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Echolocation and passive listening by foraging mouse-eared bats *Myotis myotis* and *M. blythii*

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Summary

The two sibling mouse-eared bats, *Myotis myotis* and *M. blythii*, cope with similar orientation tasks, but separate their trophic niche by hunting in species-specific foraging microhabitats. Previous work has shown that both species rely largely on passive listening to detect and glean prey from substrates, and studies on other bat species have suggested that echolocation is 'switched off' during passive listening. We tested the hypothesis that mouse-eared bats continuously emit echolocation calls while approaching prey. Echolocation may be needed for orientation while simultaneously listening for prey. Because these sibling species forage in different microhabitats and eat different prey, we also compared their echolocation behaviour and related it to their ecology. Both species used echolocation throughout prey approach, corroborating a functional role for echolocation during gleaning. Captive bats of both species emitted similar orientation calls, and pulse rate increased during prey approach. Between the search to approach phases, call amplitude showed a sudden, dramatic drop and bats adopted 'whispering echolocation' by emitting weak calls. Whispering echolocation may reduce the risks of masking prey-generated sounds during passive listening, the mouse-eared bats' main detection tactic; it may also avoid alerting ultrasound-sensitive prey. In several cases *M. myotis* emitted a loud buzz made of 2–18 components when landing. We hypothesise that the buzz, absent in *M. blythii* at least when gleaning from the same substrate, is used to assess the distance from ground and refine the landing manoeuvre. Our findings have implications for niche separation between sibling species of echolocating bats, support a role for echolocation during passive listening and suggest a functional role for buzzes in landing control.

Key words: bioacoustics, cryptic species, gleaning, mouse-eared bat.

Introduction

Besides echolocation, several bat species use other mechanisms such as passive listening (listening for prey-generated sounds), vision and olfaction for the detection and localisation of prey (e.g. Suthers and Wenstrup, 1987; Anderson and Racey, 1991; Faure and Barclay, 1994; Eklöf et al., 2002; Swift and Racey, 2002; Eklöf and Jones, 2003; Jones et al., 2003). Bats gleaning prey from substrates [i.e. ca. 30% of echolocating bats worldwide (Arlettaz, 1996)] often detect it by listening for prey-generated cues. Passive listening might represent a major foraging tactic for nocturnal vertebrates relying chiefly on the auditory sense for capturing relatively immobile prey in structurally complex microhabitats.

It has been suggested that when hunting by passive listening, gleaning bats interrupt echolocation, or largely reduce call intensity, shortly (often ca. 1 s or less) before capturing prey or landing (Anderson and Racey, 1991; Faure and Barclay, 1992; Faure and Barclay, 1994; Arlettaz et al., 2001; Swift and Racey, 2002; Ratcliffe and Dawson, 2003).

Switching off echolocation would bring about some benefits. First, bats have difficulty in processing two overlapping streams of information, such as those associated with returning echoes and prey-generated sound (Barber et al., 2003). Under these conditions, interrupting echolocation would avoid this interference. Besides allowing avoidance of overlap between echoes and sounds made by the moving prey, keeping silent when approaching prey might prove useful when capturing tympanate insects that are sensitive to the ultrasonic echolocation calls of bats (e.g. Waters, 2003). A quiet approach prevents the prey being alerted in time to evade the attack (Anderson and Racey, 1991; Faure et al., 1993).

However, several specialised gleaners produce broadband, high-frequency pulses while approaching prey (Schmidt et al., 2000; Swift and Racey, 2002; Ratcliffe et al., 2005).

Echolocation may be useful for detecting and gleaning prey from simply structured surfaces (Schmidt, 1988; Schmidt et al., 2000; Schnitzler and Kalko, 1998; Arlettaz et al., 2001; Swift and Racey, 2002), but these are in fact uncommon in nature (Ratcliffe and Dawson, 2003). Rhinolophids can detect fluttering prey on substrate by employing constant frequency echolocation calls specialised for the detection of moving targets in clutter (Schnitzler and Ostwald, 1983).

The persistence of echolocation during passive listening for prey hidden in cluttered surfaces may have different functions. The most obvious is spatial orientation: bats continuously need echo information so they do not collide with obstacles while they are searching for prey by passive listening (e.g. Neuweiler, 1989; Fenton, 1990; Arlettaz et al., 2001; Schnitzler et al., 2003). Ancillary roles of echolocation in prey detection have also been hypothesised, such as helping the bat to circumscribe the prey's probable position, in order to increase the likelihood of predation success (Ratcliffe and Dawson, 2003). Even when searching for prey hidden in complex surfaces, a role for prey detection may be imagined: as soon as prey moves, the compound prey-clutter image will also change, possibly providing the bat with cues on the presence of prey. Echolocation calls produced during gleaning would be especially important to bats hunting in unfamiliar environments, where spatial memory cannot be of help (Ratcliffe et al., 2005).

Echolocation is highly adaptable, offering one of biology's most compelling examples of convergent evolution (Siemers et al., 2001; Jones and Teeling, 2006). Echolocation call design is often shaped by environmental factors such as the proximity of clutter, and is therefore related to niche differentiation. Closely related, cryptic species, in particular those sharing a recent common ancestor [usually termed 'sibling species' (e.g. Stearns and Hoekstra, 2005)], very often show contrasted patterns of resource use, feeding upon different prey found in different habitat types, or even foraging in species-specific microhabitat structures selected within common foraging grounds (e.g. Johnston, 1971; Arlettaz, 1996; Arlettaz, 1999; Maurer and Sih, 1996; Amiet, 2004). Through clearcut niche specialisations, sibling species occurring in sympatry avoid otherwise severe competition and can co-exist in a stable way, despite exhibiting similar morphologies that would *a priori* make a large overlap in resource use seem likely.

The sibling mouse-eared bats *Myotis myotis* (Borkhausen 1797) and *Myotis blythii* (Tomes 1857) separated from a common ancestor in the Pleistocene (Arlettaz et al., 1997a), and achieve niche segregation by selecting different foraging microhabitats and exploiting different prey. *M. myotis* gleans prey from bare ground, short mown grass or forest leaf litter, and feeds mostly on carabid beetles in woodland, orchards and in freshly cut meadowland (Arlettaz, 1999). *M. blythii* takes its prey mostly from the dense grass sward, and specialises on bush crickets obtained from dense grassland such as steppe or hay meadows (Arlettaz et al., 1997b; Arlettaz, 1999). Both species largely rely on passive listening to detect prey hidden on the substrate (Arlettaz et al., 2001).

Using the same model as previously (Arlettaz et al., 2001), we tested the hypothesis that bats routinely 'switch off' echolocation completely during gleaning or, alternatively, whether they continue to echolocate using calls of very low intensity. We also explored the existence of differences in echolocation during passive listening in these sibling species to test the hypothesis that echolocation behaviour is related to ecological niche because structural differences in echolocation during prey approach may reveal adaptations to exploit divergent, species-specific niches (Arlettaz, 1999). Immediately before landing, mouse-eared bats have been found to emit a brief but loud buzz, i.e. a short call sequence made of steep frequency modulated calls produced with a high repetition rate (Arlettaz et al., 2001). Therefore, we determined whether the buzz is produced by both species during gleaning and discuss its possible functional value in relation to niche partitioning in *M. myotis* and *M. blythii*.

Materials and methods

Experimental design and data recording

Experiments were conducted in Sion (Switzerland) during September 2004. Bats *Myotis myotis* (Borkhausen 1797) and *Myotis blythii* (Tomes 1857) were temporarily captured at summer roosts by mistnetting them on emergence, and were kept in a flight room 4.30 m×1.70 m×2.30 m (L×W×H). The room was acoustically and visually isolated from the outside, and artificially illuminated according to the local natural photoperiod. The experiments were conducted at night (21:00 h–05:00 h) beginning on the night following capture. Bats were fed *ad libitum* on mealworms and crickets; water was made constantly available, and roosting spaces were provided beneath thick sheets and carpets hung on the walls. Duration of captivity was kept to the strict minimum (up to 4 days), both to minimise stress and to limit the potential role of spatial memory in prey detection (Ratcliffe et al., 2005).

In the flight room we placed a 100 cm×70 cm wooden tray filled with natural dry leaf litter. The litter increased the noise produced by prey movement, encouraging predation (Arlettaz et al., 2001). During each trial we hid 6–10 field crickets in the litter, and occasionally provided other orthopterans from alpine meadows. Prey movement was restricted by securing a small metal load to the thorax or legs of the insects, using cotton thread.

All bats were banded with coloured rings for easy identification during the experiments. No adverse reaction to bands was noticed. Bats were generally tested individually, the others being kept in cloth bags. Occasionally, several bats were kept together during foraging tests to enhance motivation. In such situations, after a bat had made an attack, its identity was checked immediately. For each subject, a trial was considered to be over when about 2 h had elapsed following the last predation attempt. If a bat failed to forage over two consecutive nights, it was hand-fed and released at its original roost. Each bat was weighed both after capture and immediately before

being released back at the roost: in no case did we observe loss of body mass. All bats maintained their health during captivity.

Bat activity was watched remotely using an IR video-camera placed at 1 m from the feeding arena and recorded with a videotape recorder. The video system consisted of a time-lapse video recorder (Sanyo, bSRT-7168P, Osaka, Japan) and an infrared camera (Videotronic, CCD-7012P, Neumünster, Germany) with an automatic iris. The focus and sharpness of the image were controlled with a small portable monitor (Sony, GV-D800, Tokyo, Japan), which was also used for surveying the experiments. The operator stayed outside the flight room and was visually sheltered by a panel covering the cage wall. We confirmed that equipment in the flight room did not produce ultrasound by listening with a bat detector. Bat echolocation calls were monitored using the frequency division mode of a Pettersson D980 bat detector (Pettersson Elektronik AB, Uppsala, Sweden). The microphone, placed inside the room (at ca. 15 cm from ground and 1.5 m from the leaf litter tray), was connected to the detector with a 5-m cable. The detector was operated outside the room. Directional effects of the echolocation calls were not considered in power measurements. However, such factors are unlikely to have affected our analysis significantly because (1) the microphone was set close to the feeding tray, i.e. to prey; (2) the directionality of the recording microphone at the relevant frequencies (~50 kHz) is very broad and thus results in a maximum potential underestimation of –2 to –9dB for an angle of ±20° at frequencies of 30 and 50 kHz, respectively (L. Pettersson, personal communication); and (3) during the final approach to prey, bats followed a direct trajectory. Moreover, any influence from directional effects probably affected each sequence randomly so we expected no significant effect on the comparison between species that we carried out.

As a bat flew towards the tray, 3 s (more rarely 12 s) of sound were time-expanded (10×) by the detector. The detector sampling frequency was 350 kHz. Call sequences were saved as WAV-files to a Toshiba laptop computer with BatSound 3.31 (Pettersson Elektronik AB, Uppsala, Sweden). Sound was digitised with a sampling frequency of 44.1 kHz at 16 bits/sample.

To describe buzzes sometimes emitted by mouse-eared bats soon before landing (Arlettaz et al., 2001), we analysed two separate datasets. Besides examining all sequences including a buzz recorded in the course of the experiments, we also selected recordings taken during previous work carried out in Bristol, UK (Arlettaz et al., 2001) under similar experimental conditions. In that case, each bat was kept under investigation for several months, so we were able to record greater individual variation in buzz structures. In such experiments, prey was placed on either natural leaf litter or on an artificial lawn (Arlettaz et al., 2001). In all, we examined a sample of 50 buzzes produced on landing by 9 bats, 38 from four bats studied in Bristol (respectively 8, 12, 8 and 10 recordings) and 12 from five bats observed in Sion (four from one individual bat and two from each of the remaining subjects). We preferred not to lump together the datasets for presentation because recordings were taken with different equipment [in Bristol, an Ultra Sound Advice S25 bat detector and a Racal high speed recorder were used (Arlettaz et al., 2001)].

Sound and video analyses

In all, we recorded at least two attack sequences from 18 bats, eight *M. myotis* (three juvenile females, two adult females, one juvenile male, and two adult males), and ten *M. blythii* (seven adult females, three juvenile males). We analysed two attack sequences per bat. When more than two attacks were available, we randomly selected two of them for analysis. Typically, after a series of active search signals, echolocation calls showed a marked decline in amplitude prior to landing; this transition also corresponds to switching to the passive-listening tactic, as described (Arlettaz et al., 2001). When a bat started prospecting for prey, it generally circled several times in the flight room before approaching the feeding arena. To avoid biases in call power measurement, we concentrated on the terminal part of prey capture manoeuvres and used video recordings to confirm that weak calls were actually emitted during gleaning.

We analysed calls starting from the last (generally three) ones preceding the 'weak' phase (see below), which were likely to have been produced close to the microphone. Most sequences that were analysed lasted ⩽2 s real time. Maximum relative power of calls (expressed in dB) was plotted over time, and calls grouped into consecutive phases, as follows (Fig. 1A,B):

Phase 1

The initial, loudest calls in the sequence, with little variation in power among calls (i.e. within an approximately ±5 dB range).

Phase 2

One to several consecutive calls following search phase, showing a decreasing trend in power over time. When >1 call was present, we included in phase 2 all calls of a progressively reduced power (i.e. those showing a declining power trend, such as those illustrated in Fig. 1B).

Phase 3

In this phase power may either be more or less constant, or sometimes may increase in calls emitted shortly before either a landing buzz (see below) or landing.

Phase 4 (terminal phase)

This sequence (the 'buzz') comprised at least two frequency modulated components (Fig. 1A) characterised by a sudden, dramatic decrease in pulse interval, >70% relative to the previous phase (range 71–97%, mean ± s.d. 87.3±7.4%). This feature made the buzz easy to recognise visually from spectrograms as a final distinct 'batch' of calls, exhibited in several sequences either soon before or during landing. Although the most obvious criterion to recognise the buzz was the above-mentioned increase in pulse rate, the mean amplitude

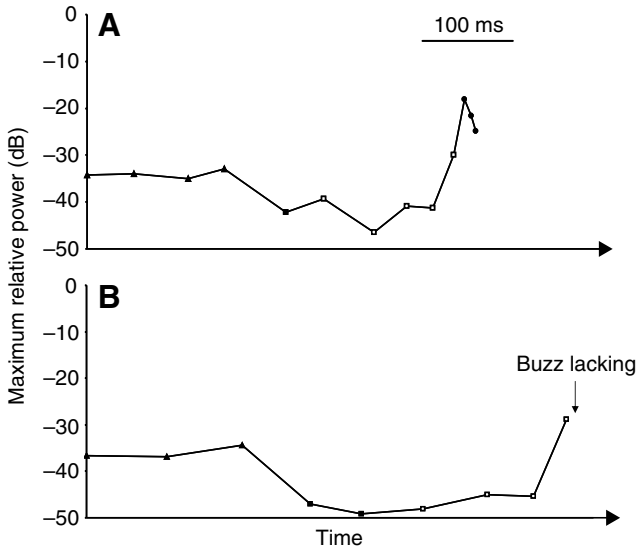

Fig. 1. Trend of maximum relative power (dB) over time measured from power spectra in typical *M. myotis* (A) and *M. blythii* (B) foraging sequences. Each sample point corresponds to a different call, the latter representing the signal emitted before touching down. In both cases, amplitude dropped from phase 1 to phase 2. Filled triangles: phase 1 (search); filled squares: phase 2 (transition); open squares: phase 3 (attack); filled circles: phase 4 (buzz) See text for definitions. The '0 dB' value is an arbitrary reference level, corresponding to the maximum allowable signal level that can be represented in the given digitisation format.

of buzz components was also markedly higher than that of the previous phase (difference >10 dB).

Phases 2 and 3 correspond to (and are hereafter together referred to as) the 'approach' phase. The actual correspondence between this call sequence and the approach manoeuvre was checked from video recordings. Mouse-eared bats emit weak calls during gleaning (Arlettaz et al., 2001), so in most cases the behavioural interpretation of audio recordings would have been unequivocal even in absence of video recordings. By examining video tapes, however, we avoided all risk of misclassifying as genuine 'weak phase' calls those appearing weak in the recordings because they were emitted by bats distant from the microphone. Classifying calls *a posteriori* based on video observations rather than in the way we did would imply some subjectivity in determining the actual start of the approach phase (especially when this was short), i.e. a high risk of overlooking the brief transitory phase 2. The conspicuous sound produced by landing bats was used to match video and audio recordings (Ratcliffe and Dawson, 2003). To test whether the emission of a buzz was related to landing angle, video recordings were also examined in which we categorised attacks as sub-horizontal (attack angle 0–30° from the ground), oblique (30–60°), or sub-vertical (60–90°).

Sound analysis was performed with BatSound 3.31. From each call, we measured the following variables: frequency of maximum energy (f_{MAXE}, in kHz), and call maximum relative power (dB), both taken from power spectra; approach phase duration (ms) and mean pulse rate (expressed as number of calls in phase/phase duration in s), measured from oscillograms. For phases 2 and 3, we refrained from measuring further variables commonly employed in echolocation studies (e.g. Vaughan et al., 1997) such as call highest frequency and duration, since these might have been greatly affected by the weak intensity of calls. Duration was measured from good quality calls in phase 1. For each sequence selected, when more than one call was present in a phase, we calculated a mean value for f_{MAXE} and maximum power. Then, we calculated mean individual values from the two sequences selected for each bat and used these in final analyses. For a description of terminal buzzes, we took the following measurements: number of components; minimum and maximum buzz frequencies (kHz), i.e. highest and lowest frequency values of all components in a buzz, as taken from spectrograms (a 512 pt FFT, 98% overlap, with a Hamming window was applied); f_{MAXE} (kHz) and maximum relative power (dB) of each buzz component; overall duration (ms), taken from the onset of the first to the end of the last component, and duration of single components (ms). Time measurements were taken from oscillograms. Measurement of maximum and minimum frequencies were taken from spectrograms as, respectively, the highest and lowest frequencies that clearly had more energy than the background noise. For consistency across measurements, in all cases the spectrogram threshold in the BatSound software was kept at a constant level (13). We checked this method by also producing power spectra from a selection of signals and taking measurements from these to determine the signal level relative to the peak energy (e.g. Surlykke and Moss, 2000). Frequency values measured from spectrograms corresponded closely (generally within 1 kHz) to values on power spectra that were 30 dB below the peak energy in the signal.

Sounds other than echolocation calls, such as rustling noise, were occasionally present in recordings (Fig. 2). In all cases the difference between noise and echolocation call structure was obvious, so noise was easily discarded from analysis. Overlap of echolocation calls with background noise was negligible.

We entered species and phase as factors in an analysis of variance (General Linear Model) to test for their effect on spectral and temporal variables of echolocation calls. Although difference in amplitude was the criterion used to separate calls into phases, our General Linear Model, aimed to detect interspecific differences in call power, also included phase as a main factor to control for its effects.

Data were first checked for test assumptions of normality of residuals (with a Ryan–Joiner test). When necessary, we used log transformations to meet the test's assumptions. We removed between-factor interactions from final models when non-significant.

To explore the association between the production of a buzz and landing angle as taken from video recordings, we employed a Fisher's exact test. Significance was set at $P<0.05$. All

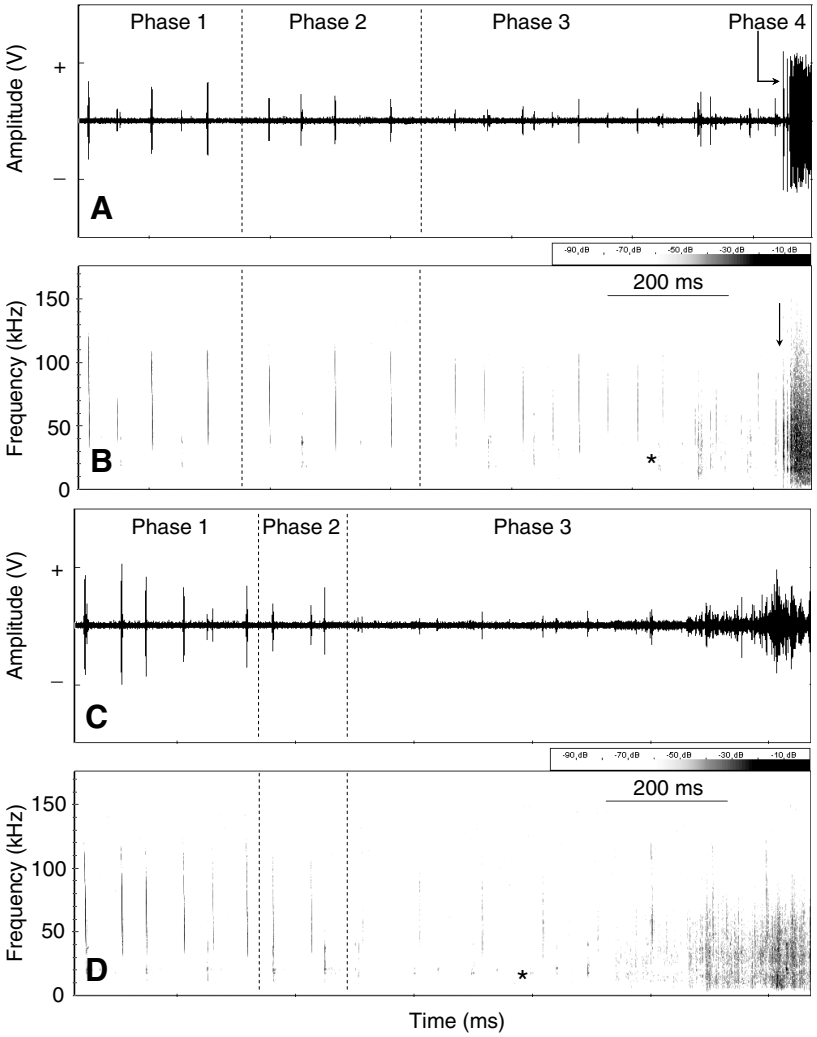

Fig. 2. Oscillograms (A,C) and spectrograms (B,D) of attack sequences in mouse-eared bats (A,B, *Myotis myotis*; C,D, *Myotis blythii*). In both cases, amplitude drops from phase 1 (search) to phases 2, 3 (prey approach). Arrows in A, B point to a buzz emitted only by *M. myotis* before landing. *Rustling noise produced by prey (low frequency sound). The increase in call amplitude during this buzz is especially apparent in the oscillogram. The noise produced by the landing bats may be noticed at the end of the sequences.

statistical analyses except Fisher's test were performed with Minitab for Windows release 13.32.

Results

In no case did a bat fully interrupt echolocation when approaching prey (Fig. 2). Under such circumstances, both species adopted a 'whispering mode' of echolocation, in several cases calls being so faint that they could hardly be detected (Fig. 3). In most sequences, we recognised phases 1, 2 and 3. One *M. myotis* omitted phase 3 in one case, and of the two trials by one individual *M. blythii*, one lacked phase 3 while the other showed no clear variation in call power (i.e. the whole sequence was classified as belonging to phase 1).

Analysis of video recordings clearly confirmed that the calls of high amplitude (categorised as phase 1 calls) were emitted just before the bat reached the feeding arena or its immediate surroundings. During the approaching manoeuvre, a reduction in call amplitude occurred when bats circled over the feeding arena or briefly hovered above prey before touching down. In a few circling events, we noticed that air turbulence caused by the bat's wing beat moved the litter, favouring prey reaction. In some instances, especially when the attack followed previous circling events (probably used to carry out a preliminary screening of the hunting spot), the bat returned to the feeding arena and performed a straight touch down. During the approach phase, bats generally flew within a height of ca. 50 cm above the ground. Once a bat landed and caught the prey, the prey item could be either eaten at place or carried away from the feeding arena. Some *M. myotis*, but no *M. blythii*, exhibited a buzz on landing (Fig. 1A, Fig. 2, Fig. 4). Three *M. myotis* emitted a buzz on both attacks considered for the analysis, two emitted it only in one sequence, whereas three did not produce any buzz. An analysis of the entire dataset of 27 trials recorded from *M. myotis* led to similar conclusions. Buzzes were present in 12 attacks. Three bats always produced buzzes (two attacks each). Three bats emitted no buzz out of respectively two, three and eight trials recorded. Of the remaining two subjects, one produced a buzz in four out of five attacks, the other in two out of three cases.

Besides the 20 *M. blythii* sequences analysed, another 35 recorded (but not selected for detailed bioacoustical analysis) all led to the same conclusion, i.e. that this species emitted no buzz on touch down. We ruled out that *M. blythii* might be a

faster learner, losing the buzz more quickly than *M. myotis*, because in several cases we examined the recording of the first attack made by *M. blythii* after bats were released into the flight room, and established that buzzes were absent.

M. myotis showed no association between buzz production and the angle of approach followed by landing bats (Fisher's exact test, P=1.00). No significant difference was found in the attack angle by the two species (P=0.74). The analysis of the two buzz datasets considered revealed that buzzes are made of 2–18 frequency-modulated components. Buzz components were typically of high amplitude, and in several cases a tightly overlapping multi-harmonic structure was recognisable. Spectrograms of buzz calls often showed amplitude modulations caused by interference between calls reaching the microphone and echoes reflected by the nearby ground. In some cases, this pattern made the calls' multi-harmonic structure less evident. The highest frequency of top harmonics typically exceeded 100 kHz; buzz duration averaged up to ca. 20–30 ms (Table 1). Obviously, duration depended upon the number of buzz components. Pulse rate and end frequency did not show distinct changes over time, so no further subdivision of buzz structure was possible.

Echolocation call f_{MAXE} did not differ between phases, but was significantly lower in *M. blythii* (Table 2). However, search calls recorded from 14 bats (including subjects used for trials) hand-released inside the same flight room (one call selected at random per each bat) had values showing no significant differences (ANOVA, F=0.34, n.s.), i.e. 51.7±1.9 kHz in *M. myotis* (N=4) and 50.1±5.5 kHz in *M. blythii* (N=10). We also compared the bandwidth of the best recorded search calls (i.e. those for which maximum frequency measurements were most reliable) selected from these

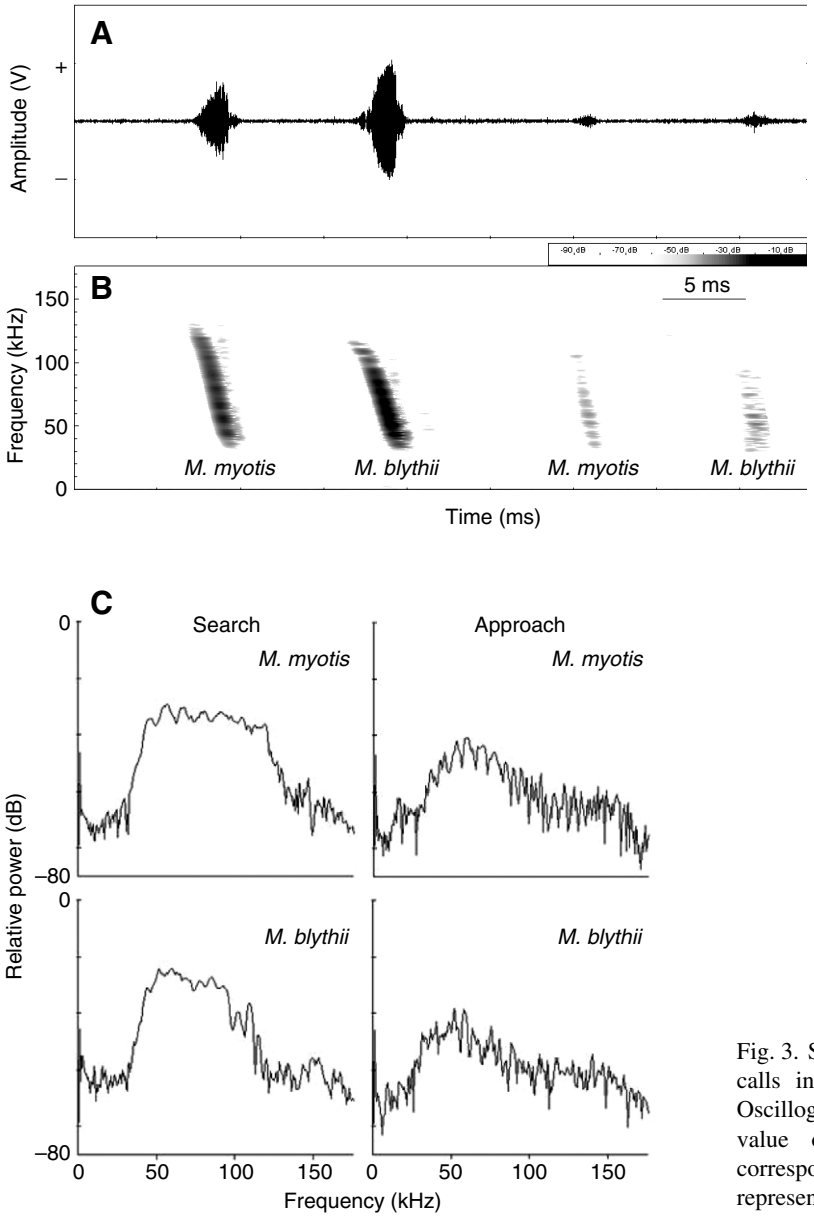

Fig. 3. Search (i.e. phase 1) and approach (phase 3) echolocation calls in mouse-eared bats *Myotis myotis* and *M. blythii*. (A) Oscillograms, (B) spectrograms, (C) power spectra. The '0 dB' value on power spectra is an arbitrary reference level, corresponding to the maximum allowable signal level that can be represented in the given digitisation format.

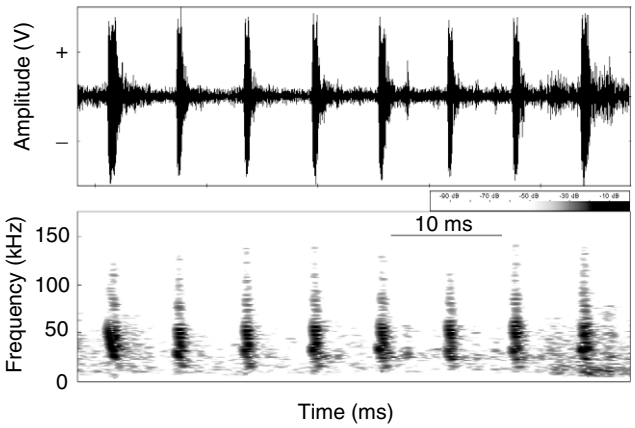

Fig. 4. A typical buzz emitted by a landing *Myotis myotis*. The background noise is due to the bat's touch down on litter.

recordings: no significant difference between species was found for both single call bandwidths (*M. myotis*=78.6±5.5 kHz; *M. blythii*=85.1±11.9 kHz; ANOVA, F=1.09, n.s.) and those calculated as individual means (three calls/bat; *M. myotis*=76.9±5.5 kHz; *M. blythii*=81.7±8.8 kHz; ANOVA, F=0.99, n.s.).

Maximum relative power did not differ between species, but the power difference among echolocation phases that was assessed visually from power trends over time (Fig. 1) was confirmed statistically: phase 1 contained calls with significantly more power on average than calls in phases 2 and 3 (Tukey test, P<0.001), which did not differ from each other.

Pulse rate did not differ between species. Phase 1 pulse rate did not differ from phase 2 (GLM on log-transformed values); phase 3 differed from both phases 1 (Tukey test, P<0.001) and 2 (P<0.005), highlighting a progressive increase in pulse rate (Table 2). Duration of the approach phase (phases 2 and 3 lumped together) tended to be longer in *M. myotis* than in *M. blythii* (Table 2), but the difference barely approached significance.

Discussion

Our study proved that during hunting by passive listening, mouse-eared bats adopted a 'whispering echolocation' mode. It also showed the occurrence of a species-specific trait (a buzz emitted on landing), which may have implications for niche separation and support new hypotheses on the functional role of buzzes for landing control in these sibling species.

Production of weak calls by mouse-eared bats

In our study, neither species fully ceased echolocating when approaching prey, i.e. we had no evidence for silence. Bats mostly emitted very weak echolocation calls, corresponding to those we categorised as phases 2 and 3. The occasional presence of calls recorded as stronger in phase 3 relative to phase 2 was probably due to the bat being extremely close to the microphone during phase 3. However, no significant

Table 1. *Mean values of variables for buzzes produced on landing by Myotis myotis*

Bat	N	Number of components	Minimum frequency (kHz)	Maximum frequency of top harmonic (kHz)	Maximum frequency of fundamental (kHz)	Mean duration of buzz pulses (ms)	Duration (ms)	Mean f_{MAXE} (kHz)	Mean relative power (dB)
Bristol									
A	8	2.9 (0.8)	13.0 (2.0)	145.4 (15.4)	34.1 (6.8)	1.3 (0.2)	14.2 (5.2)	35.2 (7.3)	–18.8 (4.0)
B	12	5.3 (0.9)	10.4 (2.5)	148.0 (10.1)	24.3 (3.2)	1.5 (0.3)	29.7 (6.1)	29.1 (7.8)	–17.6 (2.9)
C	8	10.5 (4.8)	12.5 (2.4)	103.5 (23.7)	24.6 (3.0)	1.2 (0.2)	55.2 (30.6)	27.8 (3.6)	–21.6 (3.9)
D	10	4.6 (3.0)	10.3 (2.9)	129.0 (27.0)	26.5 (3.3)	1.4 (0.3)	23.6 (18.3)	32.3 (8.1)	–20.3 (4.7)
Mean		5.8 (3.3)	11.6 (1.4)	131.5 (20.5)	27.4 (4.6)	1.4 (0.1)	30.7 (17.6)	31.1 (3.3)	–19.6 (1.7)
Sion									
E*	4	4.7 (1.0)	12.0 (0.8)	154.5 (14.8)	33.0 (1.4)	1.6 (0.4)	25.8 (8.0)	28.6 (4.1)	–21.0 (0.6)
F*	2	3.0 (0.0)	13.0	157.1	56.0	1.2 (0.2)	17.4	37.2 (2.2)	–23.9 (0.5)
G	2	3.0 (0.0)	14.0 (0.0)	119.5 (0.7)	28.5 (0.7)	1.4 (0.2)	14.6 (0.0)	32.6 (0.1)	–25.4 (0.3)
H*	2	3.5 (0.7)	19.0	109.0	38.0	1.3 (0.3)	20.6	30.2 (5.8)	–30.8 (3.2)
I*	2	3.5 (0.7)	15.0	119.0	33.0 (1.41)	1.4 (0.2)	21.4	32.4 (8.5)	–24.6 (1.6)
Mean		3.5 (0.7)	14.6 (2.7)	131.8 (22.3)	37.7 (10.8)	1.4 (0.1)	20.0 (4.2)	32.2 (3.3)	–25.2 (3.6)

Values shown refer to four bats (38 sequences) recorded for behavioural analyses (Bristol; Arlettaz et al., 2001) and five bats recorded in Switzerland (Sion; 12 sequences; this study). *For a few bats, variables other than number of components were calculated for a subset of recordings (bat E, N=2; bats F,H,I, N=1), because in the remaining cases maximum frequency exceeded the top value reliably represented (175 kHz) at the sampling rate (350 kHz) adopted. Samples were not lumped together because of the different recording equipments employed in the two cases (Bristol: Ultra Sound Advice S25 bat detector and Racal high speed recorder; Sion: Pettersson D980 bat detector and laptop computer for file storage).

Values are means (±s.d.); N=number of trials/bat; f_{MAXE} = mean frequency of maximum energy; maximum frequency of top harmonic = maximum frequency value reached by the highest harmonic component in the buzz.

Table 2. *Descriptive statistics for echolocation sequences produced by Myotis myotis and M. blythii*

Variable	*Myotis myotis*	*Myotis blythii*	ANOVA (GLM) level of significance (*P*)	
			Species	Phase
f_{MAXE} (kHz)			0.023	0.884
Phase 1	55.1 (8.9)	47.6 (5.3)		
Phase 2	55.8 (13.6)	49.5 (9.0)		
Phase 3	54.0 (5.2)	51.2 (7.4)		
Maximum relative power (dB)			0.111	<0.001
Phase 1	–39.83 (3.66)	–36.0 (3.3)		
Phase 2	–49.16 (3.93)	–48.0 (3.0)		
Phase 3	–46.98 (5.73)	–46.2 (5.6)	0.002	
Call duration (ms)				
Phase 1	1.9 (0.3)	2.3 (0.3)		
Pulse rate (s^{-1})			0.217	0.001
Phase 1	10.1 (3.1)	13.0 (7.6)		
Phase 2	11.0 (5.4)	18.3 (9.0)		
Phase 3	26.8 (17.5)	23.9 (21.8)		
Approach phase duration (ms)	972 (668)	522 (286)	0.072	

Values are means (±s.d.); *N*=8 *Myotis myotis*; *N*=10 *M. blythii*.

f_{MAXE}, frequency of maximum energy; pulse rate, number of calls in phase/phase duration (s).

All between-factor interactions in GLM failed to reach significance (*P* levels are not shown). Variable values are means of individual means from two sequences/bat. Call duration was measured only from phase 1 calls with a high signal-to-noise ratio.

difference was found between such two phases, both phases including calls of low amplitude emitted during prey approach. Proximity to the microphone may have slightly reduced the significant difference found in maximum power between search and approach phase calls. The persistence of weak calls in these species, as opposed to a real ‘silent phase’, seems to be more frequent than previously thought (Arlettaz et al., 2001). Whether this discrepancy is due to the difference in the duration of captivity (shorter in this study), possibly implying a different ‘weight’ of spatial memory in hunting behaviour (Ratcliffe et al., 2005), in sample size (larger in this study) or in recording equipment sensitivity, may be debated. In several of the sequences we examined, sound was hardly audible when time-expanded recordings were played back, and spectrograms of calls could barely be visualised during sound analysis. Indeed, ‘silent phases’ by gleaning bats, in these (Arlettaz et al., 2001) as well as other species (Ratcliffe and Dawson, 2003), may partly contain calls so weak as to be overlooked because unrecorded, or unnoticed during analysis (Schmidt et al., 2000; Schnitzler et al., 2003). If so, ‘weak’ rather than fully ‘silent’ approaches might be more common than is supposed.

Echolocation call sequences produced by *M. myotis* and *M. blythii* during gleaning differ from those produced during aerial hawking. During aerial hawking, a steady stream of calls is produced and call repetition rate increases through the buzz. In *Myotis daubentonii*, call intensity is reduced steadily and most strongly in the last 500 ms of the capture manoeuvre (Boonman and Jones, 2002). Typically, call intensity decreases by 4–6 dB/halving of distance (Hartley et al., 1989; Hartley, 1992a; Boonman and Jones, 2002). Hearing sensitivity also decreases when bats approach aerial targets (Kick and Simmons, 1984; Hartley, 1992b; Patheiger, 1998) to compensate for increases in echo strength as target range shortens. Such ‘automatic gain control’, concomitant with decreases in call intensity, may give the bats a constant sensation level in the auditory system during target approach when performing aerial hawking, although clearly this situation is very different from that in gleaning.

Antrozous pallidus (Le Conte 1856) forced to echolocate while performing passive listening increased echolocation interpulse intervals, probably to reduce temporal overlap between incoming signals (Barber et al., 2003). Unlike *Antrozous*, both *M. myotis* and *M. blythii* increased pulse rate during prey approach, a pattern commonly observed in bats foraging on the wing. *Megaderma lyra* E. Geoffroy 1810 also increases pulse rate when approaching prey (Schmidt et al., 2000; Ratcliffe et al., 2005). Production of faint calls may actually represent an alternative to decreasing pulse rate as a mechanism to reduce interference between echolocation and passive listening. In fact, calls and echoes may mask the faint prey-generated noises. Weaker signals are less effective in masking and therefore more appropriate during localisation of prey by passive listening. The constant occurrence of echolocation during passive listening suggests that its functional value offers advantages that outweigh the costs mentioned above. Although prey detection in clutter relies upon prey-generated sound or visual cues (sometimes olfaction), detecting the surroundings and dealing with the task of spatial orientation near background objects still requires echolocation (e.g. Fenton, 1990; Schnitzler et al., 2003). To detect its immediate surroundings, a bat probably only needs faint calls, as long as these produce intelligible echoes.

Moreover, the bat will not need to deal with superfluous echoes received from more distant objects away from its immediate surroundings.

Weak calls are routinely employed by *Plecotus auritus* (Linnaeus 1758), specialised in hunting in clutter (Waters and Jones, 1995; Swift, 1998). However, this species stops echolocating during the hovering phase (Swift and Racey, 2002). A mouse-eared bat calling weakly while approaching prey will probably be able to avoid collision with surrounding obstacles. *Mystacina tuberculata* Gray 1843 (Jones et al., 2003) emits echolocation calls on the ground at a low repetition rate for orientation while searching for food by prey-generated sound and possibly by olfaction.

Besides being employed for orientation, echolocation calls emitted soon before landing may still be valuable for tracking sudden prey movements. In some circumstances, for instance, prey might be alerted by an approaching bat flying low over the substrate, and react by jumping or flying (Swift, 1998). A fully 'silent' bat would probably miss the escaping prey, i.e. it would be unable to track it to the new position. By detecting prey movement through using echolocation, the bat might be able to adjust its gleaning manoeuvre, track the target to its new position or even attempt to catch it on the wing before the prey lands again.

Echolocation calls may alert prey that can hear ultrasound: calls produced immediately prior to landing might then decrease the bat's capture success rate. This is all the more true for *M. blythii*, whose diet largely includes tettigoniids that can hear ultrasound (Arlettaz et al., 1997b) and that may then evade capture by detecting the bat's calls early on (Schul et al., 2000; Schulze and Schul, 2001). Weak pulses can probably reduce this risk considerably, because prey will detect them too late to avoid capture. *M. nattereri* emits buzzes when gleaning, and feeds mostly on prey species that cannot hear echolocation pulses (Swift and Racey, 2002), whereas *P. auritus*, which approaches prey quietly, mostly captures moths sensitive to ultrasound (Waters and Jones, 1995; Swift and Racey, 1983; Swift and Racey, 2002).

Species-specific characteristics of echolocation during foraging

In general, *M. myotis* and *M. blythii* exhibited substantially similar echolocation patterns when approaching prey. The absence of marked differences between the two species matched our predictions, because both species have to cope with a comparable general orientation task and adopt a broadly similar foraging strategy (Schnitzler et al., 2003). The clearest difference in echolocation found between species is the occurrence, in some *M. myotis* foraging sequences, of a loud buzz.

Our observations clearly showed that buzzes emitted on landing are not part of *M. blythii*'s behavioural repertoire, at least in the experimental conditions adopted in this study. Arlettaz et al. also noticed the occurrence of the buzz, but their sample size was too small to highlight interspecific differences (Arlettaz et al., 2001). However, in those experiments too, only *M. myotis* emitted buzzes on touch down (R.A., unpublished observations). The presence or absence of conspecifics certainly did not affect buzz production, since buzzes were observed in both situations (D.R., personal observations). Note that both species are capable of emitting feeding buzzes (i.e. buzzes used to detect prey) when prey is airborne or gleaned from simple substrate such as Plexiglas (Arlettaz et al., 2001). This suggests that *M. blythii* may emit buzzes, but unlike *M. myotis* these are not produced soon before landing.

Feeding buzzes are widespread in the *Myotis* genus, and are commonly employed by both aerial hawkers and trawlers (e.g. Kalko and Schnitzler, 1989; Faure and Barclay, 1994; Britton et al., 1997; Siemers and Schnitzler, 2000; Siemers and Schnitzler, 2004). In *M. daubentonii*, as well as in the buzzes we recorded, buzz pulses are multi-harmonic (Kalko and Schnitzler, 1989). Several gleaning bats in the genus *Myotis* are versatile in their foraging behaviour, hunting both on the wing and by gleaning. In such cases, buzzes are produced during aerial hawking attacks, but not during substrate gleaning (Faure and Barclay, 1994; Ratcliffe and Dawson, 2003).

We hypothesise that by emitting a buzz, *M. myotis* may rapidly update information on distance to its landing spot and hence ensure a safe touch down. During touch down, call patterning is most likely driven by the informational needs for landing control and not for prey localization (achieved by passive listening).

'Landing buzzes' are also mentioned for another substrate-gleaning *Myotis* (*M. lucifugus*) (Buchler, 1979). Moreover, such signals are emitted by non-gleaning bats such as *Eptesicus nilssoni* (Rydell, 1990) and *Rhinolophus ferrumequinum* (Tian and Schnitzler, 1997). However, the landing buzzes in these species are quite different from the explosive sequences recorded in our study. For instance, Rydell mentions that *E. nilssonii* buzzes are 'weak' (Rydell, 1990). As with feeding buzzes by other *Myotis* species (Ratcliffe and Dawson, 2003), buzz structure could not be divided into phases I and II [a categorisation applied to feeding buzzes by several aerial hawking bat species (e.g. Kalko and Schnitzler, 1989; Surlykke et al., 1993; Kalko, 1995)].

The large occurrence of ultrasound-sensitive prey (tettigoniids) (Arlettaz et al., 1997b) in the diet of *M. blythii* may explain why such a 'landing buzz' is absent in this species. In fact, the production of such loud signals close to tympanate prey might alert it, so that the attack would probably fail. In other words, the presence of a buzz in *M. myotis* but not in *M. blythii* might be a consequence of niche segregation in these cryptic vespertilionids.

Caution is needed when attributing biological significance to the interspecific difference noticed in variables such as f_{MAXE} and duration of echolocation calls. Experiments in captivity are inevitably limited, as they generally rely on limited sample sizes and take place in conditions that only resemble those found in the wild. The f_{MAXE} values recorded are considerably higher than those documented either for free-flying (e.g. Barataud, 1996) or hand-released (Russo and Jones, 2002) mouse-eared bats. During trials, *M. myotis* called at ca. 55 kHz,

M. blythii at ca. 47 kHz. When recorded on release in southern Italy, the two species emitted calls at frequencies as low as 39 kHz and 41 kHz, respectively (Russo and Jones, 2002). 'Clutter effects', such as proximity to walls or floor, may have caused an increase in frequency values.

In conclusion, both species proved flexible in foraging behaviour, being able to deal with an identical gleaning task. However, at least one major species-specific difference found – the presence of a terminal buzz emitted on landing by *M. myotis* only – may have important implications for niche separation. The presence of landing buzzes – representing, at least in the experimental set adopted for this study, a major interspecific trait distinguishing the two sibling species – suggests the existence of bioacoustical specialisation in different prey.

Such buzzes are clearly not needed for prey detection: under the same experimental conditions (prey hidden in leaf litter) both mouse-eared bats perform equally well in prey capture (Arlettaz et al., 2001) (this study). In theory, the same results would be obtained if the two species differed in their ability to detect prey using prey-generated sounds, and *M. myotis*, but not *M. blythii*, required buzzes to track down moving prey. However, in the experimental conditions adopted for both this and an earlier study (Arlettaz et al., 2001), *M. myotis* was recorded to produce buzzes even when prey was either motionless (dead) or absent. Therefore, the buzz function we propose (i.e. to facilitate a safe landing) is the most probable.

In our experiments, considerable variation was revealed in buzz production, including some subjects that always produced buzzes, others sometimes, and the remaining never. We found that buzz emission did not depend upon the attack angle followed during landing. Moreover, it was not influenced by the presence of conspecifics. A great variation was also noticed in the number of buzz components, especially in the dataset from Bristol. In the latter case, the much longer duration of the experiments probably allowed for the detection of a greater intra-individual variability, with up to 18 components noticed in a single buzz. Individual or situation-specific differences behind these patterns remain to be understood.

Our results show that passive listening for prey-generated sounds and the production of echolocation calls are not mutually exclusive. Moreover, the species-specific nature of the landing buzz adds further evidence that echolocation is a plastic sensory system, which might readily adapt to the different tasks associated with diverging niche evolution trajectories among closely related species.

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