

Individual signatures in the frequency-modulated sweep calls of African large-eared, free-tailed bats *Otomops martiensseni* (Chiroptera: Molossidae)

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Abstract

Frequency-modulated sweep calls of *Otomops martiensseni* were recorded from individuals as they emerged from nine different building roosts near Durban, South Africa. Multiple analyses of call features, including duration (ms), lowest frequency (kHz), highest frequency (kHz) and frequency with most energy (kHz), indicated significant inter-individual variation. Discriminant function analysis of call features correctly classified the calls of individuals from four roosts > 70% on 19 of 28 times. Although other species of molossids (*Chaerephon pumilus*, *Tadarida aegyptiaca*, and one unidentified species) produced social calls as well as frequency-modulated sweep calls, *O. martiensseni* produced just the latter vocalizations and they were longer and lower in frequency than those of the sympatric molossids. Other species of molossids, but not *O. martiensseni*, produced feeding buzzes as they attacked flying insects. The frequency-modulated sweep calls of *O. martiensseni* seem to serve a communication function, but they may not be used in echolocation unlike similar calls by other molossids. Individually distinct communication signals (frequency-modulated sweep calls) enhance communication in a species that lives in year-round social groups (one adult male, females and dependent young).

Key words: communication, echolocation, variation in calls, *Otomops martiensseni*, Molossidae

INTRODUCTION

Bats are long-lived, and some species live in groups whose composition is stable over time (Wilkinson, 1985; Altringham, 1996; Neuweiler, 2000), so the discovery of colony-specific acoustic (Pearl & Fenton, 1996; Boughman & Wilkinson, 1998) or olfactory (De Fanis & Jones, 1995; Bouchard, 2001) signatures was predictable. Playback experiments (Barclay, 1982; Leonard & Fenton, 1984; Balcombe & Fenton, 1988) and analyses of call features (Habersetzer, 1981; Obrist, 1995; Pearl & Fenton, 1996) demonstrated that an echolocation signal can serve in communication, so signatures are as likely to occur in echolocation (Masters, Raver & Kazial, 1995) as in social calls (Boughman & Wilkinson, 1998).

The echolocation calls of low duty cycle, aerial-feeding microchiropteran bats (Fenton, Audet *et al.*, 1995) are tonal, typically sweeping from high to low frequency in 1–20 ms, with actual call durations, bandwidths, and

patterns of sweep depending upon species and situation (Obrist, 1995; Altringham, 1996; Neuweiler, 2000). Attacks by echolocating bats on flying insects are accompanied by ‘feeding buzzes’, high call repetition rates during the final ms before contact (Schnitzler & Kalko, 2001). The distinction between ‘echolocation’ and ‘social’ calls is arbitrary, but tonal frequency-modulated sweeps are usually placed in the former category and may be species-specific (e.g. Barclay, 1999; O’Farrell, Gannon & Miller, 1999). Compared to echolocation calls, social calls may be harsh and broadband or tonal and broadband (e.g. Barclay, Fenton *et al.*, 1979), and often are much longer in duration and more variable (Fenton, 1994).

Tonal frequency-modulated sweep calls (Fig. 1) that are audible to humans have been reported from the African molossid *Otomops martiensseni* Matschie (Fenton, Taylor *et al.*, 2002), a species with huge ears and long narrow wings (high aspect ratio and high wing loading; Norberg & Rayner, 1987). *Otomops martiensseni* is presumed to be an aerial-feeding bat that flies high and fast and takes prey (flying insects) on the wing having used frequency-modulated sweep calls to detect, track and evaluate potential targets (Rydell & Yalden, 1997). In the

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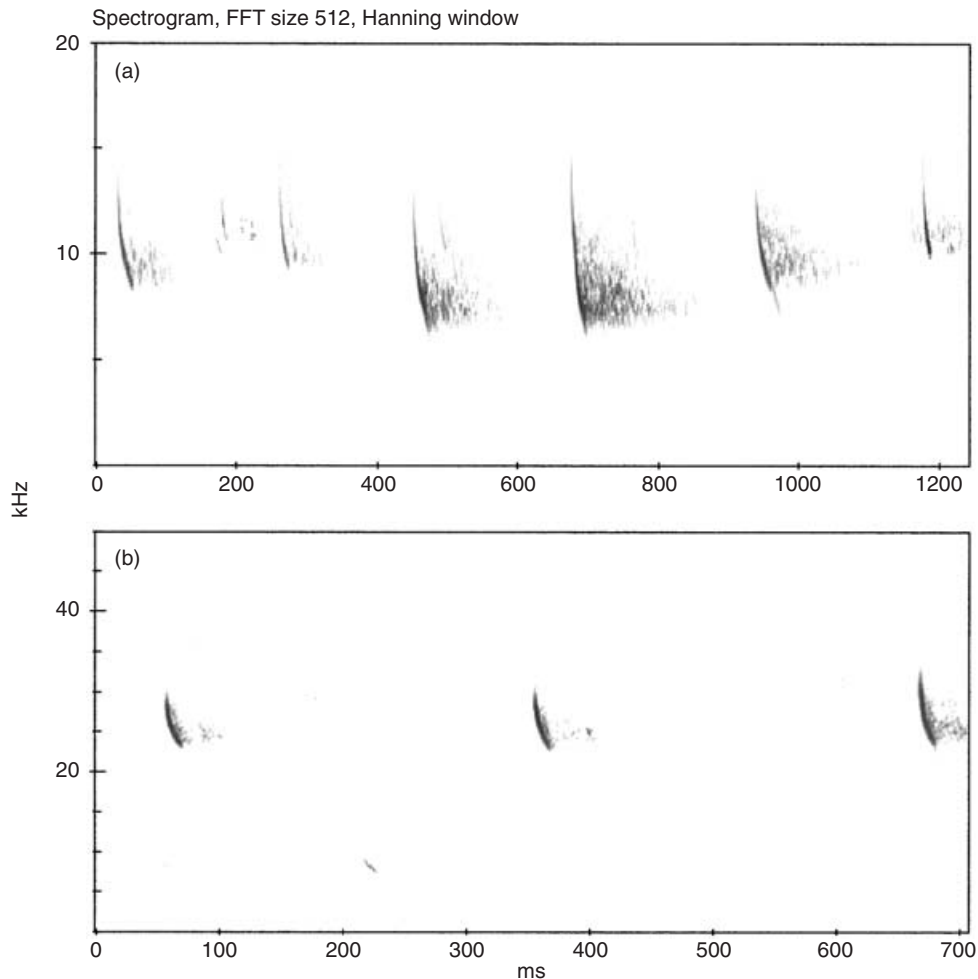


Fig. 1. Frequency-modulated sweep calls recorded from *Otomops martiensseni* (a) and *Chaerephon pumilus* (b) near Durban, South Africa (quantitative details of call features shown in Table 1). Note the strong echoes from some *Otomops* calls, and the presence of calls from at least two individuals. Horizontal and vertical axes have different scales in a and b.

Durban area of South Africa, groups of roosting *O. martiensseni* consist of one adult male, adult females and, depending upon the time of year, dependent young (Fenton, Taylor *et al.*, 2002). Roosting groups occur during the mating season (August–September; Mutere, 1973) and throughout the year. Groups of females and dependent young always include an adult male, recognizable by a well-developed chest gland, and, during the mating season, by the chest gland and enlarged testes (Harrison, 1957; Fenton, Taylor *et al.*, 2002).

The purpose of this study was to describe the frequency-modulated sweep calls of *O. martiensseni* and compare them with the vocalizations of other sympatric molossids. Statistically significant evidence was found of individual-specific frequency-modulated sweep calls in *O. martiensseni* and evidence for the role of these calls in communication. We also present preliminary evidence that, unlike sympatric molossids, these bats may not echolocate when attacking and capturing flying moths.

MATERIALS AND METHODS

Between 27 August and 7 September 2001, the vocalizations of bats were recorded as they emerged from 9 roosts in buildings near Durban, South Africa, and as they flew over other locations there. Four building roosts mentioned in detail in the text were located across the Durban area, including 1 in Durban (BR), 1 in Amanzimtoti (WE), 30 km south of the BR roost, and another (FS) 34 km south of WE. The BR roost was 37 km south of a roost in Ballito (JA). During the study, sunset occurred at 17:44 on 26 August, 17:58 on 6 September and sunrise was at 06:19 and 06:06, respectively. To observe their behaviour, 18 *O. martiensseni* were removed from a building roost (2 males and 16 females) and released 1 that flew in a large (17 × 3.5 × 2.5 m) room. This bat was recaptured and then released with the others outside.

To record the bats' vocalizations, 4 bat detectors were used: 2 Pettersson D980s (Pettersson Elektronik AB, Tallbacksvägen 51, S-756 45 Uppsala, Sweden) and a

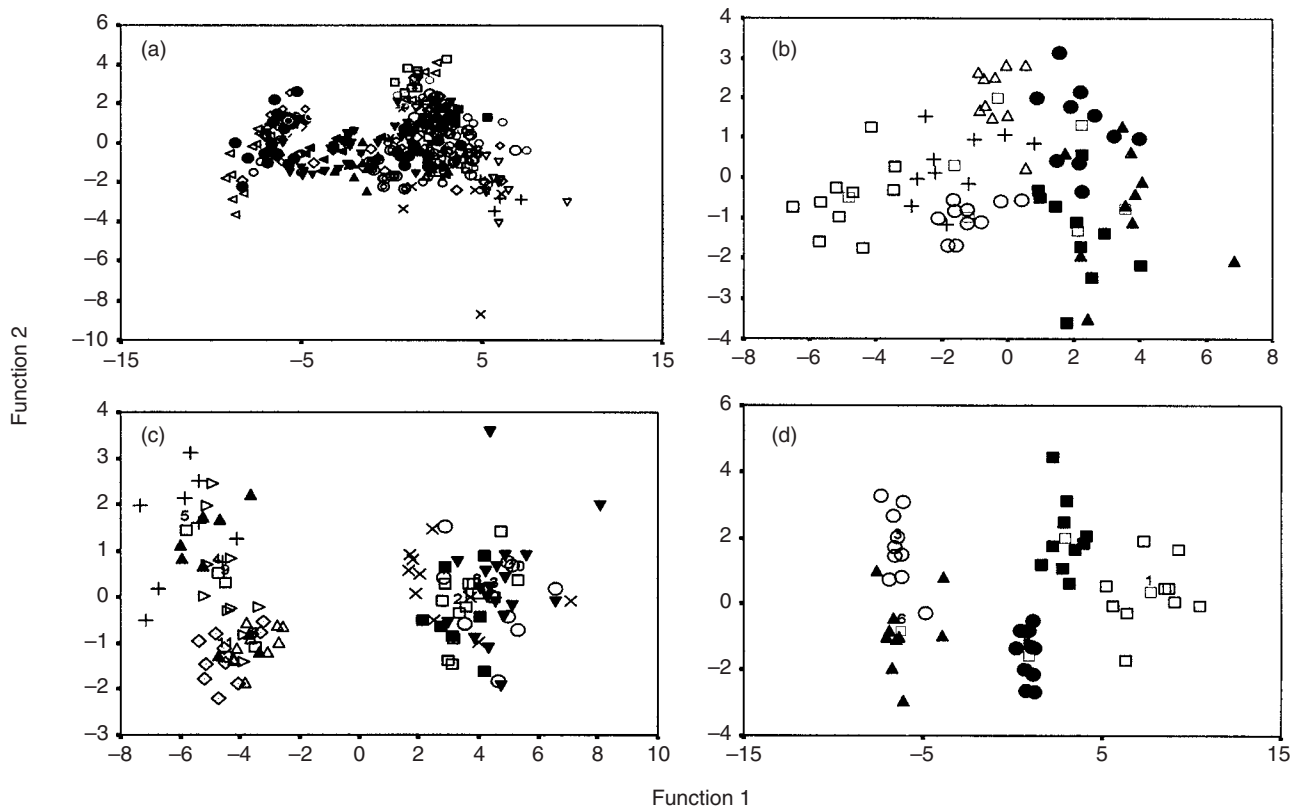


Fig. 2. Discriminant function analyses of the distribution of 328 calls from 38 recording sessions (a) showing the general features of frequency-modulated sweep calls of *Otomops martiensseni* (see also Table 3). When calls recorded from individuals emerging from one roost (10 calls per sequence; calls from each individual identified by symbols) are considered there is a clearer separation of individuals (b) when several individual bats emerge in sequence from roost BN. The separation is not as clear when the same individuals are recorded over several nights (colony WE, (c)). At another roost over 2 nights, four bats appeared to emerge from the FS colony (d). Details of analysis are presented in Tables 2 & 3, and the classification of results by calls are shown in Table 4.

Tranquility or Tranquility II (D. J. Bale, Cheltenham, Gloucestershire). Most recordings were made with a D980 through an Ines DAQ i508 high speed card to a Dell Latitude PC running BatSoundPro (Pettersson Elektronik AB) sampling at 250 kHz, 16 bit. In this situation, 60 s intervals were recorded separated by 10 s periods to reset the system. Time expansion outputs were also used from bat detectors (D980 and Tranquility or Tranquility II) to a personal computer. Pettersson D980 detectors invariably picked up the calls of the molossids at distances of 5 m, and maximum detection distances were at least 10–20 m depending upon the orientation of the bat relative to the microphone. Comparable distances for the Tranquility detectors were 5 m and 10–15 m. Recordings made with Pettersson detectors were analysed with BatSoundPro and those data were used in the quantitative aspects of this study. From each recorded signal analysed, notes were made of the interval between echolocation calls in ms (call end to call start: Fig. 2a; from the frequency change over time plot – threshold 16), duration in ms (Fig. 2b; measured from the time-amplitude plot) and, from the power spectrum (Fig. 2c), the lowest and highest frequencies (kHz at –55 dB levels) and the frequency with most energy (kHz from FFT 512, Hanning window). The

power spectrum was also used to identify the presence of harmonics.

The frequency-modulated sweep calls of *O. martiensseni* were recorded after they had emerged from building roosts, identifying individuals by the trains of pulses produced on emergence (= a recording sequence). To achieve this, a tripod-mounted D980 bat detector was used 1.4 m above the ground and angled upwards 60° from the horizontal. The detector was placed 10–15 m from the entrance to the roost and pointed away from the roost so that emerging bats flew over the detector (usually 3–5 m above it) before turning right or left as they started to vocalize. Up to 10 calls were analysed from any train of calls recorded from a bat in any recording sequence. Cumulative interpulse intervals meant that while good recordings of 10 calls could be obtained from an emerging individual, > 15 such calls were rarely recorded before the bat's calls were lost among those of others. In contrast, the sequences of frequency-modulated sweep calls of other molossids were not from single bats because the bats emerged in groups (see below). When recording the vocalizations of other molossids, the same tripod-mounted and positioned detector was used, recording from bats as they flew overhead. Up to 10 calls were also analysed from

Table 1. A comparison of features of the frequency-modulated sweep calls of four species of molossid. N_c , number of calls analysed; duration, length of call; interpulse interval, time between calls. Means are shown ± 1 SD, and CV is the coefficient of variation

| | N_c | Duration | | Interpulse interval | | Lowest frequency | | Highest frequency | | Frequency with most energy | |
|--|-------|-----------------|------|---------------------|------|------------------|------|-------------------|------|----------------------------|-----|
| | | ms | CV | ms | CV | kHz | CV | kHz | CV | kHz | CV |
| <i>Otomops martiensseni</i> | 60 | 22 \pm 3.96 | 18 | 620 \pm 103 | 16.6 | 8.9 \pm 0.91 | 10.2 | 14.7 \pm 1.68 | 10.9 | 9.9 \pm 1.11 | 1.1 |
| <i>Chaerephon pumilus</i> | 60 | 13.6 \pm 4.1 | 30 | 241 \pm 122 | 50.6 | 22.2 \pm 1.39 | 6.3 | 29 \pm 4.6 | 15.9 | 23.9 \pm 1.61 | 6.7 |
| <i>Chaerephon</i> 'other' | 60 | 9.6 \pm 3.36 | 35 | 282 \pm 230 | 81.5 | 14.5 \pm 1.13 | 7.8 | 21.8 \pm 2.87 | 13.1 | 16.3 \pm 1.36 | 6.5 |
| <i>Tadarida aegyptiaca</i> | 10 | 12.1 \pm 1.04 | 8.6 | 251 \pm 28 | 11.1 | 18.8 \pm 0.41 | 21.8 | 27.1 \pm 0.41 | 1.5 | 20.9 \pm 0.48 | 2.3 |
| <i>Otomops martiensseni</i> from Brynderyn roost | | | | | | | | | | | |
| bat 1 | 10 | 22.4 \pm 3.57 | 15.9 | | | 9.2 \pm 0.4 | 4.4 | 14.8 \pm 0.36 | 2.4 | 10.3 \pm 0.76 | 7.4 |
| bat 2 | 10 | 21.8 \pm 3.12 | 14.3 | | | 9.8 \pm 0.4 | 4.3 | 17.3 \pm 1.6 | 9.2 | 11.0 \pm 0.91 | 8.2 |
| bat 3 | 10 | 14.7 \pm 3.2 | 21.8 | | | 9.7 \pm 0.34 | 3.6 | 19.9 \pm 2.18 | 10.9 | 11.3 \pm 0.54 | 4.8 |
| bat 4 | 10 | 19.9 \pm 2.18 | 11.0 | | | 9.1 \pm 0.37 | 4.1 | 15.4 \pm 0.84 | 5.5 | 10.1 \pm 0.56 | 5.5 |
| bat 5 | 10 | 17.4 \pm 3.53 | 20.3 | | | 10.5 \pm 0.52 | 5.0 | 19.8 \pm 1.53 | 7.8 | 12.4 \pm 0.99 | 7.9 |
| bat 6 | 10 | 23.5 \pm 3.03 | 12.9 | | | 7.9 \pm 0.41 | 5.3 | 15.5 \pm 1.00 | 6.5 | 8.9 \pm 0.47 | 5.2 |
| bat 7 | 10 | 15.8 \pm 2.53 | 16.0 | | | 10.3 \pm 0.37 | 3.5 | 19.0 \pm 1.33 | 7.0 | 11.9 \pm 0.77 | 6.5 |

any train of calls recorded from a bat. When there was any question of whether or not the calls were from the same individual (assessed by interpulse intervals and signal strength), the data were not used in subsequent analysis. Wherever possible, published data about echolocation calls (Taylor, 2000) were used to identify species.

Statistical analyses were performed using SPSS version 11.0, including multiple analyses of data that were not all normally distributed, nor were the variances always equal. In discriminant analyses, data on interpulse interval were omitted because our sample sizes were always 1 less than those for other features of calls. Means are shown ± 1 SD.

RESULTS

Emergence behaviour

Otomops martiensseni began to emerge from their day roosts at *c.* 18:00 (first emergences from 17:54 to 18:10; $n = 10$), appearing alone at 3–10 min intervals. Emerging *O. martiensseni* ($n \sim 100$) flew directly away from the roost (usually on a course perpendicular to it) and then turned left (usually) or right just as they began to produce vocalizations, by now 10–30 m from the roost entrance. Observers both listened for vocalizations, and monitored the bats' vocal behaviour with Pettersson D980 bat detectors. Invariably, the first calls (frequency-modulated sweeps, see below) that emerging bats produced were simultaneously heard by human observers and recorded by the D980 systems. *Chaerephon pumilus* and *T. aegyptiaca* emerged from day roosts between 17:15 and 17:30, sometimes before 17:00. Although individual *C. pumilus* and *T. aegyptiaca* occasionally emerged singly, typically 10–15 individuals appeared as a group. Whether in groups or alone, these bats began to produce frequency-modulated sweep calls from the moment they took flight.

After emergence, *O. martiensseni* often (seven of 11 evenings) remained in the general vicinity of the roost, flying around overhead and producing conspicuous

frequency-modulated sweep calls. This behaviour continued for 5–30 min, apparently until other bats from the roost had joined the calling bats in flight, when the bats flew out of earshot of observers at the colony. Two to 4 h after emergence, groups of vocalizing *O. martiensseni* occasionally returned to roosts, flying above them and calling, but their approaches to roost entrances were silent. At night these groups of bats did not enter the colony, but flew away out of earshot.

The emergence behaviour of *O. martiensseni* permitted us to record and then analyse calls from sequences produced by different individuals.

Vocalizations

Frequency-modulated sweep calls of molossids (Fig. 1) were readily distinguishable from those of sympatric vespertilionids (most often *Pipistrellus* or *Scotophilus* species). Vespertilionids produced shorter (< 10 ms) calls of higher frequency that showed more rapid change in frequency over time, and were of broader bandwidth. Molossids produced longer, lower frequency calls that showed gradual changes in frequency over time and that were narrower in bandwidth. The frequency-modulated sweep calls of molossids rarely included harmonics but, in unsaturated recordings with very good signal-to-noise ratios, a weak second harmonic was sometimes (1% of sample) evident.

Features of the frequency-modulated sweep calls of molossids suggested that four species (Table 1) were present, three of which we could identify from the literature (Taylor, 2000; *O. martiensseni*, *C. pumilus* and *T. aegyptiaca*). A multivariate analysis of the features of these calls indicated significant interindividual variation (Table 2), and a discriminant function analysis (Table 3) accurately classified calls to each of the four 'taxa' 100% of the time.

Multivariate analysis of the features of sequences of up to 10 frequency-modulated sweep calls recorded from

Table 2. Results of a multiple analysis of variance of call features (duration, lowest frequency, highest frequency and frequency with most energy). d.f., degrees of freedom. Compared are the results from comparisons of the calls of four apparent species of molossids, all *Otomops* data and *Otomops* calls from four colonies (Wendy's, Brynderyn, Far South and Jacqueline)

| | Wilk's λ | <i>F</i> | H.d.f. | Error d.f. | <i>P</i> |
|--------------------|------------------|----------|--------|------------|----------|
| Four molossids | 0.019 | 141.599 | 12 | 484.464 | < 0.001 |
| All <i>Otomops</i> | 0.008 | 11.835 | 140 | 1264 | < 0.001 |
| Wendy's | 0.018 | 16.154 | 40 | 339.333 | < 0.001 |
| Brynderyn | 0.024 | 16.849 | 24 | 210.525 | < 0.001 |
| Far South | 0.005 | 33.806 | 20 | 170.098 | < 0.001 |
| Jacqueline | 0.017 | 17.151 | 44 | 399.833 | < 0.001 |

individual *O. martiensseni* immediately after emergence indicated significant interindividual variation (Table 2). Discriminant function analysis of the data from the calls showed general overlap between 328 calls recorded in 38 sequences across the study area (Fig. 2a, Table 3). The variability in call parameters was considerable (Table 1).

At any one roost, however, the calls of individuals (those in a sequence) were usually accurately classified by the analysis, notably at BR and FS roosts (Table 3, Fig. 2b). Records were made at the FS roost, which was occupied by > 20 *O. martiensseni*, on 2 nights. The DFA analysis suggests that four different individuals emerged, two on

each night (Table 3, Fig. 2d) indicating that most bats did not leave the roost on either night that recordings were made. At the WE roost, occupied by three *O. martiensseni*, the emergence of bats was recorded on 3 nights. When these calls were classified by discriminant analysis, the level of correct assignment was lower, reflecting repeated recordings of the same individuals (Table 4, Fig. 2c). The same situation seems to apply at the JA roost, which was visited twice.

Other species of molossids produced social calls that were very distinct from their frequency-modulated sweep calls (Fig. 3, Table 5). Social calls were four to five times longer (cf. Table 1), usually involved several changes in frequency over time, and always included at least one harmonic (Fig. 3). Although we often heard these calls when either *C. pumilus* or *T. aegyptiaca* flew in the same airspace as *O. martiensseni*, they were never heard when the other species were absent.

Foraging

Within 10–20 m of building roosts, *C. pumilus* and *T. aegyptiaca* began foraging, as evidenced by pronounced changes in flight paths that were always (*n* = 34) associated with feeding buzzes and attacks on flying insects. At one *C. pumilus* roost, bats began to attack flying insects over and beside the building within 1–2 min

Table 3. The results of discriminant function analysis of data from echolocation calls, including duration (DUR), lowest frequency (Lfr), highest frequency (Hfr) and frequency with most energy (Fme). d.f., degrees of freedom

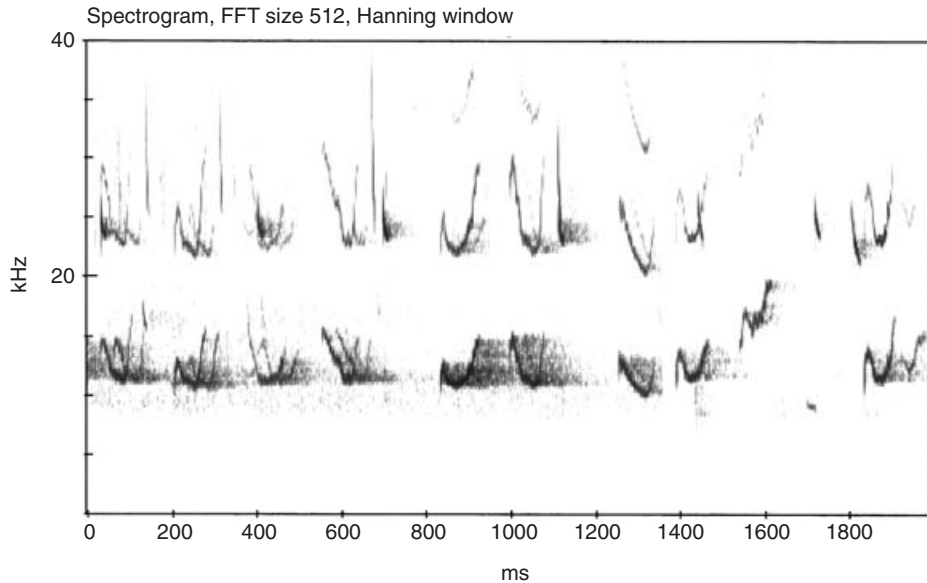
| | DUR | Lfr | Hfr | Fme | Eigenvalue | Cumulative% | Wilks λ | χ^2 | d.f. | <i>P</i> value |
|--------------------|--------|--------|--------|--------|------------|-------------|-----------------|----------|------|----------------|
| Four molossids | | | | | | | | | | |
| Function 1 | 0.994 | 0.883 | –0.175 | 0.377 | 22.752 | 94.8 | 0.019 | 736.992 | 12 | < 0.001 |
| Function 2 | 0.058 | –0.091 | 0.973 | –0.112 | 1.218 | 99.9 | 0.442 | 150.976 | 6 | < 0.001 |
| Function 3 | 0.036 | 0.451 | –0.121 | 0.699 | 0.020 | 100.0 | 0.981 | 3.574 | 2 | 0.167 |
| All <i>Otomops</i> | | | | | | | | | | |
| Function 1 | 0.451 | 1.046 | 0.082 | 0.105 | 16.946 | 85.5 | 0.008 | 1578.495 | 140 | < 0.001 |
| Function 2 | 0.721 | 0.507 | –0.856 | –0.079 | 1.648 | 93.9 | 0.152 | 622.770 | 102 | < 0.001 |
| Function 3 | 0.842 | –0.322 | 0.491 | 0.338 | 0.936 | 98.60 | 0.403 | 300.450 | 66 | < 0.001 |
| Function 4 | 0.138 | –0.758 | –0.408 | 1.395 | 0.280 | 100.0 | 0.781 | 81.835 | 32 | < 0.001 |
| Wendy's | | | | | | | | | | |
| Function 1 | 0.579 | 1.066 | –0.099 | 0.245 | 21.038 | 94.9 | 0.018 | 382.045 | 40 | < 0.001 |
| Function 2 | 0.325 | –0.636 | 0.738 | 0.580 | 0.593 | 97.5 | 0.387 | 89.778 | 27 | < 0.001 |
| Function 3 | –0.099 | 0.783 | –0.537 | 0.595 | 0.293 | 98.8 | 0.616 | 45.778 | 16 | < 0.001 |
| Function 4 | 0.245 | 0.580 | 0.372 | –1.195 | 0.256 | 100.0 | 0.796 | 21.525 | 7 | 0.003 |
| Brynderyn | | | | | | | | | | |
| Function 1 | 1.169 | 1.519 | 0.125 | 0.133 | 7.864 | 77.3 | 0.024 | 237.440 | 24 | < 0.001 |
| Function 2 | 1.519 | 0.694 | –0.427 | –1.039 | 1.488 | 91.9 | 0.211 | 98.882 | 15 | < 0.001 |
| Function 3 | 0.125 | –0.810 | 0.670 | –0.290 | 0.690 | 98.7 | 0.524 | 41.011 | 8 | < 0.001 |
| Function 4 | 0.133 | 0.186 | 0.181 | 1.828 | 0.129 | 100.0 | 0.886 | 7.686 | 3 | 0.053 |
| Far South | | | | | | | | | | |
| Function 1 | –0.066 | 0.793 | –0.058 | 0.350 | 27.436 | 88.7 | 0.005 | 287.346 | 20 | < 0.001 |
| Function 2 | 1.031 | –0.241 | 0.267 | 0.328 | 2.347 | 96.3 | 0.139 | 106.573 | 12 | < 0.001 |
| Function 3 | –0.131 | –0.762 | 0.787 | 0.663 | 1.148 | 100.0 | 0.465 | 41.338 | 6 | < 0.001 |
| Function 4 | –0.249 | 0.522 | 0.656 | –0.916 | 0.001 | 100.0 | 0.999 | 0.057 | 2 | 0.972 |
| Jacqueline | | | | | | | | | | |
| Function 1 | 0.525 | 1.092 | –0.247 | 0.178 | 7.581 | 69.3 | 0.017 | 446.226 | 44 | < 0.001 |
| Function 2 | 0.821 | 0.023 | –0.862 | 0.282 | 2.538 | 92.5 | 0.149 | 209.771 | 30 | < 0.001 |
| Function 3 | 0.725 | –0.086 | 0.630 | 0.128 | 0.719 | 99.0 | 0.525 | 70.777 | 18 | < 0.001 |
| Function 4 | 0.049 | –0.863 | –0.274 | 1.415 | 0.107 | 100.0 | 0.903 | 11.208 | 8 | 0.190 |

Table 4. Classification results of the discriminant function analysis showing the percentage of calls correctly assigned to emerging individual. $n = 10$ calls per individual

| | Bat number | | | | | | | | |
|--------------------------|------------|-----|------|-----|----|-----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| BR% correctly classified | 90 | 70 | 80 | 80 | 70 | 90 | 80 | | |
| JA% correctly classified | 70 | 50 | 60 | 100 | 80 | 100 | 80 | | |
| WE% correctly classified | 12.5 | 20 | 66.7 | 80 | 90 | 40 | 40 | 40 | 70 |
| FS% correctly classified | 100 | 100 | 90 | 100 | | | | | |

Table 5. Characteristics of social calls (Fig. 5) associated with two species of molossid. N_c , number of calls analysed; duration, length of call. Means ± 1 SD. CV, the coefficient of variation

| | N_c | Duration (ms) | | Lowest frequency (kHz) | | Highest frequency (kHz) | | Frequency with most energy (kHz) | |
|----------------------------|-------|------------------|------|------------------------|------|-------------------------|-----|----------------------------------|-----|
| | | Mean | CV | Mean | CV | Mean | CV | Mean | CV |
| | | | | | | | | | |
| <i>Chaerephon pumilus</i> | 60 | 64.47 \pm 11.1 | 17.1 | 10.9 \pm 1.13 | 10.4 | 14.69 \pm 1.34 | 9.1 | 11.8 \pm 1.17 | 9.9 |
| <i>Tadarida aegyptiaca</i> | 20 | 76.6 \pm 10.1 | 13.2 | 10.6 \pm 0.91 | 8.6 | 14.92 \pm 1.26 | 8.5 | 11.34 \pm 0.9 | 7.9 |

**Fig. 3.** A sampling of social calls of *Chaerephon pumilus* and *Tadarida aegyptiaca* (details in Table 5). Very similar calls were also recorded from the 'other' species of molossid.

of emergence. Feeding buzzes were also detected from the other molossid. On 3 August 2001, two of us (EJR, WW) observed *O. martiensseni* outside a roost. The bats had emerged from the roost at 19:00, left the area, and returned to the vicinity at *c.* 21:00. Then, for 15 min, two or three *O. martiensseni* made 10–12 flights past the house lights, attacking and capturing about nine medium-sized moths (body length 10–12 mm) that had been fluttering around the lights. Although EJR and WW monitored the vocalizations of the bats with the two Tranquility bat detectors positioned within 5 m of the foraging bats, they neither recorded nor heard any calls from these bats. Attacks on flying moths in this situation did not involve feeding buzzes or, during approaches,

frequency-modulated sweeps. In > 40 h of listening to frequency-modulated sweep calls of *O. martiensseni*, no feeding buzzes were heard, although we actively listened for the bats in areas where other species were actively feeding. The same absence of feeding buzzes prevailed in January 2001 during 8 all-night studies of *O. martiensseni* behaviour, including following radio-tagged individuals (Fenton, Taylor *et al.*, 2002).

When flying in a large room, *O. martiensseni* produce frequency-modulated sweep calls that differed from the ones recorded from flying bats in the field. Calls produced on release were short (1.8 ± 0.1 ms, $n = 6$) with four harmonics (some energy at 9.3 ± 0.6 kHz, but most energy between 20.6 ± 0.3 and 61.3 ± 0.4 kHz, $n = 6$). Interpulse

intervals also were shorter than those recorded in the field (33.8 ± 3.6 ms, $n = 4$). The differences between these calls and those produced in the field illustrate the perils of using recordings of bats flying in rooms to ascertain the nature of their calls. Calls with these frequency features could have been used in echolocation by *O. martiensseni*, and if so, they would have been registered by the Tranquility detectors used for recording foraging bats.

DISCUSSION

Long-lived mammals and birds forming long-term associations with other individuals recognize group members by acoustic signals (e.g. Novicki, 1983; Marler & Mitani, 1988; Strager, 1995; Houser, 1996; Weilgart & Whitehead, 1997; Price, 1999; Hopp, Jablonski & Brown, 2001). In the bat *Phyllostomus hastatus*, playback experiments and analysis of vocalizations indicated that screech calls were group-specific (Boughman & Wilkinson, 1998). Both screech calls (*P. hastatus*) and frequency-modulated sweep calls (*O. martiensseni*) are low in frequency, but screech calls are broadband, harsh, and much longer than the frequency-modulated sweeps, which are tonal. The levels of correct classification of screech calls by discriminant function analysis were similar to ours (Boughman & Wilkinson, 1998). Unlike *O. martiensseni* that move between roosts (Fenton, Taylor *et al.*, 2002), *P. hastatus* consistently use the same roost (Boughman & Wilkinson, 1998). Our data do not include responses to playback presentations so the behavioural significance of the variation in calls that were observed has not been demonstrated. There are currently no genetic data about the degree of isolation of the groups that were studied in this research.

In the bat *Myotis lucifugus*, echolocation calls (frequency-modulated sweeps) from individuals in nursery colonies in building roosts that were closer together (< 1 km) were more often accurately classified by discriminant function analysis than those from bats from a more distant (5 km) roost (Pearl & Fenton, 1996). *Myotis lucifugus* consistently use the same buildings as nursery roosts year after year (Neilson & Fenton, 1994), and these bats can use the echolocation calls of conspecifics to locate foraging opportunities (Barclay, 1982). Our analysis from *O. martiensseni* calls showed greater levels of significance in differences between individuals than those reported by Pearl & Fenton (1996) for groups of *M. lucifugus*. Furthermore, the roosts used by *O. martiensseni* were much farther apart (≥ 30 km), beyond the usual foraging distances covered by radio-tagged individuals (Fenton, Taylor *et al.*, 2002).

Echolocation calls may provide more details to conspecifics about a caller's identity. Using analysis of echolocation calls (frequency-modulated sweeps) recorded from captive *Eptesicus fuscus*, Masters *et al.* (1995) demonstrated group (age) specific features at about the same level of accuracy reported for the calls of either *P. hastatus* or *O. martiensseni*. While *E. fuscus* who roost in buildings

return predictably to the same roosts day after day, year after year, those bats roosting in trees regularly switch roosts (Brigham, 1991). Other species forming long-term associations between individuals (e.g. *Desmodus rotundus*, Wilkinson, 1985; *Rhinolophus ferrumequinum*, Ransome, 1990; *Saccopteryx bilineata*, Voigt & von Helversen, 1999; *Myotis bechsteinii*, Kerth, Wagner & König, 2001) can be expected to have group-specific acoustic signals.

Calling behaviour around roosts suggests that the frequency-modulated sweep calls of *O. martiensseni* may function as contact calls like the screech calls of *P. hastatus* (Wilkinson & Boughman, 1998). In both species group members roost in physical contact with one another, yet the calls are given as bats leave roosts or, in *P. hastatus*, around foraging areas. For *P. hastatus* on any night, fruit usually is localized on specific trees, while for *O. martiensseni*, food (flying insects) may be more dispersed. If *O. martiensseni* forage in concentrations of insects such as those in lees, then the frequency-modulated sweep calls may be food-sharing calls like those reported for swallows (Brown, Bomberger Brown & Schaffer, 1991).

We propose that frequency-modulated sweep calls of *O. martiensseni* synchronize activity away from roosts, which could be particularly important because on any day group members may be in different day roosts (Fenton, Taylor *et al.*, 2002) and effective communication must involve more than just the individual bats roosting together on any 1 day. Individually distinct calls offer the potential for enhanced interactions between group members, which may be particularly important for nocturnal flying animals that may be out of visual or olfactory range when foraging.

The apparent absence of feeding buzzes in *O. martiensseni* is surprising. Although the frequency-modulated sweep calls recorded from these bats are 'typical' in form for echolocation calls known from molossids (e.g. Fenton & Bell, 1981), they average almost twice as long as those of three sympatric molossids (Table 1), coinciding with differences predictable from body size. Longer duration calls mean longer periods of self-deafening (forward masking of Schnitzler & Kalko, 2001). The only time *O. martiensseni* was seen attacking and catching moths, albeit around a light, no frequency-modulated sweeps calls were detected. The situation suggests that it is unlikely that the bats produced calls which could not be heard or detected with bat detectors. Other species (e.g. *Lasiurus borealis*, *Lasiurus cinereus*) that forage around lights use echolocation and feeding buzzes when hunting flying insects (Obrist, 1995; Barclay *et al.*, 1999). *Tadarida teniotis*, another large-eared molossid similar in size to *O. martiensseni*, uses lower frequency echolocation calls (Russo & Jones, 2002), produces echolocation calls and feeding buzzes when searching for and then attacking insects around lights (M. B. Fenton, pers. obs.). We expect that *O. martiensseni* will be shown to use vision to detect and track prey.

The contrast in behaviour between *O. martiensseni* and the other three molossids whose vocalizations were

recorded deserves mention. While distinctive social calls (Fig. 3) were recorded from the other three species, *Otomops* seemed to use echolocation calls like signals in communication. The tonal calls of the other molossids are reminiscent of many social calls of other bats (e.g. *Saccopteryx bilineata*, Bradbury & Emmons, 1974; *Myotis lucifugus*, Barclay, Fenton *et al.*, 1979; *Carollia perspicillata*, Porter, 1979). Differences in emergence behaviour (noisy and in groups, the other three molossids, versus silent and solitary, the *Otomops*) may illustrate two different strategies for avoiding predators.

The identity of the fourth species of molossid in the Durban area has not been confirmed by voucher specimens so its identity remains unknown. Specimen records of molossids from the Durban area are of *C. pumilus*, *O. martiensseni*, and *T. aegyptiaca* (Taylor, 2000). In Europe, a cryptic species of *Pipistrellus* was recognized initially by its echolocation calls and later its distinctness was confirmed by DNA analysis (Barratt *et al.*, 1997). More recent studies suggest the possibility of other cryptic species in Europe (Mayer & von Helversen, 2001). The identities of southern African molossids deserve more attention.

The demonstration of individual-specific vocalizations in bats suggests the possibility of more complex social structures and interactions than previously demonstrated for most other bats. This development is particularly exciting in a species such as *O. martiensseni*, which lives in groups year-round and whose members use several roost sites and do not always roost with other members of the group. Individual-specific vocalizations within the range of human hearing could be of special importance in furthering the conservation of a widespread species such as *O. martiensseni* that has been reported from few, but widespread localities in Africa (Fenton, Taylor *et al.*, 2002). Individual-specific calls could provide a remote means of determining local populations and monitoring the presence and distribution of specific individuals.

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