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Mysterious *Mystacina*: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey

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Summary

The New Zealand short-tailed bat *Mystacina tuberculata* evolved in the absence of terrestrial mammals and initially with few potential predators. Unusual among bats, it is well adapted for the capture of prey on the ground. Bats from Fiordland, New Zealand had relatively low wing loadings and aspect ratios adapted for flight in cluttered habitats. We predicted that *M. tuberculata* would locate prey in air (uncluttered space) by echolocation. Echolocation call sequences associated with prey capture (terminal buzzes) were heard in the field, and bats detected and localized prey suspended on fishing line by echolocation in a flight cage. The bats emitted brief, multiharmonic echolocation calls at low duty cycle during search phase, and 64% of calls contained most energy in the fundamental harmonic. Approach- and terminal-phase calls were also broadband and multiharmonic. We predicted that bats would not use echolocation to locate prey hidden on the ground in leaf litter (cluttered space). Bats seemed unable to locate hidden prey precisely from the air and instead hunted for such prey while crawling. Echolocation calls were emitted at a low repetition rate on the ground, suggesting that here echolocation was used for orientation and not for prey detection. We experimentally removed cues available to the bats and showed that bats located mealworms in leaf litter by listening for prey-generated noises and possibly by olfaction.

Key words: echolocation, predation, clutter, sensory ecology, bat, *Mystacina tuberculata*.

Introduction

The New Zealand short-tailed bat *Mystacina tuberculata* (Chiroptera: Mystacinidae) has been of great interest to biologists (see Lloyd, 2001 for a review). It is one of only two extant indigenous mammals in New Zealand, the other being the long-tailed bat *Chalinolobus tuberculatus* (O'Donnell, 2001). It therefore evolved in the absence of small terrestrial mammals and, until recent introductions of predators by humans, may have been exposed to few predators. The absence of small terrestrial mammals and reduced predation risk may have permitted the exploitation of terrestrial prey by *M. tuberculata*. Dietary analyses show that *M. tuberculata* is omnivorous, eating arthropods (many of which are non-flying), pollen, nectar (Arkins et al., 1999) and fruit (Daniel, 1979, 1990). While most bats capture prey in the air, or by briefly gleaning from surfaces, *M. tuberculata* is unusual in that it searches for both plant material (Daniel, 1979) and insects (Parsons, 1998) while on the ground. *M. tuberculata* shows several adaptations for terrestrial behaviour. Strong legs and feet confer considerable agility on the ground (Dwyer, 1962; Daniel, 1976), and basal talons on the claws may be used in burrowing (Daniel, 1979). Moreover, the bats can fold their wings tightly, allowing use of the forearms for terrestrial locomotion (Dwyer, 1962; Daniel, 1979). Indeed, Daniel (1979) speculated that *M. tuberculata* might spend up to 40% of its time foraging on terrestrial and arboreal invertebrates.

The varied diet and terrestrial adaptations of *M. tuberculata* make it interesting from a sensory ecology perspective. *M. tuberculata* has relatively large ears (O'Donnell et al., 1999) and prominent nostrils (Daniel, 1979), implying that it may listen for prey-generated sounds and may use olfaction in the detection of food. Because the bats eat both volant and non-volant arthropod prey (Arkins et al., 1999), we expect that they will face different sensory challenges for the detection and localization of prey in cluttered (clutter echoes are echoes other than those from the target of interest) and non-cluttered space (Faure and Barclay, 1994). In highly cluttered space, background echoes overlap with prey echoes, and masking of prey echoes by clutter echoes makes detection of prey problematic. Bats that emit frequency-modulated (FM) calls mainly use prey-generated acoustic cues for the detection and localization of prey in clutter (Schnitzler and Kalko, 1998). The Indian false vampire bat *Megaderma lyra* may use echolocation to detect prey in limited clutter (Schmidt et al.,

2000), but one feeding situation presented here (prey buried under leaf litter) will preclude the use of echolocation for detection of prey. Recent work on mouse-eared bats *Myotis myotis* and *Myotis blythii* showed experimentally how bats used echolocation to detect aerial prey but required prey movement to rapidly detect prey in leaf litter. The bats also greatly reduced the intensity of echolocation calls emitted immediately prior to prey capture in leaf litter (Arlettaz et al., 2001).

We therefore predict that the diversity of sensory challenges that *M. tuberculata* faces when foraging will result in it adopting a range of mechanisms for the detection of arthropod prey. We first describe the echolocation calls of *M. tuberculata* from field recordings, and we show how this species has a wing shape suitable for foraging in habitats that contain considerable physical clutter, such as forest interiors. We then determine how *M. tuberculata* detects and locates arthropod prey in uncluttered space (by aerial hawking) and in leaf litter, where echolocation calls will not be able to reach prey buried in clutter. Specifically, we predict that, like another FM bat (*Myotis evotis*; Faure and Barclay, 1994), *M. tuberculata* will use echolocation to detect and localize aerial prey and will switch off echolocation when hunting for prey in clutter. Some bat species detect prey in clutter by listening for prey-generated sounds (*Plecotus auritus*: Anderson and Racey, 1991; *Antrozous pallidus*: Fiedler, 1979; Bell, 1982; Fuzessery et al., 1993), while another species (*Macrotus californicus*) locates terrestrial prey by vision (Bell, 1985). We therefore isolated cues available to the bats to determine how they found prey hidden in leaf litter. We investigated whether *M. tuberculata* detected buried prey by listening for sounds generated by prey movement. We also investigated whether olfaction plays a role in prey detection, given that the bats may locate nectar by this means.

Materials and methods

Study site

We studied bats from roosts in the Eglinton Valley, an area of temperate rainforest in Fiordland National Park, southern New Zealand (O'Donnell et al., 1999). This population consists of relatively large, short-eared *Mystacina tuberculata* Gray 1843 bats (O'Donnell et al., 1999). Tree roosts were in cavities of *Nothofagus fusca* beech trees, and the surrounding habitat (described in detail by O'Donnell et al., 1999) was forest alongside a river, with tussock grassland on the valley floor. We recorded bats flying around the roosting area (away from the roost exit) and along flight paths.

Wing shape analysis

We captured bats emerging from roosts by harp traps and by mist netting along flight paths. We traced wing outlines onto paper, digitized the tracings with a Summasketch III bitpad (Summagraphics, Seymour, CT, USA) connected to a PC. We measured the wing shape parameters described by Norberg and Rayner (1987). We measured forearm length to the nearest 0.1 mm with dial calipers, and body mass to the nearest 0.1 g with a spring balance.

Recording and analysis of echolocation calls

We used a time-expansion (10×) bat detector (D-980; Pettersson Elektronik AB, Uppsala, Sweden; frequency response ±3 dB, 20–120 kHz; Waters 1995) linked to a Sony WM-D6C Professional Walkman cassette recorder to record echolocation calls. We analysed sounds using BatSound (Pettersson Elektronik AB). Temporal characters were measured from waveforms, frequency parameters from spectrograms, with the exception of frequency of most energy, which was measured from power spectra [fast Fourier transform (FFT) size 512, Hanning window for all spectral analyses]. Maximal and minimal frequencies were measured at 30 dB below the power at the frequency of most energy.

Laboratory observations of foraging behaviour

Laboratory observations were made in a room 2.9 m×3.2 m×2.4 m. Bats were released into the room during their natural foraging hours and were observed and recorded from a covered recess on one side of the room. The room was dark, and bats were recorded under infrared illumination using a Sony TRV9E digital video camera in 'nightshot' mode. Bat echolocation calls were recorded using the equipment described in 'Recording and analysis of echolocation calls' above, with a 5 m cable leading from the bat detector to the microphone and 12 s of recording time. The microphone of the video camera recorded the frequency-divided output of the bat detector, and this allowed us to synchronise the bats' behaviour with the time-expanded recordings of echolocation calls. Synchronisation was facilitated by recording single flashes from a flashgun (Nikon SB12 Speedlight) on both audio (ultrasound from flash firing) and video tapes (light output recorded). To record bats capturing aerial prey, insects [moths (Lepidoptera), dobsonflies (Megaloptera: Corydalidae) and stoneflies (Plecoptera)] were suspended from fishing line (<1 mm diameter), and the microphone placed about 5 cm behind the prey item. To encourage foraging on the ground, a tray 120 cm×70 cm, with 7 cm-high walls, was filled with natural *Nothofagus* leaf litter. Bats learnt to land in the tray rapidly and began searching for food there without training.

Isolating cues used for the detection of prey in leaf litter

We predicted that bats might detect prey by echolocation, by vision, by listening for prey-generated sounds or by olfaction. For the detection of prey in leaf litter, we aimed to isolate cues as much as possible to determine which sensory mechanisms the bats used to detect prey hidden under leaf litter. We removed the possibility of the bats using echolocation by hiding prey under 3–4 cm of leaf litter. We argue that vision is also of no use in these situations, as the prey are concealed. Our experiments were conducted in complete darkness, under infra-red illumination. We therefore tried to isolate cues available from prey-generated sounds and smell experimentally. To isolate prey-generated sounds, we

Table 1. *Wing shape and other morphological measurements of* Mystacina tuberculata *from Fiordland*

Parameter	Females (*N*=9)	Males (*N*=9)
Body mass (g)	15.99±0.78	13.91±1.29
Forearm length (mm)	43.89±1.05	42.21±0.56
Wingspan (m)	0.315±0.008	0.296±0.0113
Wing area (m^2)	0.0160±0.0010	0.0159±0.0007
Aspect ratio	6.20±0.30	5.54±0.48
Wing loading (Nm^{-2})	9.86±0.83	8.61±0.79
Tip length ratio	1.38±0.07	1.33±0.07
Tip area ratio	0.91±0.08	0.78±0.06
Tip shape index	1.99±0.40	1.47±0.33

Wing shape parameters were defined by Norberg and Rayner (1987). Means ± S.D. are reported.

placed 25 mealworms in plastic dishes (diameter 15 cm) among leaf litter. In one dish, the mealworms were dead (killed by placing in boiling water), and hence generated no sound, in the other they were alive. The dish was covered with foil, and 25 dead mealworms were placed on the foil of both dishes as a reward for the bats finding the dish. Thus, both dishes were identical except that one contained live mealworms under the foil while the other contained dead mealworms. It is likely that the only difference in cues available to the bats under these treatments was the presence or absence of prey-generated sounds. Of course, in nature, prey movements might cause leaf litter to move, and such movement might be detectable by echolocation or by vision. The purpose of the experiment described here was to determine whether bats could locate prey by acoustic cues alone. The dishes were placed randomly in the tray of leaf litter, and we recorded which dish the released bat found first. To isolate olfactory cues, we tethered 10 dead mealworms (no prey-generated sounds) under the leaf litter (no echolocation cues) and recorded whether the bats found these in the dark (no visual cues) under infra-red lighting. The mealworms were placed at random positions within the tray. Tethering mealworms beneath the leaf litter allowed prey to be relocated easily by the experimenter and precluded the use of vision or echolocation by the bats for finding the tether. We used nine bats (adults or fully grown juveniles: seven males, two post-lactating females) and released bats at the site of capture within 10 days. All experimental sessions were performed with single bats, although groups of bats were initially allowed to familiarize themselves with the feeding arenas.

Results

Wing shape

Wing shape parameters of *M. tuberculata* are given in Table 1. When the values were converted into the size-independent principal component values Q_a (representing aspect ratio) and Q_l (representing wing loading) from equation 9 (p. 371) in Norberg and Rayner (1987), *M. tuberculata* was found to have a slightly lower aspect ratio (Q_a=–0.87) and wing-loading (Q_l=–0.45) than a species of 'average' morphology, lying in an area of morphospace that increases manoeuvrability alongside bats such as some rhinolophids and plecotines that often forage in forested habitats.

Field recordings of echolocation

We recorded 31 calls with good signal:noise ratio from nine bats flying in the forest. In addition, we analysed 11 calls from three bats recorded circling above us after release in open space away from trees (Table 2). Pulses and pulse intervals were substantially longer from bats released in the open, but frequency characteristics were similar in open and forest environments. In both situations, the calls were relatively brief and multiharmonic (Fig. 1). The frequency of most energy in the call was usually in the fundamental harmonic (64% of cases) but was often in the second harmonic (remaining cases). Pulse repetition rate was 12.4–13.8 Hz. The predicted wingbeat frequency for a bat with the body mass of *M. tuberculata* is 10 Hz (Jones, 1994), so it appears that *M. tuberculata* usually emits one pulse, sometimes two pulses, per wingbeat during search phase.

Detection of prey in uncluttered space

We sometimes heard terminal buzzes emitted by bats flying

Table 2. *Echolocation call measurements made from free-flying* Mystacina tuberculata

Call parameter	Forest (*N*=31 calls, 9 bats)	Open (*N*=11 calls, 3 bats)
Pulse duration (ms)	2.5±0.4	3.5±0.3
Pulse interval (ms)	72.3±23.4	80.7±18.9
Minimum frequency of fundamental harmonic (kHz)	18.6±0.8	19.3±0.8
Frequency of most energy in fundamental harmonic (kHz)	27.7±2.7	26.6±1.4
Maximum frequency of fundamental harmonic (kHz)	37.4±2.1	36.3±1.5
Upper frequency of third harmonic (kHz)	90.7±4.9	86.3±2.9
Frequency of most energy in second harmonic (kHz)	49.3±2.5	45.5±1.7

Calls were recorded in a forested area close to the roost or from three bats released in an open area devoid of trees. Means ± S.D. of all calls are reported.

around roost sites, suggesting that *M. tuberculata* hunts for aerial prey using echolocation. These buzzes were of relatively long duration and were clearly associated with foraging rather than obstacle negotiation. In the laboratory, *M. tuberculata* always emitted terminal buzzes when attacking prey suspended by fishing wire, showing that bats (50 captures from five individuals) detect prey in uncluttered prey by echolocation (Fig. 2). As in the field, search-phase calls were multiharmonic. Distinct approach and terminal phases were detectable during aerial feeding sequences, with calling terminated about 100 ms before striking the prey (Fig. 2). Typical of feeding sequences during aerial captures by bats, pulse duration and pulse interval decreased in the time leading up to prey capture (Fig. 2). Energy also became more concentrated in the fundamental harmonic relative to higher harmonics during the terminal phase of the buzz (Fig. 2C,D).

Detection of prey in leaf litter

Bats rapidly learnt to land on the litter tray and to search for food there. They never appeared to detect prey from the air and only started searching after landing on the ground. On the ground, bats moved rapidly and adeptly. They would frequently dig into the leaf litter with their forelimbs to find prey, sometimes disappearing completely under the litter. A typical echolocation call sequence from a bat finding prey with the presence of prey-generated sounds in a dish is shown in Fig. 3. The bat emitted search-phase calls during flight and

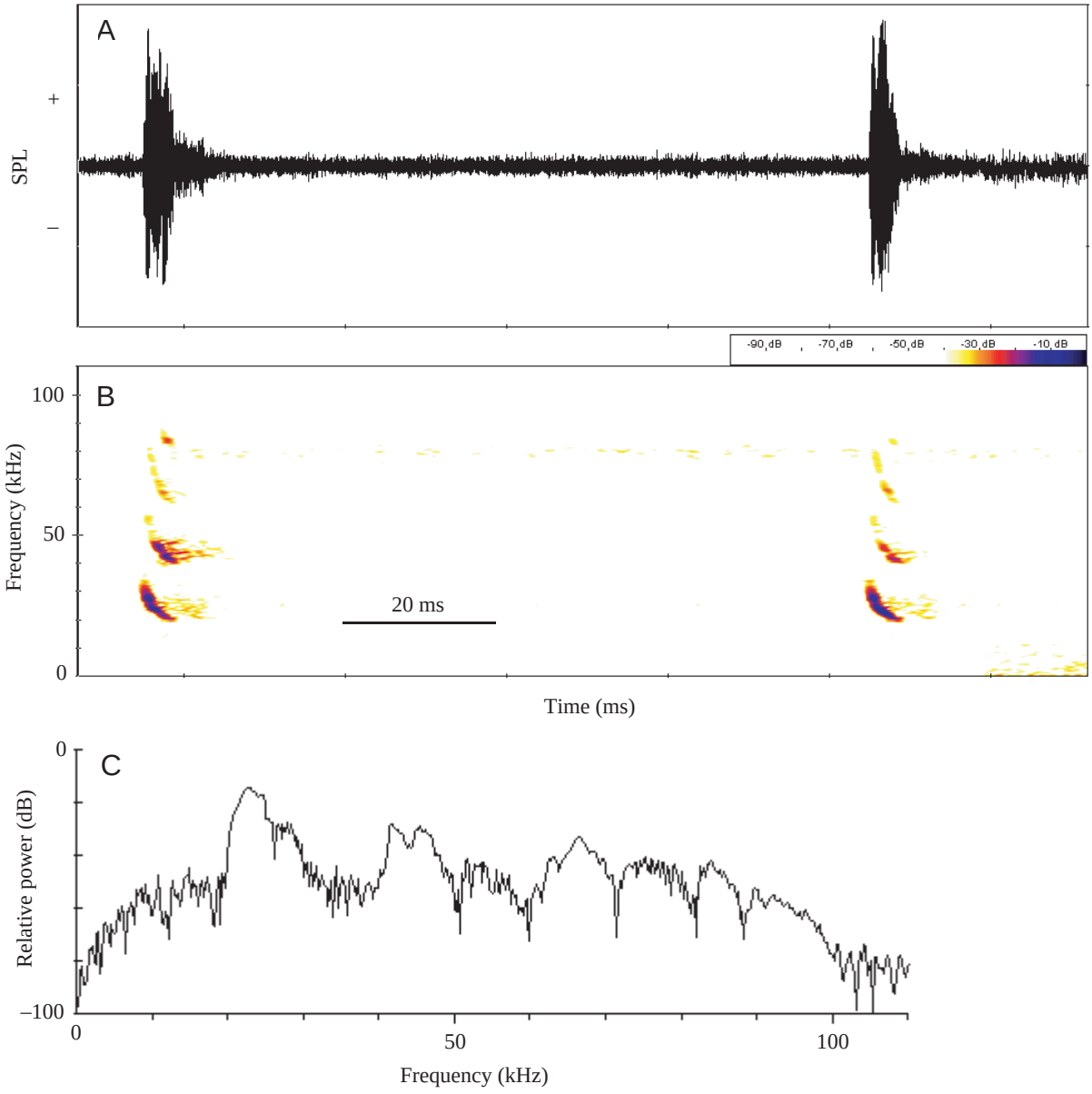

Fig. 1. Search-phase calls of free-flying *Mystacina tuberculata*. (A) The waveform and (B) the spectrogram of two consecutive calls. (C) A power spectrum of the second call. Spectral analyses were performed with a 512 point FFT and a Hanning window.

increased call repetition rate prior to landing. When on the ground, call repetition rate was low (typically <5 Hz), showing that prey are unlikely to be located by echolocation. After the bat found the prey, it took off with the prey in its mouth (sometimes prey were eaten on the ground), and call repetition rate increased again (Fig. 3).

So, as predicted, *M. tuberculata* detected prey in leaf litter by methods other than echolocation. In our experiment where rustling prey were in one dish, dead prey in the other, eight of nine bats first found the dead 'reward' mealworms above the dish containing live mealworms (χ^2 with Yates' correction = 4.0, $P<0.05$), suggesting that they were attracted to the dish by the sounds made by mealworms moving in leaf litter. Over time, however, bats often found prey in the other dish containing dead mealworms, suggesting that they did so by means other than listening. In total, five of eight bats found at least half of the buried dead mealworms overnight. One bat found six of the 10 dead buried mealworms within 10 min. These results suggest that *M. tuberculata* found dead mealworms by using olfaction.

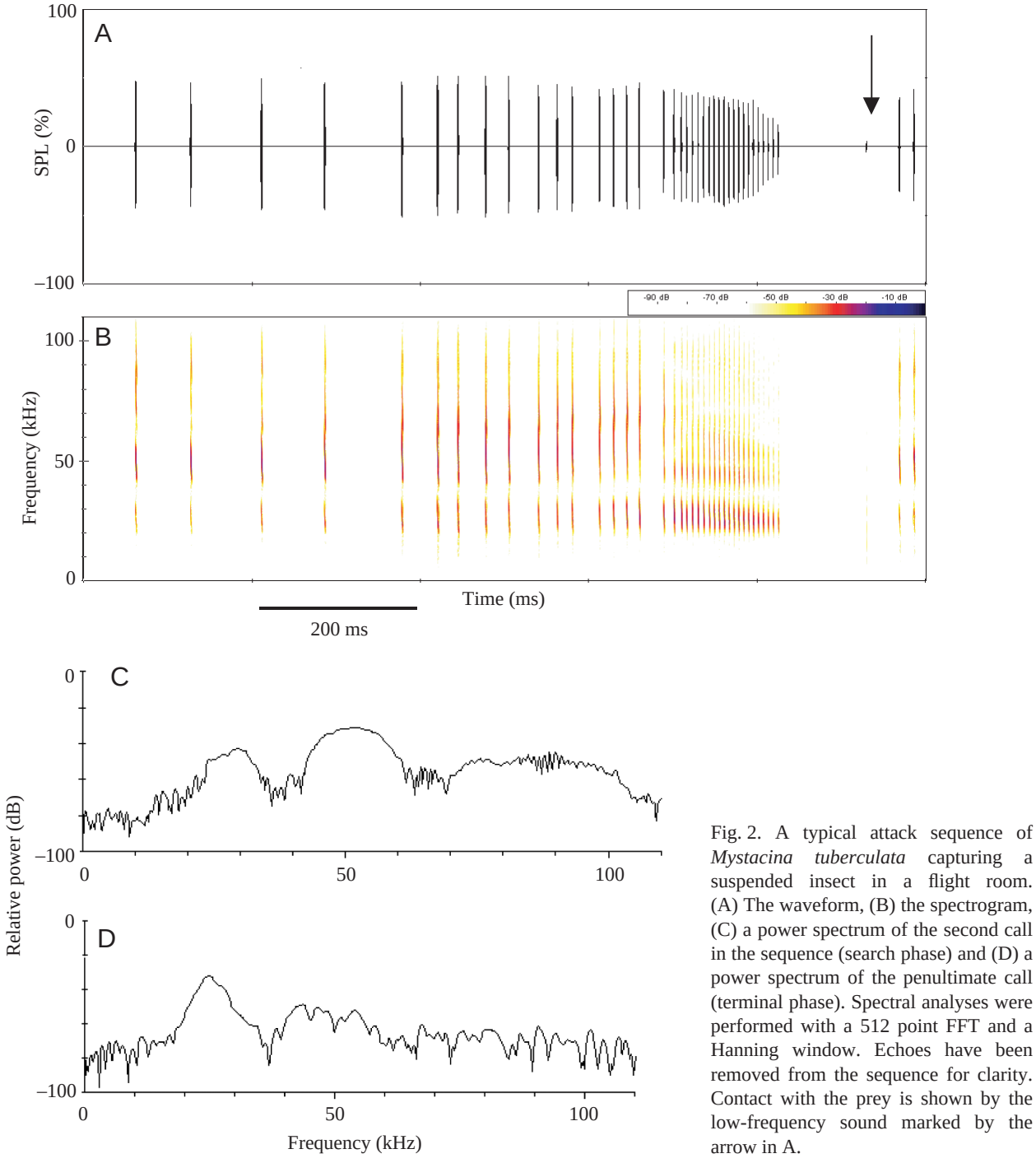

Fig. 2. A typical attack sequence of *Mystacina tuberculata* capturing a suspended insect in a flight room. (A) The waveform, (B) the spectrogram, (C) a power spectrum of the second call in the sequence (search phase) and (D) a power spectrum of the penultimate call (terminal phase). Spectral analyses were performed with a 512 point FFT and a Hanning window. Echoes have been removed from the sequence for clarity. Contact with the prey is shown by the low-frequency sound marked by the arrow in A.

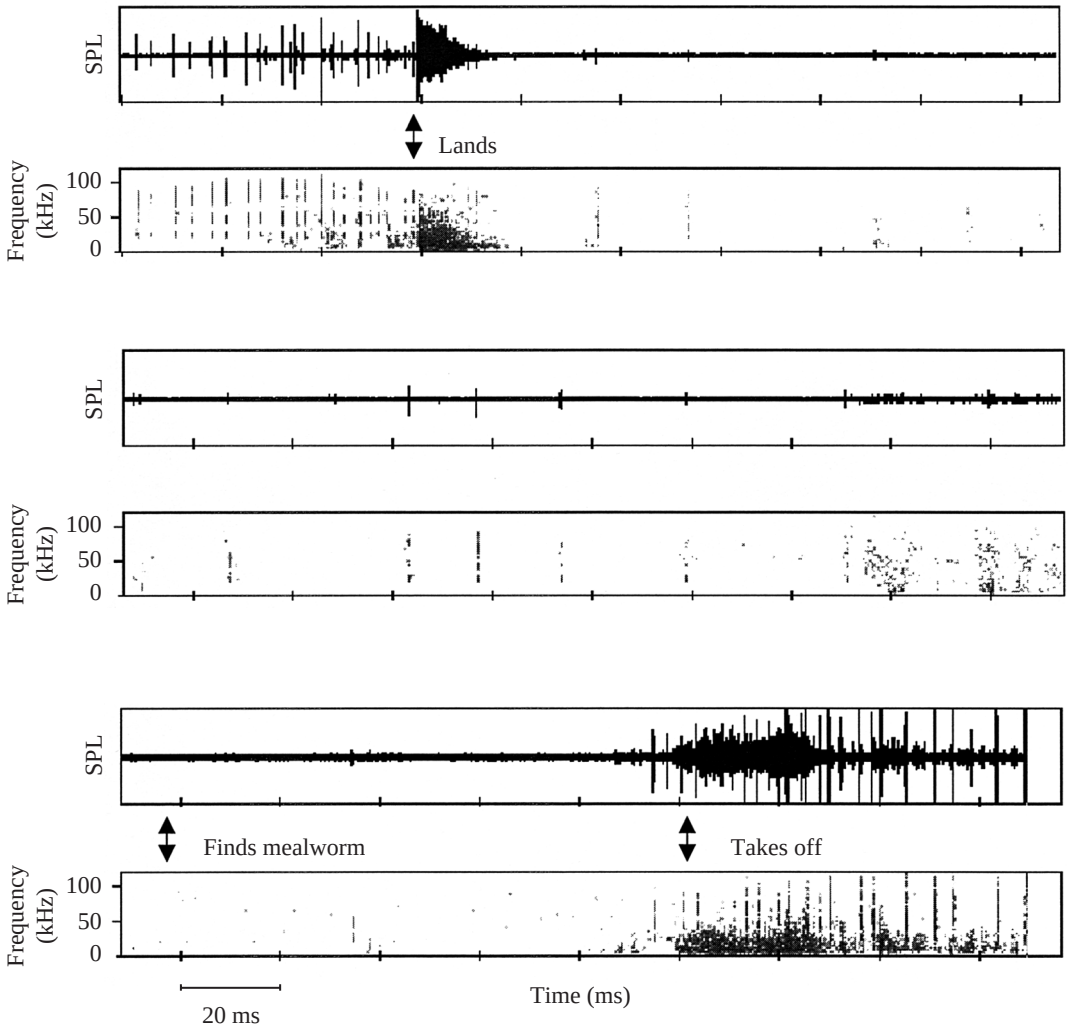

Fig. 3. A typical sequence of echolocation calls produced by *Mystacina tuberculata* locating a live mealworm buried in leaf litter. Waveforms are shown above spectrograms (512 point FFT, Hanning window) for three consecutive recording sequences. The bat emits search-phase calls as it orients in the room. It lands with a loud crash and then emits echolocation calls as it searches for the prey while on the ground. The low repetition rate of calls when on the ground and the absence of an increase in repetition rate immediately prior to finding the mealworm suggest that echolocation is not used for prey detection and localization, only for general orientation when on the ground. Notice the sudden increase in repetition rate once the bat becomes airborne again.

Discussion

M. tuberculata has an aspect ratio and wing loading that places it in the low-loading, low-aspect-ratio quarter of Norberg and Rayner's plot of principal components of flight morphology (Norberg and Rayner, 1987). Our data give a larger value for wing area (hence a lower wing loading) and a lower aspect ratio than reported in Norberg and Rayner's database, perhaps because their data were obtained from dead animals. Norberg and Rayner's analysis factors out size-dependent effects, and our data now place *M. tuberculata* alongside species such as *Myotis emarginatus*, *Leptonycteris yerbabuenae* and *Plecotus austriacus*, taxa known to forage by gleaning (Norberg and Rayner, 1987). The flight morphology of *M. tuberculata* confers manoeuvrability (Norberg and Rayner, 1987), and this is presumably adaptive in the forest habitats where the bats roost and forage (O'Donnell et al., 1999). A low wing loading also facilitates take-off from the ground (Norberg and Rayner, 1987). Extremely low values of wing loading and aspect ratio would reduce flight speed and may be selected against because the bats can commute long distances (>20 km) between roosting and foraging areas and may cross open grassland when commuting (Webb et al., 1998; O'Donnell et al., 1999). Webb et al. (1998) reported broadly similar values for wing loading and aspect ratio from bats captured on Codfish Island but argued that the bats there did not have a relatively low wing loading and aspect ratio because these parameters were similar to those of an 'average' bat of the same body mass. However, multivariate analysis using principal components involving comparisons with species whose foraging behaviours have been described makes the analysis presented here more robust.

The frequency and time parameters reported here for search-phase echolocation calls resemble those given by Parsons (2001) for short-tailed bats of a different subspecies (*M. tuberculata aupourica*) recorded on Little Barrier Island off North Island, New Zealand. Here, we provide additional information on pulse repetition rates and show that calls and pulse intervals are longer from bats flying in open areas compared with forests. Longer pulses can be produced in open habitats because echoes return later, and avoidance of pulse-echo overlap imposes fewer constraints on pulse duration (Kalko and Schnitzler, 1993). Extending pulse interval in the open may increase the time window for processing echoes from more distant targets (Fenton et al., 1998). The brief,

multiharmonic calls of *Mystacina* resemble the echolocation calls of many phyllostomid bats (e.g. Belwood, 1988; Thies et al., 1998). Such similarities may reflect the close phylogenetic affinities between bats in the families Mystacinidae and Phyllostomidae (Pierson et al., 1986; Kirsch et al., 1998; Kennedy et al., 1999; Van Den Bussche and Hoofer, 2000). If bats in these families shared a common ancestor, descendant taxa may have inherited similar constraints that shaped the evolution of their echolocation calls. Alternatively, similarities may arise through convergent evolution, although this seems unlikely given that there are no terrestrial phyllostomids, with the exception of the vampire bats.

We showed that *M. tuberculata* uses echolocation to detect and localize aerial prey. Feeding buzzes are similar to those described for aerial feeding bats (e.g. Kalko, 1995; Surlykke et al., 1993; Britton et al., 1997) in that pulse duration and pulse interval decrease as the prey is approached. Harmonics remain prominent during the approach and terminal phases, maintaining a broad bandwidth for the calls. A switch from echolocation for the detection of aerial prey to using other cues to detect prey in clutter has been shown in other bats. We know of no other bat [with the possible exception of vampire bats (*Desmodus rotundus*); Altenbach, 1979] that shows terrestrial locomotion that is as agile as that of *Mystacina*, however.

Species that glean prey from surfaces often listen for prey-generated sounds to detect and localize prey (Fiedler, 1979; Anderson and Racey, 1991; Faure and Barclay, 1992; Faure et al., 1993; Marimuthu, 1997). *M. tuberculata* is unable to locate prey in leaf litter by echolocation because echoes from leaves will mask prey echoes. Instead, the bats locate mealworms beneath leaf litter by listening for prey-generated sounds and by olfaction. Although gleaning bats such as *M. myotis* and *M. blythii* seem to locate prey in leaf litter by listening for prey sounds while flying (Arlettaz et al., 2001), *M. tuberculata* seemed unable to do this. Instead, the bats seemed to locate prey while on the ground. Whether this terrestrial location of prey is because of an inability of *M. tuberculata* to fly very slowly or hover or whether it is caused by sensory constraints remains unclear. In nature, passive cues generated by moving prey may be more conspicuous than those generated by the mealworms in our experiments.

Once on the ground, the bats often dug deep into the litter to find the mealworms. Although many frugivorous and nectarivorous bats find food by olfaction (review in Bloss, 1999), some insectivorous species can locate covered prey on the ground by olfaction (Kolb, 1961, 1973), and mealworm odours appear to stimulate prey-searching behaviour at close range in *M. emarginatus* and *P. auritus* (Dijkgraaf, 1946, 1957). Because *M. tuberculata* eats nectar as well as arthropods (Arkins et al., 1999), it is probably highly adapted for the detection of plant odours and may also use these adaptations for the detection of buried prey. We were surprised with the ease by which *M. tuberculata* found buried prey in the laboratory. This, coupled with the observation that *M. tuberculata* digs for wild beetle larvae in captivity (J. McCartney, unpublished), suggests that *M. tuberculata* may use olfaction for prey detection under natural conditions.

M. tuberculata eats a wide range of foods (Arkins et al., 1999) and is endowed with a range of sensory adaptations that allow the bats to exploit this diversity. The species is therefore a useful model to investigate how prey detection depends on ecological situation in echolocating bats. We have shown that echolocation, listening for prey-generated sounds and olfaction can all be used in the detection and localization of arthropod prey. The use of echolocation is dependent on clutter echoes not masking echoes from the prey item. We expect that olfaction is the most important sense used for the detection of nectar-producing plants and fruit. Cues used by *M. tuberculata* for the detection of plant foods, and field observations on foraging tactics, are important challenges for future researchers.

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