

Vocalizations emitted during mother-young interactions by captive eastern red bats *Lasiurus borealis* (Chiroptera: Vespertilionidae)

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We recorded acoustic signals during interactions between mother eastern red bats and their nursing young. Mothers and young produced tonal (structured change in frequency over time) frequency-modulated (FM) signals with varying harmonic components in situations ranging from reunion to just before nursing. Pups left by their mothers were usually silent, only occasionally producing tonal isolation calls. Adult females used FM signals in stressful situations, times when young usually produced clicks. Vibrational signals ('hums') composed of clicks (broadband, no structured change in frequency over time) characterized pup-pup and mother-pup interactions but pups also used other clicks that differed in frequency components from clicks comprising the hums. In stressful situations, adults produced FM signals, the pups, clicks. FM signals of pups decreased in frequencies with increasing age (size). Echolocation calls of adults and subadults hunting flying prey differed in frequency components. Differences in duration of echolocation calls coincided with setting (short calls in flight cages, open calls in the open). FM signals produced by pups searching for their mothers' nipples showed little potential for individual signatures. Calls and calling behaviour of eastern red bats that are solitary and foliage-roosting, differed from those of more gregarious species roosting in more sheltered situations.

Key words: clicks, frequency modulated signals, echolocation, harmonics, signatures, *Lasiurus*

INTRODUCTION

Most reports (e.g., Brown, 1976; Porter, 1979; Thomson *et al.*, 1985; McCracken and Gustin, 1991; Balcombe and McCracken, 1992; Zhang *et al.*, 2005) about the acoustic signals produced by mother bats and their dependent young come from colonial species, usually those roosting in protected situations (in hollows or crevices). To locate and identify their dependent young, mother bats use a combination of

spatial memory, acoustic, and olfactory cues (Gustin and McCracken, 1987; Balcombe, 1990; Loughrey and McCracken, 1991; McCracken and Gustin, 1991; Balcombe and McCracken, 1992). For bats, precision in maternal recognition of young is the rule rather than the exception (McCracken and Bradbury, 1984; Thomson *et al.*, 1985; Scherrer and Wilkinson, 1993), even for species living in very large groups. From an early age, developing young produce frequency-modulated (FM) signals, which

have been interpreted as precursors to echolocation calls (Gould, 1971; Brown, 1976; Buchler, 1980). Frequencies dominating the acoustic signals of young of some species of bats decrease with increasing age (= size — Barclay *et al.*, 1979; Thomson *et al.*, 1985; Scherrer and Wilkinson, 1993).

Eastern red bats (*Lasiurus borealis*) are solitary and roost in foliage (Barbour and Davis, 1969). In 2004 and 2005 we studied females with 1 to 5 young as well as orphaned or abandoned red bat pups that had been brought to wildlife rehabilitators during May, June, and July in central Texas. In outdoor enclosures, hand-raised young learn to use echolocation to detect, track and assess flying insects which they catch and eat, suggesting 'normal' development in captive animals (Schmidt-French and Whitaker, 2005).

The purpose of this study was to document the vocalizations emitted by mothers and young as they interact with one another as well as those of young flying and hunting in an outdoor enclosure. We compare our findings with those from colonial species of bats.

MATERIALS AND METHODS

We studied adult female eastern red bats with 1–5 young as well as orphaned or abandoned pups. The bats had been retrieved from the ground, vegetation, or the sides of buildings in June of 2004 and 2005 in Travis County, Texas, and submitted to a wildlife rehabilitator. Our sample included six orphaned young and four lactating mothers, three with three pups each and one with four pups. At birth, forearms of *L. borealis* range from 13–16 mm, those of adults from 36–42 mm (Barbour and Davis, 1969). The young we recorded had forearms 30–31 mm (smaller) and 37–39 mm (larger). The bats were observed and recorded under natural light. They were accustomed to the presence of people and appeared to call normally. Some calls were recorded from handheld bats.

Adult females were hand fed mealworms (*Tenebrio molitor*) once a day and offered canine milk replacer twice daily. Females nursed their young. Orphaned bats were maintained on canine milk replacer, mealworms, and beef baby food (Lollar and

Schmidt-French, 2002). Adults with young were housed in an outdoor flight cage constructed from a metal tube frame that measured 17.2 by 6.4 m with a peak height of 3.6 m. The cage was covered with 0.6 cm polypropylene mesh to allow insects to enter. A 1.8 m by 9.1 m section on one end of the enclosure was covered with 1.3 cm mesh. Orphans were caged together in fabric insect carriers until they began eating whole mealworms and were then transferred to the flight cage. Adults and juveniles fed on insects that entered the flight cage in the evenings.

On 19th and 22nd June 2004 we recorded interaction calls from three females as they interacted each with three pups, as well as calls produced by roosting siblings interacting with one another. On 13th June 2005, we recorded the interaction calls of a female and her four pups as well as six interacting orphan pups. On 9th July 2005 we recorded six hand-raised orphans as they interacted with one another while roosting, and then again as they flew on their fourth night in a flight cage.

We used real-time high speed recording systems to capture the interaction calls of red bats. In June 2004, this system consisted of an S-25 bat detector (Ultrasound Advice, UK) attached to a F2000 Control/Filter unit (Pettersson Elektronik AB, Sweden) and a high speed sound card (DAQCard-6062E, National Instruments, USA). Recordings were saved on the hard drive of a Dell Inspiron laptop running BatSoundPro (Pettersson Elektronik AB, Sweden). Calls were digitized with 16-bit resolution and a 250 kHz sampling rate. In June 2005, we used an integrated, high speed data acquisition system (Avisoft Germany). Calls were recorded with a CM16 solid dielectric microphone connected to an Ultrasound Gate 416 and a Dell Inspiron laptop running Avisoft Recorder USG. Recordings were digitized with 16-bit resolution at sampling rates of 225 kHz or 250 kHz.

We recorded bat calls in the outdoor flight cage and in an insulated building measuring 3.6 m by 4.9 m, with a peak height of 3.6 m. Interior walls and ceiling were covered with netting to provide roosting surfaces for bats. The microphone was placed between 1 and 15 cm from the recorded bats, depending upon the amplitude of the call, but for 'hum' signals, we gently placed an Avisoft USG microphone so the protective grid rested against the bat's back. We used a customized m file in Matlab 7.1 to analyze selected features in calls, and SPSS v. 12 for statistical analyses. We measured call duration and interpulse intervals from time-amplitude displays and, frequency with most energy (FME), lowest frequency (LF) at -5 and -10 dB from FME, and highest frequency (HF) at -5 and -10 dB from FME from 512 line fast Fourier transform (FFT) displays.

RESULTS

We recorded a variety of acoustic signals including broadband clicks (Fig. 1a–b and 1f–g; Fig. 2a–b and 2f–g), and tonal FM sweeps (Fig. 1c–e and 1h–j) associated with interactions between mothers and their

young (Figs. 1–2 and Table 1). Based on FFT displays some clicks (Fig. 1a–b and Fig. 2a–b) were too weak to permit detailed analysis of call features, while other clicks (Fig. 1f–g and Fig. 2f–g) and the FM signals were strong enough for detailed analysis (Table 1). FM signals showed variation

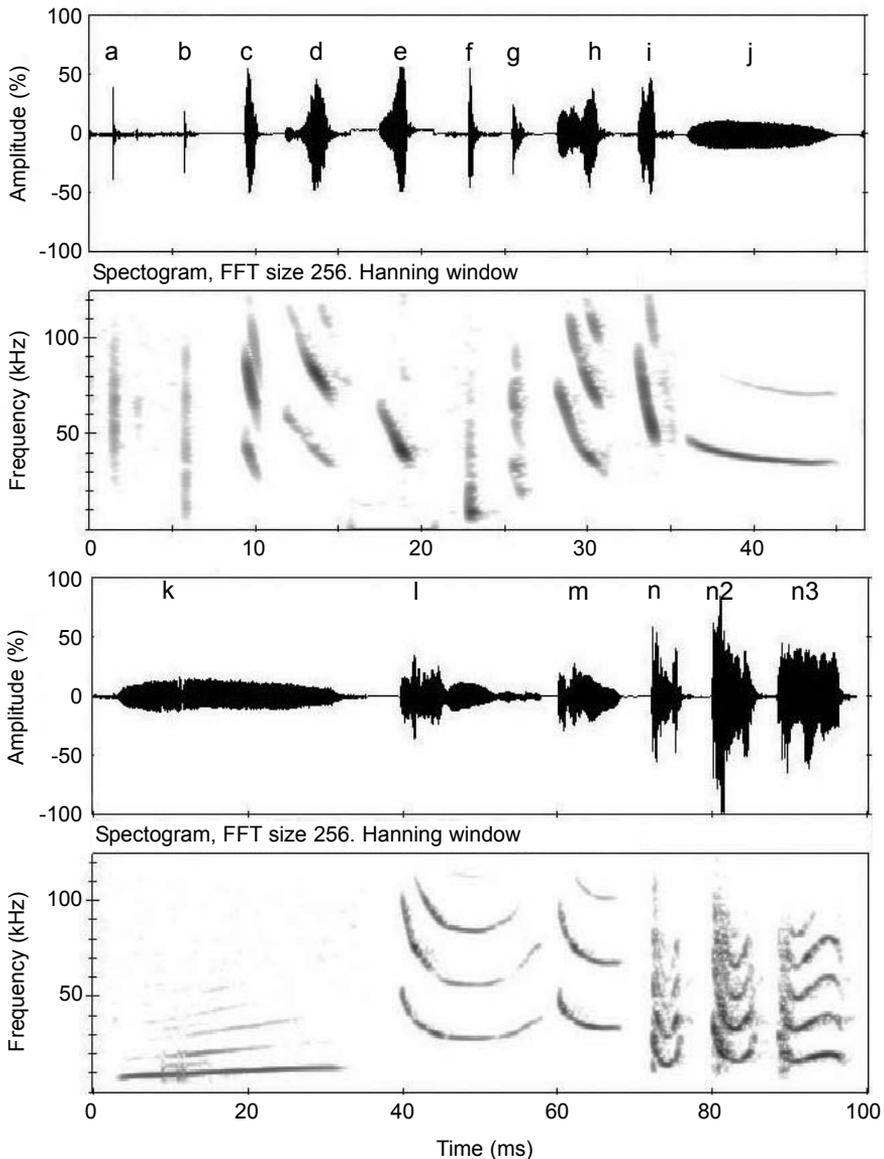
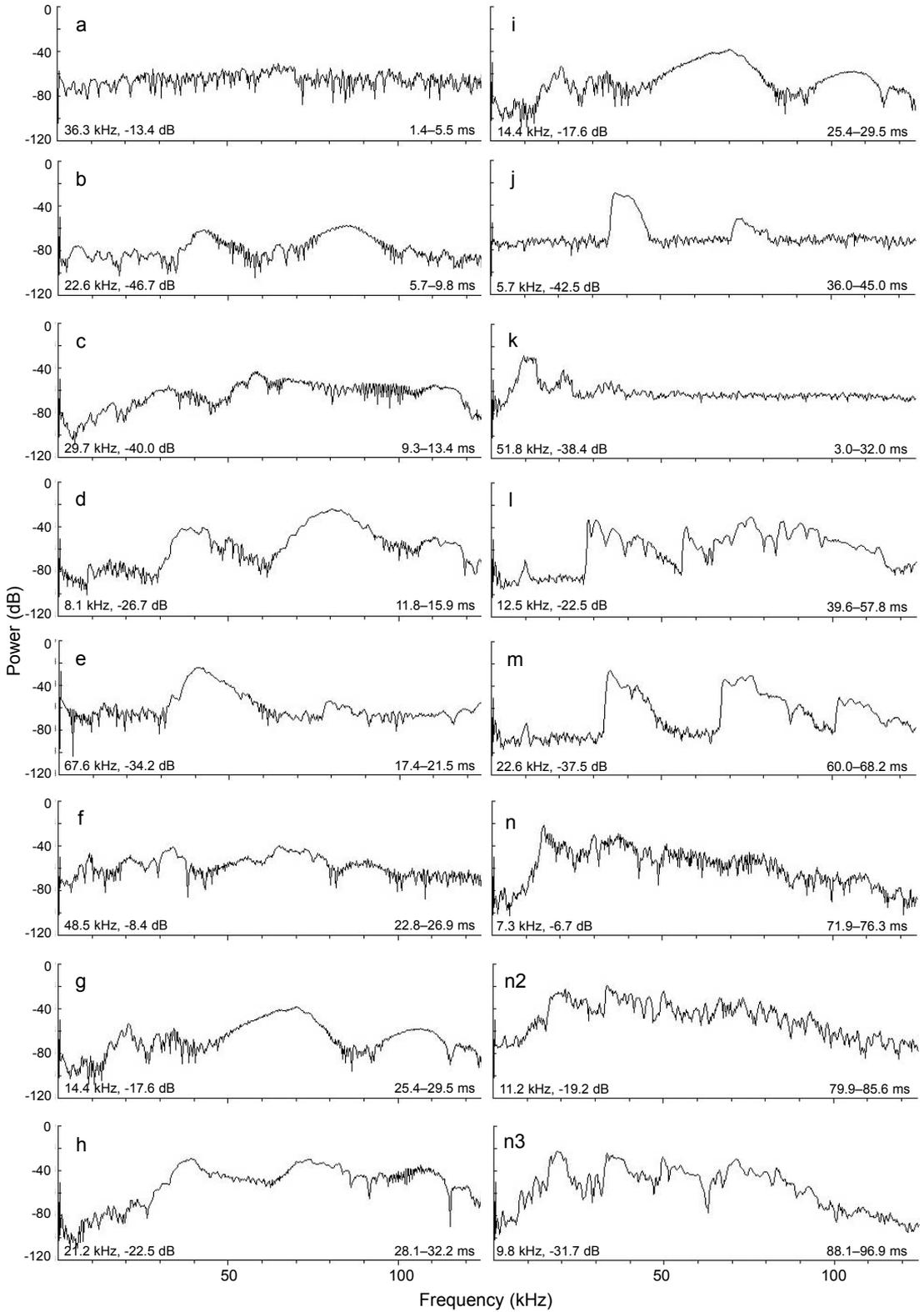


FIG. 1. We recorded clicks (a, b, c, g) and FM (other) signals from the bats, as well as echolocation calls (i, j). Each call type we recorded is presented as an amplitude and spectrogram (256 line) display (see Fig. 2 for fast Fourier transform (FFT) displays of each of the calls shown here). Where signals were strong enough, quantitative call features are presented in Table 1 (frequency data obtained from 512 line FFTs)



in the presence of harmonics (e.g., Fig. 1c–e and 1g–j, and Fig. 2c–e and 2g–j) that were obvious in both FFT and spectrogram displays, although FFT presentations provide more accurate information about the presence and relative strengths of harmonics. In low duty cycle echolocators like *L. borealis*, pulse-echo overlap precludes the use of longer signals (Fig. 1k–n and Fig. 2k–n) in echolocation.

While nursing, both mothers and pups made a vibrational humming, the elements of which differed between mothers and young (Fig. 1a and 1b, respectively), were produced at 4 to 24 ms intervals (see also Fig. 2a and 2b). These very weak humming sounds can sometimes be heard when holding a bat to one's ear. These sounds may be manifestations of a vibrational signal that occurs between pups and between pups and their mothers.

In the evenings, mothers disengaged pups from their nipples and moved them to tree branches or netting in the flight cage before flying away. Young left by their mothers were usually silent, but sometimes emitted short, tonal FM calls (Fig. 1c and Fig. 2c) and/or clicking sounds (Fig. 1b and Fig. 2b) as they clustered together, groomed, and licked each other's faces.

When a mother returned and approached (or when she was placed near) her pups, she always emitted distinctive calls (Fig. 1j–k and Fig. 2j–k) as she approached and then rubbed her muzzle against them, licked their faces and used her wings to nudge them back to her nipples. Pups searching for a mothers' nipples produced several variants of short FM signals (Fig. 1c–e and Fig. 2c–e), long search calls (Fig. 1i and Fig. 2i), and short mechanical clicks (Fig. 1f and Fig. 2f). These clicks appeared to

be louder variants of the clicks comprising hum trains. FM signals of older (larger) pups tended to be lower in frequency than those of younger (smaller) ones (Table 1).

When mothers or pups were handled, especially when we agitated them by gently rubbing their fur or opening their wings, they emitted calls that differed between pups (Fig. 1g and Fig. 2g) and mothers (Fig. 1h and Fig. 2h). In these situations, pups produced clicks while mothers emitted FM sweeps. In two cases, a pup added a long trill-like screech (Fig. 1n and Fig. 2n) to these clicks which we did not record from any adult females.

Young bats flying and hunting prey in the flight cage produced shorter echolocation calls (Fig. 1i and Fig. 2i) than adults foraging in the wild (Fig. 1j and Fig. 2j). We observed the expected differences in call durations between the two echolocation situations (shorter in the flight cage, longer out-of-doors). Furthermore, the echolocation calls of subadults in the flight cage were often dominated by higher frequency components than those of adults foraging out-of-doors (Figs. 1–2 and Table 1).

Our samples from 2004 permitted analysis of the features of sequences of six calls (types shown in Fig. 1c–e and Fig. 2c–e) recorded from each of eight individuals (forearm lengths 37.5 to 39.5 mm). A MANOVA revealed significant inter-individual variation (Wilk's $\lambda = 0.87$, $F_{49, 177.0} = 2.228$, $P < 0.001$) in call features, with call duration, and LF (at -5 and -10 dB) being most important. In a cross-validated discriminant function analysis, 39.6% of calls were correctly identified by call features, reflecting the general variability in these signals and lack of consistent individual call patterns (Fig. 3).



FIG. 2. Shown here are fast Fourier transform (FFT) displays of calls illustrated in Fig. 1, specifically clicks (a, b, c, g) and FM (other) signals from the bats, as well as echolocation calls (i, j). The FFTs are 1,024 line displays. The frequency data in Table 1 were obtained from 512 line FFTs

TABLE 1. A comparison of call features, where: Dur — duration; FME — frequency with most energy; LF and HF -5 dB — lowest and highest frequencies (FME -5 dB), respectively; LF and HF -10 dB — lowest and highest frequencies (FME -10 dB), respectively, and interpulse interval (IPI). Means are shown \pm SD; sample sizes always five calls (IPI based on four readings). Echo — echolocation calls. Forearm lengths for small pups were 30–31 mm, and 37–39 mm for large ones

Call type	Dur (ms)	FME (kHz)	LF -5 dB (kHz)	HF -5 dB (kHz)	LF -10 dB (kHz)	HF -10 dB (kHz)	IPI (ms)
Small Pup sweeps 1 (Fig. 1c–e and Fig. 2c–e)	1.6 \pm 0.6	77.7 \pm 7.5	70.6 \pm 8.1	80.5 \pm 5.7	65.6 \pm 6.3	83.6 \pm 8.2	79.2 \pm 46.2
Small Pup sweeps 2	1.2 \pm 0.5	71.7 \pm 18.0	52.6 \pm 18.3	84.0 \pm 28.2	45.9 \pm 25.2	86.5 \pm 30.7	27.6 \pm 18.3
Large Pup sweeps 1	4.4 \pm 1.3	34.3 \pm 33.3	34.1 \pm 33.1	34.6 \pm 33.4	21.8 \pm 27.1	34.8 \pm 33.4	56.8 \pm 33.3
Large Pup sweeps 2	3.0 \pm 1.0	63.2 \pm 6.2	55.2 \pm 11.0	65.1 \pm 5.6	54.2 \pm 11.2	74.8 \pm 14.2	56.0 \pm 32.9
Pup clicks (Fig. 1f)	2.8 \pm 0.5	64.5 \pm 8.8	63.2 \pm 8.7	67.0 \pm 7.5	62.6 \pm 8.9	86.0 \pm 19.0	60.4 \pm 43.6
Pup alarm (Fig. 1g)	2.8 \pm 0.5	49.0 \pm 4.6	47.5 \pm 4.6	53.2 \pm 6.8	46.4 \pm 4.2	57.0 \pm 4.8	90.2 \pm 63.0
Mother alarm (Fig. 1h and Fig. 2h)	2.6 \pm 0.9	16.3 \pm 7.4	15.1 \pm 7.8	23.3 \pm 1.9	13.5 \pm 7.8	37.3 \pm 1.9	93.2 \pm 52.2
Subadult 1 echo (Fig. 1i and Fig. 2i)	1.8 \pm 0.4	45.5 \pm 0.8	44.0 \pm 0.7	54.2 \pm 8.6	43.4 \pm 1.2	60.3 \pm 6.4	41.3 \pm 25.9
Subadult 2 echo	1.4 \pm 0.6	63.6 \pm 6.5	60.8 \pm 7.0	67.7 \pm 4.8	59.0 \pm 5.9	71.9 \pm 3.9	44.8 \pm 29.9
Subadult 3 echo	3.2 \pm 0.4	63.9 \pm 0.7	56.8 \pm 6.6	74.7 \pm 5.0	50.7 \pm 6.5	78.5 \pm 1.5	41.4 \pm 25.6
Subadult 4 echo	1.8 \pm 0.5	53.7 \pm 2.7	41.2 \pm 3.2	55.6 \pm 2.7	40.0 \pm 3.4	56.9 \pm 2.8	27.0 \pm 22.6
Adult echo (Fig. 1j and Fig. 2j)	7.8 \pm 0.8	40.4 \pm 2.5	39.5 \pm 2.4	43.2 \pm 3.6	39.3 \pm 2.3	46.4 \pm 4.1	170.8 \pm 96.0

DISCUSSION

The situation facing mother and dependent young solitary bats such as *L. borealis* differs from that prevailing for colonial species that roost in hollows or crevices. First, mothers are not challenged to find their young among those of other females, and second, foliage roosts may not offer as much protection from predators. Situational differences coincide with observed variation in calls and calling behaviour. For example, young of species roosting in more protected places call frequently when left alone, and use both long and short tonal isolation calls (Fenton, 1985; Pfalzer and Kusch, 2003), while young eastern red bats were usually silent and rarely produced isolation-like calls. Bats roosting alone in foliage may rely more on spatial memory than acoustic cues to find their young. Our data about change in call frequency with age agree with others on this topic (Thomson *et al.*, 1985; Scherrer and Wilkinson, 1993).

The repertoire of calls we observed is less than that reported from colonial species (e.g., Pfalzer and Kusch, 2003; Davidson and Wilkinson, 2004; Ma *et al.*, 2006). Furthermore, FM sweeps, the most common signals recorded from young (see Fig. 1c–e and Fig. 2c–e) are variable but a discriminant function analysis suggests little potential for individual signatures, which differs from calls that mediate mother-young interactions in other species (Scherrer and Wilkinson, 1993), calls co-ordinating group foraging (Boughman and Wilkinson, 1998) or even echolocation calls (Masters *et al.*, 1995; Fenton *et al.*, 2004). The value of echolocation signals in providing information about callers remains an active area of investigation (Siemers *et al.*, 2005; Hiryu *et al.*, 2006).

The extensive use of FM sweeps in situations ranging from echolocation to communication emphasize the potential continuum between these functions (Barclay,

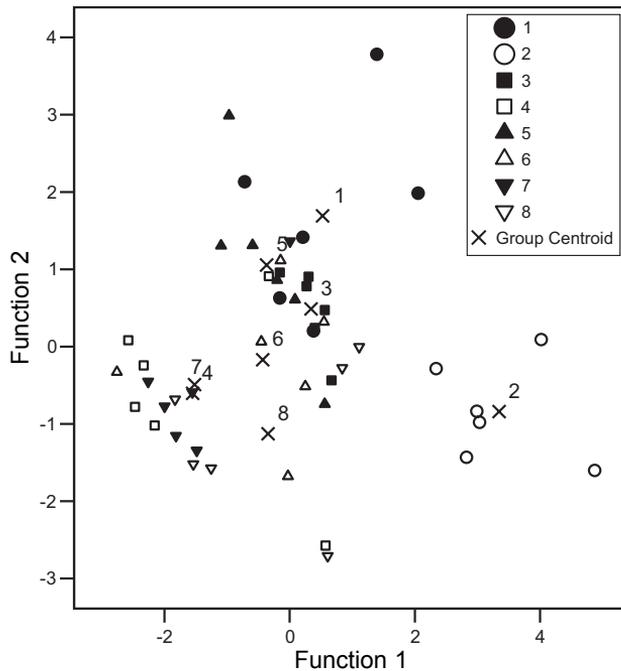


FIG. 3. The output of a discriminant function analysis (DFA) of sequences of six FM sweep calls from eight individuals (marked by different symbols) showing broad overlap in call features

1982). Of particular interest is variability in the use of harmonics. Tonal signals show structured changes in frequency over time, while harsh signals show none. The signals we recorded do not always follow Morton's (1977) motivational-structural rules about the use of tonal versus harsh signals in amicable versus agonistic settings. The clicks associated with hums and searching behaviour do not appear to be agonistic situations. The signals from agitated bats, whether pups or adults, appear to be 'distress' rather than 'alarm' signals, as defined for other animals (e.g., Fitchell *et al.*, 2005; Leavesley and Magrath, 2005; Templeton *et al.*, 2005).

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