry. Specifically, that smaller bats are constrained to higher frequencies to achieve a sufficiently directional beam, because sound beams broaden with decreasing emitter size (Fig. 1). A directional sonar beam is critical for echolocators, focusing energy in a forward-directed cone and thus

minimizing off-axis echoes and increasing on-axis intensity and therefore range^{4,6,12}.

For visual vertebrates, fields of view (FOV) depends on skull design and is relatively fixed¹³. For echolocators, acoustic FOV is the volume ensonified sufficiently to generate detectable echoes^{12,14,15}. From FOV bats build and update their auditory world¹⁶. Bats can adapt FOV (beam range and width) dynamically by changing: (1) call energy (range); (2) call frequency by laryngeal control (width); and (3) emitter size by gape control (width). Hence, the acoustic FOV of most bats should be more flexible than visual FOV and directionality an integral component of echolocation call design. In closed habitat, where range is not crucial, a broader beam provides a wider FOV, enhancing peripheral object detection. We predict that morphologically similar bats orienting in the same habitat will produce sonar signals of uniform beam shape, converging on an optimal FOV.

Vespertilionidae comprises one-third of extant bat species and exhibits pronounced negative signal frequency to body size scaling¹. We tested our predictions using six vespertilionid species of similar face and ear morphology, *Pipistrellus pygmaeus*, *Myotis daubentonii*, *Vesperilio murinus*, *Myotis dasycneme*, *Eptesicus serotinus* and *Nyctalus noctula*, that range in size from 4 to 21 g and produce calls over open field with peak frequencies of 20–55 kHz (Supplementary Table 1). We used a

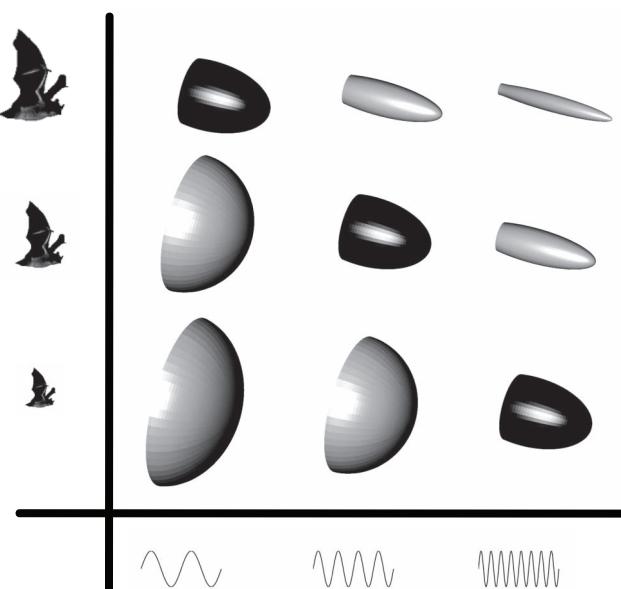


Figure 1 | Sonar beam width decreases as emitter (bat) size increases relative to wavelength. The beam width cartoons (three-dimensional figures) illustrate that for constant energy and emitter size, an increase in frequency (left to right), that is decrease in wavelength, focuses the energy in a sonar beam, to become narrower but longer, which at short distances counteracts the decrease in sonar range due to increased atmospheric attenuation at higher frequencies. The smaller the bat, the smaller is its emitter (mouth) size, and thus the broader its beam for constant frequency. Hence the smaller the bat, the higher the frequency required to maintain directionality of the biosonar beam.

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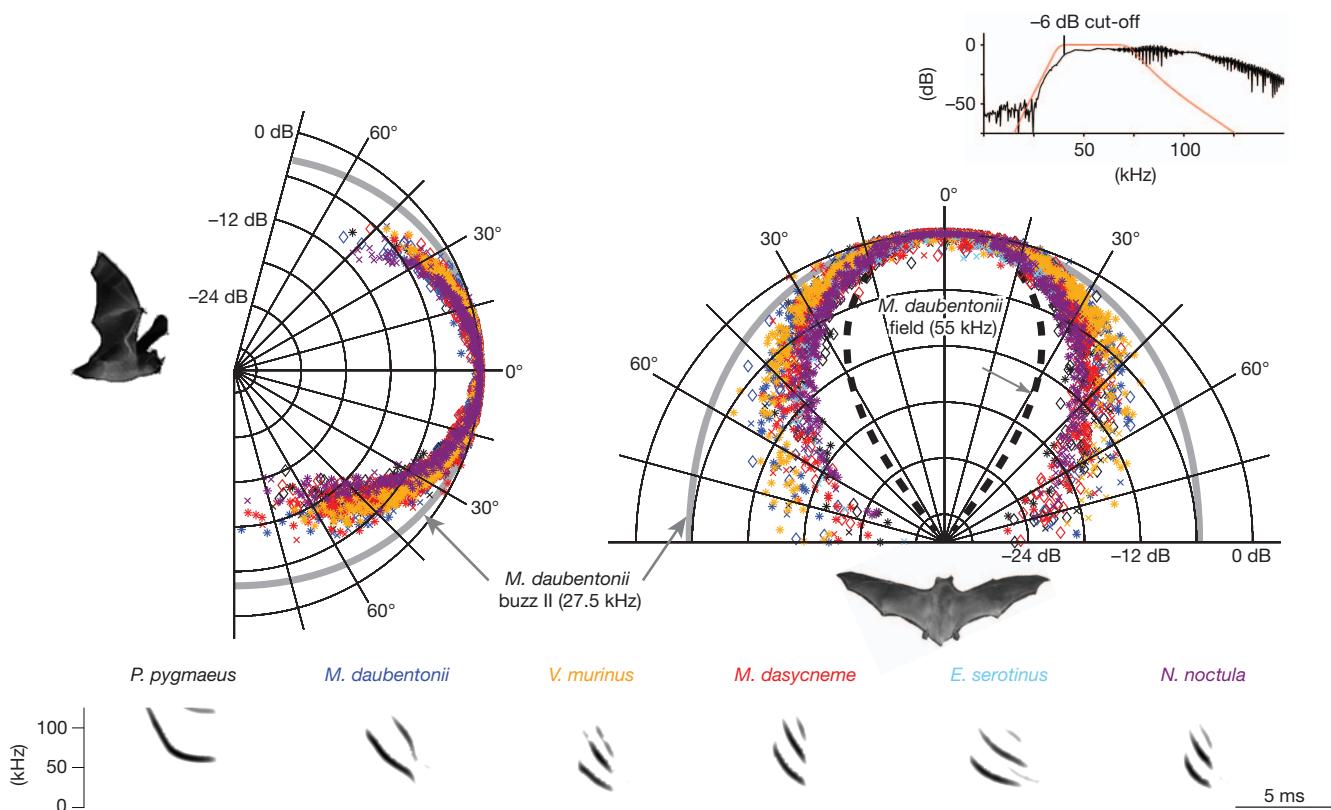


Figure 2 | Vertical and horizontal directionality in six species of vespertilionid bats. Vertical (left) and horizontal (right) directionality for *P. pygmaeus* (half-amplitude angle (HA) = 36°), *M. daubentonii* (HA = 40°), *V. murinus* (HA = 37°), *M. dasycneme* (HA = 40°), *E. serotinus* (HA = 34°) and *N. noctula* (HA = 34°). Marker colour corresponds to font colour of each species' name. Dashed black line indicates the much narrower directionality of

multi-microphone array to determine sonar beam directionality as bats oriented in a large, screened flight room, and estimated their acoustic emitter size using the piston model¹:

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

where $R_p(\theta)$ is the ratio between the pressure on-axis and at a given angle θ , J_1 is a first-order Bessel function of the first kind, $k = 2\pi/\lambda$, λ is wavelength, and a is piston radius.

We measured directionality over a full octave band starting at -6 dB down from peak (Fig. 2). All bats emitted calls with similar beam widths. Half-amplitude angles were $37 \pm 3^\circ$ (Fig. 2). Call intensities also converged across species, 108 ± 4 dB root mean square sound pressure level at 10 cm (Supplementary Table 1). To quantify measured beam patterns we computed the directivity index of each call (Fig. 3). The directivity index (DI) compares on-axis sound pressure with the sound pressure of an omnidirectional emitter producing a signal of equal energy. Calculated DI values (10.7–12.1 dB) confirm directionality as nearly identical across species despite differences in emitter size and frequency. Maximum inter-specific DI differences of 1.4 dB (Fig. 3) are negligible under ecologically relevant conditions.

These similar DI values are striking because the range of DI values available to individual vespertilionid bats is greater than the interspecific variation we observed in the flight room. *M. daubentonii* emits a narrower beam, with a DI of 16 dB, by opening its mouth wider over open field¹². In the last phase of an aerial attack *M. daubentonii* and *E. serotinus* lower their call frequency an octave, emitting broader beams (DI of 6 dB)¹⁵ (Fig. 3). Our data indicate that vespertilionids actively control directionality, adjusting emitter size and frequency, to converge on the same beam width. In closed habitats like our flight room, sonar

M. daubentonii when flying in open field, whereas grey lines in both plots indicate the broad directionality *M. daubentonii* uses in the terminal phase of the prey pursuit. The bottom panel shows spectrograms of the calls emitted in the flight room by the six species in order of size from left to right. The inset in the top right corner shows a spectrum of a *M. daubentonii* call indicating the one octave band-pass filter starting at the -6 dB low-frequency cut-off.

range is not an issue and a broader beam provides peripheral information optimal to this habitat and task. Conversely, increasing range takes precedence while over open field, where, as demonstrated for *M.*

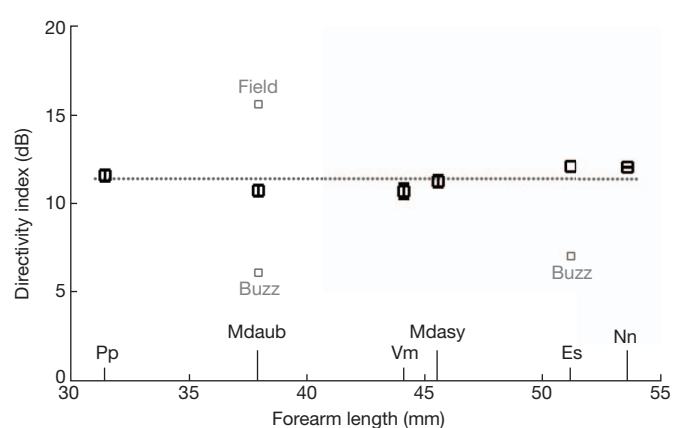


Figure 3 | Directivity index for six species of vespertilionid bats with forearm lengths ranging from 32 to 54 mm. Directivity indices (DI) (\pm s.d.) calculated from best fit of the piston model for total energy of the first harmonic (1 octave filter, see Fig. 2) of each species' echolocation call ($n = 1–3$ per species). DI compares the on-axis sound pressure with that of an omnidirectional emitter producing a signal of the same total energy that is DI = 0 dB. The larger the DI, the higher the directionality. *M. daubentonii* emits more directional search calls in the field with DI of 16 dB ('field'). *M. daubentonii* and *E. serotinus* emit broader beams with directivity indices of 6 dB in the last phase of the pursuit, the buzz II ('buzz'). The dotted line represents the mean of the DI values.

*daubentonii*¹², vespertilionid bats should emit more directional beams. Indeed, larger bats emit lower peak frequencies in open field, increasing range; in closed habitat, bandwidth is increased to include higher frequencies, enhancing resolution and temporal accuracy¹⁷. The two smallest species, particularly *P. pygmaeus*, increased peak frequency only slightly in the flight room, suggesting that, when orienting, smaller species regulate directionality almost exclusively by adjusting emitter size (Fig. 4).

To relate our acoustic models to actual species-specific mouth sizes (maximum gape) we measured upper and lower jaw length (craniomandibular joint to front teeth) and the ratio between distance from the craniomandibular joint to the origin (A) and insertion (B) of the superficial masseter (Fig. 4). The longer A is relative to B, the larger the maximal gape angle¹⁸. Assuming that inter-specific differences in A/B relate directly to differences in gape angle, we estimated gape height using a reported gape angle of 90° for *M. lucifugus*¹⁹ and a measured A/B of 2.1. We used upper jaw width at the second incisors and third molars to estimate species-specific differences in maximum gape width (Supplementary Table 1).

To verify emitter size estimates from acoustic data, we compared them to actual measured data on mouth opening. Flying *M. daubentonii* had distances between the upper and lower lip of 5–8 mm (Supplementary Fig. 1), closely matching acoustic data (Fig. 4 and Supplementary Table 1). Subsequently, we compared emitter size estimates and morphometric measures and also compared these data to acoustic data at the species-level and using independent contrasts²⁰ (see Methods for further details).

Maximum gape height and width from skull measurements were comparable, but always larger than vertical and horizontal emitter size based on the piston model, suggesting that bats did not open their mouths to the maximum (Fig. 4). Gape estimates based on skull measures better predicted open space peak frequency than body mass

(Supplementary Table 2). Similarly, emitter size estimates fitted well with second incisor distances (Supplementary Table 2). Forearm length correlated with open space peak frequency and maximum estimated gape height and width (Fig. 4 and Supplementary Table 2), as predicted by allometry and flight speed. Relationships between maximum estimated gape size and differences between open space and flight room frequencies also suggest that larger bats were using less than maximum gape in the flight room (Fig. 4 and Supplementary Tables 1 and 2).

We found that when orienting in the same context, six species of vespertilionid bats produce sonar beams with ~37° half-amplitude angles despite species-specific differences in frequency and emitter size. Over open field, larger, faster flying bats require longer detection ranges than smaller slower species to equally sample the distance they travel between calls (Supplementary Table 1). Greater range favours lower frequencies because of reduced transmission loss through atmospheric attenuation⁹. If larger bats lower peak frequency proportionally more than smaller bats, they must open their mouths wider to maintain beam width.

We propose that the requirement for a directional beam has driven the high frequencies of bat echolocation calls. Narrowing the beam focuses its energy and partially compensates for increased attenuation at higher frequencies, such that short ranges are not decreased for a given energy output (Supplementary Fig. 2). In the field, flight speed and call duration are proportional to bat size^{21–23}; in our flight room all species flew at roughly the same speed (relative to the range for open field) and used similar call intensities and durations, with no clear correlation to bat size (Supplementary Table 1). Taking into account features defining the spatial filter formed by the sonar beam (call duration, intensity, beam width and flight speed), the six species sampled almost identical volumes. For open space, flight speed was positively related to intensity and negatively related to frequency (Supplementary Table 2) suggesting FOV is adjusted such that larger, faster bats monitor greater distances than smaller, slower bats.

Our results support our prediction that sonar beam width and acoustic FOV is dynamically controlled to best monitor a particular environment. We believe that the high frequencies emitted by bats are largely dictated by FOV, which acts as an evolutionary constraint on echolocation call design²⁴. The receiving side, that is directional hearing, will also influence the bat's auditory perception²⁵, but the fact that bats adjust the beam to be narrower in open field¹² and broader in the last phase of pursuit¹⁵ demonstrates that directionality on the receiving side does not diminish the importance of the outgoing acoustic FOV. Smaller bats typically have shorter, more gracile jaws and skulls and therefore smaller maximum emitter sizes. This forces smaller bats to use high echolocation call frequencies not because of preferred prey size or body size per se, but to obtain a directional beam over open field. The lack of correlation between bat size and signal frequency in phyllostomid bats¹ is consistent with such a view. Phyllostomids are nostril-emitting echolocators and sonar beam width depends on noseleaf dimensions, which do not scale with body size. Consequently, phyllostomids are not under the constraints resulting in size-frequency scaling in mouth-emitting species. Overall, our results depict bat echolocation as not only a viable substitute for vision under conditions of uncertain lighting, but as having unique advantages owing to flexible control of field of view.

METHODS SUMMARY

We recorded one *Eptesicus serotinus*, three *Myotis dasycneme*, three *M. daubentonii*, two *Nyctalus noctula*, three *Pipistrellus pygmaeus* and two *Vespertilio murinus* as they oriented in a 7 × 4.8 × 2.5 m flight room. Calls were recorded with twelve 0.25 inch 40BF G.R.A.S. microphones, amplified by 12 AA G.R.A.S. amplifiers, and sampled at 350 kHz per channel by an Avisoft 1216 Ultrasound Gate. Seven microphones were positioned horizontally 50 cm apart and five were positioned vertically 40 cm apart (two above and three below the central horizontal microphone).

We localized bats at each call using microphone arrival-time differences, compensating for transmission loss (spherical-spreading loss, atmospheric attenuation⁸

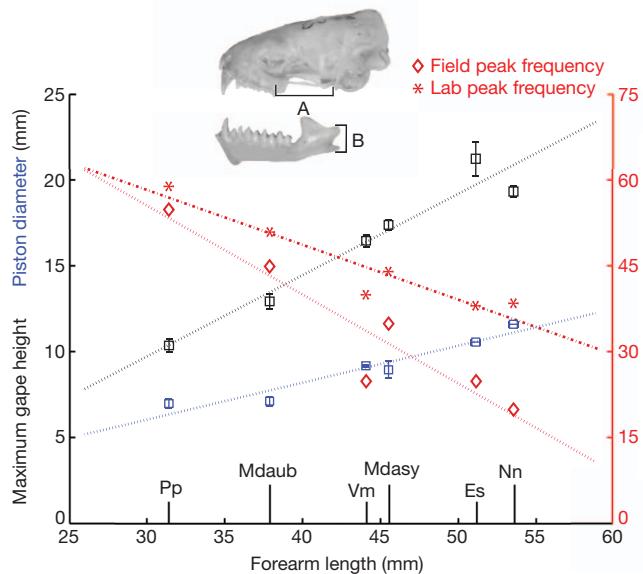


Figure 4 | Gape size estimated from skulls and from the piston model. From dry museum specimens we measured the distance from the craniomandibular joint to both the origin (A) and the insertion (B) of the superficial masseter muscle. The ratio between A and B relates directly to gape angle and was used together with upper and lower jaw length to estimate maximum vertical gape opening (black squares; see Methods). We also estimated gape diameter from the acoustic data using the piston model (blue squares). Gape size based on sonar sound beams were comparable, but always below maximum gape size based on skull metrics, indicating that the bats did not open their mouths to the maximum gape opening when flying in the flight room. Peak frequencies of echolocation calls in the flight room (red asterisks) were always higher than typical peak frequencies of the same species flying in the field (red diamonds).

and angle on microphones²⁶) by filtering the recorded signal by the impulse response of transmission loss. We filtered each call using a one-octave sixth order band-pass filter (ANSI-S1.1-1986-Standard) starting at the -6 dB low-frequency cut-off (Fig. 2 and Supplementary Table 1), which weighs directionality according to call energy distribution. We also calculated maximum beam width at minimum frequency (-6 dB low-frequency cut-off) and found similar directionality indices (8.9–10.4 dB). Root mean squared pressure of each compensated signal calculated for 95% energy content of 7.5 ms inclusive segments.

Beam aim was calculated in azimuth and elevation, using calls on-axis with the centre microphone. We fitted the piston model to emission pattern extracting equivalent piston radius, a , for each call.

We took gape heights for two flying *M. daubentonii* from the open-access repository <http://www.ChiRoPing.org/data/index>. Bats were video recorded at 500 frames per second and vertical gape heights measured. Eight flights per individual were analysed (Supplementary Fig. 1).

Skull photos ($n = 4$ –7 per species) were exported to Image J v.1.38x, measurements made as described in ref. 18. We estimated gape height as:

$$\text{Gape height}_{\text{species}} = \sqrt{a^2 + b^2 - 2 \times a \times b \times \cos \left(90^\circ \times \frac{\frac{A}{B_{\text{species}}}}{\frac{A}{B_{\text{lucifugus}}}} \right)}$$

a is upper jaw length, b lower jaw length, and A/B the ratio between distance from craniomandibular joint to origin and insertion of the superficial masseter (Fig. 4). Forearm measurements were taken from wet specimens ($n = 10$ per species).

Phylogenetically independent contrasts were generated using combined molecular phylogenies^{27–29}, actual branch lengths and the Crunch procedure (CAIC v.2.6.9, ref. 20).

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Supplementary Information is available in the online version of the paper.

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Author Contributions L.J. was responsible for conducting the experiments and programming. All authors contributed to data analyses and the writing of the manuscript.

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