Directionality of nose-emitted echolocation calls from bats without a nose-leaf (*Plecotus auritus*)

Lasse Jakobsen[1]*, John Hallam[2], Cynthia F. Moss[3] & Anders Hedenström[4]

1 Centre for BioRobotics, Dept. Biology, University of Southern Denmark, Denmark

2 Centre for BioRobotics, Maersk McKinney Moller Institute, University of Southern Denmark, Denmark

3 Johns Hopkins University, Baltimore, USA

4 Centre for animal movement research, Dept. Biology, Lund University, Sweden

* Corresponding author: lasse@biology.sdu.dk

Summary statement:

Nose-emitting bats without an obvious means of emitting a narrow bio-sonar beam still emit a highly directional beam, potentially by emitting sound through the mouth as well as the nostrils.

Journal of Experimental Biology • Accepted manuscript

Abstract

All echolocating bats and whales measured to date emit a directional bio-sonar beam that affords them a number of advantages over an omni-directional beam, i.e. reduced clutter, increased source level and inherent directional information. In this study we investigated the importance of a directional sound emission for navigation through echolocation by measuring the sonar beam of brown long-eared bats, *Plecotus auritus*. *P. auritus* emits sound through the nostrils but has no external appendages to readily facility a directional sound emission as found in most nose emitters. The study shows that *P. auritus*, despite the lack of an external focusing apparatus, emits a directional echolocation beam (Directivity index = 13 dB) and that the beam is more directional vertically (-6 dB angle at 22°) than horizontally (-6dB angle at 35°). Using a simple numerical model we find that the recorded emission pattern is achievable if *P. auritus* emits sound through the nostrils as well as the mouth. The study thus supports the hypothesis that a directional echolocation beam is important for perception through echolocation and we propose that animals with similarly un-directional emitter characteristics may facilitate a directional sound emission by emitting sound both through the nostrils and the mouth.

Introduction

Organisms throughout the animal kingdom rely on acoustic signals for a wide range of survival behaviours, including communication, territorial defence, predator evasion, and navigation (Bradbury and Vehrencamp, 2011). Acoustically guided behaviours are robust under all light conditions, but are also constrained by the transmission properties of sound (Wiley and Richards, 1978). Most bats use echolocation to forage and navigate by emitting high frequency (short wavelength) sound pulses and localizing objects in their surroundings from information carried by the returning echoes; the emission and propagation of the echolocation signals thus play a crucial role in how bats perceive their surroundings. Signal energy, frequency and directionality define the active space of bat sonar (in combination with the bats hearing threshold and ambient noise levels), i.e. the volume of space over which echoes from objects are received and processed by the animal. Bats readily adjust sonar signal parameters to suit a given environmental or behavioural context (Jensen and Miller, 1999, Surlykke and Moss, 2000). All bats investigated to date emit sound directionally, that is, sound pressure is highest in front of the bat and the pressure attenuates progressively at increasing off-axis angles (Jakobsen et al., 2013a). The directional emission likely carries a number of advantages for bats; it acts as a spatial filter, reducing echo returns from the periphery and behind the bat, and hence limiting the amount of sensory information that the animal must process. A directional sound beam also adds inherent spatial information, i.e. returning echoes probably originate from the forward direction, and it increases the source-level of the calls by focusing the sound energy in a narrower cone affording bats a longer detection range (Hartley and Suthers, 1987).

The directionality of any given sound emitter depends on the relationship between the size of the emitter and the sound frequency emitted (Kinsler et al., 2000); a small emitter is less directional than a large emitter, and an emitter of a given size is less directional when radiating low frequencies than high frequencies. The majority of bats emit sound through the open mouth, and the directionality of their emission is probably dictated by the frequency of the emitted call and the size of the open mouth (Strother and Mogus, 1970). However, of the approximately 1000 echolocating bat species, around 300 emit sound through the nostrils, often referred to as "nose-emitting." Most prominent amongst the nose-emitters are the Phyllostomidae, Rhinolophidae and Hipposideridae, accounting for more than 90% of all known nose-emitting species (Pedersen, 1993, Eick et al., 2005). A common feature for nose emitting bats is a prominent nasal structure thought to be closely

associated with sound emission from the nostrils. Phyllostomid bats have prominent nose-leaves, consisting of a lower part immediately surrounding the nostrils and a pronounced lancet extending dorsally, while rhinolophids have a complex horseshoe-like structure surrounding the nostrils (Hartley and Suthers, 1987, Schnitzler and Grinnell, 1977).

Investigations into the function of the phyllostomid nose-leaf show that it probably focuses the sonar beam in the vertical plane, accounting for much of the observed vertical directionality (Hartley and Suthers, 1987, Vanderelst et al., 2010). This is also inherently logical if the nostrils are viewed as two closely spaced small sound sources (Strother and Mogus, 1970). If two small emitters are placed close together, the interference pattern between the two will generate a more directional beam than either of the two sources independently, but only in the horizontal plane. The vertical directionality still depends on the size of the individual emitters and any related structure, e.g. a nose-leaf. With this in mind, and given the apparent benefits of emitting a directional sound beam, it is intriguing that nose-emitting bat species are found that do not have prominent nose structures, e.g. vespertilionid bats of the genera *Barbastella, Plecotus* and *Corynorhinus* (Pye, 1960, Griffin, 1958). We hypothesise that all echolocating bats emit a directional beam, including nose-emitting bats without apparent nose leaves. To test this hypothesis we investigated whether bats without prominent nasal structures emit directional sound in the vertical plan or if they radiate sound with limited vertical directionality. To this end we studied brown long-eared bats (*Plecotus auritus*) as they foraged by echolocation in a wind tunnel.

Methods

We trained three wild-caught *P. auritus* to capture mealworms in the wind tunnel at Lund University, Sweden (Pennycuick et al., 1997) over a period of two months. In between prey-captures, the bats would sit in the settling-chamber and fly into the measurement section when presented with an acoustic cue signalling that food was available. The wind-speed in the measurement section was set to 1.5 m/s for all trials. The mealworms were fastened to a thin carbon rod (1 mm diameter) located 0.25 m in front of a microphone array consisting of 9 GRAS 1/4" microphones (40 BF), 5 microphones on a horizontal line and 2 above and below the middle microphone, all with 0.2 m separation (figure 1). The microphones were high-pass filtered at 15 kHz and amplified by 30 dB using Avisoft power-modules and sounds were digitized at 300 kHz by a 1216H Avisoft USGH A/D converter. We recorded 3-second files, 2 seconds pre-trigger and 1

second post-trigger. Recordings were manually triggered when the bat attempted to land on the carbon rod. The microphones were calibrated before and after each recording session (full feeding of all three bats) using a B&K sound calibrator (type 4231). We also recorded each capture attempt with a Photron SA 1.1 high-speed camera at 1000 frames per second using BOSCH Aegis UFLED10-8BD IR lights (850 nm, 10°) to illuminate the bats. The study was performed in compliance with approved experimental guidelines (approved by Malmö-Lund animal ethics committee, M 33-13) and the animals were released at their capture site after the final experiment.

We calculated the location of the bats at the time of each call emission using triangulation of the differences in arrival-time of the sound at each of the 9 microphones. Given the location of the bats at each call emission, we compensated the recordings on each microphone for spherical spreading loss, atmospheric attenuation (ANSI, 1995) and the directionality of each receiving microphone (Kjær, 1982), by filtering the call with the impulse response of the combined loss (0.1-110 kHz) (Jakobsen et al., 2012). We then calculated the RMS sound pressure of the 95% energy content of a 2 ms window containing the call. We obtained the beam aim for each emission by fitting a second-order polynomial to the RMS sound pressure from each microphone in the horizontal and vertical planes using the peak of the polynomial as a proxy for beam aim. Given the beam aim and the bat's position, we calculated the angle at which each microphone recorded the call relative to the beam aim, which, combined with the measured RMS pressure, gives us the beam shape in the horizontal and vertical plane. We only used calls aimed within 10° of the center microphone to estimate beam shape. We calculated directionality both for the entire call and at the approximate peak frequencies of the 1st and 2nd harmonic (40 kHz and 65 kHz) using a third-octave filter centered at the selected frequencies (for details see Jakobsen et al. (2012))

For each bat we calculated the directivity index (DI) from the measured beam shape. The DI is a comparison of the measured beam pattern to that of an omnidirectional sound source, i.e. it is a measure of how much intensity increases along the acoustic axis as directionality increases (Møhl et al., 2003):

$$DI = 10log_{10}\left(\frac{2}{\sum_{i=1}^{N}(b_i \sin(v_i)\Delta v)}\right) \qquad (1)$$

b_i is the *i'th* value of an interpolation of the measured beam pattern, v_i is the angle (between 0 and π radians), Δv is the interval between the interpolation points and N is the number of values. We

obtained the beam interpolation by pooling the measured beam shapes, combining vertical and horizontal measurements, for each bat into 1° bins, averaging them and extrapolating out to 180° at 1° steps using simple linear extrapolation.

Finally, we modeled the beam pattern using five different approaches. I: a single sound source radiating sound as per the piston model (Strother and Mogus, 1970). II: two isotropic sound sources placed as the two nostrils (Strother and Mogus, 1970). III: two directional piston sources placed as the two nostrils. IV: three isotropic sound sources placed as the two nostrils and the mouth. V: three directional piston sources placed as the two nostrils and as the mouth this model includes the scenario where the mouth acts as an isotropic source. Models I and II have simple analytical solutions. Models III, IV and V were constructed numerically in Matlab (Mathworks, Inc.®) by calculating the phase differences between the sources, applying individual directionality to each source and summing the contribution from all sources across a half dome with 1° resolution. For each piston sound source we applied a Directivity Index (Urick, 1983):

$$DI = 20 \times \log_{10}(2 \times \pi \times a/\lambda) \qquad (2)$$

where a is the radius of the sound source and λ is the wavelength of the emitted sound, to account for the assumed difference in sound energy emitted by the different sources, i.e. larger sources emit more sound. We evaluated the goodness of fit for each model using standard R^2 statistics:

$$R^2 = 1 - SS_{res}/SS_{tot}, \qquad (3)$$

where SS_{res} is the residual sum of squares and SS_{tot} is the total sum of squares.

Model selection was based on the Akaike information criterion (AIC):

$$AIC = n \times \ln(SS_{res}/n) + 2 \times k, \qquad (4)$$

where n is the number of observations and k is the number of parameters in each model.

Results

We recorded echolocation signals in 214 insect capture sequences from three bats over five days. We selected four recordings from each individual where the bats flew on a straight line towards the prey and the majority of the emitted calls (> 50%) were aimed within 10° of the centre microphone. The video recordings showed no mouth movement connected to call emission or any visible mouth opening before the bat attempted to capture the mealworm (S1).

The bats emitted frequency-modulated calls containing most energy in the second harmonic, with peak frequency at 65 kHz (±2.9 kHz) (figure 2). The frequency content of the calls remained relatively unchanged as the bats approached the mealworm (linear regression of target distance vs. peak-frequency (p >> 0.05, for bat 1 & 2, bat 3 shows a slight decrease in peak frequency as it approaches the target, PF (kHz) = 5.2 × distance (m) + 63, R^2 = 0.15) and -15 dB bandwidth (p >> 0.05 for bat 1 & 3, bat 2 shows a slight decrease in bandwidth as it approaches the target, BW (kHz) = 5 × distance (m) + 21, R^2 = 0.36). Both call duration and source-level decreased continuously from approximately 0.4 meters until prey contact. At distances greater than 0.4 meters the bats emitted calls with an average duration of 0.8 ms (±0.05 ms) and average source-level of 79 dB (RMS at 0.1 m. re. 20 μPa.) (±0.5 dB). From 0.4 meter to contact, duration dropped continuously down to 0.4 ms (±0.05 ms) and source-level dropped continuously to 64 dB (RMS at 0.1 m. re. 20 μPa.) (±2 dB) (figure 3). The low values are calculated as the mean of the lowest 10% duration and source-level below 0.4 meters. Pulse interval gradually decreased as the bats approached the mealworm terminating at ca. 20 ms with no apparent plateau at distances great than 0.4 m as seen in call duration and source-level. Bats 2 and 3 consistently produced call groups consisting of two or three calls during the approach while bat 1 did so only rarely. Directionality, like frequency, remained unchanged during approach with a DI for the entire call (15 kHz – 110 kHz) of 12.5 dB (±0.5 dB), DI at 40 kHz of 9.5 dB (±0.5 dB) and DI at 65 kHz DI of 13 dB (±1 dB). The beam (15 kHz – 110 kHz) is more directional in the vertical plane than the horizontal plane, with vertical -6 dB angle at 22.0° (±1.5°) versus 34.5° (±4°) in the horizontal plane (one sided measure, figure 4). This pattern is also present at 65 kHz (vertical -6dB angle: 19.5° ±1.5°, horizontal -6 dB angle: 33.5° ±4°), but absent at 40 kHz (vertical -6 dB angle: 45.5° ±7.5°, horizontal -6 dB angle: 43° ±2.2°).

Fitting the five models to the emission pattern at 65 kHz yields a best fit for model V, with the nostrils as small pistons and the mouth as a point source (R^2 = 0.81 table 1, figure 5). Model V performs dramatically better than any of the other models. The second best fit is model III, the two piston model (R^2 = 0.59), and it is clear that the difference in the vertical emission pattern accounts for much of the observed differences between model V and the other four models. The two point-source model (model II) performs very poorly, because it is isotropic in the vertical plane. For model V, using three directional pistons, we found similar correlations to the parameters in table 1

when the mouth was a circular piston with a radius of 1 mm ($R^2 = 0.81$). Given that the two variations of model V perform equally well, and the bats show no visible mouth opening during echolocation, we selected the two-piston one point-source version because it is the most parsimonious model. At 40 kHz all models perform almost equally, except model II (two point-sources), again primarily due to its isotropic vertical component (figure 5, table 1).

Discussion

The study shows that brown long-eared bats emit directional echolocation calls both in the horizontal plane and the vertical plane, without any elaborate external structures connected to the nostrils, as seen in many other echolocating bats that emit sonar signals through the nostrils, a.k.a. nose-emitting bats (e.g. the pronounced lancet in phyllostomid bats). The DI of *P. auritus'* sonar beam is comparable to other vespertilionid bats (Jakobsen et al., 2013b). It is noteworthy that the directionality of the sonar beam of other vespertilionid bats is roughly the same in the horizontal and vertical planes, while the sonar beam of *P. auritus* is clearly more directional in the vertical plane. The same asymmetric directionality of the sonar beam pattern is also observed in other free flying nose-emitting bats (Brinkløv et al., 2011, Surlykke et al., 2013, Matsuta et al., 2013), but these all have elaborate nose-leaves and the vertical directionality is believed to be produced primarily by the lancet (Hartley and Suthers, 1987). It is clear that *P. auritus* is not using a similar directional mechanism, because this species lacks the nose-leaf structure of other nose-emitting bats. Instead, supported by our modelling, we propose that sound is also radiated from the mouth, and the interference pattern generated between the two nostrils and the mouth generates the observed directionality of *P. auritus* sonar signals. Our video recordings show no measurable mouth opening; hence, if sound is emitted through the mouth, the emitter size is too small to register with our video recordings, which is in line with our model predicting an isotropic source at the position of the mouth. Furthermore, Griffin (1958) observed a significant reduction in the emitted intensity of echolocation calls produced by *Corynorhinus rafinesquii* (~6 dB) when the mouth was covered with a tight layer of collodion, consistent with our hypothesis that sound is radiated from the nostrils and the mouth at the same time to generate the observed beam pattern. Further experiments are needed to determine empirically if the observed beam pattern is indeed generated by this three-source interference pattern. An obvious setup is be to repeat Griffins approach; if indeed the emitted pattern is generated by interference between sound coming from the two nostrils and the mouth, vertical directionality should diminish substantially when the mouth is covered.

It is clear that the two point-source model does not adequately explain the emission pattern from nose-emitting bats, mainly because the vertical plane is isotropic, but also because of the very large side-lobes generated if the distance between the two points exceeds half the emitted wavelength. Most sonar beam patterns of free flying nose-emitting bats measured to date are considerably more directional than the pattern generated by the two point source model at $\lambda/2$, and none of them show large side-lobes in their emission pattern (Brinkløv et al., 2011, Surlykke et al., 2013, Matsuta et al., 2013). Substituting the two isotropic sources with directional piston sources reduces the size of the side-lobes substantially, and may, as proposed by Vanderelst et al. (2010), explain the horizontal directionality measured from nose-emitting bats. Questions still remain surrounding the vertical directionality, and while it has been shown that the nose-leaf plays a key role in shaping the beam (Hartley and Suthers, 1987), there are multiple nose emitting bats with very small (e.g. bats from the genus Leptonycteris) or highly modified nose-leaves (e.g. the vampire bats and the wrinkle-faced bat, *Centurio senex*). Many phyllostomid species are known to echolocate with the mouth open (Surlykke et al., 2013; Fenton, 2013) and consequently, variations on the sound emission scheme that we propose may apply to many of these. The relatively simple model that we employ has its limitations; the equivalent piston sizes of the nostrils clearly exceeds the physical size of the actual nostrils, such that the directional characteristics are higher than what can be generated by a simple emitter of similar size. As discussed by Pedersen and Müller (2013), many plecotine bats have fleshy masses in connection with the nostrils and these may very well function to increase directionality of the nasal emissions. Future work should be directed at understanding the mechanisms influencing directionality of the emitted beam pattern from nose-emitting bats, not only the ones without nose-leaves.

In comparison with previous studies of *P. auritus*, bats in our study emitted calls with lower intensity and lower duration than previously reported. Waters and Jones (1995) measured maximum source-levels above 90 dB (peak at 0.1 m. re. 20 μPa) and durations of 2 ms. This substantial difference is probably caused by the relatively confined space in the wind tunnel and the different behavioural scenarios (prey capture versus orientation flight). Similar to Waters and Jones (1995), our results show that *P. auritus* adjust their echolocation output as they approach the target, lowering the source-level and the duration of the calls. Unlike some previous studies of *P. auritus*

and other gleaning bats, we did not observe any capture attempts in which the bats stop echolocating (Anderson and Racey, 1991, Faure and Barclay, 1994), but given the extremely low source levels emitted prior to prey capture (65 dB RMS at 0.1 m. re. 20 μPa) and the high directionality, it is easy to envision a scenario where these calls are not detected by the recording equipment.

To the best of our knowledge this is the first study of echolocation-beam directionality in a gleaning vespertilionid bat. Previously, directionality measurements of the sonar beam patterns of two species of free-flying phyllostomid gleaners (*Carollia perspicillata* & *Trachops cirrhosus*, (Brinkløv et al., 2011, Surlykke et al., 2013)) and one megadermatid gleaner (*Megaderma lyra*, (Möhres and Neuweiler, 1966)) has been measured. Both phyllostomids emit very directional echolocation beams (DI ≈ 17 dB) while *M. lyra* shows roughly the same directionality as *P. auritus* (DI = 12 dB). It has been proposed that gleaning bats emit a narrow echolocation beam to reduce the impact of clutter (Surlykke et al., 2013) and to focus the acoustic signals used by the animal's sonar receiver on a much smaller area and thus increasing the probability of detecting inconspicuous prey (Dukas, 2004, Brinkløv et al., 2011). However, the current study, in conjunction with results from *M. lyra,* indicates that a very directional echolocation beam is not needed to glean prey. Conversely, given the wind-tunnel setup, the bats were effectively chasing a prey item moving at 1.5 m/s, this may have affected their echolocation behaviour, potentially evoking the emission of a broader echolocation beam than a stationary prey would have, but given the capture behaviour of the bats (landing on the carbon rod) and the very low air speed, we believe that the sonar calls recorded in this experiment are still representative of a gleaning scenario.

As more studies on echolocation beam directionality emerge, both in bats and whales, it is becoming increasingly apparent that emitting a directional beam is a common element for all echolocators (Au, 1993, Rasmussen et al., 2004, Yovel et al., 2011, Jakobsen et al., 2013a, Wisniewska et al., 2015, Ladegaard et al., 2017). The current study emphasizes this in showing that even bats without an obvious directional emission system, i.e. nose emission without a prominent nose-leaf, broadcast a directional sound beam. Our study thus strongly supports the hypothesis that a directional echolocation beam is a key element for perception through echolocation, and we propose that bat species with similar emitter characteristics may also achieve directionality of the sonar beam through simultaneous mouth and nose emission.

Competing interests

The authors declare no competing or financial interests.

References

Anderson, M. E. and Racey, P. A. (1991). Feeding behaiour of captive brown long-eared bats, *Plecotus auritus. Animal Behaviour* **42**, 489-493.

ANSI. (1995). American national standard. Method for the calculation of the absorption of sound by the atmosphere. Standards Secretariat. Acoustical Society of America. 335 East 45th Street, NewYork, NewYork 10017.

Au, W. W. L. (1993). The Sonar of Dolphins: Springer.

Bradbury, J. W. and Vehrencamp, S. L. (2011). Principles of Animal Communication: Sinauer Associates, Inc.

Brinkløv, S., Jakobsen, L., Ratcliffe, J. M., Kalko, E. K. V. and Surlykke, A. (2011). Echolocation call intensity and directionality in flying short-tailed fruit bats, *Carollia perspicillata* (Phyllostomidae). *JASA* **129**.

Dukas, R. (2004). Causes and consequences of limited attention. *Brain Behav Evol* **63**, 197-210.

Eick, G. N., Jacobs, D. S. and Matthee, C. A. (2005). A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (chiroptera). *Mol Biol Evol* **22**, 1869-86.

Faure, P. A. and Barclay, R. M. R. (1994). Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behavior of the long-eared bat, Myotis evotis. *J.Comp.Physiol.A* **174**, 651-660.

Fenton, M. B. (2013). Questions, ideas and tools: lessons from bat echolocation. *Animal Behaviour,* **85,** 869-879.

Griffin, D. R. (1958). Listening in the dark. New York: Yale Univ. Press, 2.ed 1986 Cornell University.

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.

Jakobsen, L., Brinklov, S. and Surlykke, A. (2013a). Intensity and directionality of bat echolocation signals. *Front Physiol* **4**, 89.

Jakobsen, L., Kalko, E. and Surlykke, A. (2012). Echolocation beam shape in emballonurid bats, *Saccopteryx bilineata* and *Cormura brevirostris. Behavioral Ecology and Sociobiology* **66**, 1493-1502.

Jakobsen, L., Ratcliffe, J. M. and Surlykke, A. (2013b). Convergent acoustic field of view in echolocating bats. *Nature* **493**, 93-6.

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.

Kinsler, L. R., Frey, A. R., Coppens, A. B. and Sanders, J. V. (2000). Fundamentals of Acoustics. New York: John Wiley & Sons.

Kjær, B. (1982). Condenser microphones and microphone preamplifiers for acoustic measurements. Data Handbook. Nærum, Danmark: Brüel & Kjær.

Ladegaard, M., Jensen, F. H., Beedholm, K., da Silva, V. M. F. and Madsen, P. T. (2017). Amazon river dolphins (Inia geoffrensis) modify biosonar output level and directivity during prey interception in the wild. *J Exp Biol* **220**, 2654-2665.

Matsuta, N., Hiryu, S., Fujioka, E., Yamada, Y., Riquimaroux, H. and Watanabe, Y. (2013). Adaptive beam-width control of echolocation sounds by CF-FM bats, Rhinolophus ferrumequinum nippon, during prey-capture flight. *J Exp Biol* **216**, 1210-8.

Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A. and Lund, A. (2003). The monopulsed nature of sperm whale clicks. *JASA* **114**, 1143-1154.

Möhres, F. P. and Neuweiler, G. (1966). Die Ultraschallorientierung der Grossblatt-Fledermäuse (Chiroptera - Megadermatidae). *JCP* **53**, 195-227.

Pedersen, S. C. (1993). Cephalometric correlates of echolocation in the chiroptera. *J Morphol* **218**, 85-98.

Pedersen, S. C. & Müller, R. (2013). Nasal-Emission and Nose leaves. *In:* Adams, R. A. & Pedersen, S. C. (eds.) *Bat Evolution, Ecology, and Conservation.* New York, NY: Springer New York.

Pennycuick, C. J., Alerstam, T. and Hedenstrom, A. (1997). A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *J.exp.Biol.* **200**, 1441-1449.

Pye, J. D. (1960). A theory of echolocation by bats. *The Journal of Laryngology & Otology* **74**, 718-729.

Rasmussen, M. H., Wahlberg, M. and Miller, L. A. (2004). Estimated transmission beam pattern of clicks recorded from free-ranging white-beaked dolphins (*Lagenorhyncus albirostris*). *JASA* **116**, 1826-1831.

Schnitzler, H.-U. and Grinnell, A. D. (1977). Directional sensitivity of echolocation in the horseshoe bat, *Rhinolophus ferrumequinum*. I Directionality of sound emission. *J.Comp.Physiol.A* **116**, 51-61.

Strother, G. K. and Mogus, M. (1970). Acoustical beam patterns for bats: some theoretical considerations. *JASA* **48**, 1430-1432.

Surlykke, A., Jakobsen, L., Kalko, E. K. and Page, R. A. (2013). Echolocation intensity and directionality of perching and flying fringe-lipped bats, Trachops cirrhosus (Phyllostomidae). *Front Physiol* **4**, 143.

Surlykke, A. and Moss, C. F. (2000). Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *JASA* **108**, 2419-2429.

Urick, R. J. (1983). Principles of underwater sound. New York, NY: Peninsula Publishing.

Vanderelst, D., De Mey, F., Peremans, H., Geipel, I., Kalko, E. K. V. and Firzlaff, U. (2010). What Noseleaves Do for FM Bats Depends on Their Degree of Sensorial Specialization. *PLoS ONE* **5**, e11893 (1)-e11893 (13).

Waters, D. A. and Jones, G. (1995). Echolocation call structure and intensity in five species of insectivorous bats. *J.exp.Biol.* **198**, 475-489.

Wiley, R. H. and Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav.Ecol.Sociobiol.* **3**, 69-94.

Wisniewska, D. M., Ratcliffe, J. M., Beedholm, K., Christensen, C. B., Johnson, M., Koblitz, J. C., Wahlberg, M. and Madsen, P. T. (2015). Range-dependent flexibility in the acoustic field of view of echolocating porpoises (Phocoena phocoena). *Elife* **4**, e05651.

Yovel, Y., Falk, B., Moss, C. F. and Ulanovsky, N. (2011). Active Control of Acoustic Field-of-View in a Biosonar System. *Plos Biology* **9**, e1001150.
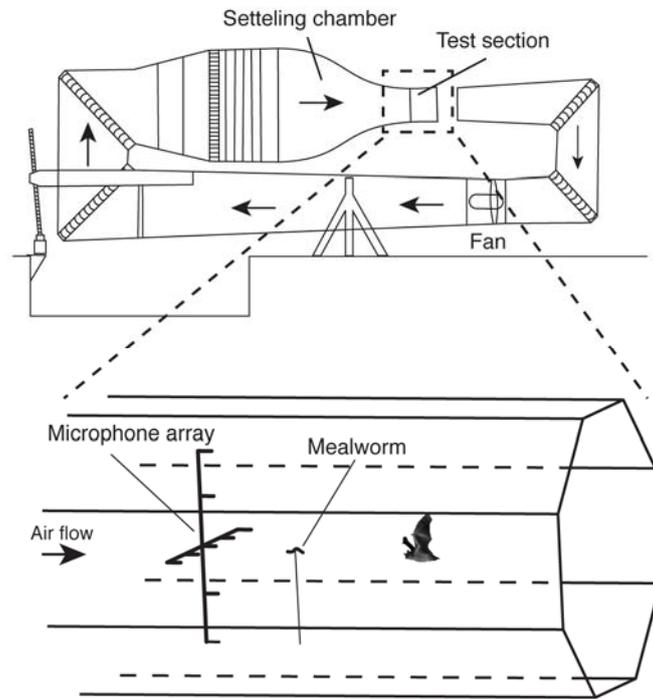
Figures

Figure 1. Experimental setup. Schematic of the wind-tunnel (adapted from Pennycuick et al., 1997) and zoom of the test section showing microphone placement and feeder positioning.
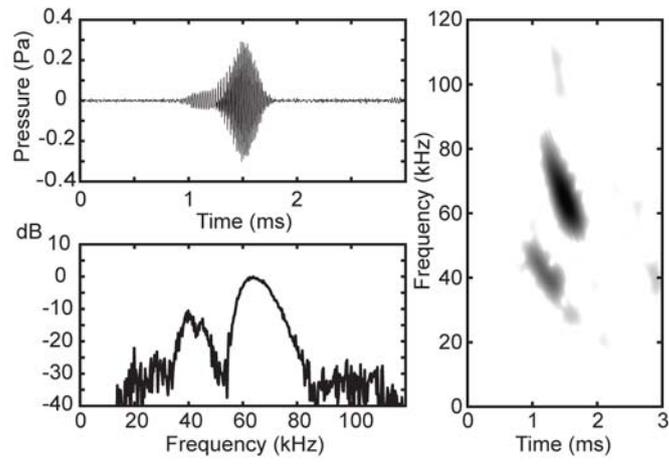
Figure 2. Call structure. Oscillogram (top left), frequency spectrum (bottom left) and spectrogram (right) of an exemplary call emitted during prey capture in the wind tunnel.
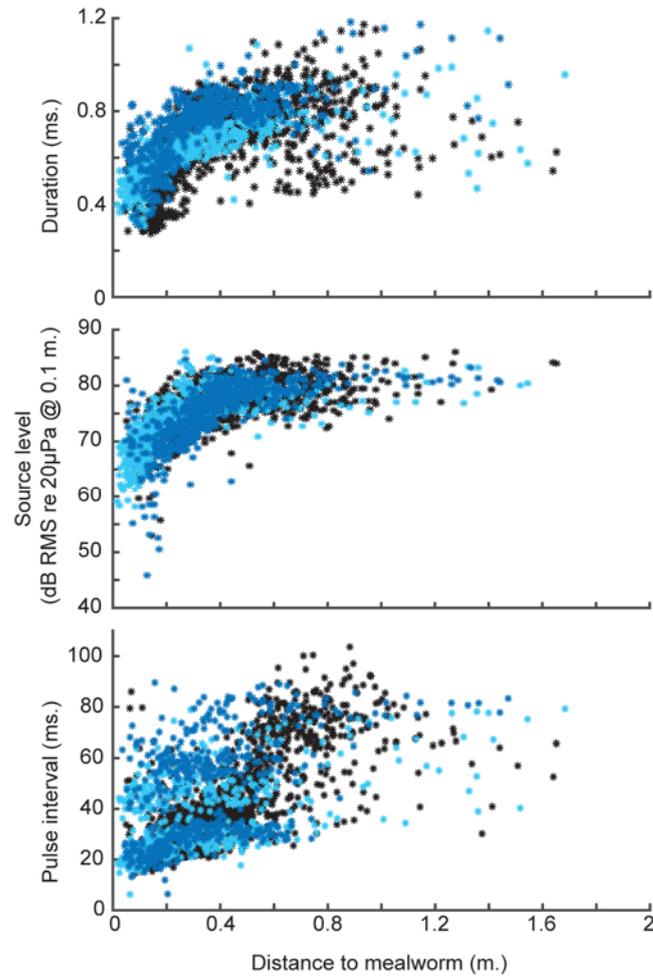
Figure 3. Prey-capture call parameters. Measured duration, Source level and pulse interval (from call start to call start) as a function of distance to prey, individuals are separated by colour: black - bat1, cyan - bat 2, blue - bat 3.
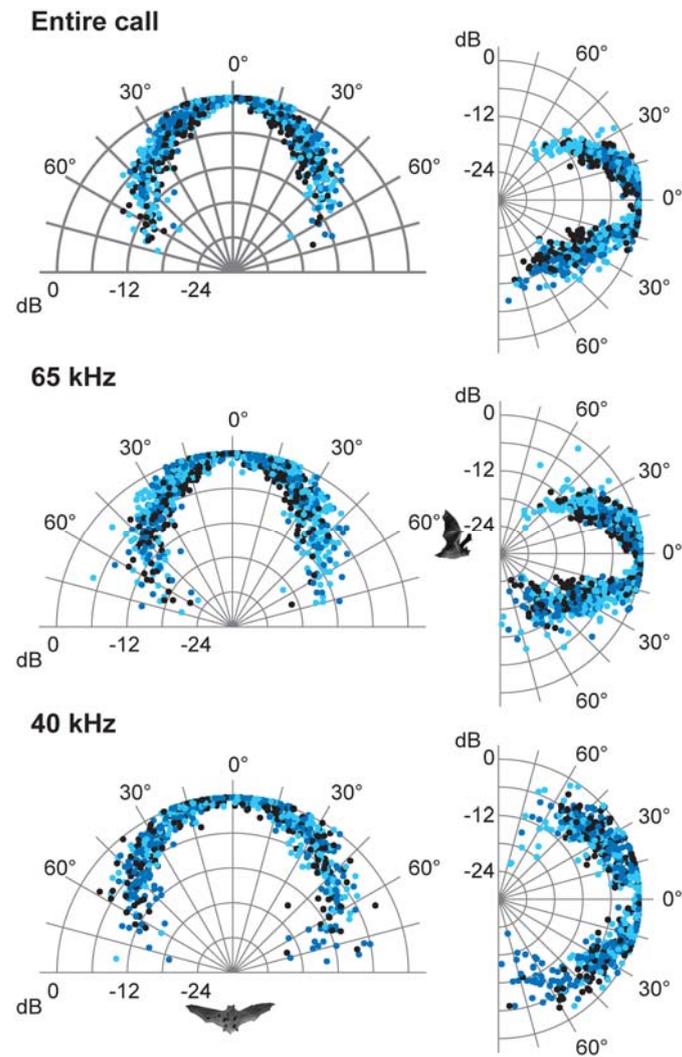
Figure 4. Measured horizontal and vertical beam pattern for the entire call (0.1 – 110 kHz), at 40 kHz and at 65 kHz, individuals are separated by colour: black - bat1, cyan - bat 2, blue - bat 3.
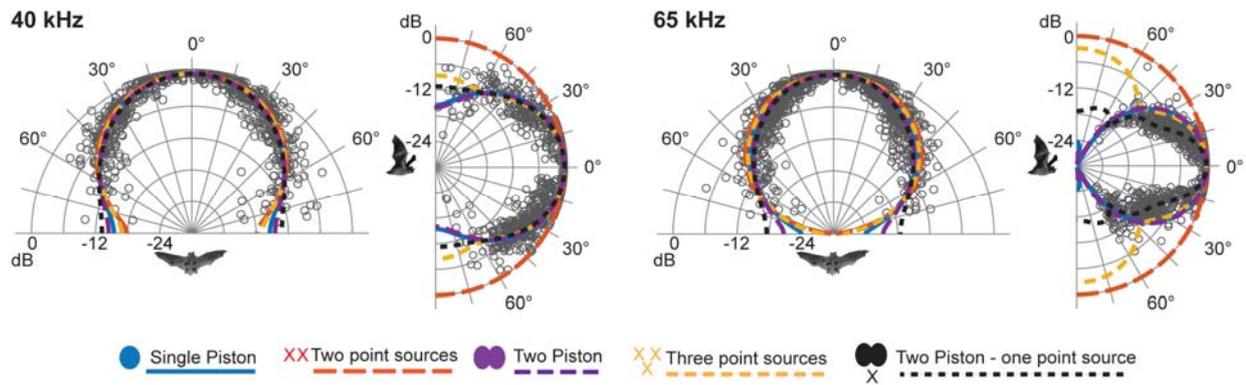
Figure 5. Modelled beam pattern fitted to measurements. Best fit of each model to the measured emission pattern at 40 kHz and 65 kHz. Individual models are colour coded as indicated and the overall model configuration is indicated with X representing a point source and a solid circle representing a piston source.

Table 1. Model fit parameters at 65 kHz and 40 kHz, 40 kHz values are given in parentheses.

Model 65 kHz (40 kHz)	R²	AIC (re. lowest value)	Parameters
Piston model	0.58 (0.61)	1631 (57)	Horizontal a = 3 mm (4.4 mm) Vertical a = 3.5 mm (4.4 mm)
Two point sources	-0.51 (-0.25)	4386 (1847)	Nostril distance = 2.6 mm (3.9 mm)
Two pistons	0.59 (0.61)	1609 (104)	Horizontal a = 2.5 mm (3.7 mm) Vertical a = 3.4 mm (4.4 mm) Nostril distance = 1.9 mm (2.6 mm)
Three point sources	0.54 (0.60)	1871 (47)	Nostril distance = 3.4 mm (5.1 mm) Mouth – nostril line distance = 3.9 mm (4.8 mm)
Two piston, one point source	0.81 (0.63)	0 (0)	Nostrils: Horizontal a = 2.6 mm (3.3 mm) Vertical a = 4.1 mm (3.0 mm) Nostril distance = 2.4 mm (4.0 mm) Mouth nostril line distance = 6.8 mm (5.0 mm)

Movie S1

Plecotus auritus flying in the windtunnel, recorded at 1000 fps and played back at 40 times reduced speed - synchronised with the audio recording.