

SOCIAL CALLS IN CLEAR-WINGED WOOLLY BATS KERIVOULA PELLUCIDA FROM MALAYSIA

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ABSTRACT

Kerivoula pellucida is a small (4.5 g) vespertilionid bat, which forages in the understorey of tropical rainforests in Southeast Asia. Most echolocation signals are characteristic for the subfamily (very high-frequency, broadband FM calls (sweeping down from 178 kHz to 58 kHz) of low intensity and short duration (< 3.0 ms)), but this species also produces stereotypical calls of a markedly different structure. The arrangement of signal elements in these calls is unusual, and we present here a detailed analysis of calls from thirteen adult individuals (nine males and four females). These multiharmonic calls are of much lower frequency (fundamental peak frequency of 36 kHz), higher intensity and longer duration (12.0 ms) than the orientation calls, and are composites comprising a long quasi-constant frequency (QCF) syllable followed by an upward frequency modulated sweep (UFM). From considerations of signal design and preliminary field observations, we consider possible functions of these calls.

Keywords: Chiroptera, communication, echolocation.

INTRODUCTION

Biosonar signals are shaped by the task of detecting, locating and classifying prey items given the acoustic constraints of the foraging habitat (Griffin 1958, Schnitzler and Kalko 1998). Although microchiropteran bats use a wide variety of signal types, they can be essentially resolved to three main components: constant frequency (CF), quasi-constant frequency (QCF) and downward frequency modulated (FM) elements (Schnitzler and Kalko 1998). The com-

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ponents vary in absolute frequency, bandwidth, harmonic structure and sound pressure level (Fenton 1985a, Schnitzler and Kalko 1998). While some of these features may be correlated with morphology (e.g. body size and call frequency (Jones 1996)), their parameters and arrangement in each pulse depend to a large extent on the information the bat is trying to extract from the echo. Echoes can convey the presence of an item, or encode distance, velocity, vertical and horizontal location. The relevance of these different types of information will vary with the food item, the foraging habitat, and the stage of prey pursuit (see Fenton 1995 for review).

Call components differ in the information they encode best. QCF elements are best suited for detection. Most of the signal energy is concentrated in a narrow band of frequencies and this maximises the likelihood that small or distant prey items will be detected (Schnitzler 1987). Detection is further enhanced if the call is long enough to encompass "acoustic glints" – increases in sound pressure created if the pulse hits a flying insect when its wings are perpendicular to the soundwave (Kober and Schnitzler 1990, Moss and Zagnesi 1994). Since they favour prey detection, QCF components contribute most to the bats' signal during the search phase of a hunting sequence. Two limitations of narrowband calls restrict their use both temporally (to the search phase), and spatially (to relatively open spaces). First, narrowband signals provide only inaccurate time markers for estimating the delay between the pulse and the echo and as a consequence are poor estimators of target range (Simmons 1973, Simmons and Stein 1980). Second, if a bat is using long duration signals as it approaches an object it may be in danger of receiving the echo before it has finished emitting the pulse (Schnitzler 1987, Kalko and Schnitzler 1993). As a result, the QCF component tends to be reduced or lost altogether as a bat forages nearer to obstacles, or closes in on its prey.

In contrast, FM components sweep rapidly through a wider range of frequencies (about an octave) in a relatively short time, providing accurate time markers for range determination. They are also well suited for localising prey, with respect to both horizontal and vertical angle (Schnitzler and Henson 1980, Simmons and Stein 1980). However, because the signal energy is spread throughout a wide range of frequencies, the effective range is limited and they are therefore less suited for detection.

Kerivoula pellucida (Waterhouse 1845) is a small (4.5g) vespertilionid restricted to Peninsular Malaysia, Sumatra, Java, Borneo and the Philippines (Corbet and Hill 1992). It is a highly manoeuvrable species that forages in the forest understorey. *Kerivoula* produce very high frequency, broadband echolocation calls of low intensity and short duration that seem particularly suited to a gleaning habit in the densely cluttered environment of the rainforest understorey (Neuweiler and Fenton 1988, Kingston et al. 1999).

Kerivoula pellucida emits groups of pulses that start at about 178 kHz and sweep down to approximately 58 kHz in 2.5 ms. In the course of a detailed comparison of echolocation calls produced by a community of seven Kerivoulinae and three Murininae species (Kingston et al. 1999) it became apparent that *K. pellucida* also produce stereotypical calls of a markedly different structure. Not only do these calls differ from the species' own orientation calls, but they also represent an unusual combination of signal elements, as yet unreported for Microchiroptera, and their integration into the orientation sequence illustrates an extreme of vocal plasticity. We present here a detailed examination of these unusual calls (which we will refer to hereafter as quasi-constant frequency – upward frequency modulated (QCF-UFM) calls (after Kanwal et al. 1994)) and discuss their possible function.

METHODS

Study site

The study was conducted between January 1996 and March 1997 at Kuala Lompat Research Station, Krau Wildlife Reserve, Pahang, Peninsular Malaysia (3° 43' N, 102° 10' E). The reserve encompasses 53,014 ha of lowland evergreen dipterocarp forest. A detailed description of the reserve is given in Caldecott et al. (1986).

Bat capture and identification

Bats were captured in the forest understorey using four-bank harp traps (Francis 1989) positioned across trails originally cut for primate studies (Chivers 1980). Species were identified following Medway (1982), Payne and Francis (1985) and Lekagul and McNeely (1977). Juveniles were distinguished from adults by the presence of cartilaginous epiphyseal plates in the finger bones (Anthony 1988). Adult individuals were sexed and weighed, and the length of forearm measured.

Sound analysis

Kerivoula pellucida uses low intensity echolocation signals. To ensure adequate samples for each individual, bats were recorded while flying in an outdoor wire mesh cage (dimensions – 5 m long × 1.5 m wide × 2 m high). Each bat was recorded as it flew past the recording equipment, which was positioned to one side of the middle of the flight cage. Recordings were made with an Ultra Sound Advice (USA) S-25 bat detector linked to a USA S-350 digital signal processor sampling at 400 kHz. Time-expanded (10×) output was recorded on a Sony WM-

D6C Walkman cassette recorder. Time-expanded sequences were analysed by using a Kay 5500 DSP Sonagraph, giving a frequency resolution of 400 Hz on the real-time signal.

Call parameters were measured from all QCF-UFM calls of high signal-to-noise ratio for each individual. Power spectra were used to derive three measures of frequency (in kHz) for the fundamental frequency: *start frequency*, *end frequency*, and *peak frequency*. *Peak frequency* was also measured for the second and third harmonic. The sound pressure level (dB) at *peak frequency* for each harmonic was noted. Given the recording conditions, sound pressure level was not an absolute measure, but was recorded to provide a comparison of the distribution of energy between the harmonics and between QCF-UFM calls and the more typical orientation calls (FM sweeps). The bandwidth of the QCF component was measured from the *start frequency* to the *peak frequency*. The duration of each call (*call duration*, ms) was measured from the waveform. The number of calls per individual varied from 8 to 20. The interval between two QCF-UFM calls was measured as the time between the start of one call and the start of the next (*interpulse interval QCF-UFM - QCF-UFM*). Similarly, the time between the start of a QCF-UFM call and that of an FM sweep immediately after it was also recorded (*interpulse interval QCF-UFM - FM*).

In addition to the QCF-UFM calls, a number of less stereotypical social calls were also recorded. The recording protocol was such that bats waiting to be recorded were held in individual cloth bags within the flight cage, while FM sweeps and QCF-UFM calls of a flying bat were recorded. The low intensity of the FM sweeps and the directionality of the QCF-UFM calls ensured that it was the focal rather than the bagged individual that was recorded. However, on several occasions, holding bags containing *Kerivoula pellucida* individuals elicited responses from the flying *K. pellucida*. These responses included flying to the bag, hovering in front of it, landing on it, and emission of social calls. Social calls were recorded as above with the microphone located approximately 0.5–1 m from the interacting bats.

Statistical analysis

The extent to which individuals could be distinguished by their QCF-UFM calls was tested using MANOVA (with calls nested within individual) and stepwise discriminant analysis techniques. Sex differences could confound findings of individual distinctiveness, particularly as females were slightly larger than males with respect to forearm length (female 31.3 ± 0.75 mm (mean \pm std); male 30.1 ± 0.65 mm; ANOVA, $F_{1, 15} = 11.6$, $p = 0.039$). Unfortunately, sex differences could not be modelled explicitly because of the uneven representation

of males and females and small female sample size (9 male 4 female). Therefore, individual distinctiveness was tested using males only. The parameters modelled were the fundamental *start frequency*, *end frequency*, *peak frequency* and *call duration*, and the *peak frequencies* of the *2nd* and *3rd harmonics*. In the discriminant analysis, the covariance matrices were heterogeneous so the quadratic discriminant function was used for classification. Prior probabilities were set proportional to sample size (8 to 20 calls per individual). To estimate classification success, Lachenbruch's (1967) jackknife procedure was employed (Stevens 1992).

All parameters exhibited univariate normality, but the data did not conform to the multivariate normal distribution. However, this deviation from multivariate normality is considered to have only a small effect on type I error (Stevens 1992). Analyses were conducted using SAS for Unix version 6.12.

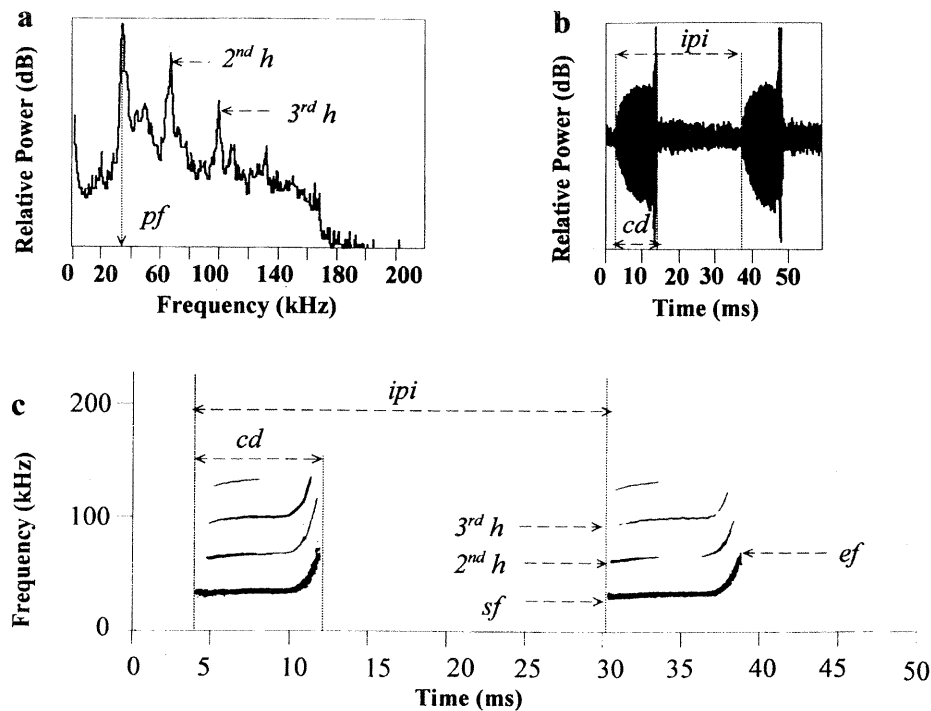


Figure 1. Structure of QCF-UFM calls of *Kerivoula pellucida*. a) power spectrum, b) waveform, c) sonograms. Parameters measured are illustrated: *pf* – peak frequency, *2nd h* – second harmonic, *3rd h* – third harmonic, *cd* – call duration, *ipi* – interpulse interval, *sf* – start frequency, *ef* – end frequency.

TABLE 1

Descriptive statistics for parameters of QCF-UFM and FM sweep calls. The sound pressure levels given are not absolute values, but should be used for comparison between harmonics of QCF-UFM calls and between these calls and FM sweeps.*
Kingston et al. (1999)

Call Parameter	QCF-UFM			FM sweep*		
	mean \pm SD	min - max	n: bats, calls	mean \pm SD	min - max	n: bats, calls
<i>Start frequency</i> (kHz)	29.6 \pm 4.25	22.4-54.4	13, 149	178.5 \pm 6.57	159.2-188.8	18, 107
<i>End frequency</i> (kHz)	58.1 \pm 9.74	37.2-90.4	13, 149	58.5 \pm 9.31	30.4-79.2	18, 107
<i>Peak frequency, fundamental</i> (kHz)	36.0 \pm 3.18	27.2-46.4	13, 165	96.4 \pm 20.74	57.6-138.4	18, 100
Sound Pressure Level at fundamental Peak frequency (-dB)	14.0 \pm 2.78	9.0-54.0	13, 178	36.4 \pm 4.9	33.0-72.0	18, 106
<i>Peak frequency, 2nd harmonic</i> (kHz)	74.0 \pm 11.30	60.8-124.8	13, 143			
Sound Pressure Level at 2 nd harmonic Peak frequency (-dB)	38.4 \pm 4.46	28.0-48.0	13, 142			
<i>Peak frequency, 3rd harmonic</i> (kHz)	110.5 \pm 12.15	91.2-155.2	13, 156			
Sound Pressure Level at 3 rd harmonic Peak frequency (-dB)	37.9 \pm 5.25	14.0-56.0	13, 157			
<i>QCF bandwidth</i> (kHz)	6.6 \pm 1.91	3.2-13.6	13, 155			
<i>Call duration</i> (ms)	12.0 \pm 1.58	7.5-15.9	13, 158	2.4 \pm 0.62	1.0-4.4	18, 107
<i>Interpulse interval</i> <i>QCF-UFM - QCF-UFM</i>	36.5 \pm 10.47	17.2-91.9	10, 107			
<i>Interpulse interval</i> <i>QCF-UFM - FM</i>	20.5 \pm 4.19	15.3-40.0	6, 44			
<i>Interpulse interval, FM-FM</i> for pulses emitted in groups of three (modal pulse group size)				15.3 \pm 2.5	9.4-22.5	18, 124

RESULTS

Of 23 adult *K. pellucida* recorded, 14 emitted QCF-UFM calls. Both males (9/13) and females (4/10) emitted QCF-UFM calls. Figure 1 illustrates the structure of two such calls, and call parameters are given in Table 1. Figure 2 illustrates three echolocation calls (FM sweep) for comparison. The QCF-UFM call consists of an initial quasi-constant frequency (QCF) portion (constituting at least three-quarters of the total *call duration*). The call then sweeps rapidly upward through 20 kHz to finish (UFM). Typically the QCF portion rises from the *start frequency* to the *peak frequency* (mean rise 6.2 kHz), but on two occasions the *start frequency* was higher than the *peak frequency* and actually swept down by 16 kHz and 12 kHz to the CF portion (see Figure 3a – first QCF-UFM call). At least four harmonics are present with most energy concentrated in the lowest. The second and third harmonics have a similar mean intensity, but within any given call it was more usual for one or the other to be of greater intensity (compare Figure 3b with 3c). It is apparent from the sonagrams in Figures 1 and 2 that these QCF-UFM calls differ dramatically in their spectral design from the orientation FM sweeps. The former also represent a

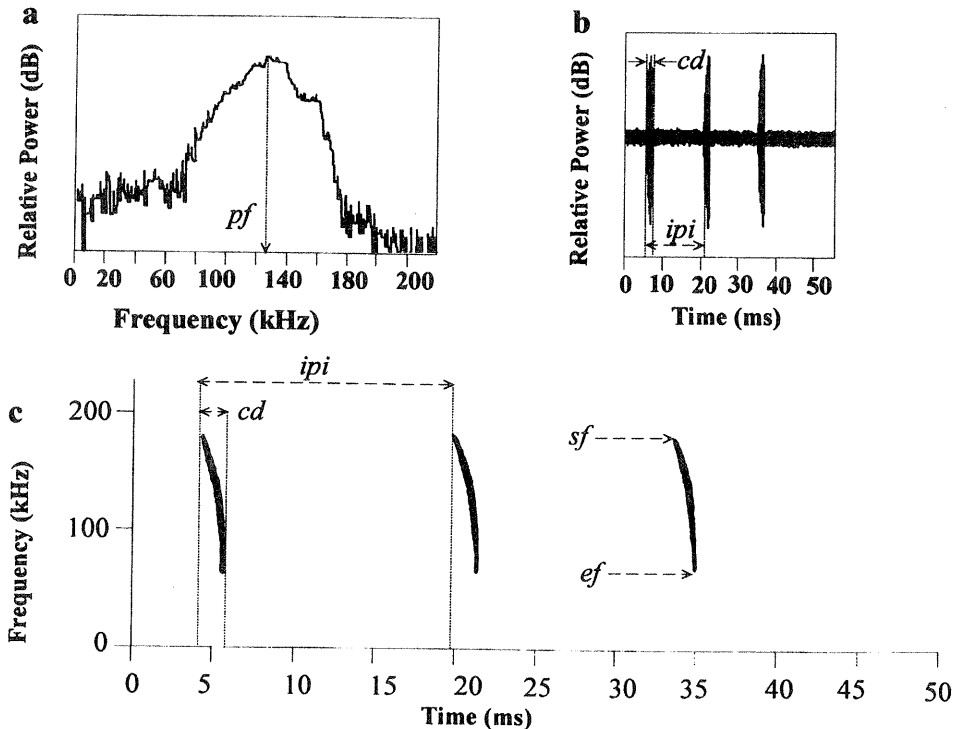


Figure 2. Structure of FM Sweep echolocation calls of *Kerivoula pellucida*. a) power spectrum, b) waveform, c) sonagram. Abbreviations as for Figure 1.

TABLE 2

Distribution of variance in call parameters. Variance components were calculated using the univariate statistics from MANOVA. For each parameter the variance components describe the percentage of the total variability explained by individual, call nested within individual and the error term. *** $p < 0.001$; ns = not significant
– $p > 0.05$

Source of variance	Call Parameter					
	<i>Start Frequency</i>	<i>End Frequency</i>	<i>Peak Frequency</i>	<i>Call duration</i>	<i>2nd Harmonic</i>	<i>3rd Harmonic</i>
Individual	15.7 ns	54.7***	0 ns	34.3***	31.0***	24.7***
Call within individual	0 ns	0.1 ns	5.7 ns	1.8 ns	0.3 ns	0 ns
Error	84.3	42.3	94.3	65.9	68.7	75.3

TABLE 3

Contribution of variables to individual discrimination, from stepwise discriminant analysis. Partial R^2 describes the variability attributable to each variable when controlling for those already in the model. λ values indicate the cumulative strength of the discrimination as each variable is added.
F ratio: * $p < 0.05$, ** $p < 0.005$, *** $p < 0.0001$.

Variable (in order of entry into the model; significance level for entry = 0.001)	Partial R^2	Wilks' λ (cumulative for model at that point)
<i>End Frequency</i>	0.62***	0.38219, $p = 0.0001$
<i>2nd Harmonic</i>	0.39***	0.23668
<i>Call Duration</i>	0.29***	0.16872
<i>Start Frequency</i>	0.22***	0.13090
<i>Peak Frequency</i>	0.24***	0.09973
<i>3rd Harmonic</i>	0.06 ns ($p = 0.5516$)	not entered into model

considerably greater energetic investment, as revealed by a comparison of the waveform displays (Figure 1b cf. Figure 2b). Indeed, a QCF-UFM call is typically about 22 dB more intense than an FM sweep emitted immediately before or after it, and lasts four to five times as long.

Over half (55.8%) of QCF-UFM calls were produced in sequences with other QCF-UFM calls, but 44.2% were followed immediately by FM sweeps (Figure 3). In the latter case, the QCF-UFM calls were always emitted at the start of a group of FM pulses. QCF-UFM sequences comprised from 7 to 22 calls.

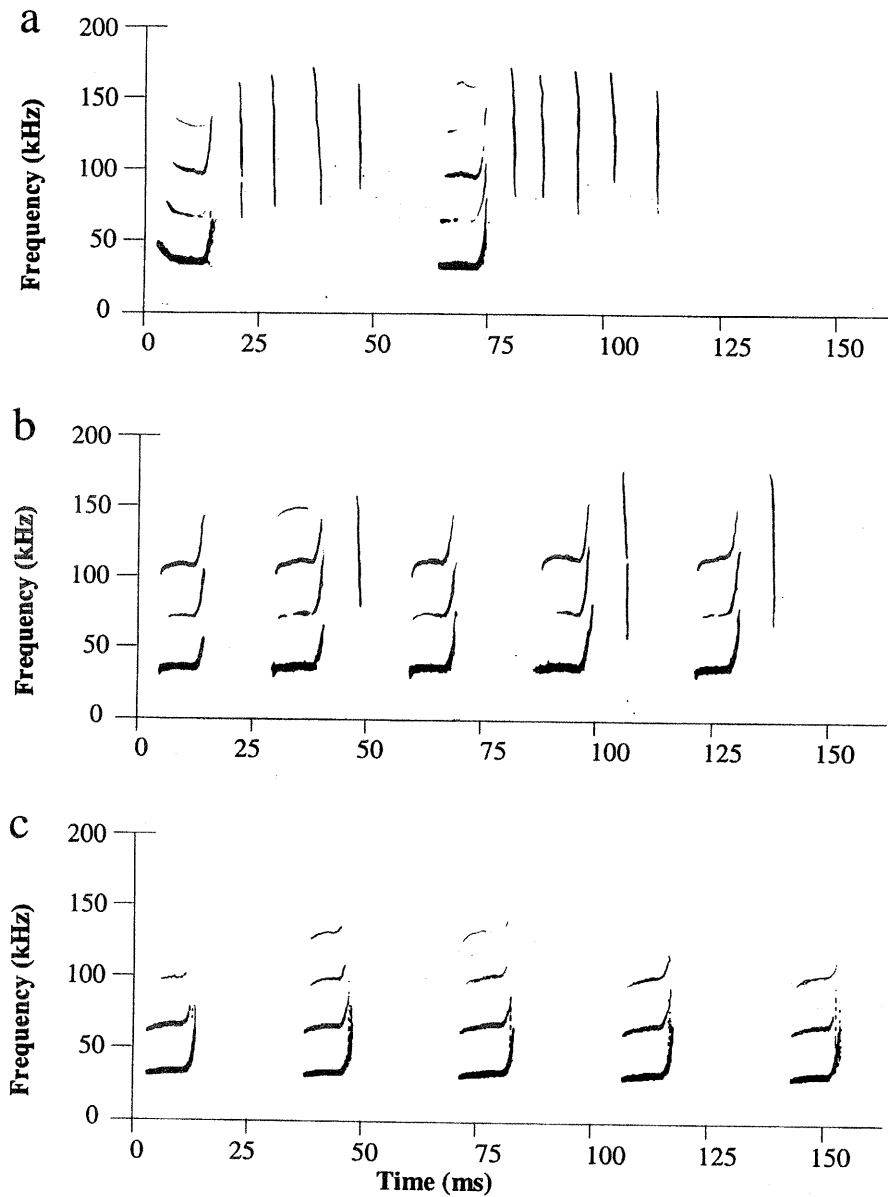


Figure 3. Sonograms of three call sequences to illustrate temporal arrangements of QCF-UFM calls and FM sweeps. a) QCF-UFM calls followed by four and five FM sweeps. b) sequence of QCF-UFM calls with occasional single FM sweeps interspersed. c) QCF-UFM sequence only.

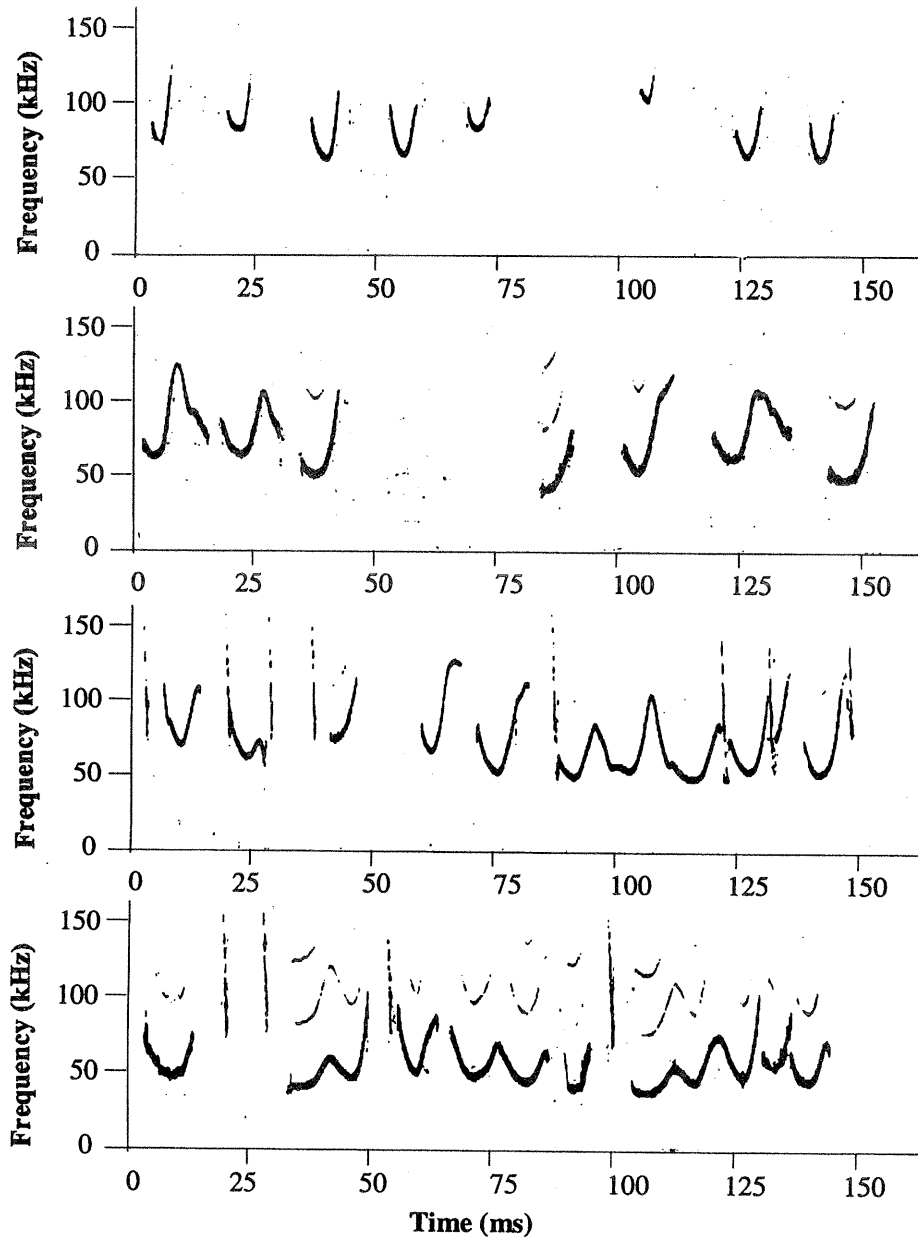


Figure 4. Sonagrams of four sequences of social calls produced during interactions between bagged and flying individuals. It was not possible to determine which of two interacting individuals was producing which calls, so these recordings should be considered a mix of calls produced by two individuals.

Despite the smaller female sample size, there was no significant difference in the tendency of either sex to produce QCF-UFM calls ($\chi^2_{0.05, 1} = 1.93$; $p > 0.1$). The structure of the QCF-UFM calls differed significantly between individual males (MANOVA with call nested within individual; Wilks' $\lambda_{42, 308} = 0.0103$, $p = 0.0001$). *End frequency*, *call duration*, *2nd harmonic* and *3rd harmonic* each differed between individuals, but none of the parameters varied significantly within individuals (Table 2). The amount of variability attributable to individual varied from 54% for *end frequency* to 0% for *peak frequency*. *End frequency* was consequently the most useful variable for discriminating between individuals, *peak frequency* the least. For each parameter, much of the variability lay within the error term (ranging from 42.3% for *end frequency* to 94.3% for *peak frequency*). The stepwise discriminant analysis found that five of the six parameters contributed to the model (Table 3). *End frequency* was again the most distinctive variable (partial $R^2 = 0.62$) and provided significant discrimination in its own right (Wilks' $\lambda_{7, 92} = 0.38219$, $p = 0.0001$). Classification success was relatively low at 52%, but varied considerably between individuals, ranging from 33.3% to 81.0%.

Figure 4 illustrates a range of social calls emitted by individuals of *Kerivoula pellucida* during intraspecific interactions. Calls were composed primarily of simple FM syllables with both upward and downward components grouped into trains or phrases (*sensu* Kanwal et al. 1994). They are clearly far less stereotyped than the QCF-UFM calls, and suggest a rich vocal repertoire for this species.

DISCUSSION

The QCF-UFM calls are highly unusual and distinctive calls unlike any previously reported in bats. Structurally they have no equivalent in bat biosonar or communication signals and are particularly distinguished by the terminal FM upsweep. Not only are the QCF-UFM calls themselves unusual, but their integration into the orientation sequence is also highly sophisticated. Thus any postulated function for these calls must explain both signal design and sequence integration.

QCF-UFM calls differ substantially in their design from FM pulses. They are high intensity signals with sound energy largely concentrated into a narrow band of low frequencies; features that favour long-distance sound propagation. Sound attenuates by 6 dB for every doubling of distance by spherical spreading alone (inverse square law). Thus for a given hearing threshold, the QCF-UFM calls should travel more than eight times as far as the FM echolocation calls as a consequence of their greater intensity (22 dB). In addition, atmospheric attenuation is highly frequency dependent; consequently, in addition to the spreading losses, orientation calls, with *peak*

frequencies of 95 kHz should attenuate nearly 2 dB/m faster than the 36 kHz QCF-UFM emissions (at 25°C and 50% relative humidity) (Lawrence and Simmons 1982).

What might be the function of these long distance calls, and how do putative functions correlate with the other parameters of QCF-UFM calls? We consider two alternatives; first that these calls play a role in orientation, and second that they function as communication calls.

The low intensity, high frequency, large bandwidth FM pulses should provide highly accurate estimates of range, and possibly spectral discrimination of stationary prey, necessary for gleaning prey items from surfaces (Kingston et al. 1999). The trade-off, however, is that these calls have a very limited functional range (Griffin 1971), and this was evident in the proximity necessary for recording (<1.5 m). Although these are small and highly manoeuvrable bats capable of responding quickly to obstacles, additional information on more distance objects may be advantageous and potentially could be provided by the QCF-UFM calls. There are, however, problems with this interpretation. First, QCF-UFM calls would not provide very accurate measures of the distance to these objects, because of their narrow bandwidth. Conceivably, more accurate time marking could be provided by the UFM component, but this would represent a rather unusual capability. Although UFM signals are used in radar systems (Skolnik 1982) they are rarely used in echolocating bats. Orientation calls of rhinolophid and hipposiderid bats frequently include an initial UFM component (followed by a CF element and variable terminal downward FM sweep), but it is uncertain whether the upsweep conveys any information or is just a by-product of intonation (Vogler and Neuweiler 1983, Tian and Schnitzler 1997). In addition, sensitivity to the time-frequency structure of FM signals has been demonstrated in *Eptesicus fuscus* and *Noctilio albiventris*, both of which have difficulty extracting range estimates from upward FM sweeps (Masters and Jacobs 1989, Roverud 1995). Second, *Kerivoula pellucida* is a narrow-space forager of the forest understorey. In such cluttered space, narrowband, long duration calls might well experience considerable pulse-echo overlap.

High intensity, long-distance calls could also serve for communication between individuals. Communication calls must be designed to be apparent to the receiver, and should be sufficiently distinctive to convey the intended information. In bats, these design requirements frequently conflict with those shaping the structure of the biosonar calls. The limited functional range of the typical orientation calls of *K. pellucida* restricts their use in communication. In contrast, the QCF-UFM calls are structurally suited for relatively long-range communication. Furthermore, some of the signal features that are difficult to reconcile with a function in orientation might be

advantageous in a communication call. Long duration would increase the probability that a conspecific would hear the call, while harmonics and frequency modulation make the call more easy to locate (Marler 1955, Hauser 1996) and may also permit encoding of individual distinctiveness (Fenton 1985b, Bradbury and Vehrencamp 1998). In accord with this, individual distinctiveness of calls in the present study was conferred primarily by differences in *end frequency* and *2nd* and *3rd harmonics* (from both the variance components and the discriminant analysis). The QCF-UFM calls also share a number of structural elements that characterise separation calls that are used by a variety of taxa. Such calls tend to have a long CF component with initial or terminal FM sweeps and frequently include harmonics (see Bradbury and Vehrencamp 1998 for a review). Typically, they are emitted by individuals who have become separated from a foraging group, as in the directive calls of the social bat *Antrozous pallidus* (Brown 1976).

Most echolocating bats modify call structure to some degree as the call sequence progresses, for example during prey capture (Griffin 1958), or as the bat approaches vegetation (Kalko and Schnitzler 1993). Furthermore, several species alternate between calls during search phase that differ in lowest frequency, harmonics, or the relative contribution of FM and CF components (Ahlen 1981, Miller and Degn 1981, Barclay 1983, Heller 1989, 1995, Jones and Corben 1993, Waters et al 1995). Other species readily mix social signals with echolocation calls (e.g. Bradbury and Emmons 1974, Miller and Treat 1993, Barlow and Jones 1997). The integration of call types seen in *Kerivoula pellucida* represents an extremely sophisticated expression of this vocal plasticity. *Kerivoula pellucida* is capable of rapidly alternating between calls that differ substantially in terms of both spectral characteristics and sound pressure level. Individuals can switch from the high intensity, low frequency QCF-UFM calls to low intensity, high frequency FM sweeps and back in less than 50 ms (Figure 3b). This dramatic alternation and integration of calls could facilitate contact during flight, even in cluttered situations that require high levels of environmental information.

From the signal design and interspecific comparisons, we are inclined to infer that these calls are used primarily as contact calls rather than for orientation, but there are clearly a number of avenues for further research that would clarify this position. One objective would be to determine under what circumstances free-flying bats use these calls. This may represent something of a challenge, because the low intensity FM pulses cannot be detected more than 1.5 m away under field conditions (with current equipment), making it difficult to track individuals unless they are actively emitting the more intense QCF-UFM calls. These difficulties may be circumvented to some extent by altering the conditions experienced by captive bats;

manipulating the degree of clutter within the flight cage, or presenting possible prey items. Establishing sociality is another key area for future research. Preliminary field observations suggest that *Kerivoula pellucida* may well contrast in this respect with other species of *Kerivoula* (*K. papillosa*, *K. intermedia*, *K. minuta*) captured at the study site. This was the only species in which we observed the intense social calling between bagged and flying bats during recording (Figure 4); tight clustering of individuals in harp trap bags (up to five bats clinging together so tightly that they appear superficially to be a single individual); and interactions between individuals on release ('dancing' together - two to three individuals spiralling around one another in flight before leaving the release point). Further investigations should include playback experiments to test the response of individuals to QCF-UFM calls, and radiotelemetry studies to elucidate roosting ecology and social structure.

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