



Discrimination of infant isolation calls by female greater spear-nosed bats, *Phyllostomus hastatus*

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In colonial species, recognition of offspring should be under strong selection. For accurate identification to occur, offspring must produce individually distinctive signals and parents must be able to discriminate between signals. Female greater spear-nosed bats roost in stable social groups and use infant vocalizations, termed isolation calls, to locate and identify their young. In this study, we investigated both the production and perception of isolation calls in *P. hastatus*. First, we measured acoustic features of calls and found that, after controlling for ontogenetic effects, sufficient variation exists between pups for isolation calls to function as individual signatures. Moreover, calls of pups from the same social group were more similar in spectral and spectrotemporal features than were calls of pups from different social groups, indicating that these features are probably heritable. We used psychoacoustic experiments in the laboratory to determine whether adult females could discriminate between calls from pups in the same or different social group. Females discriminated between pups when faced with a template-matching task and their performance was correlated with the salience of spectral and spectrotemporal features. We found no difference in performance when females had to discriminate between pups from the same and different social groups. These results indicate that females should be able to accurately identify their young using isolation calls.

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The process of identifying offspring is expected to be under strong selection to ensure that parental care is confined to related individuals. For animals living in large groups, the probability of confusing related offspring with others can be high. Consequently, parent–offspring recognition systems have evolved in many colonial species (e.g. Trillmich 1981; Stoddard & Beecher 1983). For bats, offspring recognition can be a particularly vital but difficult task because mothers typically leave their pups behind in large colonies. Accurate offspring recognition requires fulfilment of two criteria: (1) offspring must produce individually distinctive signals and (2) parents must be able to discriminate

between these signals (Beecher 1982). Here, we examine these two components of parent–offspring recognition in greater spear-nosed bats.

In Trinidad, West Indies, *P. hastatus* form stable social groups of 8–40 adult females attended by one adult male (McCracken & Bradbury 1981). Unlike most other group-living mammals, females are typically unrelated to group members (McCracken & Bradbury 1981). Males have high reproductive control over harems (McCracken & Bradbury 1977), and socially mediated birth synchrony occurs within groups (Porter & Wilkinson 2001). Consequently, pups reside in clusters of predominantly paternal half-siblings of similar age from a single social group.

Most infant bats, including *P. hastatus*, produce frequency-modulated multiharmonic vocalizations known as isolation calls, which are used in parent–offspring recognition (Gould et al. 1973). In some species, isolation calls contain enough information to serve as individual signatures (e.g. Thomson et al. 1985; Gelfand &

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McCracken 1986; Scherrer & Wilkinson 1993) and often change as pups age (reviewed in Altringham & Fenton 2003). In *P. hastatus*, females sometimes visit and retrieve group members' pups that have fallen to the cave floor (K. M. Bohn & G. S. Wilkinson, personal observation). This observation raises the possibility that isolation calls may not contain sufficient information for a female to recognize her pup from others in her social group.

Females probably use a template-matching mechanism (Lacy & Sherman 1983) to recognize their own pups' calls. By template matching, females compare incoming isolation calls to a signal template represented in memory. Offspring recognition should then depend on a female's ability to form a template and discriminate among offspring signals. Psychoacoustic studies suggest that bats should be able to discriminate between isolation calls. For example, adult female *Phyllostomus discolor* can discriminate among frequency-modulated sounds similar to isolation calls (Esser & Lud 1997), and other studies have demonstrated maternal recognition of pup calls (Balcombe 1990; de Fanis & Jones 1996). No study has yet examined the acoustic features used by mothers to recognize their pups' calls.

Here we present a comprehensive study of parent-offspring recognition in *P. hastatus*. First, we investigated signal production. We examined how isolation calls change with pup age and then we controlled for age effects to assess how acoustic features vary among bats in different caves or social groups. Next, we used psychoacoustic experiments in the laboratory to examine signal perception. We tested whether females can discriminate between pup isolation calls in a template-matching procedure, which mimics the perceptual task faced by females in the wild. We then determined which acoustic features were correlated with female performance and compared the results with the analysis of isolation call variation to infer potentially salient cues. Finally, in a second perceptual experiment, we tested whether call similarity within social groups affects female discrimination of individual pups.

METHODS

Isolation Call Recordings

We recorded isolation calls from infant *P. hastatus* at Guanapo and Tamana caves (McCracken & Bradbury 1981) in Trinidad, West Indies, in April and May, 2002 and 2004. In the evening, we captured nonvolant pups by hand for measuring and recording and then returned them to their crèche before the adult bats returned from foraging. We banded each pup with numbered stainless steel bands (National Band and Tag, Newport, Kentucky, U.S.A.) and used callipers to measure forearm length (FA) to a tenth of a millimetre. We estimated age in days as $0.77 \times \text{FA} - 24.6$ (Stern & Kunz 1998). We recorded spontaneously produced isolation calls from pups that were placed in a cardboard box (approximately $0.75 \times 0.5 \times 0.5$ m) lined with acoustic foam (Sonex, Seattle, Washington, U.S.A.). Calls were digitized at a sample rate of 250 kHz into Bat Sound Pro (Pettersson Elektronik, Uppsala, Sweden) on a laptop computer

equipped with a data acquisition card (INEES, Daq508, 12 bits) using a bat detector as a high-frequency microphone (Ultra Sound Advice, S-25) and an external amplifier (SHURE, FP-2).

Infant *P. hastatus* produce multiple types of isolation calls composed of different numbers of notes. Double-note calls are the simplest and most frequently produced calls in *P. hastatus* and in many other species of bats (Gould et al. 1973). For both simplicity and consistency, we used double-note calls for all analyses and psychoacoustic experiments (see below).

Isolation Call Measurements

We used SIGNAL (version 3.0, Engineering Design, Belmont, Massachusetts, U.S.A.) to band-pass filter isolation calls between 5 kHz and 85 kHz, normalize amplitudes by dividing each signal by its peak amplitude, and measure 12 call features (Fig. 1). We measured three temporal features, eight spectral features and one spectrotemporal feature, the relative location of the frequency minimum of the first note (MNT1) using the formula $\text{MNT1} = (\text{end time} - \text{time of minimum frequency})/\text{end time}$. In addition to these measurements, for perceptual experiments, we used SIGNAL to calculate spectral

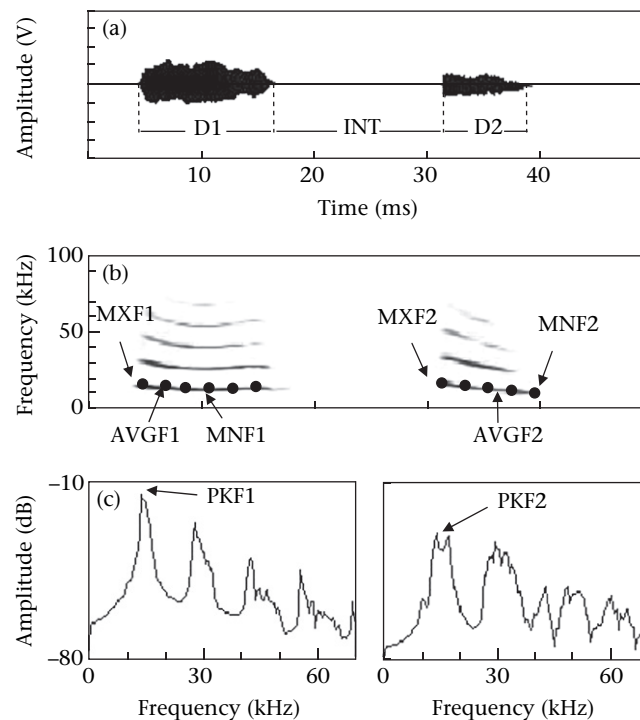


Figure 1. (a) Oscillogram, (b) spectrogram and (c) power spectra of a typical double-note isolation call. Measurements taken are first note duration (D1), second note duration (D2), interval between notes (INT), average frequency of the first (AVGF1) and second (AVGF2) notes, minimum frequency of the first (MNF1) and second (MNF2) notes, maximum frequency of the first (MXF1) and second (MXF2) notes, and peak frequency of the first (PKF1) and second (PKF2) notes. Large dots in (b) represent spectral contours, which were averaged over the duration of the calls to calculate AVGF1 and AVGF2. Spectral contours were calculated by determining the peak frequency at each point in time of the call (Beeman 1996).

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