

Habitat structure, wing morphology, and the vertical stratification of Malaysian fruit bats (Megachiroptera: Pteropodidae)

Robert Hodgkison^{*1}, Sharon T. Balding^{*}, Akbar Zubaid[†] and Thomas H. Kunz[‡]

^{*} School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK

[†] Department of Zoology, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor, Malaysia

[‡] Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, Massachusetts 02215, USA

(Accepted 11 January 2004)

Abstract: This study investigated the vertical stratification of Old World fruit bats (Chiroptera: Pteropodidae) in relation to habitat structure and wing morphology, in a lowland Malaysian rain forest. In total, 352 fruit bats of eight species were captured within the subcanopy of the structurally complex old-growth forest during 72 306 m² mist net hours of sampling. Fruit bat species that were grouped in relation to capture height were also grouped in relation to wing morphology – with those species predicted to have more manoeuvrable flight (i.e. lower wing-loadings and lower aspect-ratios) captured in increasingly cluttered airspaces. Thus, small differences in wing morphology are likely to be ecologically significant to the vertical stratification of bats. Hence, habitat heterogeneity may be a key factor promoting fruit bat species diversity in old-growth palaeotropical forests.

Key Words: Chiroptera, habitat partitioning, Pteropodidae, rain forest, vertical stratification, wing morphology

INTRODUCTION

Vertical stratification has long been recognized within tropical forests, with well-documented examples among birds (Bell 1982, Pearson 1971, 1975; Roth 1976), bats (Bernard 2001, Bonaccorso 1979, Cosson 1995, Francis 1994, Ingle 1993, Kalko & Handley 2001, Zubaid 1994), and squirrels (Emmons 1980). This partitioning is often believed to relate to spatial heterogeneity in forest structure, which promotes species diversity through adaptations in body size and morphology (e.g. wings and limbs) (Schoener 1986). However, in the case of Old World fruit bats (Chiroptera: Pteropodidae), the functional link between morphology and microhabitat use has yet to be quantitatively tested in the field. Thus, the influence of habitat structure on the maintenance of fruit bat species diversity is poorly understood.

The aim of this study is to investigate the vertical stratification of fruit bats (Chiroptera: Pteropodidae) in a lowland Malaysian rain forest, and to test the hypothesis that fruit bats partition this habitat in relation to wing morphology. Based on the mechanical and aerodynamic theories of flight (Norberg & Rayner 1987), performance

testing (Stockwell 2001), and field observations of bats described by other researchers (Heideman & Heaney 1989, Kitchener *et al.* 1990, McKenzie *et al.* 1995, Richards 1995, Start 1974, Uzzurum 1995) we predict that small species of fruit bat, with short, broad wings will be captured in cluttered habitats below the forest canopy, and that large species with long, narrow wings, will be active in uncluttered habitats within the airspace above. However, due to the structural complexity of lowland forests (Richards 1983), coupled with the morphological variation in fruit bat wings (Norberg & Rayner 1987), we suggest that further sub-divisions may also be possible. Hence, in the present study, we describe habitat use by fruit bats in relation to the distribution of vegetation clutter throughout the forest profile.

STUDY SITE AND METHODS

Study site

This study was conducted at Kuala Lompat (3°43' N, 102° 17' E), within the Krau Wildlife Reserve, Pahang, Peninsular Malaysia during two 12-mo field seasons, between May 1997 and November 1999. Some additional data were also collected during a pilot project in 1996.

¹ Corresponding author. Email: rhodgkison@hotmail.com

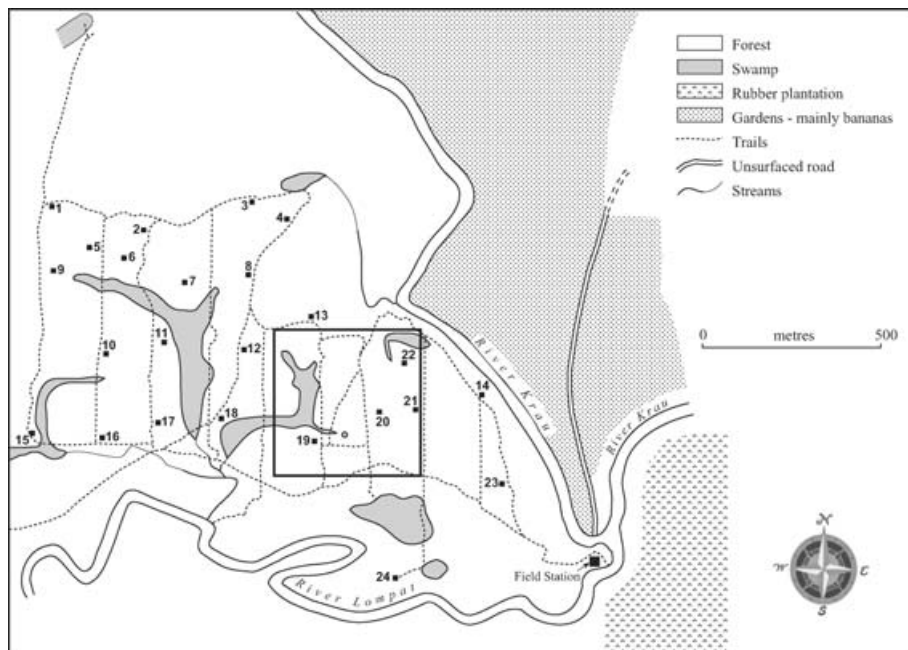


Figure 1. Map of the study site at Kuala Lompat, showing the positions of 24 stacked mist net systems and the position of the 16-ha forest plot.

The Krau Wildlife Reserve consists of a large area of old-growth forest (Clark 1996), which rises from 50 m, at Kuala Lompat, to over 2000 m at the summit of Gunung Benom. Since it lies in the rain shadow of Gunung Benom, Kuala Lompat is comparatively dry for the region, averaging around 1982 mm of rain annually (Raemaekers *et al.* 1980). Although the rainfall pattern is variable, there is a slight trend towards a relatively dry season at the beginning of the year, particularly in February, followed by a wet season from October to December (Hodgkison 2001, Raemaekers *et al.* 1980). Temperature is stable throughout the year, with maximum and minimum daily air temperatures ranging from 30 to 35 °C, and 20 to 25 °C, respectively (Hodgkison 2001, Raemaekers *et al.* 1980).

The vegetation at Kuala Lompat can be classified as lowland evergreen mixed dipterocarp forest. However, because it is relatively poor in dipterocarps, and unusually rich in large Leguminosae, the site is not characteristic of most dipterocarp forest sites within the area (Raemaekers *et al.* 1980).

The fruit bat fauna at Kuala Lompat includes at least 11 species (Francis 1990, 1994; Medway & Wells 1971, Zubaid 1993), including: *Balionycteris maculata* (Thomas), *Chironax melanocephalus* (Temminck), *Cynopterus brachyotis* (Müller), *Cynopterus horsfieldi* (Gray), *Dyacopterus spadiceus* (Thomas), *Eonycteris spelaea* (Dobson), *Macroglossus sobrinus* (Andersen), *Megaerops ecaudatus* (Temminck), *Megaerops wetmorei* (Taylor), *Penthetor lucasi* (Dobson), and *Rousettus amplexicaudatus* (Geoffroy). A previous study, by Francis (1994), has shown that

fruit bat capture rates at Kuala Lompat are up to 100 times higher in the subcanopy (10–30 m) than they are at ground level (< 3 m). However, in contrast to many studies in the Neotropics (Bernard 2001, Bonaccorso 1979, Kalko & Handley 2001), no evidence was found to suggest that any species favour the understorey.

Although the study site was described in detail by Raemaekers *et al.* (1980), the area surrounding the reserve has undergone significant changes in recent years. In particular, the forest that once bordered the reserve at Kuala Lompat has been converted into gardens and plantations, without a buffer zone (Figure 1). Several Malaysian fruit bats, particularly *C. brachyotis* and *C. horsfieldi*, are known to be particularly abundant in gardens and plantations, whereas several others (*B. maculata*, *C. melanocephalus*, *D. spadiceus* and *M. ecaudatus*) are believed to be strongly associated with the forest interior (Lim 1966, Tan *et al.* 1998).

Habitat structure

The structure of the habitat partitioned by fruit bats was sampled within a 6 × 60-m forest transect (after Richards 1983), the position of which was randomly selected within a 16-ha block of old-growth forest (Figure 1). All trees within this transect were labelled, with individually numbered aluminium tags, mapped, and then measured for girth at breast height (gbh). The heights of all trees (> 15 cm gbh) were then measured with a clinometer and tape measure – recording the complete

vertical extension of the crown, and the heights of major forks and branches. Crown widths were then measured on either side of the bole, and sketches made of each tree in the field. These measurements and sketches were then used to reconstruct the forest graphically, in the form of a forest profile diagram. This diagram was then used to investigate patterns in the distribution of vegetation clutter throughout the forest subcanopy.

One hundred randomly generated coordinates were used to investigate the distribution of vegetation clutter throughout the forest profile diagram. These coordinates sampled vegetation clutter at all heights up to 30 m over the entire 60-m length of the area drawn. To sample vegetation clutter, the position of each coordinate was located on the diagram, and scored either as a hit or a miss – according to whether or not there was any vegetation cover at that point within the diagram. A 3×2 contingency table was then constructed, which expressed forest structure as the frequency of vegetation ‘hits’ and ‘misses’ at 10-m height intervals, within the understorey (< 10 m), midstorey (10–20 m), and canopy (20–30 m). A G-test of independence, with William’s correction (Sokal & Rohlf 1995), was then used to test the association between vegetation cover (% hits) and height.

In addition to the forest transect, a 1-ha forest plot was also established in the study area, at a randomly selected site. The girths of all trees equal or greater than 15 cm gbh were then measured and recorded within the plot. A G-test of independence, with William’s correction (Sokal & Rohlf 1995), was used to compare the cumulative frequency distribution of trees, in relation to girth size, between the transect and the forest plot. This comparison was made on the assumption that similar frequency distributions in girth size would indicate similar forest structure and, hence, comparable patterns in the distribution of vegetation clutter throughout the forest profile.

Vertical stratification of fruit bats

The vertical stratification of fruit bats was investigated throughout the forest profile using mist nets (Avinet, Inc, New York, USA). These nets were stacked together to create a continuous wall of net, extending from ground level to the lower forest canopy (Hodgkison *et al.* 2002). Two pulley systems (one at each end of the net) were used to hoist the nets into position, and the whole system was held in place by a main support rope, which was positioned across two sturdy branches in the canopy.

Twenty-four rope-and-pulley systems were established at sites located throughout the 1.5-km² study area (Figure 1). All systems were positioned away from trails beneath closed to semi-closed canopy cover, as opposed to open and exposed tree fall gaps, and were high enough to hoist open between five and nine 6×3 -m mist nets

(36 mm mesh, 50 denier/2 ply nylon). The nets were tied together, along their adjoining margins, with fine black nylon thread, and each pocket was numbered at the side, to indicate its position in the stack. To reduce the risk of bats learning the positions of the mist nets, the 24 sites were netted on rotation. Only rarely was any single net operated on two consecutive nights. However, some nets were eventually run more frequently than others.

Netting protocol was influenced by both weather, and moon cycles. For the safety of fieldworkers, nets were never opened during, or immediately after high winds and heavy rains. Several pulley systems were partially, or completely destroyed by falling trees and branches, particularly after wet weather. Netting was also avoided during brightly moonlit nights; as it appeared, but was not demonstrated, that bats may have detected the nets more easily on such occasions. It is also possible that some species may have been lunar phobic.

Nets were usually opened at dusk (19h30–20h00) and inspected every 15–30 min for bats until they were closed, between midnight and 03h00. Bats were removed from stacked nets by lowering the nets to a manageable height with the pulleys. The capture height of each individual bat was then recorded from the pocket number at the side of the net. Height data were excluded for all captures made when the extension of the net was unknown (i.e. whilst the net was being hoisted).

Captured fruit bats were identified to species, following Payne *et al.* (1985) and Medway (1983), and records were made of forearm length, body mass, sex, age, and reproductive status. Most individuals were marked with stainless steel ball-chain necklaces (Ball-Chain Manufacturing Company, New Jersey, USA), for larger species (*Cynopterus brachyotis*, *C. horsfieldi*, *Megaerops ecaudatus*, *Dyacopterus spadiceus*, *Rousettus amplexicaudatus*) or monel wing bands (Lambournes Ltd., UK) for smaller species and the nectarivorous Macroglossinae (*Chironax melanocephalus*, and *Eonycteris spelaea*) (after Kunz 1996). Recaptured *Balionycteris maculata* were recognized by their distinctive wing-markings (Hodgkison *et al.* 2003). Individuals of larger species that were too small (i.e. immature) to be fitted with a necklace were marked temporarily by wing punching.

Vertical stratification data analysis

Because mist nets vary in size (thus confusing between-site comparisons with other studies), capture rates in this study were defined as the number of individual fruit bats captured per 100 m² mist net hour (mnh) of sampling effort (after Zubaid 1994). To investigate vertical stratification, this figure was calculated within the understorey (< 10 m), midstorey (10–20 m) and canopy (20–30 m) for each of the 24 mist net rig sites established

throughout the study area. The significance of any vertical stratification was then tested for each species using a Kruskal–Wallis test (Sokal & Rohlf 1995).

Wing morphology

The wing morphology of fruit bats was investigated from measurements of wing span (m) and wing area (m²) recorded from live captured bats using wing tracings (after Norberg & Rayner 1987). Together with measurements of body mass (kg), these data were then used to calculate the values of two flight indices: aspect-ratio (AR) and wing-loading (WL). Each flight index was calculated using the following formulae: $AR = B^2/S$, where B equals wingspan and S equals wing area, and $WL = Mg/S$, where M equals body mass and g equals gravitational acceleration (after Norberg & Rayner 1987). Thus, aspect-ratio provides an index of relative wing shape (with high aspect-ratios usually indicating long, narrow wings and low aspect-ratios usually indicating short, broad wings), whereas wing-loading provides a measure of body weight per unit area of wing (N m⁻²). Where possible, at least 10 individuals of each sex were sampled for each species.

Analysis of flight morphology

The normality of each flight index was tested for each species of fruit bat using the Kolmogorov–Smirnov one-sample test (Sokal & Rohlf 1995). Inter- and intraspecific variance in aspect-ratio and wing-loading were then compared using one-way ANOVA. The GT2-method (Sokal & Rohlf 1995) was then used to test for significant morphological variation between species, with an experiment-wise error rate of 5%. All individual bats included in this analysis were either adult males or non-pregnant adult females.

RESULTS

Habitat structure

The 74 trees (> 15 cm gbh), within the 6 × 60-m forest transect, created a structurally complex environment for the locomotion of bats (Figure 2). This was characterized by a dense understorey (up to 10 m), and a more or less continuous canopy (c. 30 m high), punctuated by tree fall gaps and emergent trees rising to 50 m. The distribution of vegetation cover varied significantly throughout the forest profile ($G_{adj} = 6.58$, $df = 2$, $P < 0.05$) and was lowest within the midstorey (29%) and highest in the understorey and canopy (58% and 53%, respectively). However, the exclusion of small trees and shrubs (< 15 cm

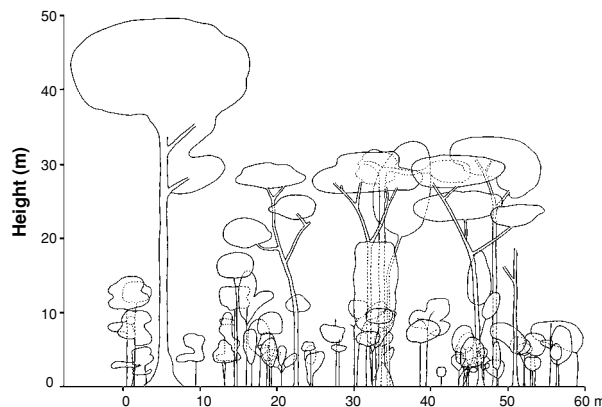


Figure 2. Forest structure at Kuala Lompat, based on measurements and sketches of all trees >15 cm gbh within a 6 × 60-m transect in old-growth lowland rain forest.



Figure 3. Cumulative frequency distributions of tree girth, recorded in one 6 × 60-m forest transect (Figure 2) and one 100 × 100-m forest plot in old-growth lowland rain forest at Kuala Lompat, Malaysia. Measurements include all trees > 15 cm gbh.

gbh) from this analysis is likely to have resulted in an underestimate for the amount of vegetation clutter within the understorey. No significant difference in the cumulative girth size frequency distribution was found between the 74 trees within the 0.036-ha transect, that was used to sample vegetation cover in the forest profile, and the 1378 trees (> 15 cm gbh) located within the 1-ha forest plot ($G_{adj} = 0.89$, $df = 15$, $P > 0.05$) (Figure 3).

Vertical stratification of fruit bats

In total, 352 fruit bats of eight species were captured during 72 306 m² mist-net hours (mnh) of sampling, which included 29 232 m² mnh in the understorey, 29 898 m² mnh in the midstorey, and 13 176 m² mnh in the canopy. Five fruit bat species (*Balionycteris maculata*, *Chironax melanocephalus*, *Cynopterus brachyotis*,

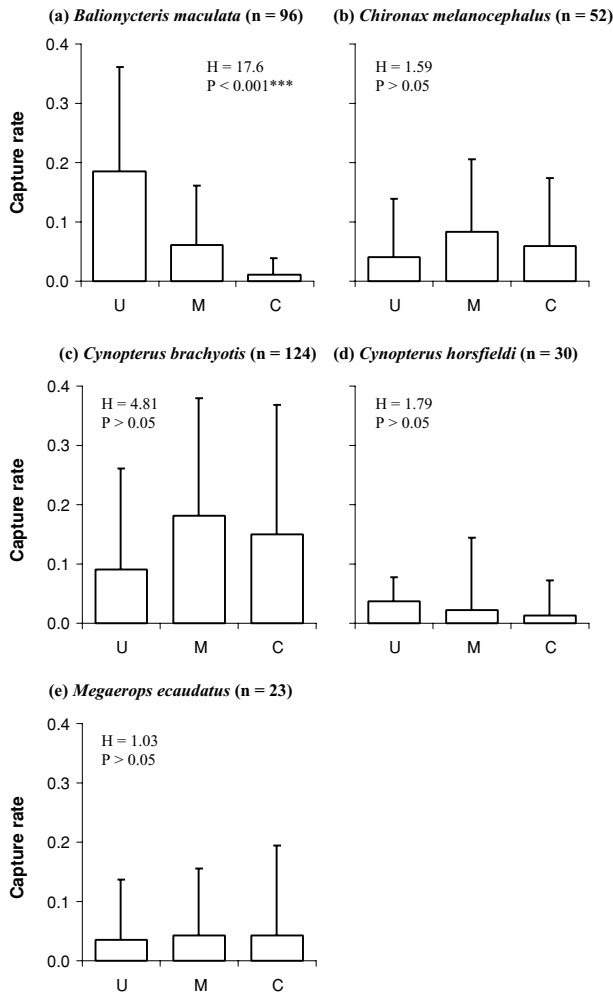


Figure 4. Capture rates and sample sizes (n) of five fruit bat species (a–e) within the understorey (U), midstorey (M), and canopy (C) of an old growth lowland rain forest at Kuala Lumpur, Malaysia. Capture rates are expressed as bats per 100 m² mnh, and are based on 72 306 m² mist net hours of sampling at 24 sites. Bars indicate standard deviations. Statistics refer to Kruskal–Wallis tests.

Cynopterus horsfieldi and *Megaerops ecaudatus*) accounted for 98.3% of the total captures within the 1–28 m height range of the mist nets, whereas the remaining three species (*Dyacopterus spadiceus*, *Eonycteris spelaea* and *Rousettus amplexicaudatus*) accounted for only 1.7%. Measurements of capture height were recorded for 331 bats.

No significant difference was found between the capture heights of the males and females of any fruit bat species commonly captured within the forest subcanopy (Mann–Whitney U, $P > 0.05$). Although all five species were captured throughout the forest profile (Figure 4), only one species (*B. maculata*) had a capture rate that varied significantly with height, with a strong preference for the understorey (Figure 4).

Table 1. Body mass and wing morphology measurements of eight species of fruit bat captured at Kuala Lumpur, Malaysia, showing mean \pm 1 SD with a sample size of n.

Species	n	Mass (kg)	Wing span (m)	Wing area (m ²)
<i>Balionycteris maculata</i>	20	0.0134 ± 0.0009	0.2836 ± 0.0118	0.01385 ± 0.00106
<i>Chironax melanocephalus</i>	16	0.0184 ± 0.0021	0.3119 ± 0.0098	0.01625 ± 0.00098
<i>Cynopterus brachyotis</i>	28	0.0279 ± 0.0029	0.3734 ± 0.0167	0.02301 ± 0.00186
<i>Cynopterus horsfieldi</i>	7	0.0556 ± 0.0089	0.4584 ± 0.0258	0.03613 ± 0.00427
<i>Dyacopterus spadiceus</i>	10	0.0757 ± 0.0101	0.4852 ± 0.0282	0.03773 ± 0.00339
<i>Eonycteris spelaea</i>	11	0.0539 ± 0.0058	0.4247 ± 0.0175	0.02911 ± 0.00231
<i>Megaerops ecaudatus</i>	17	0.0234 ± 0.0031	0.3508 ± 0.0174	0.02016 ± 0.00143
<i>Rousettus amplexicaudatus</i>	5	0.0675 ± 0.0059	0.4864 ± 0.0108	0.03737 ± 0.0023

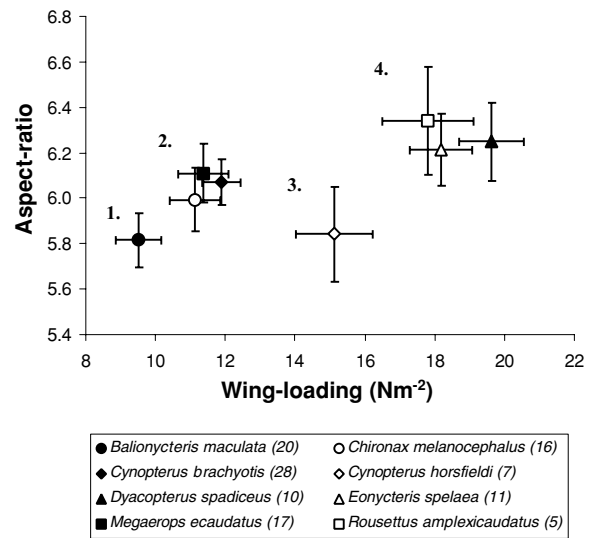


Figure 5. Aspect-ratio versus wing-loading of eight species of fruit bat captured at Kuala Lumpur, Malaysia. Data points show the species mean values of each flight parameter. Bars indicate 95% comparison intervals, calculated by the GT2-method (Sokal & Rohlf 1995). Sample sizes for each species are shown in parentheses within the legend. Species, or species clusters that are significantly different in morphology (1–4) have mean intervals of aspect-ratio and wing-loading that do not overlap.

Wing morphology

Measurements of aspect-ratio and wing-loading did not differ significantly from a normal distribution in the case of all eight fruit bat species captured at Kuala Lumpur (Kolmogorov–Smirnov one-sample test $P > 0.05$). With the exception of two species (*Eonycteris spelaea* and *Cynopterus horsfieldi*), wing-loading and aspect-ratio increased in relation to body mass and wing span (Table 1, Figure 5). Variance in aspect-ratio and wing-loading

was significantly lower within species than between species ($F_{7,108} = 5.92$, $P = 0.001$, and $F_{7,108} = 96.2$, $P = 0.001$, respectively), and multiple comparisons between the mean aspect-ratio and wing-loading of each fruit bat species revealed four morphologically distinct species/clusters (Figure 5).

DISCUSSION

The lowland rain forest, at Kuala Lompat, created a structurally complex environment for the locomotion of bats. Vegetation clutter, which has the potential to impede the flight of some species of bat (Kalko *et al.* 1996, Norberg & Rayner 1987), was not uniformly distributed throughout the forest profile, but was concentrated in the understorey (up to 10 m) and the canopy (20–30 m). The airspace in the midstorey (10–20 m), by contrast, was relatively open. Although only sampled over a small area of forest, this pattern mirrored that observed within a similar area of lowland forest at Pasoh, in Peninsular Malaysia (Kira 1978), and that of an old-growth lowland forest in Amazonia (Terborgh & Petren 1991). Hence, this study supports the idea, proposed by several other authors (Francis 1994, Zubaid 1994), that the area within the midstorey is more open.

Of the eight fruit bat species captured at Kuala Lompat, only five species were commonly captured within the 1–28 m height range of the mist nets (*Balionycteris maculata*, *Chironax melanocephalus*, *Cynopterus brachyotis*, *Cynopterus horsfieldi* and *Megaerops ecaudatus*). The remaining three species, by contrast (*Dyacopterus spadiceus*, *Eonycteris spelaea* and *Rousettus amplexicaudatus*) were mainly active in open airspaces above the forest canopy, where they fed on the fruits and flowers of large emergent trees and strangler figs (Hodgkison 2001). Only one species (*B. maculata*) was significantly associated with the dense vegetation clutter of the forest understorey. This was also the species with the shortest, broadest wings and the lowest wing-loading.

Although these results need to be interpreted with caution, they suggest that flight performance, and habitat structure, may have an important influence on the vertical stratification of fruit bats in Malaysian lowland forests. If the forest transect sampled for clutter is representative of closed-canopy forest as a whole (as supported by the 1-ha forest plot), there was a close correspondence between habitat use and the predicted flight performance of each bat, with those species predicted to have slower and more manoeuvrable flight captured in increasingly cluttered airspaces. This manoeuvrability is largely achieved as a result of lower wing-loadings (Norberg & Rayner 1987, Stockwell 2001). Thus, most fruit bat species that were grouped in relation to habitat use were also grouped by morphology, with three recognizable categories: (1) above-canopy

bats, with high wing-loadings (*D. spadiceus*, *E. spelaea* and *R. amplexicaudatus*); (2) below-canopy bats, with medium wing-loadings (*C. melanocephalus*, *C. brachyotis* and *M. ecaudatus*); and (3) understorey bats, with low wing-loadings (*B. maculata*). The only exception to this pattern was *C. horsfieldi*, which was morphologically distinct but grouped together with three other species in relation to habitat use. However, with only 30 captures, the small sample size of this species is likely to have limited the level of ecological discrimination. We predict that further netting may reveal this species to be more common within the midstorey. Notwithstanding, the present study supports the hypothesis that even small differences in morphology are likely to be ecologically significant to the vertical stratification of bats. Thus, habitat heterogeneity is likely to be a key factor promoting fruit bat species diversity in old-growth palaeotropical forests.

ACKNOWLEDGEMENTS

We wish to express our thanks to the Department of Wildlife and National Parks (Malaysia), for their generous support throughout this project, and for providing us with the use of the field station facilities at Kuala Lompat. This study would not have been possible without the kind permission of the Economic Planning Unit of Malaysia. Valuable assistance and encouragement in the field was given by Ahmad Bin Dagu, Tigga Kingston and Zamiza Bin Zainal. Constructive comments that significantly improved the manuscript were offered by Paul A. Racey, M. B. Fenton, J. Altringham, U. Lindhe and three anonymous referees. The map of the study site was prepared by Alison Sandison. This study was supported by a grant from the Lube Foundation Inc., Florida, to T. H. Kunz. Additional sponsorship, to R. Hodgkison, was provided by the Carnegie Trust for the Universities of Scotland, the Royal Society South East Asia Rain Forest Regeneration and Recovery Programme (RS-112) and Bat Conservation International.

LITERATURE CITED

- BELL, H. L. 1982. A bird community of lowland rain forest in New Guinea. III. Vertical stratification of the avifauna. *Emu* 82:143–162.
- BERNARD, E. 2001. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. *Journal of Tropical Ecology* 17:115–126.
- BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum of Biological Sciences* 24:359–408.
- CLARK, D. B. 1996. Abolishing virginity. *Journal of Tropical Ecology* 12:735–739.
- COSSON, J. 1995. Captures of *Myonycteris torquata* (Chiroptera: Pteropodidae) in forest canopy in South Cameroon. *Biotropica* 27:395–396.

- EMMONS, L. H. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* 50:31–54.
- FRANCIS, C. M. 1990. Trophic structure of bat communities in the understorey of lowland dipterocarp rain forest in Malaysia. *Journal of Tropical Ecology* 6:421–431.
- FRANCIS, C. M. 1994. Vertical stratification of fruit bats (Pteropodidae) in a lowland dipterocarp rain forest in Malaysia. *Journal of Tropical Ecology* 10:523–530.
- HEIDEMAN, P. D. & HEANEY, L. R. 1989. Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rain forest. *Journal of Zoology (London)* 218:565–586.
- HODGKISON, R. 2001. *The ecology of fruit bats (Chiroptera: Pteropodidae) in a Malaysian lowland dipterocarp forest, with particular reference to the spotted-winged fruit bat (Balionycteris maculata, Thomas)*. Ph.D. thesis. University of Aberdeen, Scotland.
- HODGKISON, R., AHMAD, D., BALDING, S. T., KINGSTON, T., ZUBAID, A. & KUNZ, T. H. 2002. Capturing bats (Chiroptera) in tropical forest canopies. Pp. 160–167 in Mitchell, A. W., Secoy, K. & Jackson, T. (eds). *The global canopy programme handbook: techniques of access and study in the forest roof*. Global Canopy Programme, Oxford.
- HODGKISON, R., BALDING, S. T., ZUBAID, A. & KUNZ, T. H. 2003. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. *Journal of Tropical Ecology* 19:667–676.
- INGLE, N. R. 1993. Vertical stratification of bats in a Philippine rainforest. *Asia Life Sciences* 2:215–222.
- KALKO, E. K. V. & HANDLEY, C. O. 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology* 153:319–333.
- KALKO, E. K. V., HANDLEY, C. O. & HANDLEY, D. 1996. Organization, diversity, and long-term dynamics of a Neotropical bat community. Pp. 503–553 in Cody, M. & Smallwood J. (eds). *Long-term studies of vertebrate communities*. Academic Press, Los Angeles.
- KIRA, T. 1978. Community architecture and organic matter dynamics in tropical lowland forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. Pp. 561–590 in Tomlinson, P. B. & Zimmermann, M. H. (eds). *Tropical trees as living systems*. Cambridge University Press, Cambridge.
- KITCHENER, D. J., GUNNELL, A. & MAHARADATUNKAMSI. 1990. Aspects of the feeding biology of fruit bats (Pteropodidae) on Lombok Island, Nusa Tenggara, Indonesia. *Mammalia* 54:561–578.
- KUNZ, T. H. 1996. Methods of marking bats. Pp. 304–310 in Wilson, D. E., Cole, F. R., Nichols, J. D., Rudran, R. & Foster, M. S. (eds). *Measuring and monitoring biological diversity: standard methods for mammals*. Smithsonian Institution Press, Washington DC.
- LIM, B. L. 1966. Abundance and distribution of Malaysian bats in different ecological habitats. *Federation Museums Journal* 9:61–76.
- McKENZIE, N. L., GUNNELL, A. C., YANI, M. & WILLIAMS, M. R. 1995. Correspondence between flight morphology and foraging ecology in some palaeotropical bats. *Australian Journal of Zoology* 43:241–257.
- MEDWAY, LORD 1983. *The wild mammals of Malaya (Peninsular Malaysia) and Singapore*. (Second edition). Oxford University Press, Kuala Lumpur. 130 pp.
- MEDWAY, LORD & WELLS, D. R. 1971. Diversity and density of birds and mammals at Kuala Lumpur, Pahang. *Malayan Nature Journal* 24:238–247.
- NORBERG, U. M. & RAYNER, J. M. V. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London, B* 316:335–427.
- PAYNE, J., FRANCIS, C. M. & PHILLIPPS, K. 1985. *A field guide to the mammals of Borneo*. The Sabah Society with World Wildlife Fund Malaysia, Kota Kinabalu. 332 pp.
- PEARSON, D. L. 1971. Vertical stratification of birds in a tropical dry forest. *Condor* 73:46–55.
- PEARSON, D. L. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. *Condor* 77:453–466.
- RAEMAEKERS, J. J., ALDRICH-BLAKE, F. P. G. & PAYNE, J. 1980. The forest. Pp. 29–62 in Chivers D. J. (ed.). *Malayan forest primates: ten years' study in tropical rain forest*. Plenum Press, New York.
- RICHARDS, G. C. 1995. A review of ecological interactions of fruit bats in Australian ecosystems. *Symposia of the Zoological Society of London* 67:79–96.
- RICHARDS, P. W. 1983. The three-dimensional structure of tropical rain forest. Pp. 3–10 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forest: ecology and management*. Blackwell Scientific Publications, Oxford.
- ROTH, R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773–782.
- SCHOENER, T. W. 1986. Resource partitioning. Pp. 91–126 in Kikkawa, J. & Anderson, D. J. (eds). *Community ecology: pattern and process*. Blackwell Scientific Publications, Oxford.
- SOKAL, R. R. & ROHLF, F. J. 1995. *Biometry: the principles and practice of statistics in biological research*. (Third edition). W. H. Freeman and Company, New York. 887 pp.
- START, A. N. 1974. *The feeding biology in relation to food sources of nectarivorous bats (Chiroptera: Macroglossinae) in Malaysia*. Unpublished Ph.D. thesis, University of Aberdeen, Scotland.
- STOCKWELL, E. F. 2001. Morphology and flight manoeuvrability in new world leaf-nosed bats (Chiroptera: Phyllostomidae). *Journal of Zoology (London)* 254:505–514.
- TAN, K. H., ZUBAID, A. & KUNZ, T. H. 1998. Feeding ecology of *Cynopterus brachyotis* (Chiroptera: Pteropodidae) in Peninsular Malaysia. *Journal of Tropical Ecology* 14:299–307.
- TERBORGH, J. & PETREN, K. 1991. Development of habitat structure through succession in an Amazonian floodplain forest. Pp. 28–46 in Bell, S. S., McCoy, E. D. & Mushinsky, H. R. (eds). *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, London.
- UTZURRUM, R. C. B. 1995. Feeding ecology of Philippine fruit bats: patterns of resource use and seed dispersal. *Symposia of the Zoological Society of London* 67:63–77.
- ZUBAID, A. 1993. A comparison of the bat fauna between a primary and fragmented secondary forest in Peninsular Malaysia. *Mammalia* 57:201–206.
- ZUBAID, A. 1994. Vertical stratification of pteropodid bats in a Malaysian lowland rainforest. *Mammalia* 58:309–311.