

Echolocation signal design in Kerivoulinae and Murininae (Chiroptera: Vespertilionidae) from Malaysia

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Abstract

Echolocation signal design in nine syntopic vespertilionid bats from the Malaysian rain forest understorey was studied. Four species of *Kerivoula*, two species of *Phoniscus* (Kerivoulinae) and three species of *Murina* (Murininae) all emitted calls that are typical of species that glean insects from surfaces: broadband, frequency-modulated (FM) calls of low intensity and short duration. However, calls were highly distinctive in the use of very large bandwidths (range: 89–123 kHz) and extremely high frequencies (start frequency 152–180 kHz; end frequency 43–86 kHz). Furthermore, calls were produced in groups of 2–15 at very high pulse repetition rates (37–105 Hz). The functional significance of these characteristics with respect to foraging strategy is discussed. Large signal bandwidths facilitate highly accurate target localization in terms of both range and angle estimation and can thus be interpreted as an adaptation to foraging in the highly cluttered environment of the forest understorey. The use of high frequencies so far in excess of those seen in other FM gleaning bats of the same size is less easily explained, but may represent a mechanism by which these species distinguish prey items using echolocation alone, without recourse to visual or auditory cues. Species exhibited differences in echolocation parameters, particularly the end frequency and the number of calls per group of calls. The two subfamilies differed from each other in multivariate space derived from echolocation parameters; calls of the Murininae were of lower frequency than the Kerivoulinae and were typically produced in smaller groups or singly. Within the subfamilies there was considerable overlap between species of *Murina*, but the *Kerivoula* spp. were clearly distinct from one another but not from the two *Phoniscus* spp.

Key words: echolocation, Chiroptera, *Kerivoula*, *Murina*, *Phoniscus*

INTRODUCTION

The design of echolocation calls is shaped by the need to detect, localize and classify prey (Schnitzler & Kalko, 1998) within the physical constraints imposed by foraging space (Schnitzler & Henson, 1980; Fenton, 1988; Neuweiler & Fenton, 1988; Neuweiler, 1989). Bats that hunt in cluttered forest environments are faced with the challenge of distinguishing insect echoes from those reflecting from the vegetation (Neuweiler, 1990). Many species of these ‘narrow-space’ bats (*sensu* Schnitzler & Kalko, 1998) employ calls of broad bandwidth (Neuweiler & Fenton, 1988), enabling the precise target location in clutter, and good textural resolution (Simmons, Lavender *et al.*, 1974; Habersetzer & Vogler, 1983; Schmidt, 1988*a, b*) necessary for gleaning insects from surfaces and negotiating dense vegetation. Calls are of short duration (< 3 ms) to prevent the overlap of

the signal by echoes, and auditory overloading by the background is further minimized by emitting calls at low intensities (Kober & Schnitzler, 1990).

Bandwidth can be broad through the use of several harmonics (up to five), as in the Palaeotropical Nycteridae and Megadermatidae, and the Neotropical Phyllostominae (Phyllostomidae) (e.g. Fenton, Gaudet & Leonard, 1983; Habersetzer, 1983; Neuweiler, 1984; Neuweiler & Fenton, 1988). However, these medium-large (> 10 g) multiharmonic (MH) gleaners also rely to varying extent on other cues to detect and classify prey. Passive sound localization is common to all three groups (e.g. Fiedler, 1979; Tuttle & Ryan, 1981; Fenton *et al.*, 1983), and it is likely that they only use echolocation to orient themselves in space and localize the target with respect to the background during the final attack (Schnitzler & Kalko, 1998).

Alternatively, broad bandwidth can be achieved by

the use of uniharmonic frequency-modulated (FM) sweeps. Steep FM sweeps are seen in several genera of vespertilionid gleaners, but many have extended low frequency hearing similar to the MH gleaners that is indicative of passive listening, and respond to prey-generated sounds (e.g. *Plecotus auritus*: Coles *et al.*, 1989; *Nyctophilus gouldi*: Guppy & Coles, 1988; *Antrozous pallidus*: Bell, 1982; Brown, Narins & Grinnell, 1984). Gleaners in the genus *Myotis* may rely more upon echolocation. Most of the *Myotis* gleaners that have been studied emit higher frequency FM sweeps that begin around 110+ kHz and drop to 50 kHz, with only weak harmonics, if any (e.g. *Myotis septentrionalis*: Miller & Treat, 1993; *Myotis auriculus*: Fenton & Bell, 1979; *Myotis evotis*: Faure, Fullard & Barclay, 1990; *Myotis emarginatus*: Schumm, Krull & Neuweiler, 1991). Whereas gleaning *M. septentrionalis* and *M. evotis* commonly cease calling before the final attack (Faure, Fullard & Dawson, 1993; Faure & Barclay, 1994), both *M. auriculus* and *M. emarginatus* continue to produce very brief broadband signals when picking up prey from surfaces. However, neither emits terminal buzzes (increase in pulse repetition rate immediately before attempted prey capture (Griffin, Webster & Michael, 1960)) when gleaning (Fenton & Bell, 1979; Schumm *et al.*, 1991).

The use of broadband, high frequency FM sweeps is taken to extremes in the Palaeotropical subfamilies Kerivoulinae and Murininae (Vespertilionidae) (the present study). These small (< 10 g), manoeuvrable bats forage in and around the clutter of the forest understorey (Payne & Francis, 1985). There are 15 species of Murininae in two genera (*Murina* 14 species, *Harpiocephalus* one species) and 21 species of Kerivoulinae in two genera (*Kerivoula* 18 species, *Phoniscus* three species) (Corbet & Hill, 1992). Despite their relative diversity and an extensive Palaeotropical range, there is little information on the echolocation calls of these species.

Palaeotropical bat communities rarely support more than three species of MH gleaners, possibly a consequence of their relatively large size (> 10 g) and catholic diets (e.g. Advani & Makwana, 1981; Fenton *et al.*, 1983; Davison & Zubaid, 1992). In contrast, the small narrow-space FM bats may compose guilds of eight species or more (Francis, 1990, 1995; the present study). Furthermore, with the greater deployment of harp traps, it has become increasingly apparent that these bats constitute a substantial component of the insectivorous fauna in Palaeotropical rain forests. Surveys using harp traps in Malaysia have found that members of the Kerivoulinae and Murininae can constitute from 13% of all individuals captured (Pasoh Forest Reserve: Francis, 1990) to nearer 30% (Sepilok Forest Reserve 34%, Temengor Forest Reserve 28%: Francis, 1990, 1995; Krau Wildlife Reserve 36%: present study). With such large and speciose communities of small narrow-space FM bats, the question arises as to whether there is evidence that these co-existing species may partition resources. One potential line of evidence may come from comparative studies of

echolocation. The functional relationship between echolocation and foraging strategy has been demonstrated on numerous occasions (e.g. Neuweiler 1984, 1989; Fenton, 1988, 1990; Jones & Rayner, 1988; Neuweiler & Fenton, 1988; Kalko & Schnitzler, 1993; Surlykke *et al.*, 1993), and there are clear indications that in tropical environments at least, interspecific differences in echolocation within foraging guilds reflect differences in foraging strategy. These differences may reflect the abilities of bats to detect prey of different sizes (Heller & Helversen, 1989) or structure of the foraging habitat (Kalko, 1995).

The likelihood that ecological differences between species will be expressed by differences in echolocation call structure depends to a large extent on the exclusivity of echolocation as a perception mechanism. If other cues, such as the passive listening typical of MH gleaners, are used for prey detection the direct relationship between echolocation and foraging strategy is weakened. A comparison of the brain structure of MH gleaners and the Kerivoulinae suggests that Kerivoulinae are in fact highly dependent upon echolocation (summarized in Baron, Stephan & Frahm, 1996). MH gleaners and other species that rely upon passive listening for prey detection exhibit greater development and differentiation of the dorsal cochlear nucleus than do insectivorous species that rely upon echolocation alone. The dorsal cochlea nucleus is extremely small in the Kerivoulinae, contrasting with a large ventral cochlear nucleus and superior olive (which analyses binaural cues). Furthermore, the nucleus sensorius nervi trigemini is also exceptionally small, suggesting that Kerivoulinae do not rely on somatosensory information from oro-facial hairs, as is the case in some gleaners (Haffner & Ziswiler, 1989). Echolocation is thus predicted to assume a predominant role in prey detection and sensory perception of the environment (Baron *et al.*, 1996). The situation in the Murininae is less clear as the dorsal cochlear nucleus is large. This is most likely indicative of passive auditory prey detection, although it has also been suggested that acute low frequency hearing is important for species roosting in vulnerable places, as do some *Murina* (Nowak, 1994; Schulz & Hannah, 1996), to enable early detection of predators. The Murininae are also characterised by extremely large olfactory structures (the main olfactory bulb and palaeocortex), and tube-like nostrils, indicating a key role for olfaction in their sensory perception.

The first goal of the present study was to provide detailed descriptions of the echolocation calls of nine species of these little-studied bats, and the second to test for interspecific differences in call structure.

METHODS

Study site

The study was conducted between January 1996 and March 1997 at Kuala Lompat Research Station, Krau

Table 1. Descriptive statistics for call parameters. For each parameter, species means with the same letter are not significantly different (Ryan-Einot-Gabriel-Welsh multiple range test). Mean length of forearm (mm) and body mass (g) are from this study

Species (FA/mm, BM/g)	No. bats	Call parameters				
		Start frequency (kHz) mean \pm SD (min–max) <i>n</i>	End frequency (kHz) mean \pm SD (min–max) <i>n</i>	Peak frequency (kHz) mean \pm SD (min–max) <i>n</i>	Centre frequency (kHz) mean \pm SD (min–max) <i>n</i>	Call duration (ms) mean \pm SD (min–max) <i>n</i>
<i>Kerivoula intermedia</i> (29.3, 3.4)	29	173.1 \pm 8.58 b (132.0–184.8) 174	77.1 \pm 5.31 b (67.2–96.8) 174	101.4 \pm 9.18 b (83.2–137.6) 174	131.3 \pm 9.30 d e (100.8–160.0) 173	1.7 \pm 0.45 f (0.7–3.0) 174
<i>Kerivoula minuta</i> (27.1, 2.4)	12	175.2 \pm 7.0 b (151.2–185.6) 78	85.8 \pm 8.31 a (66.6–101.6) 78	112.9 \pm 10.86 a (83.2–134.4) 78	137.8 \pm 7.41 b c (115.2–153.6) 78	2.3 \pm 0.51 b c (0.9–3.3) 78
<i>Kerivoula papillosa</i> large (41.1, 9.6)	24	174.0 \pm 6.64 b (154.4–187.2) 142	66.6 \pm 5.88 d (46.4–80.8) 142	93.1 \pm 13.58 c d (61.6–133.6) 139	136.7 \pm 8.57 c (102.4–153.6) 142	2.7 \pm 0.59 a (1.3–4.4) 142
<i>Kerivoula papillosa</i> small (39.4, 7.0)	11	179.9 \pm 3.98 a (172.0–187.2) 66	72.7 \pm 5.58 c (60.0–83.2) 66	96.6 \pm 13.14 b c (81.6–136.8) 62	148.4 \pm 6.44 a (128.0–160.0) 58	2.3 \pm 0.30 b c (1.3–3.1) 65
<i>Kerivoula pellucida</i> (30.9, 4.5)	18	178.5 \pm 6.57 a (159.2–188.8) 107	58.5 \pm 9.31 e (30.4–79.2) 107	96.4 \pm 20.74 b c (57.6–138.4) 100	148.1 \pm 8.16 a (121.6–161.6) 106	2.4 \pm 0.62 b (1.0–4.4) 107
<i>Kerivoula</i> sp. (30.3, 3.1)	3	173.6 \pm 5.89 b (164.0–181.6) 18	50.3 \pm 10.58 g (33.6–68.8) 18	99.6 \pm 21.92 b c (57.6–133.6) 18	140.5 \pm 10.99 b (121.6–160.0) 18	2.4 \pm 0.77 b (1.4–3.6) 18
<i>Phoniscus atrox</i> (33.4, 4.8)	7	166.1 \pm 9.86 c d (145.6–183.2) 42	60.0 \pm 5.39 e (51.2–72.0) 42	86.9 \pm 15.81 d e (62.4–122.4) 42	127.1 \pm 10.72 e (96.0–140.8) 42	2.8 \pm 0.63 a (1.9–3.9) 42
<i>Phoniscus jagorii</i> (40.4, 9.6)	3	169.3 \pm 8.66 c (154.4–184.8) 18	70.4 \pm 4.7 c (61.6–76.0) 18	94.4 \pm 11.80 b c (79.2–117.6) 18	127.1 \pm 6.57 e (120.0–140.8) 17	2.2 \pm 0.51 c d (1.6–3.2) 18
<i>Murina aenea</i> (35.2, 7.3)	2	152.4 \pm 3.90 e (145.6–159.2) 12	43.3 \pm 5.22 h (37.6–52.8) 12	83.0 \pm 14.2 e f (65.6–112.8) 12	128.1 \pm 11.03 e (114.0–147.2) 12	2.4 \pm 0.26 b (2.1–2.9) 12
<i>Murina cyclotis</i> (35.7, 8.4)	22	165.2 \pm 7.42 d (143.2–180.0) 131	51.6 \pm 6.96 g (37.6–72.8) 131	77.2 \pm 13.45 f (54.4–136.8) 127	135.1 \pm 12.72 c d (89.6–166.4) 131	2.0 \pm 0.56 e d (1.2–4.1) 131
<i>Murina suilla</i> (29.5, 3.9)	20	165.0 \pm 6.63 d (143.2–180.0) 118	55.2 \pm 8.52 f (33.6–73.6) 118	85.0 \pm 16.56 e (44.8–127.2) 116	135.1 \pm 10.83 c d (102.4–153.6) 118	2.0 \pm 0.48 e (1.0–3.6) 11

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).

Species

Bats were captured in the forest understorey using 4-bank harp traps (Francis, 1989) positioned across trails originally cut for primate studies (Chivers, 1980). Species were identified following Medway (1982), Payne & Francis (1985) and Lekagul & McNeely (1977). Juveniles were distinguished qualitatively from adults by the presence of cartilaginous epiphyseal plates in the finger bones (Anthony, 1988) and were excluded from the study. Adult individuals were sexed and weighed and the length of forearm measured.

The 10 species of narrow-space FM bats were all captured within a 2 km² area. Seven species belonged to the subfamily Kerivoulinae: *Kerivoula intermedia* Hill

and Francis, 1984; *K. minuta* Miller, 1898; *K. papillosa* Temminck, 1840; *K. pellucida* Vespertilio pellucidus Waterhouse, 1845; *Kerivoula* sp.; *Phoniscus atrox* Miller, 1905; and *P. jagorii* Peters, 1866. *Kerivoula* sp. was clearly a discrete species, but its identity remains unconfirmed, and it may represent an undescribed

species. *Kerivoula intermedia* and *K. minuta* are extremely difficult to differentiate in the hand, and were largely separated by size (*K. intermedia*, length of forearm (FA) > 27.0 mm (range: 27.4–31.7 mm), body mass (BM) > 2.5 g (range: 2.6–5.0 g); *K. minuta*, FA \leq 27.0 mm (range 23.9–27.0 mm), BM \leq 2.5 g (range: 2.0–2.5 g)). During the study it became apparent that adult size variation in *K. papillosa* was extensive. Similar findings by Payne & Francis (1985) prompted them to suggest that >1 species might be included. Adults were therefore divided into 2 arbitrary size classes: *K. papillosa* small (FA \leq 40.0 mm (range 37.8–40.0 mm), BM \leq 7.0 g (range; 6.0–7.0 g)) and *K. papillosa* large (FA > 40.0 mm (range: 40.5–45.0 mm), BM > 7.0 g (range 7.5–11.0 g)), and treated separately for the purpose of the present study. Three species of the subfamily Murininae were also captured: *Murina aenea* Hill, 1964; *M. cyclotis* Dobson, 1872; *M. suilla* Temminck, 1840. The number of individuals captured of each species is given in Table 1. Individuals were released at the original point of capture within 18 h.

Sound analysis

Narrow-space FM bats use very low intensity echolocation signals. To ensure adequate samples for each individual, echolocation calls of bats were recorded while flying in an outdoor wire mesh cage (5 m

long \times 1.5 m wide \times 2 m high). Because these species habitually hunt in clutter, flight cage recordings should be adequately representative of those produced by free-flying bats (but see Discussion). 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 \times) output was recorded on a Sony WM-D6C Walkman cassette recorder. Time-expanded sequences were analysed by using a Kay 5500 DSP Sonagraph, with a frequency resolution of 400 Hz on the real-time signal. The bat detector microphone had a frequency response of $-57 \text{ dB} \pm 3 \text{ dB}$ (ref. 1 V/ μbar) from 20–120 kHz.

Call parameters were measured from 6 calls of high (ref. 1 V/ μbar) signal-to-noise ratio for each individual. Power spectra were used to derive 4 measures of frequency (in kHz): start frequency, end frequency, peak frequency and centre frequency (frequency at half the call's duration). The duration of each call (call duration, ms) was measured from the waveform. All species produced groups of calls, the limits of which were defined when the interval between 1 call and the next exceeded that between the same call and the previous 1 by a factor of 1.5. The 6 calls we measured were selected from different call-groups whenever possible. The position of the call within a group of calls (call position) and the number of calls in the group from which it was selected (call-group size) were noted. Additional sequence parameters were recorded or measured from the whole of the recorded sequence (which comprised up to 3 passes by an individual) - frequency of each call-group size, intercall interval (time between the start of 1 call and the start of the next within a call-group), and intergroup interval (time between the start of the last call in a call-group and the start of the first call in the next group). For each sequence, a maximum of 18 call-group size counts were noted, a maximum of 10 call-groups were measured for intercall interval, and 15 intergroup intervals. Sequence measurements were taken sequentially from the start of the sequence until the maxima were reached, or the sequence ended.

Statistical analysis

Analysis of variance and discriminant analysis were used to test for species differences in call and sequence parameters. All analyses were conducted using SAS for Unix version 6.12.

Species differences in call structure

Multivariate analysis of variance (MANOVA), with individuals nested within species, was used to test for

differences in call structure between species and among individuals. Variance components were calculated (Sokal & Rohlf, 1981) for each call parameter (start frequency, end frequency, peak frequency, centre frequency, call duration) to describe the variation attributable to species, individuals and the error term which represented variability among calls within individuals. Means of call parameters were compared between species with the Ryan–Einot–Gabriel–Welsch (REGW) multiple range test (Day & Quinn, 1989). The effects of sex, call-group size and call position were investigated using a multiple-factor nested MANOVA (with interactions), and the specific relationship between call duration and call-group size for each species was modelled using regression analysis. Simple linear correlation was employed to assess relationships between mean values for species echolocation call parameter values and the mean values of forearm and body mass.

Species differences in sequence structure

ANOVAs with individuals nested within species were conducted to determine the effect of species on call-group size and intergroup interval. REGW tests on mean call-group size identified species that differed significantly from one another. A 2-factor nested ANOVA was used to test for differences between species in intercall interval and inspected the influence of call-group size on intercall interval. The specific relationship between call-group size and intercall interval was then examined for each species with simple linear regression. Intercall interval was also sorted by call-group size to test for differences between species for call-groups of the same size using a nested 1-factor ANOVA. A REGW test was employed to distinguish significant differences among species.

Call-group duty cycles (percentage of intercall interval for which the bat is calling) were calculated for each species using mean intercall interval and mean call duration for each call-group size. Sequence duty cycles (percentage of all sequences for each species for which a bat was calling) were derived from the total number of calls, intercall intervals and intergroup intervals, and average values for call duration and intercall interval for any given call-group size.

Discrimination into species

Species were also compared using stepwise discriminant analysis with resubstitution. Means of individual bats were calculated for all 5 call parameters (start frequency, end frequency, peak frequency, centre frequency, call duration) and for the sequence parameter call-group size. The covariance matrices were heterogeneous so the quadratic discriminant function was used for classification. Prior probabilities were set proportional to sample size. To estimate classification

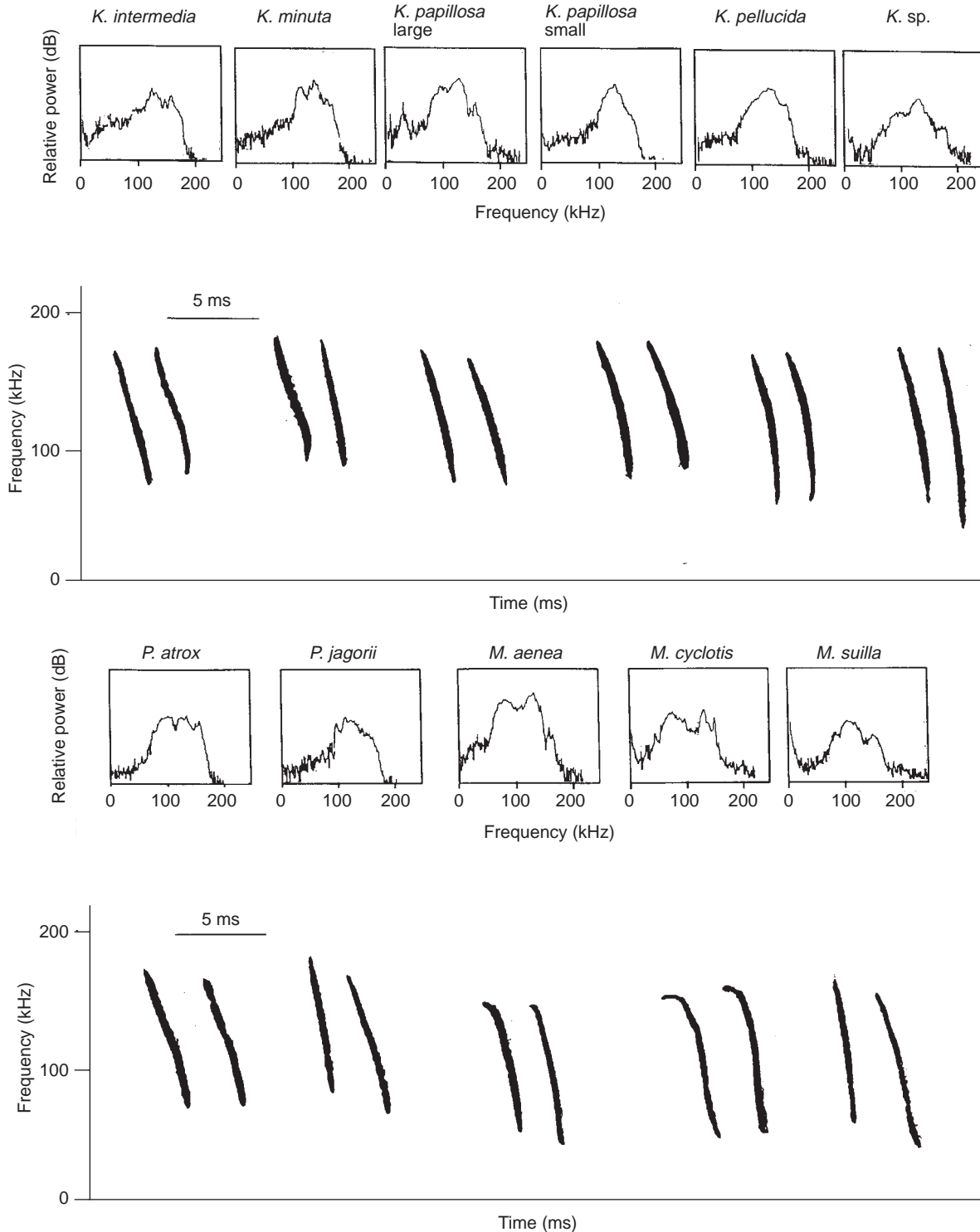


Fig. 1. Power spectra and sonograms to illustrate call structures of narrow-space FM bats captured at Kuala Lompat, Malaysia. Two calls from different individuals are shown in the sonograms (temporal separation not to scale). The power spectra refer to the first call for each species. *K*, *Kerivoula*, *P*, *Phoniscus*, *M*, *Murina*.

success, Lachenbruch's (1967) jack-knife procedure was employed (Stevens, 1992). Canonical discriminant analysis was used to compute and test Mahalanobis distances for pairwise comparisons between species in multivariate space. To provide a visual representation

of the relationship between the calls of individuals and species, multivariate means were calculated from canonical discriminant analysis and plotted.

All parameters exhibited univariate normality, but the data did not conform to the multivariate normal

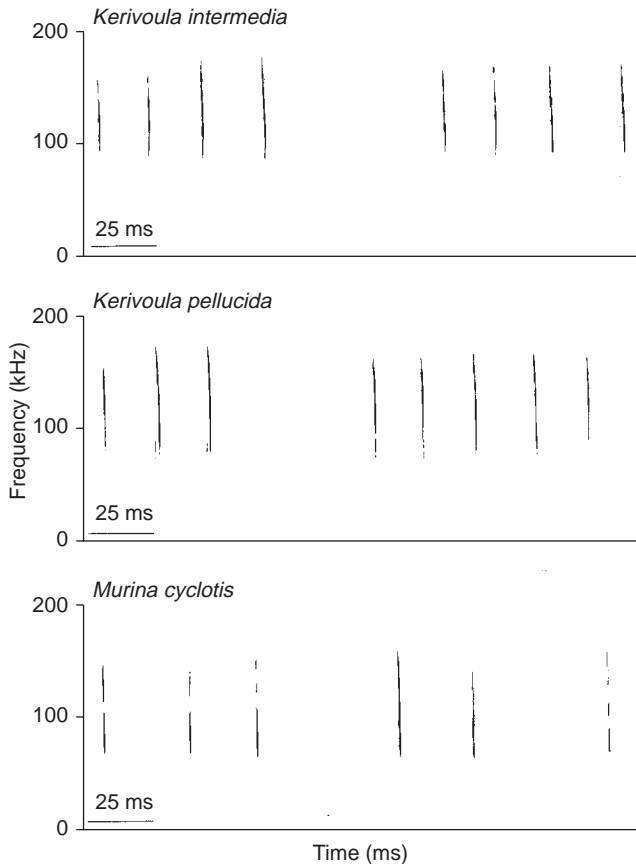


Fig. 2. Sonograms to illustrate sequence structure of three species of narrow-space FM bats at Kuala Lumpur, Malaysia.

distribution. However, this deviation from multivariate normality is considered to have only a small effect on type I error (Stevens, 1992).

RESULTS

General description

All species produced high-frequency, broadband FM sweeps of short duration (Figs 1 & 2, Table 1). Frequency sweeps were nearly linear with time, or in some cases slightly concave. In calls of both *Murina aenea* and *M. cyclotis* an initial 'hook' was present in recordings with good signal to noise ratio. Power tended to be evenly distributed throughout the frequencies, with only slight or multiple peaks apparent. Each

species produced calls in groups of variable size (Fig. 2). Calls were of such low intensity that adequate recordings could not be made if a bat was more than *c.* 1.5 m from the microphone.

Species differences in call structure

Call structure differed significantly between species (MANOVA with individual nested in species; Wilks' $\lambda_{50, 3301} = 0.0099$, $P < 0.0001$). Each parameter differed significantly between species and among individuals (Table 2). The amount of variability attributable to species varied from 73% for end frequency to 26% for call duration. End frequency was consequently the most useful variable for discriminating between species, call duration the least. Intraspecific variation was greatest for call duration at 53.5% and was high for start frequency (40.3%) and centre frequency (42.2%). Variation between calls within individuals was particularly pronounced for peak frequency (41.9%). The groupings generated by REGW multiple range testing showed no consistency across parameters (Table 1), but groupings were most distinct (highest number of groups) for end frequency and least distinct for peak frequency.

Call structure differed significantly between sexes (MANOVA; Wilks' $\lambda_{5, 723} = 0.9496$, $P < 0.0001$). Sex had a significant effect on start frequency ($F_{1, 727} = 5.81$, $P = 0.0162$) (higher in males than females in *K. intermedia* and *M. suilla*), centre frequency ($F_{1, 727} = 7.32$, $P = 0.0070$) (higher in males of *K. intermedia* and *M. cyclotis* and in females of *K. papillosa* small), and call duration ($F_{1, 727} = 6.89$, $P = 0.0880$) (longer in males of *K. intermedia*, *Phoniscus atrox* and *M. suilla* and in females of *K. papillosa* large), the three parameters exhibiting greatest intraspecific variation, but was just non-significant for peak frequency ($F_{1, 727} = 3.77$, $P = 0.0526$) and clearly not significant for end frequency ($F_{1, 727} = 2.11$, $P = 0.1471$). However, there was a significant interaction between sex and species for all five parameters ($P = 0.0001$), thus sex was not treated as a separate factor in these analyses (variation attributable to sex was included within intraspecific variation). Call-position was also found to influence call structure (MANOVA; Wilks' $\lambda_{50, 2781} = 0.8712$, $P = 0.0015$) but this was largely due to the impact of call position on peak frequency ($F_{10, 613} = 3.81$, $P = 0.0001$) and call duration ($F_{10, 613} = 3.04$, $P = 0.0009$); there was no significant effect of call-position on start frequency, end

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 species, individual and call (error term). *** $P < 0.001$

Source of variance	Call parameter				
	Start frequency	End frequency	Peak frequency	Centre frequency	Call duration
Species	37.1 ***	73.0 ***	33.8 ***	28.3 ***	26.0 ***
Individual within species	40.3 ***	17.7 ***	24.3 ***	42.2 ***	53.5 ***
Error = call within individual	22.6	9.3	41.9	29.5	20.5

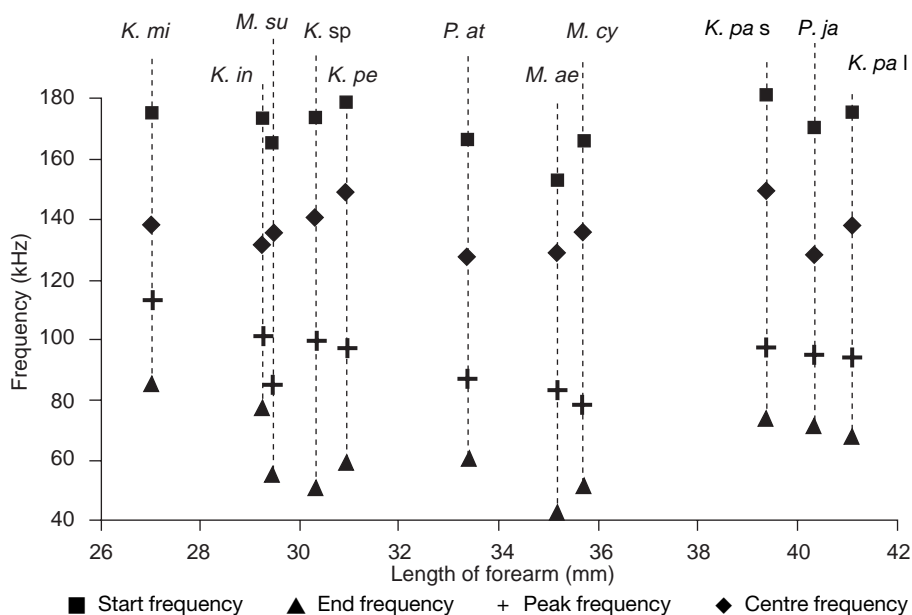


Fig. 3. Relationship between mean length of forearm and mean values of four call parameters for each species. Dotted lines link each species to improve visual interpretation. *K. mi* = *Kerivoula minuta*, *K. in* = *K. intermedia*; *K. pa l* = *K. papillosa* large, *K. pa s* = *K. papillosa* small, *P. at* = *Phoniscus atrox*, *P. ja* = *P. jagorii*, *M. ae* = *Murina aenea*, *M. cy* = *M. cyclotis*, *M. su* = *M. suilla*.

frequency or centre frequency. Overall call structure was not significantly affected by call-group size (MANOVA; Wilks' $\lambda_{80,2936} = 0.8523$ $P = 0.0761$), although call duration was influenced by call-group size ($F_{10,613} = 2.49$, $P = 0.0011$). Simple linear regressions for each species described this relationship further. There was a very slight but significant decrease in call duration as call-group size increased for four of the Kerivoulinae (*K. minuta* $P = 0.0001$, $r^2 = 0.31$; *K. papillosa* large $P = 0.0013$, $r^2 = 0.07$; *K. papillosa* small $P = 0.0247$, $r^2 = 0.08$; *K. pellucida* $P = 0.0012$, $r^2 = 0.09$), and for *M. cyclotis* ($P = 0.0008$, $r^2 = 0.08$).

There was no relationship between the species means for either length of forearm (Fig. 3) or body mass and for any of the five call parameters (Pearson's correlation coefficients all non-significant at 0.05 level). Moreover, no relationships were apparent when the Kerivoulinae

(seven species), the *Kerivoula* (five species), or the *Murina* (three species) were tested separately. End frequency did decrease with increasing length of forearm within three of the species: *K. intermedia* (simple linear regression, $P = 0.184$, $r^2 = 0.21$), *K. papillosa* large ($P = 0.0299$, $r^2 = 0.22$) and *M. cyclotis* ($P = 0.0028$, $r^2 = 0.38$).

Species differences in sequence structure

Call-group size differed significantly between species (nested ANOVA; $F_{10,2220} = 119.1$, $P = 0.0001$; Table 3) and within species ($F_{137,2220} = 4.8$, $P = 0.0001$) (see Fig. 2). Variance components showed that 55.4% of the variation was the result of species effects, 8.6% to individuals nested within species, and 36% was

Table 3. Descriptive statistics for call-group size. Species means with the same letter are not significantly different (Ryan–Einot–Gabriel–Welsh multiple range test)

Species	No. bats	Call-group size				No. call-groups
		Mean \pm SD	REGW	Mode	Min–max	
<i>Kerivoula intermedia</i>	29	3.2 \pm 1.42	c	3	1–11	467
<i>Kerivoula minuta</i>	11	2.8 \pm 1.16	c	2	1–8	181
<i>Kerivoula papillosa</i> , large	25	4.4 \pm 2.20	a b	3	1–17	387
<i>Kerivoula papillosa</i> , small	10	4.7 \pm 2.08	a	4	1–14	182
<i>Kerivoula pellucida</i>	16	4.5 \pm 3.10	a b	3	1–22	215
<i>Kerivoula sp.</i>	2	4.0 \pm 2.83	b	3	1–15	36
<i>Phoniscus atrox</i>	7	2.7 \pm 0.68	c	3	1–6	122
<i>Phoniscus jagorii</i>	3	3.1 \pm 1.11	c	3	1–5	54
<i>Murina aenea</i>	2	1.2 \pm 0.41	e	1	1–2	25
<i>Murina cyclotis</i>	23	1.7 \pm 0.81	d	1	1–5	370
<i>Murina suilla</i>	18	1.6 \pm 1.27	d e	1	1–9	329

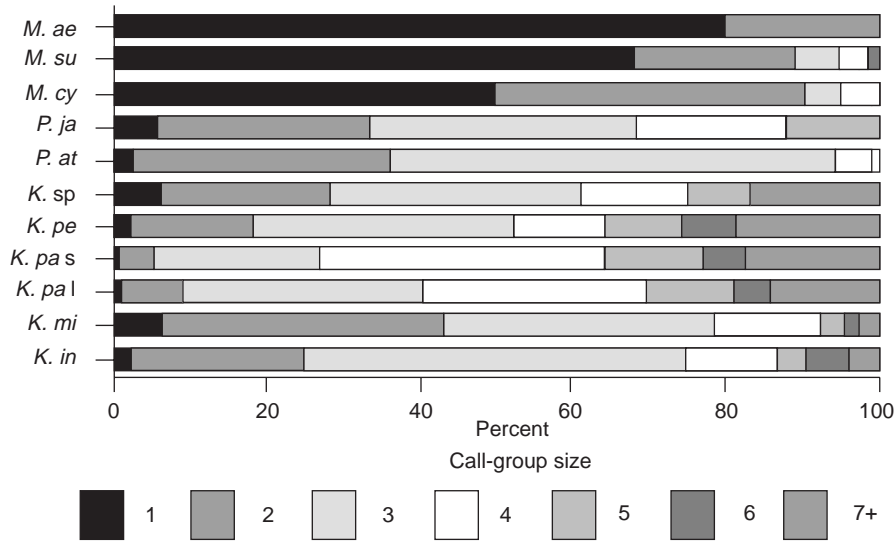


Fig. 4. Percentage of call-group size for each species. Species abbreviations as for Fig. 3.

attributable to differences between call-groups within an individual. *Murina* spp. used significantly fewer calls per call-group (REGW grouping, Table 3 and Fig. 4) than the Kerivoulinae, generally emitting calls singly or in groups of two. In contrast, call-groups of two, three or four calls dominated Kerivoulinae call sequences.

Significant differences among species were observed in intercall interval which was itself affected by call-group size (two-factor ANOVA; $F_{10,2429} = 62.65$, $P = 0.0001$; $F_{11,2429} = 36.77$, $P = 0.0001$, respectively). Since the interaction between species and call-group size was also very highly significant, ($F_{49,2429} = 9.31$, $P = 0.0001$), the species were treated separately and the relationship between call-group size and intercall interval explored further. Each species of Kerivoulinae exhibited significant differences in intercall interval between call-group sizes although individual variation was also significant (two-factor ANOVA, significance at 0.001 level). Simple linear regression analyses showed that intercall interval decreased slightly with increase in call-group size for all Kerivoulinae except *Kerivoula intermedia* (Table 4). In *Murina cyclotis* and *M. suilla* there was also a significant effect of call-group size on intercall interval ($P < 0.05$) and a negative relationship (Table 4). Call-group size for *M. aenea* did not exceed two, precluding these analyses. Species varied significantly within each call-group size with adequate sample size, (nested ANOVA, $P < 0.001$) except for call-group size two. Intraspecific variation was also significant. Comparisons of species means of intercall interval (REGW multiple range tests) revealed the *Kerivoula pellucida* consistently used short intercall intervals (this species was either in the last or penultimate (shortest) REGW grouping for each call-group size). *Kerivoula intermedia* exhibited the opposite trend and was consistently in the first REGW group (with the exception of call-group size two and three) suggesting that it generally uses longer intercall intervals. For call-group sizes two and three, the *Murina* spp. produced the

longest intercall interval. No other consistent trends were identified.

Species also differed on intergroup interval (one-factor nested ANOVA, $F_{10,1352} = 33.72$, $P = 0.0001$) but species effects accounted for only 11.9% of the variability in the data (variance component). Intraspecific variation was significant ($F_{141,1352} = 5.98$, $P = 0.0001$) and contributed 29.9%, but 53.4% of the variation lay within individuals (the error term) (this was probably attributable to the tendency of intergroup interval to decrease as the preceding call-group size increased (Table 5).

Species averages for call-group duty cycles ranged from 9.6% in *Kerivoula intermedia* to 17.3% in *K. pellucida*. There was a slight increase in call-group duty cycle with call-group size (simple linear regression, $P = 0.0081$, $r^2 = 0.11$) across species (reflecting the decrease in intercall interval), although this did not hold true when the species were treated separately (sample sizes too small). As would be expected, estimates for sequence duty cycle were considerably lower than for call-group duty cycles (Table 5).

Discrimination into species

The discriminant analysis was based on the five call variables and the sequence variable call-group size. Intercall interval was not used because of the interaction with call-group size (it was not possible to take values from a single call-group size without reducing the overall sample size owing to variable representation of call-group sizes between individuals). In addition, the high intra-individual variation in intergroup interval was considered reason to exclude this parameter.

Stepwise discriminant analysis revealed that all six parameters contributed to the model (Table 6) ($\alpha = 0.0001$ for Wilks' λ and the average squared canonical correlation at each step). As might be

Table 4. Descriptive statistics for intercall interval for each call-group size. DC = duty cycle (%)

Species	Intercall interval (ms)							
	2 calls / group Mean ± s D, n (min–max) DC	3 calls / group Mean ± s D, n (min–max) DC	4 calls / group Mean ± s D, n (min–max) DC	5 calls / group Mean ± s D, n (min–max) DC	6 calls / group Mean ± s D, n (min–max) DC	7 calls / group Mean ± s D, n (min–max) DC	8 calls / group Mean ± s D, n (min–max) DC	
<i>Kerivoula intermedia</i>	19.1 ± 2.37, 88 (13.8–29.1) 9.5	17.9 ± 1.87, 331 (13.1–24.4) 10.6	18.33 ± 2.69, 72 (12.5–24.4) 9.3	18.7 ± 2.61, 56 (12.8–25.0) 11.1	18.0 ± 2.29, 85 (13.1–24.1) 9.4	18.0 ± 1.49, 36 (15.6–22) 8.1	18.8 ± 3.24, 7 (11.6–20.9) 9.9	
<i>Kerivoula minuta</i>	20.4 ± 1.77, 35 (15.9–23.1) 12.5	17.2 ± 2.63, 100 (12.8–23.8) 13.6	16.4 ± 2.32, 24 (12.8–23.8) 12.7	18.8 ± 2.52, 24 (14.7–23.1) 9.4	21.2 ± 1.68, 10 (18.1–23.1) 7.9	18.3 ± 2.19, 18 (14.4–22.2) 11.2		
<i>Kerivoula papillosa</i> l	18.4 ± 1.64, 14 (15.6–21.6) 15.4	18.0 ± 2.17, 154 (12.5–24.0) 14.7	17.5 ± 2.72, 210 (16.9–25.0) 15.8	18.0 ± 2.38, 132 (11.3–23.1) 14.6	17.7 ± 2.93, 50 (10.9–23.8) 14.4	17.2 ± 2.12, 36 (13.1–22.5) 16.5	17.2 ± 2.5, 49 (12.5–21.9) 14.4	
<i>Kerivoula papillosa</i> s	16.2 ± 2.04, 7 (14.1–19.4) 16.4	15.5 ± 1.80, 52 (11.3–20.0) 14.5	15.4 ± 1.63, 141 (11.6–21.6) 15.5	15.2 ± 2.11, 72 (11.3–20.3) 14.8	15.3 ± 1.90, 40 (12.2–20.3)	15.6 ± 1.84, 41 (11.9–20.3)	14.1 ± 1.74, 22 (10.9–16.9) 15.0	
<i>Kerivoula pellucida</i>	17.1 ± 2.92, 29 (9.1–22.5) 15.4	15.3 ± 2.5, 124 (9.4–22.5) 16.6	14.1 ± 2.56, 69 (8.75–21.6) 16.7	12.7 ± 2.25, 70 (6.9–18.8) 17.4	13.2 ± 2.28, 55 (9.1–19.1) 16.9	12.4 ± 2.07, 55 (8.8–21.6) 17.4	12.9 ± 2.28, 19 (9.1–18.8) 14.5	
<i>Kerivoula</i> sp.	17.1 ± 1.87, 7 (13.8–19.7) 15.7	15.7 ± 1.83, 24 (11.6–18.8) 14.5	13.5 ± 2.08, 18 (9.4–16.9) 19.4	16.1 ± 2.52, 20 (11.3–21.3)		15.3 ± 1.55, 11 (13.1–17.8) 14.6		
<i>Phoniscus atrox</i>	21.2 ± 2.11, 44 (15.3–25) 13.2	19.9 ± 3.04, 102 (13.8–27.5) 14.0	15.3 ± 0.95, 3 (14.4–16.3) 13.0					
<i>Phoniscus jagorii</i>	18.2 ± 3.01, 12 (14.4–23.1) 11.3	19.6 ± 3.19, 30 (13.1–25.6) 11.2	17.8 ± 3.07, 15 (12.5–21.3) 12.5	12.8 ± 1.76, 12 (10.0–16.3) 17.1				
<i>Murina aenea</i>	27.2 ± 1.64, 6 (25.3–28.8) 8.3							
<i>Murina cyclotis</i>	22.5 ± 3.11, 16 (12.8–32.5) 8.5	18.1 ± 3.73, 22 (14.7–31.9) 9.3	16.9 ± 3.01, 9 (12.8–23.1) 11.1					
<i>Murina suilla</i>	22.6 ± 3.55, 68 (17.2–31.9) 8.4	19.0 ± 2.56, 30 (14.1–25.0) 12.7	18.0 ± 1.64, 15 (15.3–21.3) 12.7	16.7 ± 1.40, 8 (14.4–19.1) 13.8		16.2 ± 0.51, 13 (15.3–17.2) 13.7	16.8 ± 1.64, 7 (15.0–18.4) 14.0	

Species	Intercall interval (ms)						Regression	
	9 calls / group Mean ± s D, n (min–max) DC	10 calls / group Mean ± s D, n (min–max) DC	11 calls / group Mean ± s D, n (min–max) DC	12 calls / group Mean ± s D, n (min–max) DC	15 calls / group Mean ± s D, n (min–max)	Intercall interval = call-group size P, r ²	Mean call-group duty (%)	
<i>Kerivoula intermedia</i>	17.9 ± 0.94, 16 (16.3–19.4) 9.3					0.4478, 0.00	9.6	
<i>Kerivoula minuta</i>					10.5 ± 2.03, 15 (8.4–14.7) 12.2	0.0001, 0.26	11.3	
<i>Kerivoula papillosa</i> l	16.5 ± 1.87, 64 (11.6–19.4) 16.4	12.2 ± 0.63, 9 (10.9–13.1) 17.3	14.5 ± 2.51, 30 (9.1–20.0) 16.0			0.0001, 0.08	15.5	
<i>Kerivoula papillosa</i> s	15.0 ± 1.47, 24 (12.5–17.8) 16.4	15.7 ± 0.87, 9 (14.4–16.6)		13.3 ± 0.81, 11 (11.6–14.7) 14.4		0.0011, 0.03	15.3	
<i>Kerivoula pellucida</i>	11.0 ± 1.93, 100 (7.8–18.4) 17.2	9.9 ± 0.89, 14 (8.1–11.6) 21.3	12.1 ± 3.4, 20 (8.1–17.8) 11.3	13.0 ± 1.38, 11 (10.3–14.4)	9.5 ± 0.70, 14 (8.1–10.6) 24.5	0.0001, 0.31	17.3	
<i>Kerivoula</i> sp.	13.1 ± 1.05, 9 (11.3–14.4)				12.3 ± 1.30, 6 (10.3–13.8)	0.0001, 0.15	16.1	
<i>Phoniscus atrox</i>						0.0009, 0.07	13.4	
<i>Phoniscus jagorii</i>						0.0001, 0.25	13.0	
<i>Murina aenea</i>							8.3	
<i>Murina cyclotis</i>						0.0001, 0.22	9.6	
<i>Murina suilla</i>						0.0001, 0.35	12.6	

Table 5. Descriptive statistics for intergroup interval. Species means with the same letter are not significantly different (Ryan–Einot–Gabriel–Welsh multiple range test)

Species	No. bats	Intergroup interval (ms)				
		Mean ± sD	REGW	Min–max	No. of intervals	Mean sequence duty cycle (%)
<i>Kerivoula intermedia</i>	27	57.5 ± 14.9	b c	28.1–115.6	263	5.7
<i>Kerivoula minuta</i>	11	66.2 ± 21.9	a	39.4–176.9	95	6.6
<i>Kerivoula papillosa</i> large	25	62.0 ± 13.3	a b	35.6–101.2	206	9.5
<i>Kerivoula papillosa</i> small	11	63.0 ± 13.6	a b	28.4–94.4	101	7.9
<i>Kerivoula pellucida</i>	19	50.3 ± 25.8	d e	14.0–182.5	156	10.4
<i>Kerivoula</i> sp.	3	61.9 ± 13.0	a b	39.4–85.6	35	7.1
<i>Phoniscus atrox</i>	7	57.0 ± 14.4	b c d	29.7–113.1	82	8.1
<i>Phoniscus jagorii</i>	3	47.4 ± 9.54	e	29.4–64.4	32	8.1
<i>Murina aenea</i>	2	55.1 ± 16.4	c d	35.9–131.6	30	4.8
<i>Murina cyclotis</i>	22	48.3 ± 13.7	e	20.9–117.5	256	5.4
<i>Murina suilla</i>	20	47.3 ± 13.3	e	10.0–118.0	248	5.5

Table 6. Contribution of variables to species 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

Variable (in order of entry into the model)	Partial R^2	Wilks' λ (cumulative for model at that point)
End frequency	0.7843 ***	0.2157, $P = 0.0001$
Call-group size	0.5574 ***	0.0958
Duration	0.3398 ***	0.0630
Start frequency	0.2588 ***	0.0467
Peak frequency	0.1434 *	0.0400
Centre frequency	0.1275 NS	0.0349

F ratio: * $P < 0.05$, ** $P < 0.005$, *** $P < 0.0001$.

expected from the MANOVA and ANOVA, end frequency was the most useful variable (partial $R^2 = 0.78$) and provided significant discrimination in its own right (Wilks' $\lambda_{10,132} = 0.2157$, $P < 0.0001$). Call-group size was the second variable entered, and also had a high partial R^2 at 0.56. Centre frequency was of borderline significance ($P = 0.057$), but still contributed to the overall discrimination. All six variables were therefore used in the classification procedures. Classification success as estimated by the jack-knife procedure was 61.9%, but varied considerable between species, ranging from 0 to 88.9% (Table 7). *Kerivoula* sp. and *M. aenea* were excluded from the analysis due to small sample size. *Kerivoula intermedia*, *K. minuta*, *K. papillosa* large and *K. pellucida* were classified correctly on the majority of occasions. *Kerivoula papillosa* small was frequently misclassified as *K. papillosa* large. The two species of

Phoniscus were not successfully classified, but sample sizes were small. Interestingly, neither *Phoniscus* species was misclassified as the other. *Murina cyclotis* and *M. suilla* were only correctly classified approximately half the time, and were largely misclassified as each other.

There was no overlap in multivariate space between the Kerivoulinae and the Murininae (Fig. 5). Within each subfamily, species distributions overlapped, but the multivariate means showed significant separation in 92% of species pairs (canonical discriminant analysis, pairwise tests that the squared distance between species exceeds Mahalanobis distance; $F_{6,127}$, $\alpha = 0.05$) (Table 7). *Kerivoula* sp. could not be distinguished from *K. pellucida*, and *Phoniscus jagorii* did not differ significantly from *K. intermedia*, *K. papillosa* large, *K. papillosa* small or *P. atrox*. The three species of *Murina* could not be separated by these pairwise tests. The first canonical variable is primarily a spectral function derived from end frequency and start frequency (by examination of the standardized canonical discriminant coefficients) while the second canonical variable is most heavily influenced by call-group size and call duration.

DISCUSSION

Echolocation signal design in the Kerivoulinae and Murininae

Echolocation signal design in the Kerivoulinae and Murininae is highly distinctive. As would be expected for putative gleaners, calls are of short duration and low

Table 7. Discriminant function analysis for species showing the percent of individuals classified to species, excluding *Kerivoula* sp. and *M. aenea*. The probability that species pairs differ significantly in multivariate space is indicated (canonical discriminant analysis; $F_{6,127}$ * $P < 0.05$, ** $P < 0.005$, *** $P < 0.0001$). Boxed values are percentage correct classifications for each species. Species abbreviations as for Fig. 1

Actual species, No. bats	Assigned species										
	<i>K. in</i>	<i>K. mi</i>	<i>K. pa l</i>	<i>K. pa s</i>	<i>K. pe</i>	<i>K. sp</i>	<i>P. at</i>	<i>P. ja</i>	<i>M ae</i>	<i>M. cy</i>	<i>M. su</i>
<i>K. intermedia</i> , 27	88.9 ***	7.4 ***	0 ***	0 ***	0 ***	0 ***	0 ***	0 NS	0 ***	0 ***	3.7 ***
<i>K. minuta</i> , 12	25.0 ***	75.0 ***	0 ***	0 ***	0 ***	0 ***	0 ***	0 ***	0 ***	0 ***	0 ***
<i>K. papillosa</i> l, 24	0 ***	0 ***	75.0 ***	4.2 *	16.6 ***	0 **	0 **	0 NS	0 ***	0 ***	4.2 ***
<i>K. papillosa</i> s, 9	22.2 ***	0 ***	66.7 *	11.1 ***	0 ***	0 **	0 ***	0 NS	0 ***	0 ***	0 ***
<i>K. pellucida</i> , 16	0 ***	0 ***	18.8 ***	0 ***	75.0 ***	0 NS	0 ***	0 **	0 ***	0 ***	6.2 ***
<i>K. sp.</i> , 2	***	***	**	**	NS	NS	*	*	**	**	*
<i>P. atrox</i> , 7	0 ***	0 ***	57.1 **	0 ***	14.3 ***	0 *	0 NS	0 NS	0 **	0 ***	28.6 **
<i>P. jagorii</i> , 3	66.7 NS	0 **	33.3 NS	0 NS	0 **	0 **	0 NS	0 ***	0 ***	0 NS	0 NS
<i>M. aenea</i> , 2	***	***	***	***	***	**	**	***	***	NS	NS
<i>M. cyclotis</i> , 22	0 ***	0 ***	0 ***	0 ***	4.5 ***	0 **	0 ***	0 ***	0 NS	54.5 NS	40.9 NS
<i>M. suilla</i> , 19	0 ***	0 ***	5.3 ***	0 ***	0 ***	0 *	0 **	0 **	0 NS	42.1 NS	52.6 NS

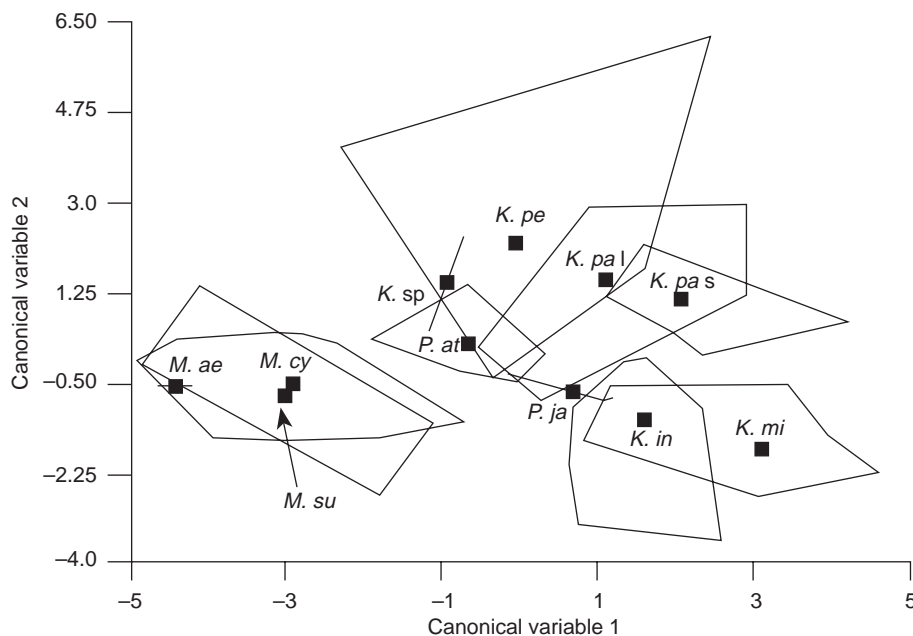


Fig. 5. Species distributions in multivariate space. The outline for each species groups the individual canonical variables for that species. Species canonical means are represented by filled squares. Species abbreviations as for Fig. 3.

intensity, but they are distinguished by the very high frequencies and extreme bandwidths used, and by high pulse repetition rates. Bandwidths ranged from 89 to 123 kHz, extremes only comparable with that seen in *M. nattereri* (Siemers & Schnitzler, 1997) and exceeding most species by at least 30 kHz. Large signal bandwidths facilitate highly accurate target localization in terms of both range and angle estimation (Schnitzler & Kalko, 1998). Accurate spatial resolution is undoubtedly of prime importance to bats hunting relatively small prey items (as a consequence of their small body size) in dense vegetation.

While large bandwidths can be appreciated as an adaptation to foraging in highly cluttered space, the use of such high frequencies is less readily explained. Not only do the observed peak frequency values exceed those predicted for aerial insectivores of equivalent size (Barclay & Brigham, 1991) by a minimum of 28.5 kHz (*M. suilla*) and a maximum of 53 kHz (*K. papillosa* large), but they are also considerably higher than those used by other vespertilionid FM gleaning bats. This is not simply a consequence of small body size as several of the species are in the same size range as the gleaners of the genus *Myotis*. Consider the five species in the present study with body mass between 7.0 and 10.0 g; *K. papillosa* large, *K. papillosa* small, *P. jagorii*, *M. aenea*, *M. cyclotis*. Start frequency for this group ranged from 152.4 kHz (*M. cyclotis*) to 179.9 kHz (*K. papillosa* small). Of comparable body mass are five species of gleaning *Myotis*: *M. septentrionalis*, *M. evotis*, *M. auriculus*, *M. nattereri* and *M. emarginatus*. The highest mean start frequencies are seen in *M. emarginatus* and *M. nattereri*, but do not exceed 130 kHz (Schumm *et al.*, 1991; Siemers & Schnitzler, 1997), and

are as low as 80 kHz in *M. evotis* (Faure & Barclay, 1994). We consider two possible explanations for these observations. First, high frequencies represent a sophisticated texture resolution mechanism enabling the spectral discrimination of stationary prey. Second, this may be an attempt by these species to avoid detection by moths.

It is highly probable that FM bats are capable of using spectral cues to assess target texture (Habersetzer & Vogler, 1983; Schmidt, 1988*a,b*, 1992; Mogdans, Schnitzler & Ostwald, 1993; Moss & Schnitzler, 1995). A signal reflected from an uneven surface will include peaks and notches in the frequency spectrum where the various echo components either enhance or cancel each other through interference (Mogdans & Schnitzler, 1990; Simmons, Moss & Ferragamo, 1990). The frequencies at which the peaks and notches occur are correlated with the depth of the surface feature creating them. By analysing the spectral pattern of the echo (possibly by transformation into temporal representations along the range-axis (Simmons, Moss *et al.*, 1990)), a bat should be able to characterize the textural structure of a target surface or discriminate between complex targets (Neuweiler, 1990; Mogdans *et al.*, 1993).

Experiments by Schmidt (1988*a,b*, 1992) strongly suggest that the multiharmonic gleaner, *Megaderma lyra* uses spectral interference patterns to determine the textural structure of simulated targets, and is capable of resolving textural features as small as 0.2 mm. Since the textural resolution attained by a bat increases with frequency (Neuweiler, 1990), the frequencies employed by the species in this study, which are considerably higher than the 100–20 kHz MH calls of *Megaderma*

lyra, should improve on this 0.2 mm resolution, enabling an extremely detailed representation of surface texture. The question then remains as to whether such sophisticated discrimination can be achieved under natural conditions. Barclay & Brigham (1994) found that the temperate FM aerial insectivores *Myotis lucifugus* and *M. yumanensis* only distinguished between prey of different sizes when free-flying, and did not discriminate between edible and inedible items of similar size. They proposed that rapid flight and sound attenuation combine to reduce the interval between prey detection and prey capture to such an extent that only the most rudimentary target discriminations are possible. However, it is unlikely that the Kerivoulinae and Murininae experience the same constraints as aerial insectivores. These are slow-flying bats (both *Murina cyclotis* and *M. suilla* are capable of hovering; T. Kingston, pers. obs.) that are probably gleaning stationary prey. The combination of slow flight and stationary prey may well provide sufficient time to distinguish spectral patterns generated by prey from the noise of background clutter (Simmons & Stein, 1980; Neuweiler, 1990). Some of the *Myotis* gleaners are able to distinguish items using echolocation alone and take silent prey, although the echolocation cues may have been learned through association with visual or auditory cues (Schumm *et al.*, 1991; Schnitzler & Kalko, 1998). The extremely high frequencies used by the narrow-space FM bats in this study would be predicted to provide sufficient textural resolution to distinguish prey from clutter, particularly if the prey item produces a distinctive pattern that can be discerned from the background irrespective of aspect angle. Schulz & Wainer (1997) found that spiders constituted 91% of the diet of *K. papuensis* and web fragments were frequently found on the bats' fur. *Murina florium* has also been reported as taking spiders (Schulz & Hannah, 1996). This situation would indeed constitute recognition of a stationary, distinctive shape (that could not be identified by flutter detection or prey-generated noise) on a relatively non-reflective background (the web).

An alternative explanation for the high frequencies employed by these species is derived from the interaction between bats and tympanate moths. Many moths are sensitive to the echolocation frequencies commonly used by bats, particularly those between 20 and 50 kHz (Fullard, 1987), and upon detecting a bat they may take evasive action (Roeder, 1967). To avoid detection, bats could employ echolocation frequencies above or below the moth's best hearing response (allotonic frequency hypothesis: Fenton & Fullard, 1979; Fullard & Thomas, 1981; Fullard, 1987), and it appears that this strategy is indeed employed by some moth specialists (e.g. Woodsworth, Bell & Fenton, 1981; Jones, 1992) including several of the *Myotis* gleaners (Faure, Fullard & Barclay, 1990; Faure, Fullard & Dawson, 1993). The extent to which the Kerivoulinae and Murininae use this strategy is unknown, although it has been proposed for *K. argentata* (Fullard, 1987). Certainly the end frequencies of the Kerivoulinae and Murininae are all

above 50 kHz (with the exception of *M. aenea*), but this does not explain why the calls start at such high frequencies – some 30 + kHz above the start frequencies of the *Myotis* spp. In addition, moths represented only a small dietary component in *K. papuensis* (present in only 11.3% of pellets, 3% volume; Schulz & Wainer, 1997) and were not present in a preliminary analysis of *M. florium* diet (Schulz & Hannah, 1996). Although the allotonic hypothesis cannot be discounted, and may well account for the lower limit of the FM sweep, it seems more likely that these high-frequency FM sweeps are associated with prey detection in clutter.

The task of detecting prey and manoeuvring in cluttered situations may also account for the extremely high pulse repetition rates within call groups. The minimum repetition rate was 37 Hz for *M. aenea*, when using two calls, and the maximum was 105 Hz for the group of 15 calls produced by *K. pellucida*. Pulses emitted at such high rates are not coupled to wingbeats (predicted wingbeat frequency ranged from 12.2 Hz in *P. jadorii* to 19.1 Hz in *K. minuta* (based on relationship between body mass and wingbeat frequency given in Jones, 1994). Rather, scaling arguments (Jones, 1994) suggest that batches of pulses are produced every one to three predicted wingbeats; the *Kerivoula* spp. call groups commonly extended over two predicted wingbeats, whereas the Murininae tended to produce one call group per wingbeat. High pulse repetition rates have also been reported for other gleaning species (e.g. *Myotis emarginatus* (Schumm *et al.*, 1991), *Nycteris macrotis* (Jones, 1994)) and some *Hipposideros* species (Jones *et al.*, 1993). The link between wingbeat and pulse emission also breaks down during the feeding buzz of all species, when repetition rate increases, while bandwidth and call intensity are reduced. Pulse–wingbeat coupling substantially reduces the energetic cost of echolocation (Rayner, 1991; Speakman & Racey, 1991), but calls for the narrow-space FM bats are of such low intensity that they are relatively energetically inexpensive (Jones, 1994). Furthermore, the very high frequencies coupled with the low intensity of these calls means that they will have a particularly limited functional range (Griffin, 1971). Consequently, to obtain sufficient environmental information to avoid collisions while foraging in dense clutter, species may need to emit more calls per unit time than can be provided if calls are coupled to wingbeats, which may themselves be erratic as the bat manoeuvres through the vegetation.

The echolocation calls for the *Kerivoula* spp. and *Murina* spp. described in this paper are considerably higher in frequency than those reported for *K. argentata* (120–85 kHz: Fenton & Bell, 1981), *K. hardwickii* (79–56 kHz: McKenzie *et al.*, 1995) and *M. hilgendorfi* (107–47 kHz: Drobachev *et al.*, 1968 cited in Airapet'yants & Konstantinov, 1973); although high frequency calls have been reported for *M. leucogaster* (start frequency 140–160 kHz) (Simkin & Patlyakevich, 1973). We cannot discount the possibility that the former three species do indeed use rather different

echolocation, although the disparities may alternatively be attributable to methodological differences; particularly with respect to the frequency response of the recording equipment and microphone. In fact, it is quite possible that the importance of the higher frequencies was underestimated in this study, because of the combined effects of the time expansion factor (10), the sampling rate (400 kHz), and tail-off in both microphone and Walkman frequency response at higher frequencies.

Currently we can offer no satisfactory explanation of the observed effect of sex on call parameters, particularly given the lack of relationship between size (measured as length of forearm or body mass) and call parameters for most species. In some FM bats frequency may decrease as body size increases (Jones, 1995), as did end frequency within *K. intermedia*, *K. papillosa* large and *M. cyclotis*. However, end frequency did not vary with sex. The parameters that did respond to sex in some species (start frequency, centre frequency and call duration) did not exhibit an intraspecific relationship with body size. Thus, although females were larger (length of forearm) than males in four species (*K. intermedia*, *K. papillosa* small, *K. pellucida* and *M. cyclotis* (data not presented)) sexual dimorphism with respect to body size cannot be invoked to explain the effect of sex on call parameters. In addition, *M. suilla* was sexually dimorphic for call frequency but not for body size. Jones (1995) concludes that there is no general rule to relate sexual differences in call frequency to sexual size dimorphism in rhinolophoid bats, and we find similarly for the Kerivoulinae and Murininae.

As a cautionary note, we reiterate that the recordings we made were in a flight cage. For species that habitually hunt in clutter, the dimensions of the flight cage are no more restricting than those they encounter while foraging, and may in fact be less cluttered than their typical foraging space. It is thus unlikely that the signal modifications employed by many species as they approach cluttered situations will be much in evidence. Species that normally hunt in uncluttered situations or with back-ground clutter (*sensu* Schnitzler & Kalko, 1998) typically reduce the CF component of calls, decrease call duration and increase pulse repetition rate and bandwidth (Neuweiler, 1984; Kalko & Schnitzler, 1993). These modifications are necessary to avoid signal-echo overlap and to maximize information about approaching obstacles; design requirements that are already met by narrow-space FM bat signals. Call parameters from a single individual of *K. pellucida* and two *K. papillosa* large recorded after release in the field were all within the range characterizing each species. Miller & Treat (1993) found that *M. septentrionalis* calls recorded from bats flying freely did not differ spectrally from those flying within a confined porch (although duration was slightly reduced in the latter situation). Flight cage recordings of narrow-space FM bats should therefore be adequately representative of those produced in the field situation, and have been used in several studies (e.g. Faure & Barclay, 1992, 1994; Faure

et al., 1993; McKenzie *et al.*, 1995). None the less, more recordings from free-ranging bats are clearly desirable to evaluate this assumption more fully.

Interspecific differences in echolocation signal design

Members of the narrow-space FM guild exhibited differences in echolocation parameters, both in terms of call structure and sequence structure. As in the studies on echolocation-mediated resource partitioning by Heller & Helversen (1989) and Kalko (1995), the observed differences between species could not be attributed to size alone. Species means for call parameters were not correlated with length of forearm or body mass, even within genera. End frequency and call-group size were the most important variables for differentiating between species. Start frequency, end frequency and centre frequency were all lower in the Murininae than in the Kerivoulinae (REGW groupings Table 1), and while the latter generally emit calls in groups of two or three upwards, the Murininae tend to produce calls singly or in groups of two only (Table 3). Murininae showed considerable overlap in multivariate space and could not be successfully discerned from each other, five of the *Kerivoula* spp. were clearly distinct from one another but not from the two *Phoniscus* species.

Interpretations of the functional significance of interspecific differences in end frequency and call-group size must be of a speculative nature given the current lack of knowledge. However, it is conceivable that differences in end frequency might translate to functional differences in maximum target depth (i.e. the thickness of an insect target that can be differentiated from a surface). Further work is clearly needed to determine whether maximum target depth is of any influence in the detection and discrimination of prey items, and, if such is the case, whether the differences in end frequency between species in the present study result in functionally significant differences in target depth.

We suggested above that high pulse repetition rates may in part be an adaptation to foraging in cluttered environments. Certainly, individuals may increase pulse repetition rate as they switch from foraging in uncluttered to cluttered space (Kalko & Schnitzler, 1993; Kalko, 1994), from which it might be predicted that species in the present study with high repetition rates forage in more cluttered habitats than those with lower repetition rates. Just as echolocation call design is shaped by the habitat in which a bat forages, wing morphology is similarly determined by the degree of clutter in which a bat hunts (McKenzie & Rolfe, 1986; Norberg & Rayner, 1987; Crome & Richards, 1988; McKenzie *et al.*, 1995) and should be compatible with signal design (Aldridge & Rautenbach, 1987). Thus we predict that bats that use high pulse repetition rates to negotiate clutter should also exhibit greater manoeuvrability in flight. Overall pulse repetition rate will be highest for those species that either have short intercall

interval, or large call-group size, or both. Within the Kerivoulinae, *K. pellucida* consistently used short intercall intervals and large call groups, while *K. intermedia* used long intercall intervals and slightly smaller call groups, and *K. papillosa* large was intermediate with respect to intercall interval, but used large call groups. Manoeuvrability experiments for these three species (T. Kingston, pers. obs.), indicate that *K. intermedia* is in fact the least manoeuvrable of the three, *K. pellucida* the most, and *K. papillosa* intermediate, which is what might be expected if intercall interval indicates the degree of clutter tolerance. Field observations of bats upon release supported this hypothesis. *Kerivoula pellucida* frequently disappeared into thick stands of understorey vegetation, often flying quite low (<1 m). In contrast, *K. intermedia* tended to use small trails, or the spaces between branches of different heights at the understorey/midstorey boundary. The Murininae used both long intercall intervals and small call-groups, suggesting that they forage in more open areas than do the Kerivoulinae. It should be recalled that all recordings were made in a flight cage which represented a relatively open space to these species. It is quite possible that intercall interval is reduced (repetition rate increased) when species are flying in more cluttered situations. The data presented here should perhaps be considered the 'background' repetition rate; we assume that this will be in some way related to the repetition rate in clutter.

The two subfamilies clearly differed from each other in multivariate space. It is possible that this is manifested in terms of either foraging microhabitat or detectability of prey items. From the above, based on differences in call-group size and intercall interval we predict that the Murininae will forage in slightly less cluttered situations. Maximal target depth is slightly greater in the Murininae, and this may have implications for the size of target that can readily be discriminated from the background. Within the subfamilies, there was considerable overlap between species of *Murina*, particularly *M. suilla* and *M. cyclotis* for which sample sizes were large, suggesting that resource partitioning, if it exists, is by some mechanism other than echolocation. Size is a likely candidate; *M. cyclotis* is over twice the body size of *M. suilla* (mean 8.4 g vs 3.9 g) and this will influence both the size of prey that can be eaten and access to prey as the greater wing loading in *M. cyclotis* (T. Kingston, pers. comm.) reduces manoeuvrability (Norberg & Rayner, 1987).

In contrast, the *Kerivoula* clearly used different echolocation designs (with the exception of *K. sp.* for which sample size was small), as might be expected given their assumed reliance upon echolocation for perception. *Phoniscus jagorii* could not be statistically separated in multivariate space from several of the *Kerivoula* spp., nor from *P. atrox*. The small sample size for *Phoniscus jagorii* means this should be interpreted with some caution, but it is worth noting that this species was only captured on three occasions (out of a total of 494 Kerivoulinae captures), and was a new record for

Peninsular Malaysia (Kingston *et al.*, 1997). This species may be genuinely rare, or may be spatially separated from the other Kerivoulinae, possibly foraging in the higher levels of the canopy and only rarely descending to the understorey. Spatial partitioning may thus be of greater significance than that mediated by echolocation differences.

In conclusion, the extreme bandwidths, high frequencies and high pulse repetition rates employed by the Kerivoulinae and Murininae distinguish them from all other narrow-space FM bats studied to date. How the specifics of these features relate to foraging strategy clearly requires further study. Two particularly fruitful avenues for future research would be a thorough investigation of diet, and recordings of echolocation during prey capture to determine whether echolocation is used throughout capture, or if passive listening is used in the final moments.

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