IDENTIFYING LITTLE SANDY DESERT BAT SPECIES FROM THEIR ECHOLOCATION CALLS

N.L. MCKENZIE AND R.D. BULLEN


In combination, the frequency maintained for the greatest number of cycles (\(F_{\text{peakC}}\)) and the width of this peak (quality factor) identified search-mode echolocation calls of nine species comprising the bat fauna of Australia's Little Sandy Desert. These data were derived from the frequency spectrum profile of frequency-divided calls. Differences between \(F_{\text{peakC}}\) quality factors of arid-zone emballonurid and molossid calls were functionally consistent with their different foraging strategies.

Key words: bat, echolocation, call identification, spectral profile, foraging strategy.

N.L. McKenzie, Department of Conservation and Land Management, PO Box 51, Wanneroo, Western Australia 6065, Australia. R.D. Bullen, 43 Murray Drive, Hillarys, Western Australia 6025, Australia. Manuscript received 29 July 2002; accepted 5 March 2003.

A number of factors influence sonar design in bats. Within a species, apparent variation can be related to differences between individuals and between populations (e.g., Parsons 1997; Barclay et al. 1999; Murray et al. 2001), to Doppler effects (e.g., Guppy and Coles 1988), to signal recording and analysis techniques (Parsons et al. 2000), to habitat differences and presence of conspecifics (Obrist 1995), and to the foraging context in which a bat is emitting calls (including the 'search', 'approach' and 'interception' phases in call sequences e.g., Griffin et al. 1960; Schnitzler et al. 1987; Kalko and Schnitzler 1993).

Search-mode calls are known to be useful for acoustic identification of species (e.g., O’Farrell et al. 1999; Murray et al. 2001). They are prominent above background noise levels and, by measuring call repetition-rates, can be uniquely discriminated from other phases of call sequences, thereby reducing the variability problem.

Most published attempts to differentiate Australian bat species from their calls have relied on parameters derived from zero-crossing analysis in time domain (Fenton 1982; Jones and Corben 1993; Chick et al. 2000). When we applied this technique in the Carnarvon Basin of Western Australia (McKenzie and Muir 2000), we were often unable to distinguish between molossid and emballonurid call sequences, even when the analysis was confined to search-mode calls (e.g., yellow-bellied sheathtail-bat *Saccopteryx bilineata*, and common sheathtail-bat *Eumops perotis*, and common sheathtail-bat *Taphozous georgianus* from Beccari's freetail-bat *Mormoops beccarii*). In approximately 50% of cases across the range of frequency values observed, the identifications were confounded by overlap in species’ parameter values.

In this paper we use spectral analysis in frequency domain in an attempt to more clearly differentiate the search-mode echolocation calls of nine microbat species from the Little Sandy Desert. This fauna includes arid zone populations of the molossids and emballonurids listed above. Reliable identification of these nine bats from their echolocation calls allowed us to compile data on the foraging niches and flight capabilities of free-flying bats in the Desert (McKenzie et al. 2002).

METHODS

Echolocation calls

Species nomenclature follows Strahan (1995) except for the white-striped freetail-bat *Tadarida australis* Gray, 1838. During field work in 1996, echolocation call sequences by free-flying bats of known identity were recorded from: 1) bats captured in mist nets set over pools and in riparian woodlands, then released with bioluminescent tags (Buchler 1976) and recorded on subsequent passes. 2) bats that we collected while their echolocation calls were being tape-recorded (CALM Animal Ethics Permit No. 14/93). 3) recordings of species in surrounding regions if we were unable to record then in the study area. We excluded sequences in which a second bat was present. The emballonurid and molossid call sequences used were from bats flying in uncluttered air spaces.
Call sequences were recorded using the frequency-division function of Anabat II (Titley Electronics, Australia) or D940 (Pettersson Elektronik, Sweden) ultrasound detectors (divided by 16 or 10, respectively). The frequency-division function using Zero-crossing analysis within these detectors is known to operate on the strongest harmonic present (Parsons et al. 2000), normally the fundamental harmonic. Output was stored directly onto Metal IV cassette tapes using a Sony Walkman Professional (WMD6C) tape recorder.

COOL EDIT 95 (Syntrillium Software, USA) was used to digitize the analogue tape recordings as '.wav' files using a sampling rate of 44100 at 16-bit resolution, then to display each call sequence in time domain. We measured only consistently shaped, regularly spaced, sequential sets of calls emitted at a rate of no more than one call per wing-beat, and with a clean, well-defined shape. These were calls of bats in 'search' mode, rather than 'approach', 'interception' or 'departure' phases of sequences (Schnitzler et al. 1987; Kalko and Schnitzler 1993, 1998; McKenzie and Muir 2000). Search-mode echolocation calls are emitted during the wings’ down-stroke in most species (Lancaster et al. 1995). Unlike 'approach' and 'interception' calls, only a single search-mode call is emitted during every down-stroke, or every second or third etc, so the time between successive search-mode calls is an integer multiple (x 1, x 2, ...., x n etc) of wing beat frequency. Given that microbat species all flap their wings at similar frequencies (7 - 12 Hz: Schnitzler et al. 1987; Bullen and McKenzie 2002a), call repetition rates can be used to distinguish periods of 'search mode' in sequences recorded from free-flying bats. Typically, at least three seconds were required before bats settled into a normal search mode call sequence following hand-release (Obrist and Wenstrup 1998; McKenzie and Bullen unpubl. data). During the course of the study, we noted that call characteristics changed once the bat was illuminated by the spotlight. Calls emitted after this point were excluded from analyses.

We used COOL EDIT 95 to carry out a 2048-point Blackmann-Harris fast-Fourier transformation of each call (Fig. 1). This analysis provided the frequency spectrum of the call’s strongest harmonic. The analysis window’s width was selected so that it covered the entire duration of each call. The frequency that was maintained for the greatest number of cycles (Fpeak) could be determined from the frequency profile (see Fig. 1). Each search-mode call was transformed to obtain this value, then the mean and standard deviation of Fpeak was calculated for each species. Where the range of Fpeak values for different species overlapped, we measured the quality factor (Q) of the strongest harmonic (Laverghetta 1981): Q = Fpeak/width of Fpeak. By convention the Q-factor is measured at 50% of the cycle-count at Fpeak in the frequency spectrum (equivalent to 6 dB below peak from the fast-Fourier transformation) (Fig. 2).

Regression analysis was used to test the relationship between Fpeak and Q in each species, then an 'homogeneity-of-slopes test' was applied to determine whether the regression lines for each species had the same slope (SAS General Linear Models procedure). While the Q-factor data was found to be mildly heteroscedastic when diagnostic tests were carried out as part of the regression procedure, they were not appreciably (or significantly) different from a normal distribution.

**RESULTS**

Fpeak could be used to uniquely identify five of the nine Little Sandy Desert species (Fig. 3). *S. flaviventris* calls >16.5 kHz overlapped with the observed range of *C. jobensis* calls, while *T. georgianus* calls >24.3 kHz overlapped with the observed range of *M. beccarii* calls.

Although not recorded from the Little Sandy Desert, Hill’s sheath-tail-bat *Taphozous hilli* occurs in all surrounding regions in Western Australia’s arid zone, so its call data were included in the subsequent analysis for completeness. The regression equations relating Fpeak and Q-factor for *S. flaviventris*, *C. jobensis* and *M. beccarii* showed gradients that were significantly different from zero (Fig. 4). Homogeneity-of-slopes tests showed that *S. flaviventris* had a different slope to *C. jobensis* (F = 108.6, d.f. = 211, P < 0.0001), and *M. beccarii* had a different slope to both *T. georgianus* and *T. hilli* (F = 16.2, d.f. = 355, P < 0.0001). At low Fpeak values in their strongest harmonic, calls emitted by *S. flaviventris* had significantly higher Q-factors than calls of equivalent Fpeak emitted by *C. jobensis* (Fig. 4).

Similarily, *T. georgianus* and *T. hilli* regression lines were compared, their Q-factors (y-axis intercepts) were significantly different (estimated difference in intercepts = 1.19, s.e. = 0.25, P < 0.0001) even though their gradients were not (estimated difference in slopes = -0.27, s.e. = 0.44, P = 0.54).

The third molossid in the Little Sandy Desert is *Tadarida australis*. While the Fpeak values of its search mode calls are unique in the fauna (Fig. 3), their Q-factors are consistently low, with values comparable to the other molossids (5.82, s.d. = 1.14, n = 13 calls, N = 3 individuals)(see Fig. 4). Thus, the three arid-zone emballonurids used calls with higher Q-factors than the three molossids belonging to the same faunas.
Fig. 1. *Mormopterus beccarii* search-mode call recorded using an ANABAT II detector, and displayed in frequency-time domain using COOL EDIT. Results of a spectral analysis of the entire call (‘Analysis window’) are included on the right-hand side of the figure as a plot of ‘dB’ (a direct measure of the number of cycles) versus ‘frequency’. The fundamental harmonic (1), as well as higher harmonics (3 to 9), are visible in both displays. ANABAT II produces a square-wave output, so these higher harmonics are artifacts produced by COOL EDIT’s Fast Fourier Transform routine. ANABAT’s analysis result (fundamental harmonic only) has been superimposed for comparison.
Fig. 2. Typical frequency profile of the strongest harmonic in search-mode calls by *S. flaviventris*, *C. jobensis*, *T. georgianus* and *M. beccarii*. Calls of equivalent *F*<sub>peak</sub> were chosen for this comparison (*Sf* at 17.4 versus *Cj* at 17.7 kHz; *Tg* at 24.7 versus *Mb* at 25.3 kHz). Resonance width 50% below the peak number of cycles (see arrows) was used in calculating a call’s Q-factor.

Fig. 3. Peak frequency of search-mode calls by Little Sandy Desert microbats plotted against usual foraging strategy (from McKenzie et al. 2002). Standard deviation bars are shown. Species codes comprise the first letter of the genus and species names. Sample sizes (Number of individuals, average number of calls per individual +/- s.d.): *Tadarida australis* (*Ta*, 5, 14.8 +/- 10.1), *Chalinolobus gouldii* (*Cg*, 4, 14.3 +/- 7.8), *Scotorepens greyi* (*Sg*, 5, 13.0 +/- 9.2), *Vespertulus finlaysoni* (*Vf*, 6, 9.7 +/- 5.6), and *Nyctophilus geoffroyi* (*Ng*, 4, 8.3 +/- 3.4). *Saccolaimus flaviventris* (*Sf*), *Chaerephon jobensis* (*Cj*), *Taphozous georgianus* (*Tg*) and *Mormopterus beccarii* (*Mb*) sample sizes are listed in caption to Fig. 4.
Fig. 4. Scatterplot of $F_{peakC}$ versus Q-factor of the strongest harmonic in ‘search-mode’ echolocation calls by *S. flaviventris* (●), *C. jobensis* (x), *T. georgianus* (▲), *T. hilli* (Δ) and *M. beccarii* (+). Sample sizes (Number of individuals, average number of calls per individual ± s.d.): $Sf$ (13, 6.1 ± 4.1), $Cj$ (16, 8.7 ± 5.0), $Tg$ (13, 6.8 ± 3.9) and $Th$ (16, 8.4 ± 3.9). Regression lines are discussed in ‘Results’. 
DISCUSSION

The profile of the frequency spectrum of search mode calls is a useful survey tool. In combination, $F_{peak}$ and Q-factor discriminated all species (but not all calls) recorded from the Desert. Our study also reveals systematic relationships between echolocation call variables that contribute to the observed variation in call sequences. A similar analytical approach has been used to distinguish calls by the seven species of *Nyctophilus* known from Western Australia (Bullen and McKenzie 2002b), although the pattern of $F_{peak}$ values (therein termed $F_{peak}$) from call-to-call in sequences was important for *Nyctophilus*, rather than the spectral profile of the individual calls.

To explain why the Q-factor of the strongest harmonic might discriminate molossid from emballonurid calls of similar $F_{peak}$ (Fig. 2), we need to consider the functional implications of Q-factor in frequency modulated calls of low-duty-cycle. High frequency echolocation provides detailed imagery at the expense of range, so fast-flying species of open and semi-open airspaces detect prey at a distance by concentrating the energy in their brief search-mode calls at the lower end of the frequency sweep, thereby increasing their sonar range (Simmons and Stein 1980; Kingston et al. 1999). The ‘shallow sweep’, low frequency calls emitted in search mode by Little Sandy Desert molossids and emballonurids are typical examples.

Lancaster et al. (1995) concluded that even the powerful, low-frequency component of search-mode calls may be cost-neutral if produced as a by-product of the flight muscle contractions that drive the wings' down-stroke. Nevertheless, the energy-cost of these calls limits the distance at which prey can be detected, and the limit is severe because power is inversely proportional to distance squared and is further attenuated by the atmosphere (Lawrence and Simmons 1982). Bat detection-ranges for insect-sized targets are “just a few metres” (Fenton et al. 1995 p. 233). For instance, Kick (1982) reported that *Eptesicus fuscus* first detected a 19 mm diameter sphere at 5 m, while Fenton (1982) reported insect detection ranges of 3 to 5 m for *Chalinolobus nigrogriseus*, and of less than 2 m for *Eptesicus pumilis*. This means that, at its foraging speed of 5 m s$^{-1}$, *E. fuscus* has only one second from detection to contact with an insect-sized prey (Fenton et al. 1995).

If the $F_{peak}$ of search-mode calls was concentrated into an extremely narrow resonance width, range would be maximised for a given muscle power-output. Alternatively, call energy cost would be minimised without loss of range. Our data show that Little Sandy Desert emballonurids in search-mode use calls with this type of frequency peak (high Q-factor). The narrowness of the peak improves prey-detection distance, but provides less information on shape, orientation, flight-path and size of the prey than an equivalent call with more complexity in the peak of the strongest harmonic (Moss and Zagaeski 1994; Jensen et al. 2001). Given that Little Sandy Desert emballonurids are able to perform abrupt manoeuvres (McKenzie et al. 2002), they can delay characterising and tracking a target until it is close enough for the available power to be dispersed across a wider range of frequencies.

In contrast, the molossids are aerial interceptors – they rely on speed rather than agility to catch prey. They forage at 7 - 8 m s$^{-1}$ but are unable to generate abrupt turns (Bullen and McKenzie 2001; McKenzie et al. 2002), so they probably need to characterise and track airborne prey from the moment of detection. To do this, the $F_{peak}$ of the strongest harmonic in molossid search-mode calls needs to be complex as well as intense, implying width. Observed differences in the Q-factor of the $F_{peak}$ in ‘shallow-sweep’ search-mode calls by Little Sandy Desert emballonurids and molossids are consistent with these deductions (Figs 2, 4). The bats were flying in open microhabitats (as defined in McKenzie et al. 2002) at the time their call sequences were recorded, so the proximity of obstructions was unlikely to have caused the observed call differences.

Obrist et al. (1993) found that the specialisation for long-range target detection was most obvious in high-flying emballonurids and, especially, molossids. Both families used search-mode calls dominated by an intense low-frequency component, and showed “more obvious correspondence between directionality patterns [important for tracking moving targets] and echolocation calls” (p. 148) than the other nine microbat families assessed in that study. In relation to the directional sensitivity of hearing in bats, their data showed that molossid pinna features and highest ‘interaural intensity difference’ (IID) values were matched to lower frequencies (i.e. most effective at greater distances) than those of emballonurids. “In some emballonurids, pinna features best matched the FM part of their vocalizations, and in other [emballonurid] species they best matched the second harmonic of the call. In the ... three molossids ... the IID shows peaks and steepest slope at the dominant sonar component” (p.148). These data are consistent with our view that, although both families detect their prey at long range, molossids are adapted to characterise and track airborne prey from a greater distance than are emballonurids.

We suggest that the $F_{peak}$ characteristics of search mode calls by molossids and emballonurids are constrained by anatomical differences in vocal
apparatus and airframe. Both of these are associated with the evolutionary divergence of these two families towards different foraging strategies – air superiority in the case of the emballonurids, and air interceptor in the case of the molossids.

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REFERENCES


