Echolocation range and wingbeat period match in aerial-hawking bats

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Aerial-hawking bats searching the sky for prey face the problem that flight and echolocation exert independent and possibly conflicting influences on call intervals. These bats can only exploit their full echolocation range unambiguously if they emit their next call when all echoes from the preceding call would have arrived. However, not every call interval is equally available. The need to reduce the high energetic costs of echolocation forces aerial-hawking bats to couple call emission to their wingbeat. We compared the wingbeat periods of 11 aerial-hawking bat species with the delays of the last-expected echoes. Acoustic flight-path tracking was employed to measure the source levels (SLs) of echolocation calls in the field. SLs were very high, extending the known range to 133 dB peak equivalent sound pressure level. We calculated the maximum detection distances for insects, larger flying objects and background targets. Wingbeat periods were derived from call intervals. Small and medium-sized bats in fact matched their maximum detection range for insects and larger flying targets to their wingbeat period. The tendency to skip calls correlated with the species' detection range for background targets. We argue that a species' call frequency is at such a pitch that the resulting detection range matches their wingbeat period.

Keywords: echolocation; aerial-hawking bat; source level; detection range; wingbeat period

1. INTRODUCTION

Coupling call emission to wingbeat allows flying bats to produce intense echolocation signals at low cost as a by-product of flight (Heblich 1986; Speakman & Racey 1991; Wong & Waters 2001). In particular, aerial-feeding bats searching for distant prey take advantage of this by calling only once every wingbeat (Jones 1994; Kalko 1994). However, the need to minimize the high energetic costs of flight limits the range of accessible wingbeat periods (Pennycuik 1975; Norberg 1998). As an echo that arrives after the next call will be ambiguous with respect to the measured delay, the flight morphology and flight style of aerial-hawking bats determine a time window in which these bats can optimally listen for echoes. Owing to the constant propagation speed of sound in air, this also sets a window of available object distances, which we call the 'wingbeat window'.

The main tasks of echolocation—efficient foraging and successful orientation—are impaired if echoes arrive outside the wingbeat window. Unlike bats using constant-frequency (CF) calls, such as rhinolophids, the aerial-feeding bats in this study cannot detect echoes while calling as they contract their middle-ear muscles during pulse emission (Henson 1965) and accordingly miss out on all objects whose echoes arrive during their call. Echoes arriving later can be heard, yet they need to be assigned to either the first or the second call, which may result in location errors leading to unnecessary abrupt avoidance manoeuvres or the risk of collisions.

These problems are avoided if all echoes arrive within the window between calls. All insectivorous bats adopt this

strategy while approaching prey: the closer a foraging bat gets to its prey the earlier it receives the echo and the sooner it produces the next call, resulting in a characteristic 'approach phase' series of calls with gradually decreasing call intervals ending with a distinctive feeding buzz (Kalko & Schnitzler 1998). Obviously, this strategy makes sense in the presence of a target, whereas a bat that scans the empty sky must prepare for all echoes, from possible prey and from obstacles in its flight path. What call intervals might a bat prefer in this situation? To increase its foraging success it might try to maximize its detection range by producing the most intense and at the same time the lowest-pitched calls since these are least affected by absorbance (Bazley 1976; Kober & Schnitzler 1990). From experience it will know when to expect the last possible echo originating from the outer limit of its detection range. By calling after exactly that time it would gather new information without risking a call–echo overlap or call–echo assignment problems. At the same time it would not waste time by waiting in vain for further echoes.

Thus, the two perhaps most important features of a bat, its flight and echolocation, make independent and potentially conflicting demands on inter-call intervals. In a system as highly integrated as the bat, one might expect to find an optimal solution harmonizing both demands. We hypothesize that aerial-hawking bats in search flight should match their echolocation range and their wingbeat period.

We used the method of acoustic flight-path tracking (Aubauer 1994; Aubauer & Ruppert 1994) to measure source levels (SLs) of search-flight calls produced in the field by 11 aerial-feeding bat species. From these SLs we derived each species' detection range for differently sized insects and calculated their maximum detection range for flying objects and for background structures. Mean wingbeat periods were derived from call intervals. Comparing wingbeat period and detection range allowed us to judge

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whether bats were matching their wingbeat and their echolocation range and, if so, to what type of targets.

2. MATERIAL AND METHODS

Detection ranges were obtained for 11 out of the 13 aerial-hawking bat species encountered in Europe: *Pipistrellus pipistrellus* (Pp), *P. pygmaeus* (Pm), *P. kuhli* (Pk), *P. nathusii* (Pn), *Hypsugo savii* (Hs), *Nyctalus leisleri* (Nle), *N. noctula* (Nn), *N. lasiopterus* (Nla), *Eptesicus serotinus* (Es), *E. nilssoni* (En), *Vespertilio murinus* (Vm), *Tadarida teniotis* (Tt) and *Miniopterus schreibersi* (Ms). These species are low-duty cycle bats, which avoid overlap between calls and returning echoes. All bats were encountered in so-called background-cluttered situations and used the FM-QCF call type (downward frequency-modulated start and a quasi-constant-frequency end; Schnitzler & Kalko 1998). Additionally, detection ranges were calculated for *Craseonycteris thonglongyai*, a very small bat from Thailand, from published data (Surlykke *et al.* 1993) (mean call interval of 45.5 ms; SL of 115 dB peak equivalent sound pressure level (peSPL); call frequency of 73.2 kHz and at a temperature of 25 °C and a relative humidity of 40%).

Measuring the SLs of bat signals involves two steps: first, measuring the local level of the signal at a calibrated recording microphone; and, second, calculating how much the signal was attenuated before it reached this microphone. To do this the position of the bat must be known. For the first step we used microphones (Knowles BT1759 electret) of known directional sensitivity at the relevant frequency range (10° angular resolution). These microphones were calibrated in the field before and after each recording session with a 50 kHz tone (calibrated by B&K 2209, B&K 4135 without grid and B&K 4220). There was no drift in sensitivity with time, temperature or humidity. The frequency response of the microphone for the direction of call incidence was taken into account. Bat calls were sampled in the field at 500 kHz and 11 bit resolution and stored on a custom-made digital recorder. To reduce any variation caused by directionality of call emissions only calls recorded in the flight direction were included (recording microphone less than 60° below, 20° above and 40° to the side of the flight vector). In the second step, distance-related absorption was calculated using the peak frequency of the call as determined from the periodogram and the actual temperature and humidity at the microphone at the time of the call (Bazley 1976). Acoustic flight-path tracking was used to localize the bats (Aubauer 1994; Aubauer & Ruppert 1994). This method uses the different arrival times of single echolocation calls at eight microphones (Knowles BT1759) at known locations to determine the bat's position at the time of calling (figure 1). The SLs are given in dB peSPL re: 20 µPa at a reference distance of 10 cm from the bat's mouth, i.e. the value that would have been measured at a distance of 10 cm (Stapells *et al.* 1982).

Maximum detection ranges were calculated using the sonar equation (Møhl 1988)

$$DT = (SL + TLA + TLS + TS) - \text{noise term (dB)},$$

where DT is the detection threshold; TLA is the transmission loss owing to absorption; TLS is the transmission loss owing to spherical spreading and TS is the target strength. TLA and TLS are functions of distance.

The SL of the most intense echolocation call found for each species was used for calculations of detection ranges. The absorption (TLA) was calculated for the peak frequency of typi-

Figure 1. Schematic drawing of the automatic flight-path tracking equipment as used in the field. Each microphone array consisted of four microphones arranged in a symmetrical star. Two arrays were placed at known relative positions. Depending on the position of the bat its echolocation pulse reached each microphone at a different time. The time delays between the signals reaching the microphones enable the calculation of the bat's position at the time of each call.

Figure 2. Across-species comparison of the 10% highest call SLs (mean and range in dB peSPL re: 20 µPa in 10 cm) measured from a frontal direction (microphone less than 20° above, 60° below and 40° to the side of the flight vector) of 11 bat species plotted against their mean body mass. For some species data from two (Pk, Pn, Ms and Nle), four (Hs) or five (Pm) different recording sites are shown. Different symbols stand for different species. For an explanation of the abbreviations of the species names see § 2. *M*, body mass.

cal narrowband search-flight calls assuming the same temperature and humidity as for the SL measurement (Bazley 1976; the typical peak frequencies were: Pm, 55 kHz; Ms, 51 kHz; Pp, 45 kHz; Pk and Pn, 39 kHz; Hs, 35 kHz; Nle, Es and En, 26 kHz; Nn, 20 kHz and Nla, 18 kHz).

Three different types of target were considered, which were chosen to include the most distant objects a bat is likely to encounter: type 1, insect prey; type 2, largest flying objects with spherical spreading of the echo (e.g. conspecifics or flying predators); and type 3, large planar background objects reflecting the call back to the bat when ensonified perpendicularly (e.g. a rock face or wall from the front or a water surface

Table 1. Interspecies comparison of tendency to skip calls.

(Data given are the percentages of calls emitted every wingbeat, skipping one call (every second wingbeat), skipping two calls (every third wingbeat) or skipping even more calls (>) measured from call intervals. n = total number of calls per species. Wingbeat period min–max (ms) is the duration of call intervals considered as corresponding to one call per wingbeat.)

species name	percentage of calls emitted				n	wingbeat period min–max (ms)
	every wingbeat	every second wingbeat	every third wingbeat	>		
<i>Nyctalus lasiopterus</i>	55	28	10	7	121	100–200
<i>Eptesicus nilssoni</i>	52	43	5	0	1177	70–170
<i>Hypsugo savii</i>	60	31	8	1	900	60–150
<i>Pipistrellus kuhli</i>	74	19	6	1	1183	50–150
<i>Nyctalus leisleri</i>	76	21	3	0	514	50–175
<i>Nyctalus noctula</i>	79	18	2	1	1486	90–190
<i>Eptesicus serotinus</i>	85	11	3	1	2059	100–170
<i>Pipistrellus pipistrellus</i>	88	11	1	0	2522	50–130
<i>Pipistrellus nathusii</i>	91	8	1	0	936	50–150
<i>Pipistrellus pygmaeus</i>	89	9	1	1	4139	30–120
<i>Miniopterus schreibersii</i>	94	6	0	0	895	20–140

from above). They differ with respect to their TSs and their TLSs.

Types 1 and 2 targets were both treated as point sources with spherical spreading of the echo. As both call and echo are spreading spherically, TLS increases by 12 dB every time the distance between the bat and the target is doubled

$$\text{TLS} = 2 \times 20 \log \left(\frac{d}{0.1} \right),$$

where d is the distance from bat to target (in metres).

Targets of type 3 reflect the sound back to the bat resulting in a TLS increase of only 6 dB per doubling distance. Thus, their TLS is smaller than those of type 1 and type 2 targets, i.e.

$$\text{TLS} = 20 \log \left(\frac{2d}{0.1} \right).$$

The values for the TSs of the insects were taken from Waters *et al.* (1995). The TSs of insects did not change systematically over the relevant frequency range (18–55 kHz). Therefore we used the mean TS for each insect: *Noctua pronuba*, –18 dB; *Agrotis segetum*, –30 dB; Trichoceridae, –45 dB and Culicidae, –53 dB at 10 cm. Type 3 targets, which reflect all sound energy, have a TS very close to 0 dB at 10 cm. This value also served as a realistic approximation to the highest TS possibly generated by large type 2 targets.

The DT was assumed to be 0 dB SPL (Kick 1982; Neuweiler *et al.* 1984; Coles *et al.* 1989) although other authors have reported a DT of 40 dB (Troest & Möhl 1986). Thereby we assume that all bats use calls with a suitable bandwidth, frequency modulation and duration to give them a DT of 0 dB. The noise term was considered to be included in the DT.

Wingbeat periods were obtained from frequency histograms of intervals between calls (from start to start of consecutive calls). They showed several peaks because bats sometimes beat their wings once or more without producing a call. The mean wingbeat period was taken as the median of the first peak (for the chosen limits of the first peak see table 1). These multiple peaks also indicate how frequently calls were skipped (see table 1). Deriving wingbeat periods from call intervals is based on the assumption that call emission is coupled to wingbeat. This has been proven in all species studied so far (Jones 1994; Kalko

1994; Wong & Waters 2001), though it has not yet been explicitly shown for every species in this study.

3. RESULTS

A total of 2355 call SLs were obtained from 11 bat species. For this study only the highest SLs are relevant. Figure 2 shows the most intense 10% of these calls. In some species data from up to five recording sites are given separately. Several calls from the same individual can be included. All species were able to emit most intense calls of at least 124 dB peSPL. The heaviest species, *N. lasiopterus*, produced the most intense call (maximum SL of 133 dB peSPL), yet even the lightest species, *P. pygmaeus*, proved able to call at 128 dB peSPL. There was a significant trend for heavier bats to use higher SLs (figure 2; $r^2 = 0.46$, $F_{1,20} = 17$, $p = 0.0005$). The differences between recording sites, e.g. for *P. pygmaeus*, however, were of the same magnitude as the differences between species. Measurements of the highest 10% of SLs (at 10 cm standard distance) were independent of the distance between the bat and the microphone (e.g. Pp: distance to microphone 3.5–12 m; regression coefficient -0.05 dB m^{-1} ; $R^2 = 0.008$; $F_{1,28} = 0.22$; $p = 0.64$).

Across the species investigated, the call end frequency decreased with increasing body mass (figure 3a; $R^2 = 0.80/0.91$, $F_{1,12} = 51/116$, $p < 0.0001/< 0.0001$; with and without *M. schreibersii*, respectively). *Miniopterus schreibersii* calls were higher than those of similar-sized species. Wingbeat period measured from call intervals showed a positive correlation with body mass (figure 3b; $R^2 = 0.79/0.88$; $F_{1,10} = 43/75$, $p < 0.0001/< 0.0001$; with and without *M. schreibersii*, respectively). *Miniopterus schreibersii* called more frequently than expected for a bat of its size.

Figure 3c shows the detection distances for different targets calculated for a typical search call with the highest SL found for the respective species. The detection distances for insects of different sizes (circles and triangles) ranged between 5 m and 25 m for the largest insects and between 2 m and 7 m for the tiny culicid. The general trends were

Figure 3. Cross-species comparison of (a) call end frequencies (median and 90% confidence interval) and (b) mean wingbeat periods (median and quartiles) of aerial-hawking bat species with their body masses. Regressions without *Miniopterus schreibersi* (Ms). (c) Mean wingbeat period plotted against maximum detection ranges and echo delays, respectively, calculated for four differently sized insects (black and white circles and triangles), larger flying targets with spherical spreading of the echo (black diamonds) and planar background targets reflecting the echo back (white diamonds) both with 0 dB TS. Straight lines indicate perfect matching between the wingbeat period and the detection range for bats calling every second or every third wingbeat. For an explanation of the abbreviations of species names see § 2. Right inset in (c): spherical spreading of echo of type 1 and type 2 targets; left inset in (c), spreading of echo of type 3 targets (see § 2). EF, call end frequency; *M*, body mass; WBP, wingbeat period; dB/dd, dB per doubling distance.

that heavier bats achieved longer detection ranges and that the detection range increased with the TS of the insect. The maximum detection ranges for large flying targets (type 2) increased from *ca.* 7 m for the smallest up to 38 m for the largest bat species (figure 3c; black diamonds). However, for planar background targets (type 3) much higher detection ranges were derived: *ca.* 13 m for the smallest species but about 90 m for *N. lasiopterus* (figure 3c; white diamonds).

Figure 3c also gives a comparison of the species' detection range with their mean wingbeat period. The straight lines indicate perfect matching between wingbeat period and detection range for bats calling every wingbeat (1 call per wingbeat), every second wingbeat (1 call per 2 wingbeats) or every third wingbeat (1 call per 3

wingbeats). In all species all the detection ranges for insects lay within the window set by the wingbeat period (triangles and circles in figure 3c). Insect echoes were spread over a similar proportion of the wingbeat window in all species, making more or less full use of the available time window. Furthermore, for small- and medium-sized bats there was a tight matching of wingbeat and detection range for large flying targets of type 2 (black diamonds). Only in a few larger species may type 2 echoes arrive later than the following call, which is emitted after one wingbeat. There was no evidence for a matching of type 3 echoes (white diamonds) to the wingbeat period.

The tendency of a species to skip calls, that is to beat the wings once or more without calling, increased with body size. The smallest species called with every wingbeat

in ca. 90% of cases. The largest species skipped one call in 45% of cases and skipped more than one call in 17% of all vocalizations.

The three straight lines in figure 3c also indicate to what extent a certain species might profit from skipping calls: as none of the black diamonds lies to the right of the middle straight line, no species will profit from skipping more than one call while focusing on type 1 or type 2 airborne targets. If a bat does so, it wastes time by waiting for echoes in vain. However, the white diamonds for almost all species indicate that skipping two or even three calls makes sense when waiting for echoes from distant background targets (type 3).

4. DISCUSSION

Griffin (1958) was the first to stress the ecological relevance of SLs in bat echolocation. Owing to technical difficulties, however, our knowledge about SLs of echolocation calls *in the field* is relatively poor (Surlykke *et al.* 1993; Jensen & Miller 1999). The present study narrows this gap by giving maximum SLs for 11 European bat species in free flight.

It has been estimated that *Eptesicus fuscus* in free flight produces SLs of 120 dB SPL (Roeder 1966), *E. serotinus* reportedly uses 121–126 dB SPL (Jensen & Miller 1999) and *C. thonglongyai* ca. 115 dB SPL (Surlykke *et al.* 1993). All bat species in the present study achieved at least such levels, or even considerably higher levels of up to 133 dB peSPL. Even the lightest bat in Europe, *P. pygmaeus*, was surprisingly intense in its calls, with up to 128 dB peSPL.

The SL differences between the investigated species are not exclusively size dependent and might therefore also reflect adaptations to somewhat different foraging situations or differences between individuals rather than being a species characteristic. The more-or-less similar SLs of all species raise the question of whether there is a common limit to the maximum achievable SL, for example, because of problems of impedance matching in sound production.

The detection of insects in the air by echolocation is restricted to a few metres (Kick 1982; Kalko & Schnitzler 1998) in spite of the fact that aerial-hawking bats use calls with very high SLs. This is owing to the high absorption of ultrasound in air (Bazley 1976) and to the small proportion of the acoustic signal reflected by the targets. Generally, larger bat species achieved larger detection ranges because their lower-pitched calls were less affected by absorbance in air. As an exception, *M. schreibersi* has a short detection range for its size because it uses relatively high-pitched calls. Behavioural evidence of detection ranges is scarce, but pipistrelles reportedly reacted to insect prey at a distance of 2 m (Kalko & Schnitzler 1993), which is in rough agreement with their calculated maximum detection range for small insects of ca. 3.5 m. The difference most probably results from the fact that TS was measured with the insect's wings perpendicular to the direction of sound incidence (Waters *et al.* 1995), which is rarely the case in natural foraging situations. With any other wing position the detection range is reduced because the insect's echoes can be 20 dB weaker (Kober & Schnitzler 1990).

The main aim of this study was to investigate a possible match between echolocation range and wingbeat period

in aerial-hawking bats. The first important finding was that all insect echoes reached all bat species within the window set by the wingbeat period and furthermore that insect echoes were spread over almost the full wingbeat window in all species. This means that bats use the time window set by the wingbeat period fully without risking ambiguous call echoes. However, the flying insects investigated are not the most distant objects that bats can perceive. The very last echoes from flying objects come from the large type 2 targets. In fact, none of the species investigated had a maximum detection range for large flying targets significantly shorter than the wingbeat window. Thereby they avoided waiting too long for returning echoes. Furthermore, in all small and most medium-sized bat species the detection range for such large flying targets rather tightly matched the mean wingbeat period. Even the smallest bat in the world, *C. thonglongyai* (Surlykke *et al.* 1993), showed a perfect match between its maximum detection range for flying targets and its wingbeat period (figure 3c). Finally, *M. schreibersi* is particularly interesting in this respect: this species differed from similarly sized species by using an unusually high call end frequency (figure 3a) and an extraordinarily short mean wingbeat period (figure 3b). On its own, each of these deviations would lead to a detection range either too short or too long for the wingbeat window. However, in combination they cancel each other out. Like all other species investigated *M. schreibersi* achieved a perfect match between mean wingbeat period and maximum detection range for large flying targets. The example of *M. schreibersi* shows that this matching mechanism goes beyond a pure coincidence caused by the parallel increases in wingbeat period and detection range with body mass.

We conclude that aerial-hawking bats in search flight match their maximum detection range for flying targets to their wingbeat period. By doing so they take advantage of efficient call production and at the same time scan the skies without risking call–echo assignment problems and without wasting time by waiting too long for echoes.

Aerial-hawking bats are chiefly searching for flying prey and therefore it makes sense for them to adjust their detection range for flying targets (types 1 and 2) to match their wingbeat. Consequently, more distant background targets (type 3) are far out of their wingbeat window (white diamonds in figure 3c). For orientation purposes however, bats from time to time must also be interested in these distant background targets. For the largest species investigated (*N. lasiopterus* and *N. noctula*) even large flying targets are out of the wingbeat window (black diamonds in figure 3c). This longer detection range might compensate for the relative scarcity of suitably large prey insects. In both cases bats receive echoes originating from their first call after their second call, and consequently are exposed to the risks of incorrect call–echo assignment. One strategy to ease correct call–echo assignment is to mark successive calls individually by alternating peak frequencies (e.g. *N. noctula*; Ahlén 1981; *Cormura brevirostris*; O. von Helversen, personal observation), different frequency modulations (e.g. *Barbastella barbastellus*; Denzinger *et al.* 2001) or perhaps even alternating call intensities (e.g. *P. pipistrellus*; M. W. Holderied and O. von Helversen, personal observations). The drawback is that decoding this infor-

mation increases the neuronal computation effort in the sensory system.

Another strategy is to multiply the size of the wingbeat window by skipping calls. In fact we found a correlation between a species' probability of encountering echoes out of the wingbeat window (figure 3c) and its tendency to skip calls (table 1). Bats with a limited detection range (e.g. *M. schreibersi* and *P. pygmaeus*) very rarely skipped calls, whereas species with long detection ranges (e.g. *N. lasiopterus*) skipped calls almost every other time (compare figure 3c and table 1). The very long detection range of *N. lasiopterus* for background targets would even justify skipping up to three calls (figure 3c) and in fact this was the only species to skip more than two calls on a regular basis (7%; see table 1). Some species did not skip as many calls as expected presumably because they were not recorded in open space but in a more-or-less background-cluttered situation. The tendency to skip calls might also be affected by the presence of conspecifics.

The three parameters—wingbeat period, SL and call frequency—interact more than hitherto discussed. Wingbeat period sets a time window that is matched by echolocation range. Echolocation range is determined by call SL and by call frequency. As the call SL is physiologically and physically limited, call frequency is the most likely agent for a match to the wingbeat window. We therefore hypothesize that a bat species' search-call frequency is at such a level that the resulting echolocation range matches the range determined by the wingbeat period. This constraint on call frequency adds to other constraints such as a wavelength-to-body-size relation suitable for efficient call production, or a wavelength-to-target-size relation fostering sufficient acoustic resolution owing to an appropriate amount of energy reflected, diffracted and scattered.

The authors gratefully acknowledge the help of R. Aubauer who developed and built the acoustic flight-path tracking equipment, developed software and assisted in improving it. F. Oehme, G. Kilian, T. Jaumann, M. Bannert and J. Dazio (Institut für Technische Elektronik, Universität Erlangen) developed the hardware and software for digital recording in the field. We are also indebted to too many people to mention for their help in the field or because they granted access to their property. The manuscript was improved greatly by comments by G. Jones and two anonymous referees. This work was funded by grants from the 'Bayerische Graduiertenförderung' and the 'Studienstiftung des deutschen Volkes' to M. W. Holderied.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.