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## Resource partitioning in rhinolophoid bats revisited

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**Abstract** We assessed the ecomorphological structure of a guild of rhinolophoid bats in a Malaysian rainforest first described by Heller and von Helversen (1989). These authors found that the distribution of echolocation call frequencies used by 12 syntopic species was more even than expected from allometric relationships or in randomly generated communities, and that the observed minimal ratio was greater than expected by chance alone. In this study we were able to expand their guild to 15 species, but in doing so it became apparent that call frequencies might be less evenly distributed across the total frequency range than previously proposed. We replicated Heller and von Helversen's (1989) analyses with the full 15-species complement but were unable to support their suggestion that rhinolophoid bats exhibit resource partitioning through differences in frequency bands. We adopted a multivariate approach and incorporated measures of body size and wing morphology into the analysis. We used phylogenetic autocorrelation to ensure that the species were statistically independent and principal component analysis to describe the morphological space occupied by the 15 species in the community and four additional species representing the extremes of phenotypic variation. We derived interspecific Euclidean distances and tested the mean values and SDs of these distances against those of 100 guilds of "synthetic" species created randomly within the principal component space. The guild of Rhinolophoidea was not distributed randomly in multivariate space. Instead we found evidence of morphological overdispersion of the most simi-

lar species, which suggests niche differentiation in response to competition. Less similar species were nearer in morphological space than expected, and we suggest this is a consequence of ecological constraints on parameter combinations. Despite this underdispersion, many of the more distant neighbours were evenly rather than randomly spaced or clumped in morphospace, suggesting that, given the environmental constraints on morphology, species in this guild do experience limits to their similarity. Finally, we tested the influence of the relative abundance of species on morphological displacement, and found no evidence that abundant, spatially correlated species reduce interspecific overlap in morphological space.

**Key words** Community structure · *Rhinolophus* · *Hipposideros* · Echolocation · Wing morphology

### Introduction

The diversity of species in tropical bat communities has long been of interest to ecologists. With communities comprising in excess of 50 species, questions have inevitably arisen as to whether these species-rich assemblages are structured in any way, specifically as a consequence of competitive interactions. Although a number of ecomorphological studies have described patterns in bat community structure indicative of resource partitioning (e.g. O'Shea and Vaughan 1980; Aldridge and Rautenbach 1987; Crome and Richards 1988; and see Findley 1993 for a review), only a few have tested the deterministic nature of these patterns. There is little consensus regarding the role of competition in structuring bat assemblages; Schum (1984), Willig and Moulton (1989) and Arita (1997) could not reject the null hypothesis of random assembly in bat communities, whereas McKenzie and Rolfe (1986) and Heller and von Helversen (1989) both detailed guilds of bats that exhibited very little niche overlap and were more regularly spaced than those generated randomly.

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Heller and von Helversen (1989) investigated a guild of 12 rhinolophoid bats in a primary lowland rainforest in peninsular Malaysia. The guild was defined by the ability of its members to forage for flying insects in cluttered environments. Member species were characterised by specializations of echolocation signal design that enabled them to distinguish between echoes returning from a food item and those from background vegetation, and by wing morphology that ensured that they were sufficiently manoeuvrable to intercept prey items without colliding with obstacles. In their analysis of resource partitioning, Heller and von Helversen (1989) focused on the distribution of the echolocation call frequencies across the total frequency range used by the member species. Call frequency may be the key determinant of the size of prey that an insectivorous bat can detect, because echo strength diminishes rapidly once the wavelength of sound exceeds the circumference of the target object (Pye 1993; but see Waters et al. 1995). Theoretically, bats that use higher frequencies (shorter wavelengths) should be better able to detect smaller prey than bats using lower frequencies (longer wavelengths), providing a potential mechanism for dietary niche partitioning (Jones 1995, 1996). Further differences may be effected through atmospheric attenuation, because high frequencies experience greater atmospheric attenuation than low frequencies (Griffin 1971; Pye 1993). As a consequence, high-frequency echolocating bats may experience less signal interference from the background vegetation (O'Shea and Vaughan 1980), but because the operating range of the signal is also reduced, they must be sufficiently manoeuvrable to respond quickly to prey items when they are detected. Greater manoeuvrability should also promote foraging close to vegetation (O'Shea and Vaughan 1980).

Members of the Hipposideridae and Rhinolophidae (superfamily Rhinolophoidea) concentrate most of the energy of their echolocation signal into a very narrow band of frequencies. These long-duration, constant-frequency (CF) signals, combined with a specialized acoustic fovea, are used to detect fluttering insects against the acoustic interference of background vegetation (Schuller and Pollak 1979; Schnitzler 1987). The specializations required for flutter detection greatly constrain intra-individual variation in frequency (Jones 1995) and thus provide a "morphological" measurement that is both relatively stable and ecologically relevant. If competition limits the similarity between syntopic species, then call frequency values should be overdispersed across the total frequency range, and be regularly rather than randomly spaced (MacArthur and Levins 1967; Schoener 1974; Horn and May 1977). Heller and von Helversen (1989) tested these predictions and found that the observed minimal ratio between call frequencies was greater than expected by chance alone, and that the distribution of frequencies was more even than expected from allometric relationships or in communities generated randomly. In the present study, we worked at the same site as Heller and von Helversen (1989). We expanded the guild of rhi-

nolophoid bats to 15 species and replicated their analyses with the full 15-species complement to re-evaluate their suggestion that resource partitioning of frequency bands operates in rhinolophoid bats. In doing so, it became apparent that call frequencies might be less evenly distributed across the total frequency range than previously concluded.

One of the predictions of competition theory is that the more speciose a community, the more niche dimensions will be required to preserve minimal resource overlap between species (Schoener 1974). Thus, it would be unlikely that 15 species could be adequately separated along a single resource dimension (detectable prey size). We therefore extended our analysis to include body size and wing morphology. Body size not only influences the size of prey that can be handled effectively, but also has a major effect on the aerodynamic capabilities of a bat (Norberg and Rayner 1987). Both features affect the use of microhabitats. Numerous studies have demonstrated a functional relationship between foraging strategy, microhabitat use and wing morphology (e.g. O'Shea and Vaughan 1980; McKenzie and Rolfe 1986; Aldridge and Rautenbach 1987; Crome and Richards 1988; McKenzie et al. 1995). The main descriptors of wing morphology are aspect ratio ( $\text{wingspan}^2/\text{wing area}$ ) and wing loading [ $\text{mass} \times g$  (gravitational acceleration)/wing area] (Norberg and Rayner 1987). These parameters influence the energetic cost of flight, flight speed and manoeuvrability. Energetic efficiency increases with aspect ratio, and flight speed is proportional to wing loading, but both are inversely related to manoeuvrability (Norberg and Rayner 1987). Manoeuvrability (the ability to turn in a small space) is of particular relevance to the species considered in the present study, since they forage primarily in the cluttered environment of the forest understorey; species with low wing loading should be able to forage in more structurally complex situations than those with higher wing loading. The parameters selected are thus sensitive to ecological separation along both a food/feeding dimension (in that call frequency relates to detectable prey size) and a microhabitat/locomotor dimension (defined by both wing morphology and call frequency) (McKenzie and Rolfe 1986).

Guild members, by definition, exploit the same resources in a similar way (Root 1967; Simberloff and Dayan 1991). Competitive interactions should be most intense within guilds, and are more likely to produce morphological patterns within guilds than across entire communities (Willig and Moulton 1989). Restricting the analysis to the guild level also minimizes the creation of nonrandom patterns by outlier species (e.g. Schum 1984), and if morphology is phylogenetically constrained, morphological divergence is more likely to reflect differences in resource use resulting from interspecific competition (Findley and Black 1983; Brown and Bowers 1985; Ricklefs and Miles 1994). Guild members in the present study were all members of the same superfamily, thereby reducing the amount of taxonomic information implicit in morphological measurements

(McKenzie and Rolfe 1986). Nonetheless, the guild comprised two families within which were several species groups, and these distinct levels of common ancestry reduced the statistical independence of the species for comparative purposes (Felsenstein 1985, 1988; Pagel and Harvey 1988; Gittleman and Luh 1992; Garland et al. 1992, 1999). There are a number of methods by which phylogenetic effects can be removed from comparative data (Felsenstein 1985; Pagel and Harvey 1988; Losos and Miles 1994; Garland et al. 1999). In the present study we used phylogenetic autocorrelation analysis (Cheverud et al. 1985; Gittleman and Kot 1990) to partition the variables into phylogenetic and specific components.

As in many communities, a few species in the guild were very common while most were relatively rare. We might predict that interspecific competition should be most intense between the more abundant species, and that these species should consequently show the greatest degree of morphological adjustment to avoid overlap. While it is possible that rarity was simply a consequence of differential susceptibility to the sampling technique (harp traps), we assumed that this was not the case, and attempted to incorporate a measure of relative abundance into the analysis.

The species in this study constitute a closely related guild of bats sampled for an extended period from an actual, environmentally and compositionally stable community in which both food/feeding and microhabitat/locomotory dimensions were considered. Conditions were excellent for detecting deterministic community patterns. In the present study, we replicate Heller and von Helversen's (1989) analyses of frequency band distribution with the full 15-species complement. We then adopt a multivariate approach, incorporating measures of body mass and wing morphology, in which we control for phylogenetic effects; and finally test the impact of the relative abundance of species on patterns of community structure.

## Materials and methods

### Study site, species capture and parameters measured

The study was conducted between January 1996 and March 1997 at Kuala Lompat Research Station on the eastern edge of the Krau Wildlife Reserve (formerly Krau Game Reserve), Pahang, Peninsular Malaysia (3°43'N, 102°10'E). The reserve encompasses 53,014 ha and includes six distinct floristic zones. Kuala Lompat is at approximately 50 m above sea level, located at the junction of the rivers Lompat and Krau in lowland evergreen dipterocarp forest that occurs below 300 m. The dominant tree species include *Dipterocarpus cornutus*, *Dipterocarpus baudii*, *Hopea sangal*, *Shorea acuminata* and *Shorea ovalis* (Caldecott et al. 1986), but Kuala Lompat is relatively rich in large Leguminosae and poor in dipterocarps (Raemakers et al. 1980). A detailed description of the Krau Wildlife Reserve is given in Caldecott et al. (1986) and of Kuala Lompat in Raemakers et al. (1980).

Bats were captured in the forest understorey using four-bank harp traps (Francis 1989) positioned across trails cut originally 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) and were excluded from the study, as were pregnant females, to avoid skewing the wing-loading estimates for each species based on differences in body mass. Adult individuals were weighed using a Pesola scale ( $\pm 0.1$  g) and the length of the forearm was measured with dial calipers ( $\pm 0.1$  mm).

Echolocation calls were recorded with an Ultra Sound Advice (USA) S-25 bat detector linked to a USA S-350 digital signal processor sampling at 400 kHz. Animals were held in the hand approximately 30 cm from the microphone for recording. Time-expanded (10 $\times$  and 20 $\times$ ) 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. Call parameters were measured from six calls of high signal-to-noise ratio for each individual. Power spectra were used to derive the peak frequency (kHz) for each call.

Wing tracings were made by placing the ventral side of the bat on paper, extending one wing, the uropatagium and half the body, and drawing around it. Wingspan and wing area were derived from the tracings. We followed Norberg and Rayner (1987) in our definition of these variables.

Small sample sizes for some species precluded us from treating each sex separately, and preliminary analyses (ANOVA) detected only limited sexual dimorphism in the most common species. Average values were therefore used for each species.

### "Frequency ratios" in syntopic species

In order to examine the significance of the spacing of call frequencies that they observed, Heller and von Helversen (1989) applied three tests to the ratios of the call frequencies of neighbouring species; tests that we repeated with the full 15-species complement. First, we tested whether the minimal ratio was larger than might be expected if the total frequency range was divided randomly, using Simberloff and Boecklen's (1981) test. To avoid the assumption of purely random division, we then tested whether the distribution of the observed frequency ratios differed from those expected from forearm measurements. For this test, Heller and von Helversen (1989) first described the relationship between forearm length and call frequency for 48 rhinolophoid species for which data were available, and then used the regression equation for each of the two genera to predict call frequencies for the 12 species at Kuala Lompat based on their forearm lengths. We expanded the species pool used to derive the regression equations from 46 to 56 species, because additional information on the echolocation calls of rhinolophids and hipposiderids is now available. We also employed frequency values from this and more recent studies in place of previous values [Table 1 lists the additions and revisions to the original list given in Heller and von Helversen (1989) from which all other data were drawn for the regressions]. We then followed their final procedure and generated hypothetical communities by drawing 15 species randomly, without replacement, from the pool of the known recorded species (in this case 56 rather than 48).

### Multivariate comparisons of 15 syntopic species

In the present study, we expanded Heller and von Helversen's analysis to include body mass, wingspan and wing area. Our analysis was a three-step process in which we: (1) removed the phylogenetic effect from all variables; (2) plotted the species residuals in principal component space and derived Euclidean distances between all species; and (3) compared these distances with those between species in communities that were generated randomly within the principal component space.

We used the program "P.A." (Luh et al. 1995) to fit phylogenetic autocorrelations. In the absence of a phylogeny that includes all species in this study, we used three taxonomic ranks: species

**Table 1** Call and wing parameters for species used in the present study. Species groups after Corbet and Hill (1992) and Koopman (1994) (b) *Hipposideros bicolor*, (d) *Hipposideros diadema*, (s) *Hipposideros speoris*, (f) *Rhinolophus ferrumquinum*, (h) *Rhinolophus hipposideros*, (t) *Rhinolophus trifolius* (formerly *Rhinolophus philippinensis*), (p) *Rhinolophus pusillus*

Species (species group)	Call frequency kHz (n)	Forearm length mm (n)	Body mass kg (n)	Wingspan m (n)	Wing area m <sup>2</sup> (n)	Reference
<i>Hipposideros</i>						
<i>H. ater</i> <sup>b</sup> (India)	166.0	36.0				Jones et al. (1994)
<i>H. bicolor</i> <sup>a</sup> (b)	130.9 (14)	45.5 (14)	0.0081 (5)	0.282 (5)	0.0143 (5)	This study
<i>H. sp.</i> <sup>a,b</sup> (b)	141.8 (20)	43.6 (19)	0.0083 (16)	0.272 (16)	0.0124 (16)	This study
<i>H. caffer</i> <sup>b</sup>	144.1	46.0				Jones et al. (1993)
<i>H. commersonii</i> <sup>c</sup> (d)	63.5	107.0	0.0890	0.654	0.0556	Norberg and Rayner (1987)
<i>H. cervinus</i> <sup>a</sup> (b)	125.5 (49)	49.5 (48)	0.0102 (31)	0.301 (31)	0.0141 (31)	This study
<i>H. cineraceus</i> <sup>a</sup> (b)	144.0 (5)	38.4 (4)	0.0057 (7)	0.244 (7)	0.0107 (7)	This study
<i>H. diadema</i> <sup>a</sup> (d)	60.4 (16)	84.9 (17)	0.0469 (26)	0.504 (26)	0.0389 (26)	This study
<i>H. fulvus</i> <sup>b</sup>	157.0	39.0				Jones et al. (1994)
<i>H. larvatus</i> <sup>a,b</sup> (s)	100.0 (5)	58.5 (5)	0.0173 (10)	0.342 (10)	0.0186 (10)	This study
<i>H. lyeli</i> <sup>b</sup>	72.5	79.3				Robinson (1996)
<i>H. ridleyi</i> <sup>a</sup> (b)	61.9 (8)	48.4 (8)	0.0092 (11)	0.295 (11)	0.0097 (11)	This study
<i>H. ruber</i> <sup>b</sup>	133.0	48.5				Jones et al. (1993)
<i>H. sabanus</i> <sup>a</sup> (b)	195.1(2)	36.9 (2)	0.0048 (3)	0.227 (3)	0.0094 (3)	This study
<i>H. speoris</i> <sup>b</sup>	138.0	51.0				Jones et al. (1994)
<i>Rhinolophus</i>						
<i>R. acuminatus</i> <sup>b</sup>	80.0	48.2				Robinson (1996)
<i>R. affinis</i> <sup>a</sup> (f)	77.6 (4)	49.3 (4)	0.0138 (6)	0.312 (6)	0.0120 (6)	This study
<i>R. coelophyllus</i> <sup>b</sup>	77.5	44.4				Robinson (1996)
<i>R. hildebrandtii</i> <sup>c</sup>	46.0	65.0	0.0243	0.407	0.0243	Norberg and Rayner (1987)
<i>R. hipposideros</i> <sup>c</sup> (h)	110.0	40.0	0.0068	0.231	0.0094	Norberg and Rayner (1987)
<i>R. landeri</i> <sup>c</sup> (f)	121.0	42.5	0.0090	0.290	0.0132	Norberg and Rayner (1987)
<i>R. luctus</i> <sup>a</sup> (t)	42.0 (1)	63.4 (1)	0.0263 (1)	0.396 (1)	0.0283 (1)	This study
<i>R. macrotis</i> <sup>a</sup> (t)	48.0 (1)	45.5 (1)	0.0075 (1)	0.284 (1)	0.0139 (1)	This study
<i>R. malayanus</i> <sup>b</sup>	75.0	40.9				Robinson (1996)
<i>R. pearsonii</i> <sup>b</sup>	65.0	50.0				Robinson (1996)
<i>R. pusillus</i> <sup>b</sup>	92.5	38.3				Robinson (1996)
<i>R. refulgens</i> <sup>a</sup> (p)	99.7 (45)	40.5 (38)	0.0063 (34)	0.245 (34)	0.0103 (34)	This study
<i>R. sedulus</i> <sup>a</sup> (t)	66.8 (9)	40.3 (7)	0.0077 (13)	0.260 (13)	0.0125 (13)	This study
<i>R. stheno</i> <sup>a</sup> (f)	86.1 (59)	48.8 (58)	0.0089 (41)	0.286 (41)	0.0137 (41)	This study
<i>R. trifolius</i> <sup>a</sup> (t)	53.3 (26)	50.9 (22)	0.0139 (32)	0.324 (32)	0.0188 (32)	This study

<sup>a</sup> Species captured at Kuala Lumpur

<sup>b</sup> Additions or revisions to species listed by Heller and von Helversen (1989) used in the regression analyses of call frequency on forearm length

<sup>c</sup> Taxonomic extremes included in the principal components analysis

group, genus and superfamily. We assigned the species to species groups following Corbet and Hill (1992) and Koopman (1994) (see Table 1), and used a maximum-likelihood power-law autoregressive model to partition the log-transformed variables into a phylogenetic component and a specific component.

Principal component analysis (PCA) was conducted on the species residuals of the four variables, with components calculated from the covariance matrix to preserve the original positions of species in multivariate space and to ensure that factor loadings could be interpreted as ratios (Ricklefs and Travis 1980; Ricklefs and Miles 1994). For comparative purposes, we also performed PCA on the entire trait values. Several of the species at Kuala Lumpur represent the morphological extremes for the two genera in terms of the variables measured (i.e. *Rhinolophus luctus* – largest body mass and wing area, lowest call frequency; *Hipposideros diadema* – lowest call frequency; *Hipposideros sabanus* – highest call frequency and smallest body mass, wingspan and wing area), but to ensure that the morphological space was fully defined by the true evolutionary endpoints of each genus we included an additional four species in the PCA: *Hipposideros commersonii* (largest body mass, wingspan and wing area), *Rhinolophus landeri* (highest call frequency), *Rhinolophus hildebrandtii* (largest wingspan), *Rhinolophus hipposideros* (smallest wingspan and wing area) (Table 1). These species represent generic extremes for which data for each of the four variables were available for analysis. This avoids the potential bias towards even spacing of

species in morphospace that can occur if the actual range of possible morphological variables is greater than that used to define the morphospace, as may be the case if species in the assemblage are used to set the endpoints of morphological space (Simberloff and Boecklen 1981; Tonkyn and Cole 1986; Gotelli and Graves 1996).

Estimates of the morphological separation between each species pair were derived from the matrices of Euclidean distance (from principal component scores). We followed Arita (1997) in producing a series of means and SDs for each order of nearest neighbours. The first-order mean is the mean distance between each species in the community and its nearest neighbour, and equates to nearest-neighbour distance used in previous studies as a measure of species packing (Findley 1973; Ricklefs and Travis 1980; Travis and Ricklefs 1983; Arita 1997). The second-order mean is between each species and its second-nearest neighbour. Thus, for the guild of 15 species, there are 14 nearest-neighbour order means. Means that are higher than those from communities assembled at random suggest morphological displacement between species (Arita 1997). SDs that are lower than those of random assemblages suggest that species are distributed regularly rather than randomly in morphological space (Ricklefs and Travis 1980; Arita 1997).

Generating random communities was complicated by the paucity of data for the wing morphology of the species available for analysis. This meant that it was not possible to assemble random

communities by drawing from the species pool. Instead, we followed Ricklefs and Travis (1980) and created guilds of 15 “synthetic species” within the principal component space of the original 19 taxa. To produce factor scores for each synthetic species, we multiplied the square root of the eigenvalue (the SD) of each of the four components from the real-species PCA by a random normal deviate (Ricklefs and Travis 1980). We generated 100 communities of 15 synthetic species, and for each of these we derived the mean neighbour values and SD for each neighbour order. We used two-tailed probability tests to determine whether the observed mean value and SD for each neighbour order differed from those of the random communities.

#### Fifteen syntopic species adjusted for relative abundance

First we calculated the probability (interspecific encounter probability, IEP) that two species ( $k$  and  $j$ ) would encounter one another based solely on the numbers of each species relative to the total of all species captured ( $N$ ):

$$IEP_{kj} = \left( \frac{N_k}{N} \right) \left( \frac{N_j}{N} \right) \quad (1)$$

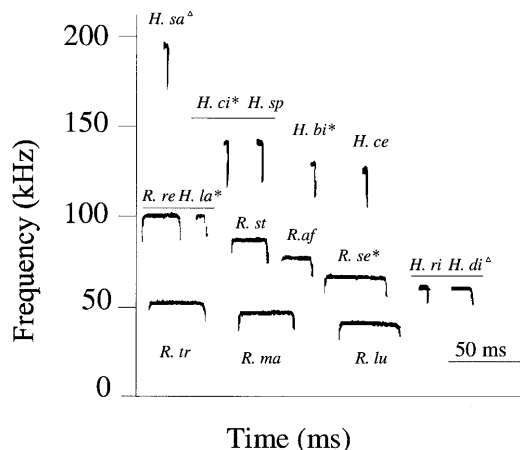
This measure assumes that the species encounter each other randomly, but in fact 21 of the 105 species pairs were positively spatially correlated (Spearman correlation coefficients for species pairs based on nightly captures significant at  $\alpha=0.05$ ). We corrected IEP by the correlation coefficient [Spearman's rho ( $R$ )] for each species pair, and derived an adjusted Euclidean distance for each species as follows:

$$D'_{jk} = \frac{D_{jk}}{(IEP_{jk})(R_{jk} + 1)}, \quad (2)$$

where  $D_{jk}$  is the Euclidean distance between species  $j$  and  $k$  derived from the principal component space. The unit addition to  $R$  avoided negative values and ensured that negative associations between species had a lesser impact on  $D'$  than did positive associations. If the organization of this guild depends on competition, common species, particularly those that are spatially correlated, should be separated by greater morphological distances. A shift in the distribution of  $D'$  towards large values (compared to a random distribution) suggests two situations that would reduce competitive interactions: (1) morphologically similar species may be rare and/or negatively associated; and (2) abundant/positively associated species may be morphologically divergent (and thus have large values for  $D$ ). To generate random communities, we followed the previous procedure to create synthetic species, and then generated relative abundances for each community randomly from a log-normal distribution, defined by the mean and SD of the observed community. Similarly, random values for  $R$  were generated from a normal distribution using the mean and SD of the original distribution.

## Results

The 15 species captured at Krau Wildlife Reserve included three additions to those studied by Heller and von Helversen (1989) (*Hipposideros larvatus*, *Hipposideros cineraceus*, *Rhinolophus sedulus*). We also included a fourth species, *Hipposideros* sp., which is potentially a cryptic species with *Hipposideros bicolor*; these two species differed in their call frequencies by approximately 11 kHz, with a silent band between them of 6 kHz. We were unable to confirm the presence of *Hipposideros armiger*, and therefore excluded it from our analysis. We note that Heller and von Helversen (1989) did not cap-



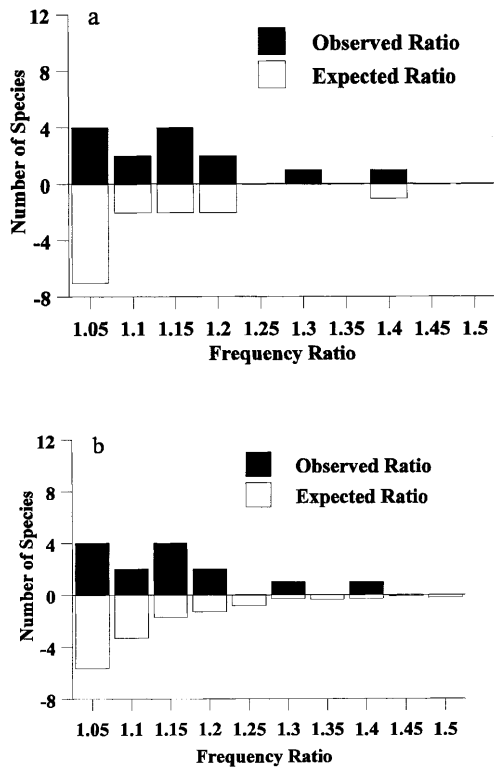
**Fig. 1** Echolocation calls of 15 syntopic Rhinolophoidea from Kuala Lumpur, Krau Wildlife Reserve, Malaysia. Species joined by *underscores* do not differ in peak frequency. \* Additions to species in Heller and von Helversen (1989),  $\Delta$  frequency value differed by  $>5$  kHz from that given by Heller and von Helversen (1989), *H. bi* *Hipposideros bicolor*, *H. ci* *Hipposideros cineraceus*, *H. ce* *Hipposideros cervinus*, *H. di* *Hipposideros diadema*, *H. la* *Hipposideros larvatus*, *H. ri* *Hipposideros ridleyi*, *H. sa* *Hipposideros sabanus*, *H. sp* *Hipposideros* sp., *R. af* *Rhinolophus affinis*, *R. lu* *Rhinolophus luctus*, *R. ma* *Rhinolophus macrotis*, *R. re* *Rhinolophus refulgens*, *R. se* *Rhinolophus sedulus*, *R. st* *Rhinolophus stheno*, *R. tr* *Rhinolophus trifoliatus*

ture this species either but included it in their study based on records in Medway and Wells (1971).

The 15 species captured at Kuala Lumpur all produce echolocation calls dominated by a relatively long CF component typical of the Hipposideridae and Rhinolophidae (Fig. 1, Table 1). Frequencies were similar to those reported by Heller and von Helversen (1989), although two of the species recorded at Templar Park by Heller and von Helversen (1989) differed by 5 kHz from those we recorded at Kuala Lumpur (*H. diadema*, *H. sabanus*). It is apparent from Fig. 1 that the additional species captured in this study have influenced the evenness of the distribution of the call frequencies. Overall, species differed in call frequency (ANOVA;  $F_{14,285}=11,166$ ;  $P<0.0001$ ), but post-hoc tests [the Ryan-Einot-Gabriel-Welsch multiple range test (Day and Quinn 1989)] revealed that three species pairs could not be distinguished from one another by their call frequencies: *Hipposideros* sp. and *H. cineraceus*; *H. larvatus* and *Rhinolophus refulgens*; and *Hipposideros ridleyi* and *H. diadema*.

#### Frequency ratios in syntopic species

In contrast to the findings of Heller and von Helversen (1989), the minimal ratio (1.003) was not significantly greater than would result from a random division of the frequency range by 15 species [Simberloff and Boecklen's (1981) test,  $P>0.1$ ]. Heller and von Helversen (1989) found that while ratios representing  $<5\%$  divergence were lacking from the observed distribution, the distribution predicted from forearm lengths showed no

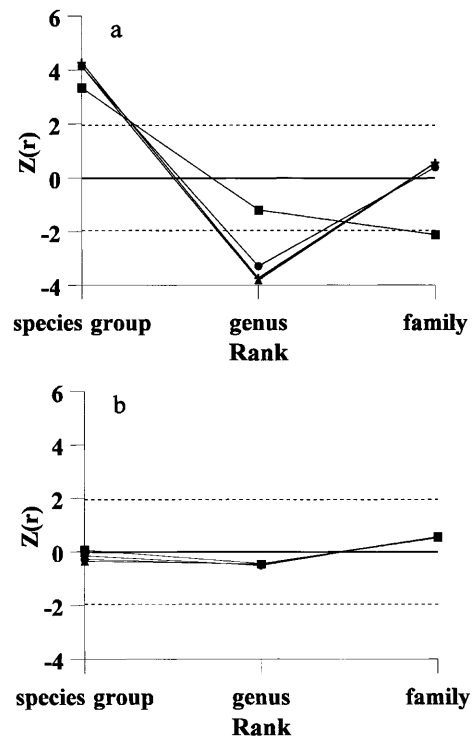


**Fig. 2a,b** Distribution of the call frequency ratios of an observed guild of 15 Malaysian bat species compared to two expected distributions. **a** Expected distribution estimated from forearm length, derived from the revised relationships between call frequency and forearm: *Hipposideros* regression line,  $\log$  frequency (kHz) =  $3.60 - 0.91 \log$  forearm (mm) ( $P < 0.001$ ,  $r = -0.77$ ); *Rhinolophus*,  $\log$  frequency (kHz) =  $4.25 - 1.42 \log$  forearm (mm) ( $P < 0.001$ ,  $r = -0.60$ ). **b** Expected distribution estimated from 100 random samples of 15 species from the 56-species pool. The observed distribution did not avoid small ratios, and in neither case did it differ from the expected distribution

avoidance of small frequency ratios and differed significantly from the observed distribution. In contrast to their findings, our observed distribution showed no avoidance of small frequency ratios and did not differ significantly from our expected distribution ( $\chi^2 = 2.57$ ,  $df = 1$ ,  $P > 0.25$ ) (Fig. 2a). Similarly, and again in contrast to the 12-species analysis of Heller and von Helversen (1989), we found no evidence that the observed distribution differed from that derived by drawing randomly from the 56-species pool ( $\chi^2 = 0.79$ ,  $df = 1$ ,  $P > 0.5$ ) (Fig. 2b).

#### Multivariate comparisons of 15 syntopic species

Although a number of species pairs used similar, if not indistinguishable, frequency bands, it was apparent that these species might be separated along other resource dimensions. For example, *H. larvatus* and *R. refulgens* used the same frequency band (ca. 100 kHz), but differed greatly in size (*H. larvatus*, 17.0 g; *R. refulgens*, 6.3 g), as did *H. diadema* (60.4 kHz; 46.9 g) and *H. ridleyi* (61.9 kHz; 9.2 g) and, to a lesser extent, *Hipposideros* sp. (141.8 kHz; 8.3 g) and *H. cineraceus* (144.0 kHz; 5.7 g).



**Fig. 3 a** Significance tests of the phylogenetic correlograms of call frequency (■), body mass (▲), wingspan (●) and wing area (+) for the 19 species of bats.  $Z(r)$  represents the randomized significance test in which Moran's  $I$  is compared to the values that are sampled from the  $n!$  permutations of the observed phenotypic trait values. Phylogenetic autocorrelation is significant at the 0.05 level if  $Z(r) > 1.96$  (dashed lines represent the 95% confidence intervals about zero autocorrelation). There are significant positive autocorrelations within the species groups and significant negative correlations between groups (within genera) for all variables. Call frequency also exhibits a significant negative correlation between the genera. **b** Significance tests of the phylogenetic correlograms of the specific component of call frequency, body mass, wingspan and wing area derived from a maximum-likelihood power-law autoregressive model. All significant correlation is removed

All four variables exhibited phylogenetic correlation (Fig. 3a, Table 2). There were significant positive autocorrelations within the species groups and significant negative correlations between species groups (within genera) for all variables. The maximum-likelihood power-law model removed all significant correlations (Fig. 3b) (Gittleman and Kot 1990; Luh et al. 1995).

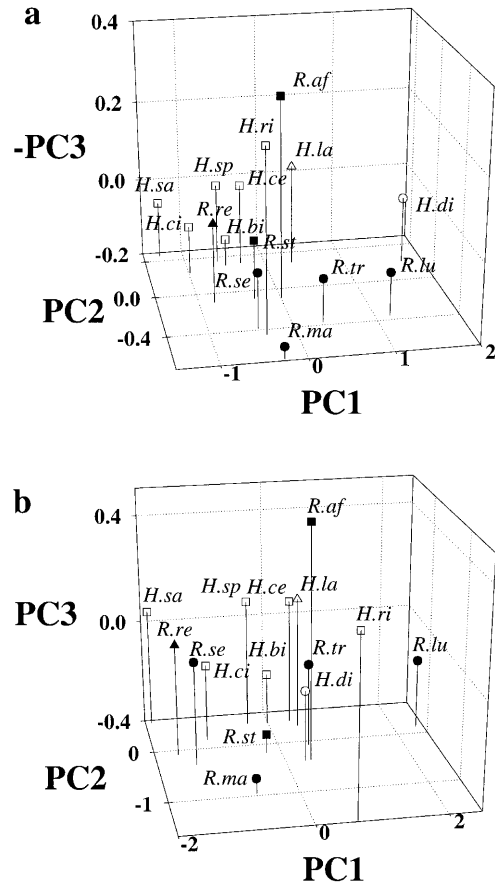
Heller and Volleth (1995) suggested that body size might be less important than wing dimensions in structuring bat communities; but this was not found to be the case in the present study. In the PCA using the species residuals, the first principal component is essentially a measure of size, with a large positive loading on body mass, wingspan and wing area, and accounted for 82% of the variance in multivariate space (Table 3). Sixteen percent of the variance was associated with the second component, which was dominated by call frequency. With a high loading for body mass and high negative loading for wing area, the third principal component relates to wing loading,

**Table 2** Statistics from the phylogenetic autocorrelation analysis of call frequency, body mass, wing span and wing area.  $R^2$  is the proportion of the total phenotypic variance that is due to phylogeny,  $\rho$  is the correlation between the purely phylogenetic value of individuals and the total phenotypic value,  $\alpha$  is the variable exponent relating taxonomic distance between individuals and the weighting function in predicting phenotypes

Variable	$R^2$	$\rho$	$\alpha$
Call frequency	0.41	0.53	4.8
Body mass	0.48	0.57	5.1
Wingspan	0.49	0.56	7.2
Wing area	0.53	0.59	7.0

independent of body size (the effect of which is removed by the first component). Species with a large value for this component have a relatively high wing loading and would be predicted to be less manoeuvrable than species with low values. Likewise, the fourth component essentially describes aspect ratio (high positive loading on wingspan, and high negative loading for wing area). Although the third and fourth components account for a small proportion of the total variance, they are ecologically relevant measures and were consequently retained in subsequent analyses (Ricklefs and Miles 1994). The principal components derived using entire the trait values were similar to those resulting from the species-residual analysis (Table 3), although the third component related inversely to wing loading.

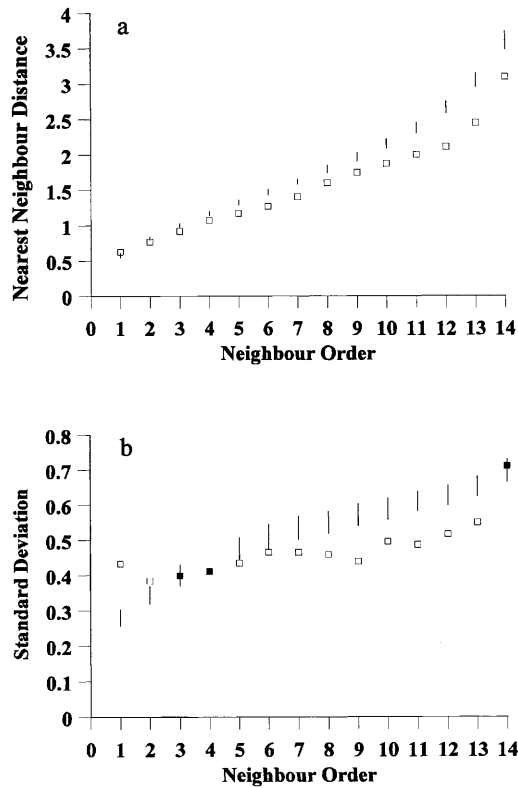
The inclusion of these additional variables greatly improved the separation of the 15 species (Fig. 4a,b). Species pairs that overlapped in call frequency are separated in multivariate space (e.g. *R. refulgens* and *H. larvatus*; *H. cineraceus* and *H. sp.*; *H. ridleyi* and *H. diadema*). Removing the phylogenetic effect improved the separation of species within the same species groups (compare Figs. 4a,b) and reduced the separation between the species groups and genera. In fact, a number of species from different species groups occupy very similar positions in phylogeny-free multivariate space, particularly *Hipposideros cervinus* and *H. larvatus* and, to a lesser extent *R. sedulus* and *H. cineraceus*, and *H. diadema* and *R. trifoliatus*, perhaps indicative of some degree of ecological



**Fig 4a,b** Distribution of 15 syntopic Rhinolophoidea from Kuala Lumpur in principal component space derived from call frequency, body mass, wingspan and wing area. **a** Principal component space described by the entire trait values. **b** Principal component space described by the species residuals. In both cases, principal component (PC) 1 is primarily a measure of size, PC 2 is dominated by call frequency and PC 3 describes size-independent wing loading. PC 3 for the full trait principal component analysis relates inversely to wing loading, so the PC 3 components are plotted with a reverse sign to assist visual comparison with the species residual PC 3. ■ *Rhinolophus ferrumiquinum* group; ● *R. trifoliatus* group; ▲ *R. pusillus* group; □ *Hipposideros bicolor* group; ○ *H. diadema* group; △ *H. speoris* group. For other abbreviations, see Fig. 1

**Table 3** Principal components analysis of call frequency, body mass, wingspan and wing area using species residuals and the full phenotypic trait value. PC Principal component

Eigenvectors	Species residuals				Phenotypic value			
	PC 1	PC 2	PC 3	PC 4	PC 1	PC 2	PC 3	PC 4
Variable ( $\log_{10}$ )								
Call frequency	-0.442	0.872	0.185	0.102	-0.307	0.951	-0.020	0.005
Body mass	0.535	0.197	0.639	-0.517	0.768	0.238	-0.529	-0.273
Wingspan	0.541	0.146	0.159	0.813	0.274	0.082	-0.059	0.957
Wing area	0.475	0.425	-0.729	-0.249	0.491	0.177	0.847	-0.103
Eigenvalue	1.806	0.351	0.042	0.010	0.949	0.122	0.014	0.001
SD	1.340	0.593	0.206	0.098	0.974	0.349	0.118	0.032
Variance explained								
Percent	0.818	0.159	0.019	0.004	0.874	0.112	0.013	0.001
Cumulative	0.818	0.976	0.996	1.000	0.874	0.986	0.999	1.000
Interpretation	Size	Fre- quency	Wing loading	Aspect ratio	Size	Fre- quency	Wing loading	Aspect ratio



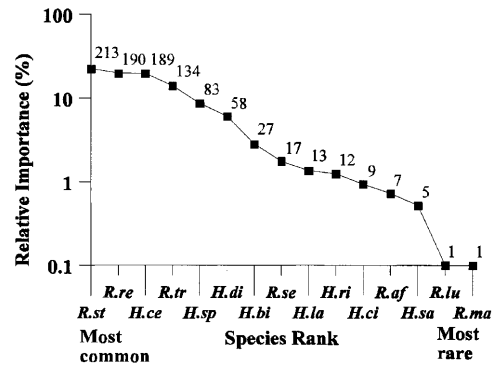
**Fig. 5** **a** Mean Euclidean distances for 14 nearest-neighbour orders. *Squares* show values for the observed guild, *vertical lines* are the 95% confidence interval for expected values from a random 100 communities of synthetic species. *Filled squares* indicate that the mean for the observed guild falls within the 95% confidence interval of the distribution of expected means; mean values with *open squares* differ significantly from the expected distribution. The first-order mean was significantly greater than expected; higher-order means were less than expected. **b** SDs of mean neighbour distances for 14 nearest-neighbour orders. Lower-order SDs were significantly greater than expected, higher-order means (with the exception of the fourteenth order) were less than expected

equivalence or convergence between phylogenetically disparate species.

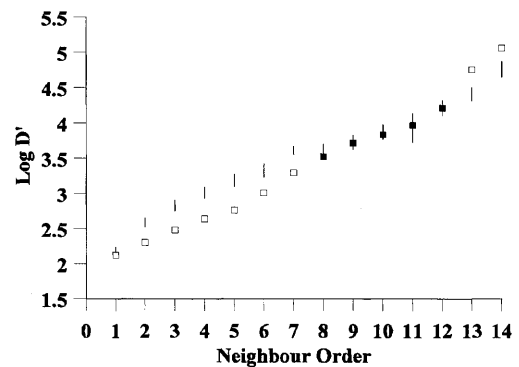
The first-order mean neighbour distances were significantly greater than those of the random communities ( $P < 0.001$ ; Fig. 5a), strongly suggesting that there is morphological displacement between species that are most similar to one another. Mean neighbour distances for all other neighbour orders were in fact less than expected. SDs for the first two neighbour orders were greater than expected, those of the third and fourth neighbour orders did not differ from those of the random community, but orders 6–13 were less than expected (Fig. 5b). Thus the higher orders exhibited smaller inter-specific separation, but were more evenly spaced than in the randomly generated communities.

#### Fifteen syntopic species adjusted for relative abundance

The relative abundance of species captured at Kuala Lompat approximated a log-normal distribution (Fig. 6).



**Fig. 6** Relationship between relative importance of species and their rank in the guild. *Data labels* indicate the number of individuals of each species captured at Kuala Lompat, Krau Wildlife Reserve. For abbreviations, see Fig. 1



**Fig. 7** Adjusted mean Euclidean distances ( $D'$ ;  $\log_{10}$  transformed) for 14 nearest-neighbour orders. *Squares* show values for the observed guild, *vertical lines* are the 95% confidence interval for expected values from a random 100 communities of synthetic species. *Filled squares* indicate that the mean for the observed guild falls within the 95% confidence interval of the distribution of expected means; mean values with *open squares* differ significantly from the expected distribution. Adjusted means for neighbour orders 2–5 of the actual guild were significantly less than generated from random communities

Contrary to our expectations, the adjusted mean neighbour distances were smaller than those from random communities for the first to the seventh orders (Fig. 7), strongly suggesting that morphological displacement was not influenced by the abundance of each species. The lower orders (the most similar species) should either have been less abundant/spatially correlated or showed a greater degree of morphological difference. Thus, we have no evidence that abundant, spatially correlated species reduce interspecific overlap in morphological space. SDs for each order except the tenth were all significantly greater ( $P < 0.001$ ) than those of the random communities, suggesting a clumped rather than regular or even spacing of species.

## Discussion

The guild of Rhinolophoidea at Kuala Lompat exhibited ecomorphological structure that was nonrandom in phylogeny-free multivariate morphospace. We found evidence of morphological overdispersion of the most similar species, which suggests niche differentiation in response to competition. The trait underdispersion exhibited by the higher neighbour orders is possibly a reflection of the ecological constraints experienced by the species (Wieher and Keddy 1995); there may be a limited set of parameter combinations that constitute an ecologically viable bat, particularly for species foraging in the cluttered environment of the forest interior. For example, the limited operating range of high call frequencies necessitates manoeuvrable flight for prey capture (Barclay and Brigham 1991). Since manoeuvrability relates inversely to wing loading (Norberg and Rayner 1987), high call frequencies are unlikely to be found in combination with high wing loading. Similarly, smaller bats may need higher call frequencies to detect prey items that are small enough for them to handle. Despite this underdispersion, many of the higher orders (fifth–thirteenth) were evenly rather than randomly spaced, or clumped in morphospace, suggesting that, given the environmental constraints on morphology, species in this guild do experience limits to their similarity – a possible response to diffuse competition (Arita 1997).

These findings suggest that competitive interactions, to some extent, determine community structure in this guild. This differs from a number of previous studies of bat communities, but in many respects we were presented with theoretically ideal conditions for detecting morphological consequences of competition. We studied an actual, localized community, rather than a dispersed fauna derived from distribution maps (e.g. Findley and Black 1983; Schum 1984), and focussed on a single guild from which we removed much of the phylogenetic effect. The use of the species residuals rather than overall trait values did not greatly influence the description of morphological space, but did influence species' distribution patterns within it. In addition, the age and temporal stability of rainforest habitats minimize both the seasonal variability in community species composition and the likelihood that species represent recent invasions; deterministic guilds are predicted if environmental conditions are stable and predictable (Sale 1977; Crossman et al. 1982).

Finally, consideration should be given to the choice of morphological characters analysed, since this frequently determines the patterns that are observed (Dayan and Simberloff 1998). It seems likely that bat communities parallel those of other insectivorous mammal and bird communities, rather than mammalian carnivore guilds, in exhibiting maximum separation along microhabitat/locomotor morphology dimensions rather than dimensions of trophic structure (McKenzie and Rolfe 1986; Dayan and Simberloff 1998). McKenzie and Rolfe (1986) demonstrated the deterministic structure of guilds of insectivorous bats in Australian mangrove communities using

wing morphology (i.e. locomotor morphology), but studies that have focussed on skull parameters (i.e. feeding morphology) report only stochastically assembled communities (e.g. Willig and Moulton 1989; Arita 1997; but see Yom-Tov 1993). Species in the present study overlapped along the original trophic dimensions (echolocation call frequency), but when microhabitat/locomotory dimensions (body size and wing morphology) were considered, deterministic patterns emerged. Birds, bats and, because of the arboreal habits of many species, insectivores, essentially forage in three-dimensional space, and this may facilitate spatial niche shifts. In contrast, the two-dimensional space in which mammalian carnivores operate may mean that adjustments along the trophic-structure dimension are more readily achieved.

We have assumed here that the effect of interspecific competition from other bat families is negligible, but the forest at Kuala Lompat also supports a diverse group of vespertilionid bats, including seven species of Kerivoulineae and four species of Murinineae. Although these bats are smaller than most of the rhinolophoids (body mass 2.5–10.0 g), it is still possible that some of the largest vespertilionids overlap along locomotory axes with the smallest rhinolophoids. However, echolocation signals in the Kerivoulineae and Murinineae differ substantially from the rhinolophoids; clutter resistance is achieved by the use of extremely broad-band frequency-modulated sweeps of short duration (Kingston et al. 1999) and it is likely that these bats primarily glean insects from foliage rather than capture prey in the aerial mode as do most rhinolophids (Schnitzler and Kalko 1998).

Although we found evidence that morphology was influenced by the distance to the nearest neighbour, we found no evidence that morphological differences were influenced by relative species' abundances. Common and spatially associated species exhibited less morphological avoidance of each other than predicted, and than did rare species. Similarly, other studies have failed to link relative abundance to morphological displacement (Weins and Rotenberry 1980; James and Boecklen 1984; Findley and Findley 1985), but our study differs from these in finding evidence of morphological displacement between similar species and even spacing. Perhaps we are glimpsing a "ghost of competition past" (Connell 1980); competitive interactions may have influenced morphology in the past, but morphological/ecological separation is now sufficient that species' populations are effectively independent of one another.

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