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# Ultrasound social calls made by greater horseshoe bats (*Rhinolophus ferrumequinum*) in a nursery roost

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Ultrasound calls made by adult *Rhinolophus ferrumequinum* in a nursery roost were recorded using a time expansion detector with a microphone on an extension cable. Initial analysis showed that in addition to the echolocation calls at 81–84 kHz there were ultrasound calls at lower frequencies. Simultaneous recordings of ultrasound and low frequency signals (1–10 kHz) showed that echolocation pulses, ultrasound social calls and low frequency social calls were quite distinct in both duration, frequency and number of calls. Twelve types of ultrasound social calls were identified. The majority of calls were in the range 20–29 kHz and 1–49 ms duration. Variability was found in the relative power of the fundamental and harmonics of the calls. This analysis has identified a substantial repertoire of calls used by *R. ferrumequinum* in a nursery roost colony. The possibility of the use of a male advertisement call in the roost is discussed.

*Key words*: *Rhinolophus ferrumequinum*, ultrasound social calls, low frequency social calls, nursery roost

## INTRODUCTION

The greater horseshoe bat *Rhinolophus ferrumequinum* (Schreber, 1774) emits long-duration, high-frequency echolocation calls. An acoustic fovea in the auditory system of this species is tuned to a narrow frequency range of 78–88 kHz (Bruns, 1976*a*, 1976*b*; Suga *et al*., 1976; Schuller and Pollack, 1979; Vater, 1987) to provide a specially high sensitivity within the call frequency range. Alternating movement of the outer ears during each echolocation pulse enables vertical acoustic orientation (Andrews, 1995).

In addition to echolocation calls, bats also produce social calls for communication, well known for several vespertilionid species (Lundberg and Gerell, 1986; Barlow and Jones, 1997*a*). Although it would be expected that *Rhinolophidae* would also have similar vocal signals, little or nothing is known about social calls in this microbat family. A colony of greater horseshoe bats (*R. ferrumequinum*) in a nursery roost in West Wales has been studied since 1977 (Andrews, 1996; McOwat, 1997). Preliminary recordings made 1995–1999 in the roost near the exit showed that in addition to the normal echolocation calls there were frequency modulated (FM) ultrasound calls at lower frequencies. These calls, longer than the echolocation calls, were found mainly in the range 20–32 kHz. When Stebbings and McOwat monitored greater horseshoe bats, in the same nursery roost used in this study, they found that there were mature males with mature and immature females in the roost (Andrews, 2000). Therefore the possibility that some ultrasound calls made below the echolocation frequency were male advertisement calls was considered. Ultrasound calls related to activity in the roost warranted investigation since clusters of *R. ferrumequinum* form in nursery roosts (Ransome, 1980) and agonistic calls are made by non-hibernating bats when they squabble over positions in a cluster (Bradbury, 1977). The aims of the study were to record and classify the ultrasound social calls made by adult *R. ferrumequinum* bats in a nursery roost in May, before the babies were born from late June to early August, and to distinguish those calls from echolocation calls and low frequency social calls.

## Materials and Methods

### *Sound Recording and Method of Analysis*

An ECO-Tranquility ultrasound bat detector (Bale, Courtpan Design Ltd., U.K.) was used with a sample time of 320 ms and × 10 expansion. The sample rate was 409.6 kHz. The detector, placed in an adjacent room, was modified to operate with an ultrasonic microphone in the roost on a long extension lead. The microphone was placed on a beam in the roof of the nursery roost that was 5 m long × 3.06 m wide × 4–5 m high. The output from the detector was fed to a microphone input on the stereo cassette tape recorder (Radio Shack, Tandy Corporation, U.S.A.) through a 20 dB attenuator to optimise the performance of the automatic record volume control. Ultrasound recordings were made on standard tape (TDK Corporation Europe S.A., Luxembourg) during selected 30–45 minute periods in May 2001. Recordings of low frequency social calls were made using an audio microphone placed inside the roof space of the nursery roost, near the ultrasound microphone described above. Low frequency sounds were recorded on cassette tape (TDK Corporation Europe S.A., Luxembourg) using a remote tape recorder (Marantz) so that detailed analysis of the spectrograms could be made. Analysis was made using BatSound (Pettersson Elektronic AB, Uppsala) with a Hanning window and the FFT size of 512. Optimal settings were used for the frequency, threshold level and power spectrum of each call. Where multiple calls were recorded simultaneously the combined oscillogram and spectrogram analysis was used to determine the beginning and end of each call. May was selected for recordings of adult bats in the nursery roost, when 200–300 *R. ferrumequinum* bats have been observed in the colony, before the birth of babies from late June to early August (Andrews 1996, 2000; McOwat, 1997).

### *Bat Activity*

Bats flying in and out of the roost passed through an array of infrared light beams and their flight direction and the time were stored on a computer (Andrews, 1996). Bat activity in the roost was monitored in 2001 and 2002 using infrared lighting in the roost and a night vision viewer (I.T.T., Night Mariner, Alana Ecology, U.K.) which was used to see the bats through a window between the roost and an adjacent observation area. The number and activity of bats that occupied numbered sections of North and South facing slopes at the apex, middle and base of the roof was recorded. The recording system was synchronised by an electronic timer set to the computer time (G.M.T).

## Results

### *Initial Identification of The Differences in The Range of Frequency of Calls*

A power spectrum of the calls recorded from the roost in a sample over a 6 s period (60 s recording time at × 10 expansion) was analyzed. The energy was high in three frequency bands. The calls from 1 to 10 kHz were designated low frequency social calls. The maximum energy of the ultrasound social calls was in the range 25–29 kHz but the fundamental and harmonics of the ultrasound social calls were found throughout the frequency range 11–78 kHz. Echolocation calls were identified by the main energy peak at the frequency of 81–84 kHz and a smaller energy peak at 40–42 kHz in the frequency range of the fundamental. In the frequency range 40–78 kHz there was an overlap between fundamental frequencies of the echolocation calls and the frequencies of the harmonics of the ultrasound social calls. The FM sweeps of the echolocation calls were also seen in this frequency range.

*Low frequency social calls (1–10 kHz)*

The low frequency social calls, in the range 1–10 kHz, were those audible to the unaided ear in the nursery roost. The main characteristics were that they were constant frequency polyharmonic calls of relatively long duration (Table 1). The range of frequencies and the lack of FM components distinguished these calls from ultrasound social calls.

*Echolocation calls (81–84 kHz)*

In the sample of 855 echolocation calls recorded in the roost the fundamental in the range 40–44 kHz was observed with 413 calls (48.3%). There was no possibility of confusing the fundamentals of echolocation calls with the harmonics of ultrasound social calls in the same frequency range because the characteristics of the calls were different. The frequency of the CF component of a sample of 286 echolocation calls in the roost (82.0 ± 0.56 kHz) was lower than in the adjacent wood (84.7 ± 4.8 kHz). Also the duration of echolocation calls in the roost were shorter (13.9 ± 5.6 ms) compared with the calls made during foraging in the wood (40.7 ± 7.4 ms).

*Ultrasound social calls (11–78 kHz)*

Although ultrasound social calls were detected over a wide range with fundamental frequencies of 11–78 kHz the main peak in the power spectrum associated with the fundamental was found between 11 and 39 kHz. Spectrogram analysis indicated that the peak frequency of the fundamental of the ultrasound social calls was at 25 kHz and the peak frequency of harmonic 2 was at 50 kHz. Comparison of the relative power at 25 kHz (0.0 dB) and 50 kHz (-20 dB) showed that the fundamental was the predominant sound in ultrasound social calls. In addition there was a gradual increase in power that corresponded with the frequency range of 61–78 kHz. Ultrasound social calls in the range 61–78 kHz were designated as modified echolocation calls because further analysis showed that the calls were similar to echolocation calls but the frequencies of the second harmonics were below those used by *R. ferrumequinum* for echolocation.

*Detailed Identification of Ultrasound Social Calls*

Analysis of ultrasound sound social calls ($n$ = 1060) showed that there were single component calls, multiple component calls, and modified echolocation calls, subdivided into categories using Roman numerals, according to the parameters of frequency, duration and number of

TABLE 1. Characteristics of low frequency social calls made in a nursery roost by adult *R. ferrumequinum*. Audio recordings (not ultrasound) made in the nursery roost. CF — constant frequency; F — fundamental frequency; H2–H5 — Harmonics 2–5

| Category of calls | Fundamental or harmonic | Frequency (kHz) ($\bar{x}$, SD) | Duration (ms) ($\bar{x}$, SD) | LF calls sampled ($n$) | Proportion LF calls (%) |
|---|---|---|---|---|---|
| CF polyharmonic | F | 1.9, 0.1 | 142.1, 49.3 | 109 | 100.0 |
| | H2 | 3.9, 0.3 | 108.1, 43.1 | 99 | 90.8 |
| | H3 | 6.0, 0.3 | 91.5, 40.0 | 81 | 74.3 |
| | H4 | 8.0, 0.5 | 72.2, 35.4 | 40 | 36.7 |
| | H5 | 9.7, 0.6 | 62.9, 29.8 | 12 | 11.0 |

components (Tables 2 and 3). The ultrasound social calls have also been given names according to the similarity of the time expanded ultrasound calls to mammalian sounds. This designation was given to facilitate sorting the calls recorded and not as an interpretation of the meaning of the social calls.

*Single component ultrasound social calls*

The term single component was used to define ultrasound social calls which had only one part, referred to as component 1 (C 1). The frequency was either constant or it rose, or it fell, during the call.

*CF I, constant frequency single component call (monotone whistle)*

The largest group of single component calls were designated category CF I (Fig. 1). These constant frequency calls sounded like a single tone whistle (Tables 2 and 4).

*FM II, single component calls, rising or falling frequency whistles*

The second largest group of the single component calls also sounded like whistles in which the frequency either rose or fell (Fig. 1, Table 2). Since both of these types of call were frequency modulated calls and had a single component they were both designated category FM II but were divided into two categories, FM II r and FM II f (Table 2 and Table 4). The majority of FM II calls were rising frequency FM II r calls.

*FM VIII, single component repeated calls, rising frequency calls (whistles)*

There were relatively few single component rising frequency calls designated category FM VIII (Fig. 1, Table 2). These calls, repeated 3 or 4 times in sequence, were considered as a separate group from the other rising frequency calls. A delay of 8.0 ± 1.9 ms between these calls was also a characteristic. The mean frequency rise of 9.2 kHz in 9.7 ms was greater than the increase of 6.6 kHz in 29.9 ms observed in the FM II r calls and the peak frequency was 26.5 kHz (Table 4).

*Multiple component calls*

The term multiple component call was used to define an ultrasound social call which had more than one part (Fig. 1, Table 2). The components were referred to as component 1 to component 5 (C1–C5). The frequency rose or fell during each component part of the call. Multiple component calls were categorised according to the number of components and subsequently allocated to sets according to the duration and frequency of the calls in each category (Table 5).

*Double component calls*

The third largest group of ultrasound social calls had two components and spectrograms of those calls were used to classify the calls into two categories (Table 2).

*FM III r-f, double component rising and falling frequency call (two tone whistle)*

A small proportion categorised as FM III double component calls sounded like a two-tone whistle in which the frequency rose in component 1 and then fell in component 2 (Fig. 1, Table 2). The majority of the FM III r-f calls were in the range 20–24 kHz (Tables 2 and 5).

*FM IV r-s, double component rising and sustained frequency call (screech)*

A large proportion of double component calls, designated category FM IV, had a distinctive screech sound in which the frequency rose in component 1 and was sustained in component 2 (Fig. 1, Table 2). The majority of the FM IV r-s calls were observed in the frequency range 20–24 kHz (Table 5).

TABLE 2. Analysis of the fundamental of single and multiple component ultrasound social calls made by adult *R. ferrumequinum* in a nursery roost. Records made in May during the morning, afternoon, exit and pre-dawn return periods. Mean, SD, and minimum-maximum range of frequency or duration (in parentheses) are shown. I-VIII, r-f, r-s = categories of call (see the text for details); CF = constant frequency; FM = frequency modulated. All frequencies given in kHz, duration in ms. [a] — frequency at the start of call; [b] — frequency of the first component; r — rising frequency; f — falling frequency

| Category of call | *n* | First component | | | Second component | | Third component | | Fourth component | | Fifth component | | Total duration |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Frequency | | Duration | Frequency | Duration | Frequency | Duration | Frequency | Duration | Frequency | Duration | |
| CF I | 305 | 20.1, 5.9[a] (10–30) | 20.1, 5.9[b] (10–30) | 43.9, 41.7 (1–266) | | | | | | | | | 43.9, 41.7 (1–266) |
| FM II r | 186 | 21.4, 4.7 (10–38) | 28.0, 6.3 (12–41) | 29.9, 28.4 (1–126) | | | | | | | | | 29.9, 28.4 (1–126) |
| FM II f | 55 | 22.0, 6.9 (10–38) | 19.3, 6.6 (10–36) | 65.8, 39.9 (3–141) | | | | | | | | | 65.8, 39.9 (3–141) |
| FM VIII repeated r | 32 | 22.2, 4.3 (13–27) | 31.4, 3.6 (27–38) | 9.7, 6.1 (3–29) | | | | | | | | | 9.7, 6.1 (3–29) |
| FM III double r–f | 87 | 18.7, 5.3 (10–29) | 25.2, 4.9 (15–38) | 18.4, 12.4 (4–23) | 21.0, 5.1 (11–33) | 55.9, 47.2 (2–206) | | | | | | | 74.4, 52.5 (10–221) |
| FM IV double r–s | 143 | 18.4, 5.5 (10–36) | 24.5, 4.7 (13–41) | 20.0, 16.2 (1–80) | 25.2, 4.9 (14–41) | 49.4, 35.0 (2–17) | | | | | | | 69.1, 41.9 (5–186) |
| FM V triple | 25 | 20.7, 4.8 (12–29) | 26.1, 4.2 (18–32) | 19.6, 14.1 (3–67) | 25.8, 3.4 (18–30) | 29.5, 28.9 (3–140) | 25.9, 6.0 (13–41) | 29.3, 20.3 (3–80) | | | | | 78.4, 43.3 (20–163) |
| FM VI quadruple | 12 | 15.2, 3.9 (10–25) | 22.6, 5.1 (13–32) | 11.6, 7.7 (5–27) | 22.6, 6.1 (10–32) | 33.3, 17.8 (13–78) | 21.1, 5.5 (14–41) | 23.1, 11.2 (10–41) | 20.2, 5.1 (11–29) | 34.6, 20.4 (9–100) | | | 102.0, 32.0 (61–157) |
| FM VII quintuple | 5 | 15.1, 4.4 (11–22) | 22.4, 4.6 (15–28) | 10.0, 7.4 (4–19) | 20.9, 6.3 (16–30) | 37.7, 24.2 (24–45) | 24.4, 5.8 (15–29) | 33.8, 38.8 (8–101) | 22.1, 5.3 (17–29) | 59.6, 30.9 (34–93) | 23.0, 5.6 (15–28) | 26.2, 23.7 (6–66) | 167.3, 48.4 (117–240) |

*FM V, triple component call (three tone whistle)*

There were relatively few FM V calls which sounded like a three tone whistle in which the frequency rose at different rates in components 1 and 2 and was then sustained or rose again in component 3 (Fig. 1). The majority FM V calls were in the range 20–24 kHz (Tables 2 and 5).

*FM VI, quadruple component call (shriek)*

There were few calls designated FM VI which had four components (Fig. 1, Table 2). The frequency rose in component 1, was ustained in component 2 then fell in component 3 fell and continued to fall more slowly in component 4. The sound produced was a prolonged piercing shriek. The majority of FM VI calls were found between 15–29 kHz and were relatively long calls (Table 5).

*FM VII, quintuple component call (squeal)*

The smallest proportion of multiple component calls had five components, designated category FM VII (Fig. 1, Table 2). This call sounded like a long squeal. There was an alternate rise and fall in frequency in components 1–5. The range of frequencies in which the fundamentals of FM VII calls were found was 15–24 kHz. The calls were the longest of all the ultrasound social calls and most of the calls ranged between 117–199 ms (Tables 2 and 5).

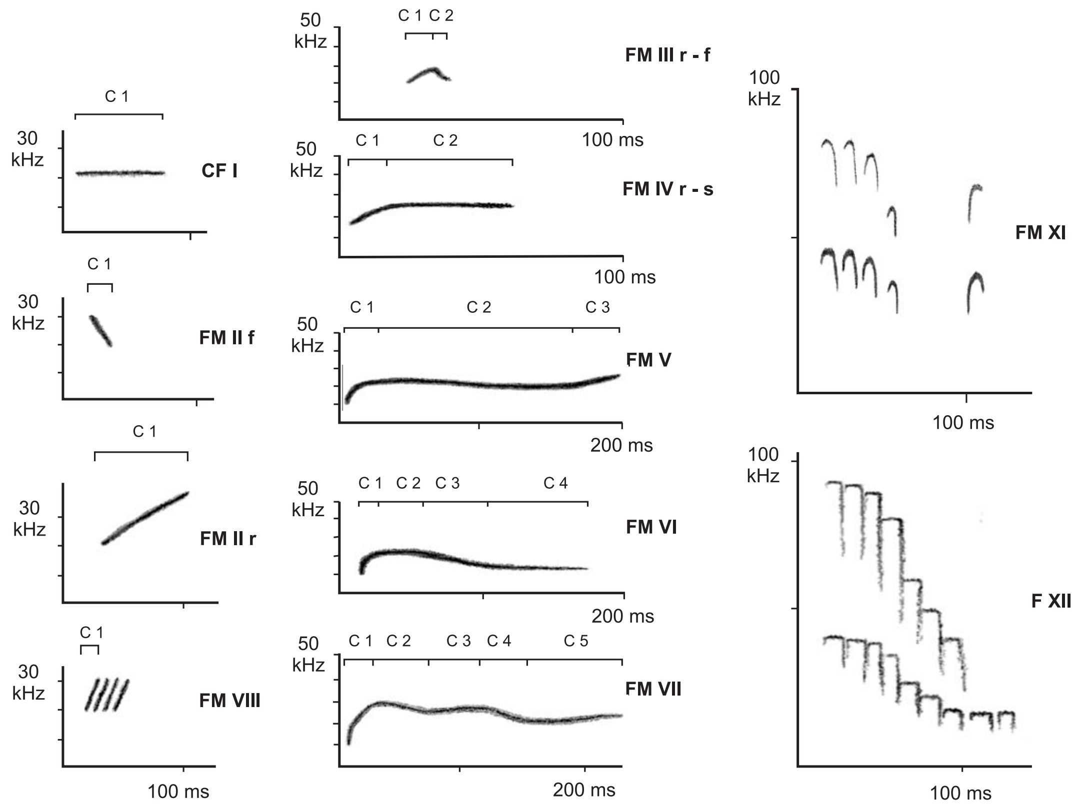


FIG. 1. Sonograms of single component, multiple component, and modified echolocation ultrasound social calls made by adult *R. ferrumequinum* in a nursery roost. CF — constant frequency, FM — frequency modulated. I–XII — categories of calls (see the text and Tables 1–5 for details), r — rising frequency, f — falling frequency, s — sustained frequency. C1–C5 — components 1–5

TABLE 3. Analysis of the CF and FM modified echolocation calls made by adult greater horseshoe bats (*R. ferrumequinum*) in a nursery roost. Records during morning, afternoon, exit and pre-dawn return periods in May. Abbreviations: CF — constant frequency; FM — frequency modulated. [1]–[4] — sequence of cascade calls. Category FM IX — see the text. Frequency range in parentheses — fundamental suppressed. Frequency and duration given in kHz and ms, respectively

| Category of call | Fundamental | | | | | | Harmonic 2 | | |
|---|---|---|---|---|---|---|---|---|---|
| | Frequency | | | Duration | Number | Proportion of | Frequency[a] | Duration | Number |
| | Range | Start ($\bar{x}$, SD) | End ($\bar{x}$, SD) | ($\bar{x}$, SD) | in set | calls in sets (%) | ($\bar{x}$, SD) | ($\bar{x}$, SD) | in set |
| CF XII cascade | | | | | | | | | |
| XII [1] | 40–44 | 40.2, 0.3 | 40.2, 0.3 | 3.7, 1.5 | 13 | 1.2 | 80.4, 0.6 | 3.7, 1.5 | 13 |
| XII [1] | 35–39 | 37.2, 1.2 | 37.2, 1.2 | 4.6, 2.1 | 25 | 2.4 | 74.3, 2.6 | 4.6, 2.1 | 25 |
| XII [1] | 30–34 | 31.4, 1.6 | 31.4, 1.6 | 4.1, 1.6 | 17 | 1.6 | 62.2, 2.9 | 4.1, 1.6 | 17 |
| XII [2] | 25–29 | 27.5, 1.7 | 27.5, 1.7 | 5.4, 4.9 | 30 | 2.8 | 54.9, 3.7 | 5.4, 4.9 | 30 |
| XII [3] | 20–24 | 21.5, 2.1 | 21.5, 2.1 | 4.2, 1.8 | 26 | 2.5 | 43.0, 4.0 | 4.2, 1.8 | 26 |
| XII [4] | 20–29 | 25.9, 3.0 | 25.9, 3.0 | 4.7, 2.3 | 21 | 2.0 | | | |
| FM XI cascade[b] | | | | | | | | | |
| XI r [1] | 30–39 | 31.4, 5.2 | 35.8, 4.9 | 13.0, 8.6 | 6 | 0.6 | 67.2, 6.4 | 13.0, 8.6 | 6 |
| XI r [2] | 25–29 | 24.9, 0.0 | 28.2, 0.0 | 9.0, 0.0 | 1 | 0.1 | 53.1, 0.0 | 9.0, 0.0 | 1 |
| XI r [3] | 20–29 | 22.4, 2.5 | 27.8, 3.9 | 3.9, 3.8 | 9 | 0.9 | | | |
| XI r [4] | 15–19 | 17.1, 0.0 | 19.0, 0.0 | 25.0, 0.0 | 1 | 0.1 | | | |
| FM XI cascade[c] | | | | | | | | | |
| XI f [1] | 35–39 | 38.0, 3.0 | 36.3, 2.1 | 5.0, 2.8 | 2 | 0.2 | 74.3, 2.5 | 5.0, 2.8 | 2 |
| XI f [2] | 30–34 | 33.1, 3.9 | 31.2, 2.6 | 5.0, 1.4 | 4 | 0.4 | 64.3, 3.3 | 5.0, 1.4 | 4 |
| FM XI single call[d] | | | | | | | | | |
| XI r | 20–29 | 19.8, 0.0 | 29.1, 0.0 | 8.0, 0.0 | 1 | 0.1 | | | |
| FM XI single call[e] | | | | | | | | | |
| XI f | 30–39 | 38.0, 2.8 | 37.0, 3.3 | 22.0, 4.2 | 2 | 0.2 | 75.0, 3.1 | 22.0, 4.2 | 2 |
| XI f | 25–34 | 31.5, 2.2 | 27.9, 2.5 | 4.2, 2.9 | 45 | 4.2 | | | |
| CF X single call | | | | | | | | | |
| X | (25–29) | | | | | 0.3 | 58.6, 1.9 | 1.0, 0.4 | 3 |
| X | (20–24) | | | | | 0.4 | 47.6, 0.5 | 1.7, 0.5 | 4 |
| Σ | | | | | *210* | *19.8* | | | *135* |

[a] — Peak frequency in the power spectrum; [b] — FM XI r rising frequency; [c] — FM XI f falling frequency; [d] — FM XI r single calls, rising frequency; [e] — FM XI f single calls, falling frequency

*FM IX, signals (trill)*

The signals designated FM IX were only observed in the nursery roost in May and need further investigation. Spectrogram analysis of the calls made by nesting swallows, which occupied the bat nursery roost, showed that the bird sonograms were dissimilar when compared with any of the calls at ultrasound or low frequencies.

*Modified echolocation CF and FM calls*

Modified echolocation (modified EL) calls were allocated to categories according to the central component of the call (CF or FM), and whether the calls were separate or occurred in a cascade of calls (Fig. 1, Table 3). The FM sweep at the start and end of the central part was present in all the CF modified EL calls but the FM sweep at the end of the call was more evident. The modification of the CF calls was the progressive reduction of frequencies in a stepwise manner with some suppression of the second harmonic, especially at the end of the cascade. The conversion of the central constant frequency (CF) pulse to a frequency modulated (FM) pulse was the alternative modification (Fig. 1). The calls were allocated to sets according to the frequency range and, where appropriate, the sequence in which they occurred in a cascade of calls (Table 3).

*CF X, constant frequency single modified echolocation calls*

The main characteristic of CF X calls was that they were very short single calls and the fundamental was not observed. There were only a few calls in category CF X which were similar to echolocation calls but found at frequencies below those used normally for echolocation by *R. ferrumequinum* (Table 3).

*FM XI f, frequency modulated falling frequency single modified EL call*

Modified echolocation calls in category FM XI were formed by the prolongation of the FM sweep at the start and end the call and the removal of the CF component. There was a wide range in the duration of the calls in the FM XI f category and they were more numerous than any other FM XI calls. Most of these single calls also lacked

TABLE 4. Sets of single component ultrasound social calls made by adult *R. ferrumequinum* in a nursery roost in May. Abbreviations: rising — rising frequency; falling — falling frequency; I, II, VIII — categories of ultrasound social calls (see the text for details); < > — frequency rises less than or more than the value given

| Category of call | Set | *n* | % | Peak duration (ms) | Peak frequencies (kHz) | Rise in frequency (kHz) |
|---|---|---|---|---|---|---|
| CF I | 1 | 110 | 10.4 | 5.0 | 11, 21, 28 | – |
| | 2 | 170 | 16.0 | 40.0 | 11, 21, 28 | – |
| | 3 | 25 | 2.4 | 75.0 | 11, 21 | – |
| Σ | | *305* | *28.8* | | | |
| FM II rising | 1 | 84 | 7.9 | 9.5 | 27 | > 5 |
| | 2 | 102 | 9.6 | 12.5 | 25 | < 5 |
| Σ | | *186* | *17.5* | | | |
| FM II falling | 1 | 40 | 3.8 | 66.0 | 22 | < 4 |
| | 2 | 15 | 1.4 | 27.0 | 24 | > 4 |
| Σ | | *55* | *5.2* | | | |
| FM VIII | 1 | 17 | 1.6 | 6.5 | 27 | 6 |
| Repeated call | 2 | 15 | 1.4 | 13.0 | 26 | 12 |
| Σ | | *32* | *3.0* | | | |

the second harmonic and were short calls (Table 3).

*FM XI r, frequency modulated rising frequency single modified EL call*

There was only 1 call observed in the category FM XI r. The rise in frequency of 9.2 kHz was notable because it was more than twice that measured in the rising frequency FM XI r cascade calls above. Harmonic 2 was not observed in this call (Table 3).

*FM XI f cascade, frequency modulated falling frequency sequential calls*

The first calls in the modified echolocation FM XI f cascades started below frequencies used for echolocation and the frequency of each successive call fell (Fig. 1, Table 3).

*FM XI r cascade, frequency modulated rising frequency cascade calls*

The rising frequency FM XI r cascade calls commonly followed the FM XI f falling frequency cascade calls when the sequence of the cascade calls occurred in reverse order at a progressively higher frequencies (Fig. 1, Table 3). Numbering of the sequence of calls [1]–[4] has been allocated for comparability with other cascade calls (Table 3). The frequencies of all the FM XI r cascade calls were below the echolocation frequency and harmonic 2 was not observed in calls at the lower frequencies (Table 3).

*CF XII cascade, constant frequency modified EL calls*

CF XII cascade was the category of ultrasound calls in which the frequency of the

TABLE 5. Sets of multiple component ultrasound social calls made by adult *R. ferrumequinum* in a nursery roost in May. FM — frequency modulated; III–VII — categories of ultrasound social call; r — rising frequency; f — falling frequency; s — sustained frequency (see the text for details of categories of calls)

| Category of call | Set | *n* | % | Peak duration (ms) | Peak frequencies (kHz) |
|---|---|---|---|---|---|
| FM III r-f | 1 | 42 | 4.0 | 29 | 16, 24 |
| (double component) | 2 | 38 | 3.6 | 104 | 20 |
| | 3 | 7 | 0.6 | 185 | 18, 21 |
| Σ | | *87* | *8.2* | | |
| FM IV r-s | 1 | 60 | 5.7 | 33 | 23 |
| (double component) | 2 | 53 | 5.0 | 77 | 23 |
| | 3 | 24 | 2.3 | 118 | 22 |
| | 4 | 6 | 0.5 | 168 | 22 |
| Σ | | *143* | *13.5* | | |
| FM V | 1 | 7 | 0.6 | 31 | 24 |
| (triple component) | 2 | 12 | 1.1 | 75 | 24 |
| | 3 | 4 | 0.3 | 132 | 27 |
| | 4 | 2 | 0.2 | 162 | 22 |
| Σ | | *25* | *2.4* | | |
| FM VI | 1 | 4 | 0.4 | 69 | 18 |
| (quadruple component) | 2 | 5 | 0.5 | 125 | 20 |
| | 3 | 3 | 0.3 | 149 | 21 |
| Σ | | *12* | *1.1* | | |
| FM VII | 1 | 2 | 0.2 | 125 | 21 |
| (quintuple component) | 2 | 1 | 0.1 | 161 | 25 |
| | 3 | 1 | 0.1 | 186 | 17 |
| | 4 | 1 | 0.1 | 240 | 24 |
| Σ | | *5* | *0.5* | | |

central component was constant but below the echolocation frequency (Fig. 1). The CF XII calls were the largest proportion of modified echolocation calls in which the central CF pulse of each successive call, [1]–[4], showed a reduction in frequency (Fig. 1 and Table 3). The last calls in the sequence, heard as guttural sounds, were usually repeated three to four times and lacked a harmonic. All the CF XII cascade calls were short (Fig. 1, Table 3).

*Harmonics of Ultrasound Social Calls and Low Frequency Social Calls*

A sample of 181 ultrasound social calls was analysed according to categories I–XII identified previously (see Tables 2 and 3) and the harmonics were also measured. The fundamental frequencies covered the same ranges and the frequencies of harmonics 2, 3 and 4 were measured within the predicted estimations. Harmonic 2 was observed in 41.4% of calls and harmonic 2 was half the duration of the fundamental in single and multiple component calls. Harmonics 3 and 4 were observed in relatively few calls (4.4% and 2.2%) and typically were the same duration or shorter than harmonic 2. In contrast harmonic 2 was present in 90.8% of the low frequency social calls and harmonics 3–5 also occurred more often than ultrasound social calls. The duration of harmonics 2–5 became progressively shorter but remained a predominant feature of low frequency social calls (Table 1).

*Bat Activity*

During the day clusters of *R. ferrumequinum* bats formed and dispersed and activity was variable in the nursery roost. The main activity was observed at the outer edges of clusters and between pairs of bats hanging in areas of the roof away from the clusters. There was some individual grooming, occasional flapping of wings and some bats flew or walked across the roof.

## Discussion

*Differentiation Between Calls Made by R. ferrumequinum in a Nursery Roost*

Since ultrasound social calls in a nursery roost used by *R. ferrumeqinum* bats have not been reported previously there is no direct comparative literature. The nearest comparable reference was the identification of a protest call made by a single *R. ferrumequinum* in experimental conditions (Long and Schnitzler, 1975), comparable with the multiple component call FM VII in both the frequency range (20–32 kHz) and the duration (125 ms). It is not known whether the threatening call of a rhinolophid bat described by Möhres (1966) had the same characteristics as the ultrasound social calls identified in this study. Möhres (1953) studied individual bats, the interaction between two bats of different species or the relationship between mother and infant rhinolophid bats in laboratory conditions, not in a nursery roost colony. The frequencies (15–32 kHz) at which the single and multiple component social calls were observed in this study corresponded with the broad sensitive region of the auditory system of *R. ferrumequinum*; quite distinct from the higher narrowly-tuned region concerned with echolocation (Neuweiler, 1970; Long and Schnitzler, 1975).

Harmonic 2 at the beginning of the sequence of the modified echolocation call cascade (70–78 kHz) was also considered too low when compared with *R. ferrumequinum* echolocation described by (Vaughan *et al*., 1997). Modified echolocation calls were not caused by Doppler shift compensation since the progressive stepwise reduction in frequency was 5–10 kHz and the maximum reduction in forward flight, estimated by Sales and Pye (1974), would have been only 2.5% from the resting frequency (2.1 kHz). The frequency shift was well outside the 2.5% lowering of the CF echolocation pulse for the Doppler shift (Schnitzler, 1968).

This study confirmed the occurrence of low frequency social calls made by *R. ferrumequinum* heard as a noisy squeal similar to the frequency calls made by the Japanese bat *R. ferrumequinum nippon* (Matsumura, 1981). Such calls are audible to the unaided ear in summer roosts (Van den Brink, 1967; Ransome, 1980). Recent mtDNA analysis indicates that the Japanese rhinolophid may be a separate species, not a subspecies of *R. ferrumequinum* (Thomas, 2003). A discrete species is also indicated by the relatively low echolocation frequency of this bat in the range of 71–72 kHz (Matsumura, 1979). Such calls are audible to the unaided ear in summer roosts (Van den Brink, 1967; Ransome, 1980).

Although vespertilionid and rhinolophid bats have different echolocation calls Vaughan *et al*., 1997) and may have little or nothing in common regarding male advertisement calls there were some similarities between FM VIII calls identified in this study and vespertilionid advertisement calls. However, there were three main differences between the FM VIII calls made by *R. ferrumequinum* and advertisement calls made by *Pipistrellus pipistrellus*, *P. pygmaeus*, *P. kuhlii* or *Plecotus auritus* (Lundberg and Gerell, 1986; Barlow and Jones, 1997*a*; Russo and Jones, 1999). The FM VIII calls were two to three times longer than the advertisement calls made the vespertilionid bats. The repetitive FM VIII calls rose in frequency as opposed to falling in frequency in pipistrelle and long-eared bats and the FM VIII calls were made inside not outside the nursery roost. Barlow and Jones (1997*b*) proposed that one type of call could have a dual function in different circumstances. Male *R. ferrumequinum* may have used an advertisement call in the nursery roost as a general social call or the adult female breeding bats may have used the FM VIII call to accept or repel the advances of mature males in the nursery roost.

Results indicated one or more of the FM ultrasound calls might represent male advertisement since mature male bats occupied this nursery roost (Andrews, 2000), and there was a temporary increase in the colony size in early to mid May (Andrews, 2002) but further investigations are needed to test this hypothesis. Although mating in *R. ferrumequinum* occurs mainly in April or October (Ransome, 1990) the mature *R. ferrumequinum* males store viable sperm in the epididymis until spring (Racey and Entwistle, 2000). Mating occasionally takes place in spring (Ransome, 1991) and births occur from late June to early August (Ransome, 1991; McOwat and Andrews, 1995). It is possible that a few *R. ferrumequinum* females, which reached maturity in the autumn too late to visit male territories, mated in the nursery roost at the beginning of May. However, mature male *R. ferrumequinum* bats habitually occupy their own mating territory with mature females from midsummer to November (Ransome, 1991; Stebbings, 1991) and mating occurs is such sites (McCracken and Wilkinson, 2000). No ultrasound advertisement calls from male greater horseshoe bats have been reported for comparison.

### *Emission of Ultrasound Social Calls, Low Frequency Calls and Echolocation Calls*

It was estimated that the single and multiple component ultrasound social calls and low frequency social calls, in which the fundamental was in the range 1–30 kHz, were uttered through the mouth since calls made during the development of *R. ferrumequinum nippon* were in the range 66–72 kHz

(Matsumura, 1979). During the development of the nasal echolocation calls Matsumura (1979) observed the ability of *R. ferrumequinum nippon* to alter the airstream from the epiglottis to the oral or nasal cavity to produce an oral to nasal shift. The last calls in the sequence of the cascade of modified echolocation calls identified in this study might have been made by a nasal to oral shift.

### *Communication Between R. ferrumequinum in The Nursery Roost and Colony Size*

This study provides evidence of extensive social communication by *R. ferrumequinum* in the nursery roost. There was sufficient scope for the diversity of calls, which would be expected for communal activity in a nursery roost (Rossiter *et al*., 2000, 2002). Low frequency social calls were louder than the concomitant echolocation calls or ultrasound social calls within the nursery roost. It was estimated that the low frequency social calls would have to be stronger, or the distance between bats would have to be short, since *R. ferrumequinum* hearing is not acute at frequencies below 15 kHz (Neuweiler, 1970; Long and Schnitzler, 1975). Low frequency social calls would only be effective between bats in close proximity in a nursery roost and would be more efficient when the background noise was minimal (Dunbar, 1993). The theory that oral communication evolved as an efficient form of social grooming in large primate groups could also apply to Rhinolophidae (Dunbar, 1993). Results from this study support the hypothesis that social communication in *R. ferrumequinum* in a nursery roost is by the emission and processing of auditory signals.

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