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Roost-mate communication in adult Indian false vampire bats (*Megaderma lyra*): an indication of individuality in temporal and spectral pattern

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Abstract The remarkable cognitive abilities of bats indicate that they may recognise particular conspecifics. Because of their highly developed auditory system, it is obvious that vocalisations of bats may give information about the individual emitting them. In a field study of the social behaviour in the Indian false vampire bat (*Megaderma lyra*), two different types of vocalisation were recorded and analysed. The bats emitted these vocalisations only while aggregating with conspecifics inside the day roost. The “landing strophe” consisted of a number of brief multi-harmonic downward frequency-modulated (FM_{down}) sounds which levelled off as a constant frequency (CF), and the “clatter strophe” was composed of a number of multi-harmonic FM_{down} sounds which became shallow at the end as a short CF. The sounds of the landing strophe and the clatter strophe differed in repetition rate, duration, harmonic components and frequency. Time pattern and peak frequency of the two sound types differed highly significantly between single, unidentified bats. The sounds were inter-individually distinct when the three parameters were combined as an acoustical space. Therefore, these vocalisations might be used for individual recognition in adult bats.

Key words Communication · Individual signature · Recognition · Social behaviour · Bats

Introduction

Bat species in which individuals associate with particular conspecifics need mechanisms to identify and locate these specific group members. This is particularly obvious when mothers that leave their pup in large maternity colonies return hours later from their foraging trips, and identify their own pup without any problems (e.g. Balcombe 1990).

Several reports on social foraging, hierarchies, territoriality and other social interactions indicate that bats know group members individually (e.g. Wilkinson 1985; Vaughan and Vaughan 1986; Kohzurina 1993; Brooke 1997). A well known example is the common vampire bat, *Desmodus rotundus*, in which individuals feed other group members on a reciprocal basis. To maintain a high level of probability for reciprocal rewards in social feeding, vampires remember and reject individual cheaters (Wilkinson 1984, 1990; DeNault and McFarlane 1995). Another example may be the Indian false vampire bat, *Megaderma lyra*, in which dominant males perform complex song flights towards females throughout the year (Leippert 1994). Males seem to establish social bonds with particular females, and thus it is likely that these animals know each other individually (Leippert 1994; D. Leippert and I. Siewert, unpublished work). Such sophisticated behaviours require an intimate knowledge of individual partners.

Bats have a highly developed auditory system (e.g. Neuweiler 1990; Neuweiler and Schmidt 1993) and thus it is likely that auditory cues play a major role in the identification of other individuals. The greater spear-nosed bat, *Phyllostomus hastatus*, uses auditory cues to recognise conspecifics and provides an impressive example of the remarkable cognitive abilities of bats. The females of this bat species use group-specific, but not individually distinctive, “screech calls” to recruit members of their roosting group and to co-ordinate foraging movements with them

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(Boughman 1997; Wilkinson and Boughman 1998). This screech call is emitted by unrelated roost-mates and is learned through vocal imitation (Boughman 1998).

Individual cues were found in sound characteristics of isolation calls of juveniles of some species (e.g. Gelfand and McCracken 1986; Rasmuson and Barclay 1992; Scherrer and Wilkinson 1993). Furthermore, playback experiments demonstrated that the mothers of *Tadarida brasiliensis* use acoustical cues to locate and identify their young ones (Balcombe 1990). However, information about distinctive individual cues in communication sounds of bats has so far been documented in only a few species. Most of these reports have identified distinctive individual cues in communication sounds between mothers and pups, but there is almost no information about such distinctive individual cues in sounds that serve communication amongst adult bats (e.g. Barlow and Jones 1997).

Our field studies on the social behaviour of Indian false vampire bats have provided information on individual variability of social calls in adult bats. Indian false vampires roost in colonies of 10–1,000 individuals in caves and buildings (Brosset 1962; Habersetzer 1983; Audet et al. 1991). Like most other bat species, they leave their roost after sunset to forage in specific foraging areas (Audet et al. 1991; Goymann et al. 2000). They spend a considerable part of the night in so-called night roosts (e.g. open buildings, verandas, trees: Audet et al. 1991; Goymann et al. 1999). At sunrise the bats return to their day roost, where they briefly search for a suitable roosting spot (Habersetzer 1983; Audet et al. 1991; Goymann et al. 2000).

Here we describe two previously unknown sound types of Indian false vampire bats. These sound types show inter-individual variability in several sound characteristics and thus have the potential to transfer information about the identity of the vocalising bat.

Methods

The data were collected from a colony of about 60 *M. lyra* roosting in an old temple in Krishnapuram, 15 km from Tirunelveli in southern India; 35 of the bats were individually marked by colour-coded forearm rings (Goymann et al. 2000).

From 9 February 1995 to 23 April 1995 the bats were observed inside the temple for a total of 335 h over 68 days. The temple was illuminated with dimmed red light (nine 15-W bulbs) for 24 h per day. Observations in the day roost were conducted by one or two people at different observation sites (Fig. 1). Gradually, the bats accepted that two human beings were also roosting in their temple. After a 2-week habituation period the bats were often asleep and were not disturbed when we sat down at an observation point. Also, they did not fly up when we read the tags of resting bats using a white-light torch. Bats in flight, however, could not be identified (see also Goymann et al. 2000).

Additionally, from 9 February 1995 to 23 April 1995, we observed four night-roosts (unused buildings) in the vicinity of the temple where individuals of the colony of Krishnapuram roosted frequently during the night, for a total of 105 h. In night roosts bats were observed at a distance of 2–4 m, mainly with a night vision scope (Litton) supported by red-light torches.

From 15 April to 6 June 1996 we observed favourite perches of identified individuals of the colony of Krishnapuram in their foraging habitat for 231 h over 28 nights. The bats, which used the

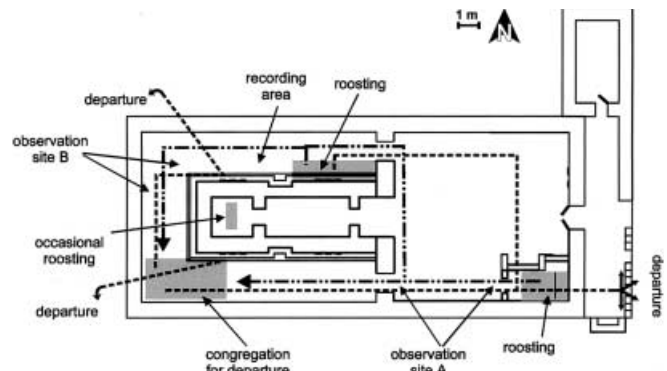


Fig. 1 A ground plan of the day roost, the Krishnapuram temple in Tirunelveli, South India, showing the roosting sites and the site of congregation for departure of *Megaderma lyra*. The dashed-dotted lines show the movements of the bats in the evening, and the dashed lines their flying out

perches frequently during the night, were observed at a distance of 1–4 m. The area around the perches was illuminated with three torches (MagLite) covered with red filters (Heliopan, red 25, ~650 nm). More detailed observations were made using binoculars (Zeiss 8 × 56, Leitz 10 × 40, Nikon 8 × 25) and a night vision scope (Litton) supported by a red-light power torch (MagLite with 4 cells). Perching bats were identified by briefly shining white light on their tags, which did not disturb them.

Vocalisations were recorded in the northern corridor of the temple roost (Fig. 1) by an electrostatic microphone (Pettersson), amplified via a Pettersson Ultrasound Detector (type D940) and stored to a Racal Store 4 DS tape recorder with a tape-speed of 30 inch s⁻¹ (76 cm s⁻¹; approximate system response: 3–100 kHz ± 10 dB). The signals were monitored on an oscilloscope. While the bats' vocalisations were being recorded, their behaviour was also reported on a dictaphone.

The bats emitted each of the previously unknown sound types in sequences of several single sounds (see Results), and therefore we were able to collect a sound sample from a single unknown individual of one of the two sound types. For that purpose, recordings of 320 min duration were first monitored by headphones at slow speed (8 times slowed down). In so doing, we identified sequences of a number of sounds emitted by individual bats flying past the microphone by the waxing and waning of sound intensities. The selected sound sequences were digitised and transferred to a PC (AT486) by an A/D card (DT 2801A) at 8 times slowed down speed and analysed by custom-made sound analysis software (Sona, M. Knipschild, Dortmund; time resolution = 0.07 ms, frequency resolution = 195 Hz). In a first step, the time course of a digitised sequence was analysed. We classify a sound sequence as a "single-bat" recording when no overlap between any two sounds occurred, and the frequency-time course of sounds was not dissimilar within the sequence. However, in the recordings, the individual emitter could not be identified. In this way seven separate "single-bat recordings" of each sound type were randomly collected and the sound durations, durations of intervals, and spectral composition (peak frequency, number of harmonics, frequency band of the harmonics at –20 dB from maximum, and the relative intensity of the harmonics) of their sounds were measured.

The intervals, durations and peak frequencies of sequences of communication sounds were tested for significant differences between single-bat recordings ($P \leq 0.05$; Kruskal-Wallis test). Single-bat recordings that differed from each other were determined by means of post hoc multiple comparisons (Conover 1980). Data are given as medians (md) and interquartile differences QD = (3rd quartile–1st quartile)/2.

Results

General behavioural situation in the day roost

The bats returned from their nocturnal foraging activity to the day roost shortly before sunrise. Inside the temple, they usually aggregated in two mixed-sex groups of 4–19 and 15–49 bats which were about 10 m apart (Fig. 1). Occasionally, they split into a third group consisting of members from the other two groups, reaching a size of about 10 bats. Generally, individuals stayed in one roosting group throughout the day, and some individuals were frequently observed at the same roosting place. In the evening many bats left their roosting groups about 1 h before sunset, and congregated for departure in a part of the temple which was not used as a day roost (Fig. 1).

During aggregating flight activities, in the morning for roosting and in the evening for departure, the bats interacted extensively and uttered two sound types, the landing and the clatter strophe, which were only emitted by aggregating

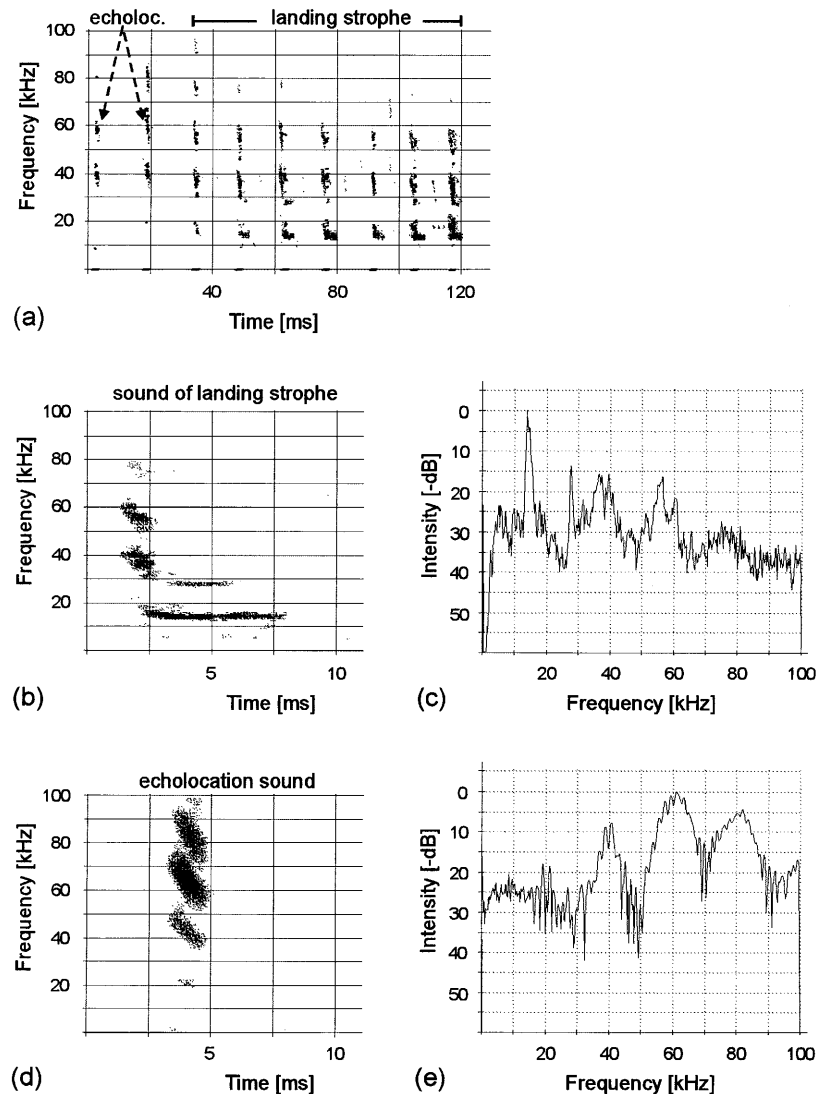
bats in flight. In addition, the bats also displayed song flights and grumbling flights already known from *M. lyra* kept in captivity (Leippert 1994).

Landing strophe

When a false vampire was landing it often emitted a sequence of audible sounds while flinging up its legs, and it did not make any difference whether the bats landed singly or in groups. We call this sequence the “landing strophe”, because it was mainly uttered during landing approaches. This sound sequence was sometimes also emitted when a bat took off due to disturbance. Interestingly, these audible sounds of landing strophes were never heard from bats landing singly or in groups at night roosts or on perches in the foraging areas.

The landing strophe consisted of a variable number of brief multiharmonic sounds (Fig. 2a–c), which were repeated with an interval of 11.0 ms (QD = 1.1 ms, $n = 44$, Fig. 3a) and lasted 4.9 ms (QD = 0.7 ms, $n = 50$, Fig. 3b).

Fig. 2 a The landing strophe and its typical sound element (b spectrogram, c power spectrum) in comparison to a typical echolocation sound (d spectrogram, e power spectrum) of *M. lyra*; a shows the spectrogram of a complete landing strophe preceded by two typical echolocation sounds in *M. lyra*



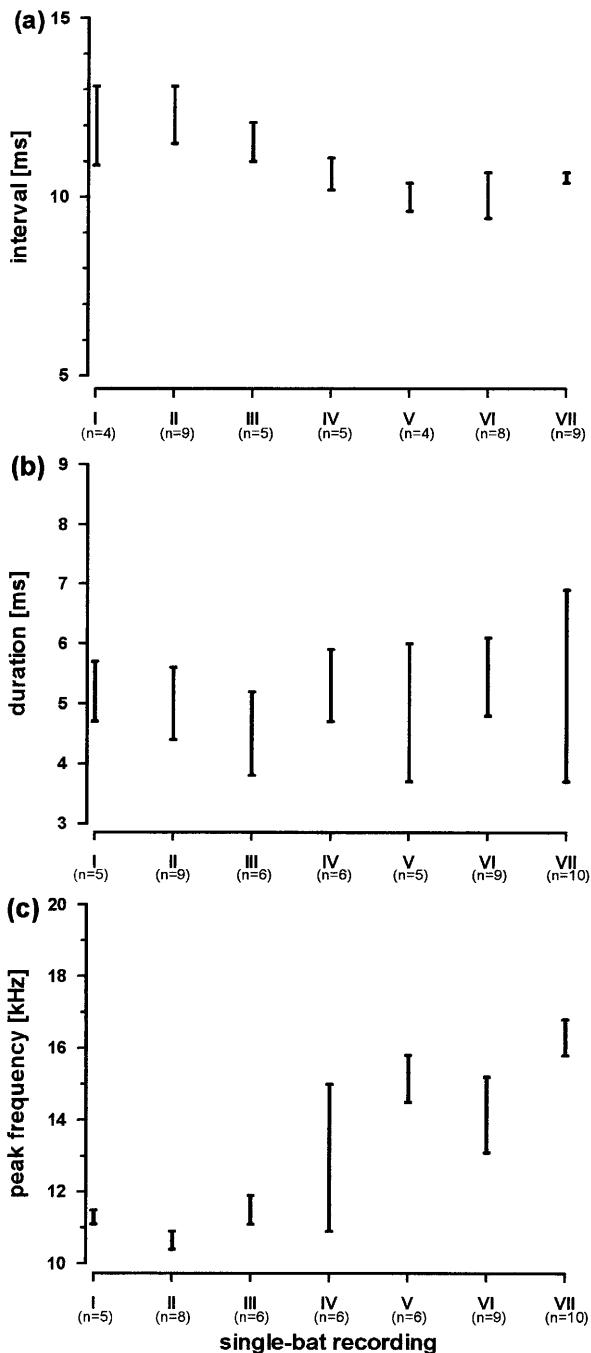


Fig. 3 Inter- and intra-individual variability of **a** interval, **b** duration and **c** peak frequency of sounds of landing strophes. The bars give minimum and maximum values of single-bat recordings (numbered I–VII); *n* is the sample size

The first of at least six downward-modulated harmonics of these landing sounds started at 16.6 kHz (QD = 1.7 kHz, $n = 51$) and levelled off as a low-frequency tone (Fig. 2a–c). The frequency of the first harmonic tone part was the loudest element of the sound and hence its peak frequency of 13.1 kHz (QD = 2.2 kHz, $n = 51$, Figs. 2c, 3c). The landing strophe sometimes (10 of 41 cases) evolved from a sequence of echolocation calls during the landing approach

(Fig. 2a), after a short pause of 7.2–25.6 ms (md = 11.6, QD = 1.4 ms, $n = 10$) between echolocation sequence and landing strophe. Sounds of the landing strophe differed from echolocation sounds by their longer duration, the tonal part and the loud and low first harmonic (Fig. 2).

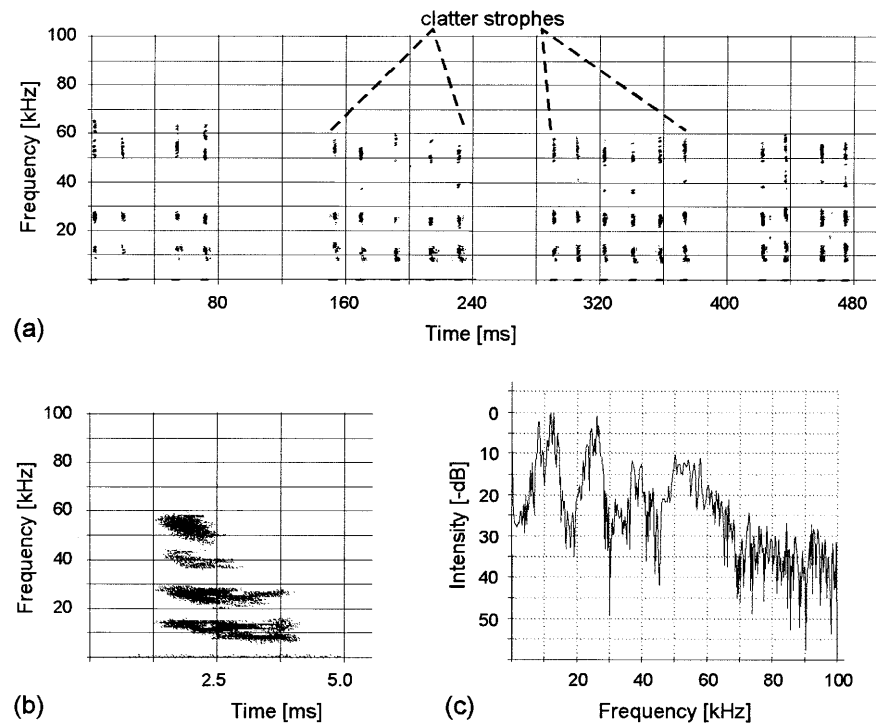
The single-bat recordings (Fig. 3a–c; $n = 7$) of the landing strophes differed significantly in interval (Fig. 3a; Kruskal-Wallis test: $H_6 = 27.9274$, $P < 0.001$) and peak frequency (Fig. 3c; Kruskal-Wallis test: $H_6 = 45.6083$, $P < 0.001$) of their sounds. The peak frequencies (85.7% of 21 pairs compared) of sounds from single-bat recordings differed more than the intervals (71.4% of 21 pairs compared). Combining these two sound parameters, 95% of the pairs of single-bat recordings can be correctly distinguished. In contrast, sound duration did not differ significantly between single-bat recordings (Fig. 3b; Kruskal-Wallis test: $H_6 = 11.6977$, ns).

Clatter strophe

In the morning, the false vampires continuously uttered audible sounds while entering the temple and flying straight to a roosting place. Because the sounds can be defined best as a clatter we called these vocalisations “clatter strophes” (Fig. 4). In the evening, and sometimes during daytime, single individuals emitted this type of sound while flying from one roosting place to another. We also several times observed two or more bats flying straight or in loops closely behind each other 30–50 cm apart, continuously emitting clatter strophes. We could not identify which one or how many of such bats were calling, except on one occasion in which a single bat entered the temple and emitted a clatter strophe. This caused another bat hanging about 2 m away from the entrance opening to take off. It followed the newcomer and immediately also emitted clatter strophes, though at a different frequency from that of the first bat. When resting bats were disturbed, for example by climbing squirrels, they uttered clatter strophes while flying to another roosting place. We could also provoke clatter strophes when we startled a group of resting bats. The bats emitted the clatter strophe in the day roost but not in night roosts or in foraging habitats, and we never heard the clatter strophes from individuals held in captivity.

The clatter strophes were composed of 2–12 sounds (Fig. 4a–c) with strophe intervals of 25.2–81.8 ms (md = 49.3, QD = 7.5 ms, $n = 11$; Figs. 4a, 5a). The sounds of the clatter strophe were repeated at a relatively constant rate (interval duration = 17.1, QD = 1 ms, $n = 84$; Fig. 4a, 5a), with a duration of 2.3 ms (QD = 0.45 ms, $n = 92$; Figs. 4b, 5b). On average the sounds of the clatter strophe were 2.6 ms shorter and repeated at intervals 7.1 ms longer than the sounds of the landing strophe. Clatter sounds consisted of at least four harmonics of a downward frequency modulated sweep (Fig. 4a–c). The first harmonic swept down from 13.9 kHz (QD = 0.75 kHz, $n = 94$) to 7.8 kHz (QD = 1.2 kHz, $n = 94$), and contained the peak frequency of 11.0 kHz (QD = 2.2 kHz, $n = 94$; Figs. 4b, c, 5c). At the

Fig. 4 a The clatter strophe and its typical sound (b spectrogram, c power spectrum)



end of the signal the sweep became shallow and levelled off into a constant frequency tail (Fig. 4b, c). Thus, sounds of clatter strophe differed from those of landing strophes by the lower number of harmonics and a lower peak frequency (11.0 kHz compared to 13.1 kHz) embedded into a lower first harmonic (Table 1).

The single-bat recordings (Fig. 5a–c; $n = 7$) of the clatter strophes differed significantly from bat to bat in interval (Fig. 5a; Kruskal-Wallis test, $H_6 = 21.4025$, $P < 0.01$), duration (Fig. 5b; Kruskal-Wallis test, $H_6 = 32.3282$, $P < 0.001$) and peak frequency (Fig. 5c; Kruskal-Wallis test, $H_6 = 64.5176$, $P < 0.001$) of their sounds. Most single-bat recordings differed significantly in the peak frequency of their sounds (81.0% of 21 possible pairs), and less frequently in interval (38.1%) and sound duration (52.4%). All (100%) pairs of single-bat recordings compared can be unambiguously distinguished by a combination of the three sound parameters.

Discussion

Do communication sounds serve as identity cards?

The single-bat recordings of the two types of vocal communications reported in this study were emitted by single, but unidentified, false vampire bats. The results of our study suggest that the temporal and spectral pattern of vocalisations in *M. lyra* carries individual signatures.

Individual recognition by vocal signals has been extensively studied in mother-infant identification by bats. In large nursery colonies of Mexican free-tailed bats (*Tadarida*

brasiliensis), mothers recognise and locate their own infant by olfaction and sounds. Mothers of *T. brasiliensis* stayed significantly longer at a box playing back isolation calls of their own pups than at a box emitting the calls of a conspecific infant (Balcombe 1990). Vocalisations of bat mothers are also individually distinct. In an analysis of the directive calls of mother Mexican free-tailed bats using nine sound parameters, 279 out of 300 directive sounds were correctly assigned by the authors to mothers who produced them (Balcombe and Mc Cracken 1992). Scherrer and Wilkinson (1993) described isolation calls of young *Nycticeius humeralis* using four sound parameters which varied among individuals but were rather stereotypic within individuals. They calculated that, in the total four-dimensional acoustic space occupied by pup calls, more than 1,800 infants could produce individual isolation calls without overlap in the combination of the four parameters. Thus, individual recognition by vocalisation between mothers and infants seems possible even within crowds of many thousands of individuals.

As demonstrated in the greater spear-nosed bat, *Phyllostomus hastatus*, adult bats may have remarkable cognitive abilities enabling them to create acoustic signatures. Females of the greater spear-nosed bat, which live in stable social groups of unrelated individuals, use screech calls to recruit social group mates to foraging groups (McCracken and Bradbury 1981; Wilkinson and Boughman 1998). The sound characteristics of the screech calls differ among social groups but not among individuals, and the bats recognise these differences (Boughman 1997; Boughman and Wilkinson 1998). If the composition of a social group changes, the females also change the call structure resulting in an increased similarity among new members (Boughman

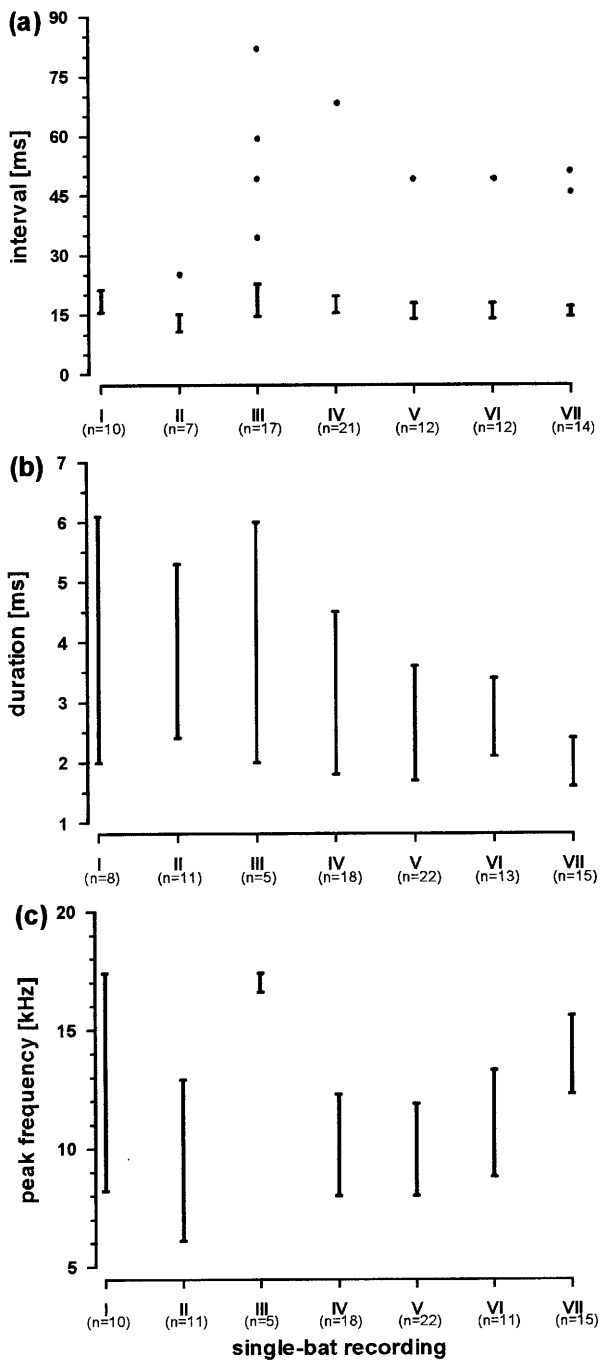


Fig. 5 Inter- and intra-individual variability of **a** interval, **b** duration and **c** peak frequency of sounds of clatter strophes. The *bars* give minimum and maximum values of single-bat recordings (*numbered I–VII*); *n* is the sample size. The *dots* in **a** show the duration of pauses

1998). It shows that adult bats may be able to create group-identity calls by vocal learning, and it is likely that they may also be able to learn and to recognise the individual acoustical cues of particular conspecifics. Such individual sound characteristics were found in songflight calls of adult males of *Pipistrellus pipistrellus* (Barlow and Jones 1997). Our own data suggest that there may

Table 1 Parameters of the sounds of landing strophes and clatter strophes

	Landing sound	Clatter sound
Interval	11.0 ms	17.1 ms
Duration	4.9 ms	2.3 ms
No. of harmonics	6	4
Peak frequency	13.1 kHz	11.0 kHz
1st harmonic sweep	16.6 to 13.1 kHz	13.9 to 7.8 kHz
1st harmonic bandwidth	3.5 kHz	6.1 kHz

also be an individual sound signature formed by temporal and spectral features in the communication of adult false vampire bats.

It seems that the social interactions that induce the clatter strophe and landing strophe only occur in the day roost. A free-ranging false vampire bat leaves the day roost for foraging and stays for the night in the foraging area (Audet et al. 1991). At sunrise the bat enters the day roost and emits the clatter strophe while aggregating with conspecifics. In contrast, captive bats which do not emit clatter strophes always stay in the same room and do not meet again daily individuals that they have left at sunset for foraging. The free-ranging bats which return from foraging at sunset may search for familiar roosting neighbours and indicate their own identity by their calls.

Several social displays indicate that false vampire bats recognise each other individually. For example, roosting individuals establish body-contact with up to five conspecifics (Goymann et al. 2000). Body-contacts occur between females, between females and males, and between males with non-prominent testes, but do not occur between males with prominent testes. Initiators of body-contacts pass over other individuals to reach their partners and so it seems that false vampire bats choose their partners particularly and not opportunistically (Goymann et al. 2000). As false vampires seem to form small stable groups in their foraging habitat (D. Leippert and I. Siewert, unpublished work) it is likely that social bonds between individuals exist. The complex song-flight behaviour of males towards females also indicates that it helps to establish and maintain social bonds (Leippert 1994; D. Leippert and I. Siewert, unpublished work). In captivity, dominant males direct their song flights preferentially to alien females although a number of familiar females is present (Leippert 1994). The various observations made suggest that false vampire bats recognise each other individually.

An analysis of the two sound types which we had recorded shows that parameters of the calls in adult bats are sufficiently distinct between individuals to be used for individual identification. Since the bats emitted the sounds in strophes of a number of sounds we were able to collect samples of sounds of single but unidentified bats. Nearly all – or even all – of the analysed strophes represent different individuals because 7 of more than 100 recorded strophes of each sound type were selected randomly. Artefacts in sound variability caused by directionality characteristics of the microphone can be excluded since the micro-

phone featured low directionality in the range of the peak frequencies of the landing strophe and clatter strophe. Therefore, our data strongly suggest individuality of the sounds in their temporal and spectral dimensions. The results of our study are supported by a recent results from our laboratory, where landing strophes emitted by identified false vampire bats were recorded and analysed. The sound characteristics of landing strophes are distinct among individuals, but also among sexes of the same colony (G. Waldau and D. Leippert, unpublished work). Only playback experiments will, however, show whether bats use vocalisations for individual recognition.

Do echolocation calls also serve as communication signals and vice versa?

In bats approaching a landing site, the sequence of echolocation calls is often changed into a landing strophe while the bats fling up their legs for landing. Therefore, it is not clear if the landing strophe is a sequence of modified echolocation calls for acoustical guidance of the landing procedure or a communicative signal to the neighbours, or if it serves both purposes. We never heard landing strophes from single bats or groups landing in roosts (e.g. buildings) which they used during the night. Also, we never detected the landing strophes in single bats or groups that landed at perches in their foraging area. In addition, when echolocating bats approach a target, echolocation sound duration is shortened and repetition rate raised, whereas the sounds of the landing strophes last considerably longer than the preceding echolocation pulses. Thus landing strophes are markedly different from echolocation sounds and appear to have a primarily communicative function. In captivity roosting *M. lyra* usually react aggressively when they are accidentally touched by a neighbour, whereas landing bats that inadvertently touch neighbours usually do not elicit an agonistic reaction. The landing strophe might be involved in subduing aggression during such landing manoeuvres.

Nevertheless, it can not be excluded that such communicative signals also serve echolocation. Many sound types are only emitted in distinct behavioural contexts (Leippert 1994), and we therefore interpret these vocalisations as communication calls. These sounds have physical features such as ultrasonic frequency range and simple time/frequency course which are typical for echolocation calls in many bat species. Conversely, echolocation sounds may also serve communication. For instance, little brown bats (*Myotis lucifugus*) are attracted to foraging conspecifics by their echolocation calls (Barclay 1982). Miller and Degn (1981) reported that *Eptesicus serotinus*, *P. pipistrellus* and *Nyctalus noctula* might communicate by echolocation signals. Ohlemiller et al. (1993) described cortical neurons in *Pteronotus parnelli* which responded to different echolocation signals and to sounds emitted during social interactions. Playback experiments might disclose if such signals are bifunctional and serve two different purposes, communication and echolocation at the same time.

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