

Species richness in an insectivorous bat assemblage from Malaysia

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Abstract: Estimates of insectivorous bat diversity in the Palaeotropics have largely been hampered by the lack of long-term studies employing appropriate capture techniques. Using a variety of trapping methods, 45 insectivorous bat species were captured in approximately 3 km² of primary dipterocarp rain forest in Malaysia over 8 y. The cumulative site list for Kuala Lompat Research Station, Krau Wildlife Reserve, now stands at 51 insectivorous species. Although this is likely still not a complete list, it is already one of the most species-rich in the world. We attribute much of our success in recording this diversity to the extensive use of harp traps. Of the 45 species, 38 were captured in an intensive harp-trapping programme (> 1030 harp-trap nights) of the forest interior (22 species exclusively so). Insectivorous bats of the forest interior are thus a key component of Old World bat diversity, particularly in South-East Asia, and are dominated by taxa capable of detecting and capturing prey in cluttered environments (Hipposideridae, Rhinolophidae, Kerivoulinae and Murininae).

Key Words: Chiroptera, Hipposideridae, Kerivoulinae, Murininae, Rhinolophidae, species abundance, species diversity

INTRODUCTION

Despite their significance to global biodiversity (Kunz & Pierson 1994), the nocturnal, volant nature of bats has limited our understanding of global patterns of species richness. Bat species richness is greatest in the tropics, increasing as latitude decreases to peak in the equatorial rain forests of South America and Asia, and the savannas and dry woodlands south of the Sahara in Africa (Findley 1993, Willig & Patterson, in press), and it is a generally held assumption that species richness of bat communities in the Neotropics is greater than in the Palaeotropics. In contrast to the 78 species recorded at Paracou, French Guiana (Simmons & Voss 1998) or the 66 species known for Barro Colorado Island, Panama (Kalko *et al.* 1996), the record for a single palaeotropical locality stands at 50 species at Ulu Gombak, Malaysia (Heller & Volleth 1995). In Africa, the highest count comes from the dry woodlands of Kruger National Park (South Africa) with 41 species (Pienaar *et al.* 1987), with only 34 species currently listed for Makokou (Gabon), one of the best-known lowland African rain-forest sites (Happold 1996). How-

ever, neotropical bat communities have also been the focus of much more attention than those of the Palaeotropics (reviewed in Findley 1993, Simmons & Voss 1998, Voss & Emmons 1996), and this begs the question as to whether neotropical bat communities are really more species-rich than their palaeotropical counterparts, or if this pattern is simply a reflection of differential sampling effort.

There is little doubt that, despite taxonomic equitability, species richness of fruit bats at regional and local levels is greater in the Neotropics (Findley 1993, Fleming 1987, Francis 1990, Wilson 1973). Whereas Paracou supports 22 species of plant-visiting bat, an intensive study by Heidemann & Heaney (1989) found only 13 species on Negros Island in the Philippines, while 11 species have been recorded at Ulu Gombak, 7 at Makokou and 4 at Sengwa Wildlife Research Area (Zimbabwe) (Fenton 1985, Happold 1996, Heller & Volleth 1995, Simmons & Voss 1998). Megachiropteran diversity in palaeotropical rain forests may have been constrained by resource availability. Two major floral radiations, that of understory shrubs in the Andes and canopy trees originating in Amazonia, have provided an abundance of resources for plant-visiting bats in the neotropics that have no parallels in the Old World (Gentry 1982), particularly in West Malesia where forests are dominated by wind-dispersed dip-

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terocarps (Fleming 1987, Francis 1990, Janzen 1980, Wong 1986). The low diversity of plant resources, in combination with the spatio-temporal patchiness of fruit may have favoured the high mobility, large size and more generalized feeding habits of the pteropodids, setting limits to local diversity (Fleming 1987, 1993). In contrast, the great diversity and relative constancy of plant foods available in the Neotropics is thought to have promoted the extensive radiation of the (generally) smaller Phyllostomidae and high local species richness (Fleming 1987).

Historical and regional processes have also shaped the taxonomic composition of the insectivorous bat faunas in the two regions. In both instances, the insectivorous bat community can be broadly divided into three guilds, defined by the degree of clutter (i.e. vegetation or other obstacles) that bats encounter when foraging (Aldridge & Rautenbach 1987, Fenton 1990, Kalko 1995, McKenzie & Rolfe 1986, McKenzie *et al.* 1995, Schnitzler & Kalko 1998). We follow McKenzie *et al.* (1995) in using wing morphology to group species into guilds. Strategy I bats (or narrow-space bats *sensu* Schnitzler & Kalko 1998) forage in the highly cluttered space within the forest interior; strategy II species (edge and gap bats) forage in small clearings in the forest, over small streams, or at the forest edge where clutter is in the background; and strategy III species (open-space bats) forage in open spaces above the forest, or in large clearings that are clear of clutter. These are broad groups that can be divided further by echolocation design and foraging strategy. Although these guilds can be recognized in both the Old and New World, their taxonomic composition varies. Diversity of the Emballonuridae (typically strategies II and I) is much greater in the Neotropics, and the Indomalayan region supports less than half the number of molossid species found in Africa and South America. Several families are restricted to the New World tropics (namely the Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, Thyropteridae and Natalidae), while the Rhinolophidae, Hipposideridae, Nycteridae and Megadermatidae, which are predominantly narrow-space foragers, are confined to the Old World. However, it has been suggested that the overall lower species richness of insectivorous bats reported for palaeotropical rain forests (mean of 29 vs. 40 species; Heller & Volleth 1995) is not so much a reflection of these processes, but rather a sampling bias attributable to lower research intensity, both spatially and temporally (Heller & Volleth 1995). The disparity is further compounded by differences in sampling techniques appropriate for the two regions. Although there are biases associated with any of the capture methods used to sample bat faunas (Kunz & Kurta 1988), mist nets, which form the backbone of neotropical sampling (Voss & Emmons 1996), are much less effective in the palaeotropics (Francis 1989, 1990). The most common families of the forest interior, the Rhinolophidae and Hipposideridae, and the vespertilionids in the subfamilies

Kerivoulineae and Murinineae are both highly manoeuvrable in flight and capable echolocators, and as a consequence are adept at avoiding mist nets (Francis 1989). In contrast, these species appear more susceptible to capture by harp traps (Francis 1989, Rautenbach *et al.* 1996), but few studies have capitalized on this (but see Francis 1989, 1990, 1995). It is conceivable therefore, that previous studies have missed much of the insectivorous bat diversity of palaeotropical bat communities, limiting both the detection of patterns at the global level, and the understanding of the processes behind them.

The aim of the present study was to assess species richness of insectivorous bats in a palaeotropical bat community. To reduce the possibility that species were overlooked due to inadequate sampling, our study was conducted over 8 y and employed a variety of sampling methods, but with particular focus on an intensive harp-trapping programme of the forest interior. The study site in Peninsular Malaysia falls within the area of maximum species richness for the Old World (Findley 1993), and has been the focus of at least eight previous bat surveys dating from Medway & Wells (1971) (Heller & Volleth 1995). Thus it supports one of the best-known bat faunas in the region, conferring two further advantages. First, comparison with previous studies allows an assessment of the thoroughness of our own sampling methods, while also providing for a more complete list by including at least some of the species missed in the current study. Second, the extent of additions to the previous list of 33 insectivorous species (Heller & Volleth 1995) can provide a conservative estimate of the degree of undersampling at other localities.

METHODS

Study area

The study was conducted 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 extends for 530 km² and includes six distinct floristic zones, but sampling was confined to approximately 3-km² area around the Research Station. Kuala Lompat is at approximately 50 m asl located at the junction of the rivers Lompat and Krau in lowland evergreen dipterocarp forest that occurs below 300 m (see Francis 1994, Kingston *et al.* 2000). Trapping was conducted along a trail system originally cut for primate studies in the 1970s (Chivers 1980), and in a 110-ha grid of trails to the west established by CMF in 1991 (Francis 1994).

Species capture and identification

Species differ in their susceptibility to the available capture techniques (Francis 1989, Kunz & Kurta 1988, Kunz

et al. 1996). To generate as complete a species list as possible we used a number of sampling methods. Within the forest, four-bank harp traps (Francis 1989) were positioned in the understorey across trails or small streams, and mist nets (12 m; 70 denier nylon, four shelves, 36 mm mesh size) were set at ground level along and across trails, and over streams. Nets were also set over the rivers Lompat and Krau at the edge of the reserve. Horizontally strung mist nets were restrung to hang vertically in the canopy following Munn (1991) (Francis 1994), or were stacked one above the other (up to 8 nets) in clearings using a pulley system (Kunz & Kurta 1988). Insectivorous species that forage around lights and fly low in open areas were captured with hand nets and by 'flick-netting', in which a short 6-m mist net held taut on two poles is flicked up into the flight path of a low-flying bat (Finnemore & Richardson 1987, Kunz *et al.* 1996). Hand nets were occasionally used to capture bats at roosts.

Sampling was conducted by CMF for all or part of 43 nights in 1991 (August–December), 25 nights in 1992 (May–September) and 6 nights in 1993 (July–September). This resulted in approximately 200 harp-trap nights (3–6 harp traps set per night), 40 canopy-net nights and 64 mist-net nights (the latter two as part of a study focusing on fruit bats; Francis 1994).

A more intensive and systematic harp-trapping programme was established by TK in the forest interior from October 1995 to May 1997 and in August 1999. The programme was restricted to the primate trail system, which encompassed an area of just under 1.2 km² with approximately 14 km of trails. Up to eight harp traps were used each night, about 50 m apart, and each trap was set for a single night then moved to a new position in the forest, until the entire trail system had been trapped twice, and some sections trapped three times. Traps were set at dusk, attended every 15–30 min until 22h00 and then left open overnight and rechecked at dawn, to catch the peaks in bat activity at dusk and dawn. The trapping protocol in 1999 was the same but fewer trails were sampled. The total survey effort was 723 harp-trap nights in 1995–1997 and 114 harp-trap nights in 1999. In addition, mist nets were set in various locations for part of 81 nights between 1995 and 1997 for a total of 786 ground-net hours, 606 stack-net hours, 147 canopy-net hours and 34 river-net hours.

Captured bats were held individually in cloth bags and identified from external characters following Medway (1982), Payne & Francis (1985), Lekagul & McNeely (1997) and Corbet & Hill (1992). Voucher specimens were taken to confirm the identification of new or uncertain records, most of which were deposited with the collections of the Malaysian Department of Wildlife and National Parks or Universiti Kebangsaan Malaysia. Individuals were weighed, measured and released at the capture point within 12 h. Juveniles were distinguished from

adults by the presence of cartilaginous epiphyseal plates in the finger bones (Anthony 1988). Most bats were marked with wing bands (Kunz 1996) for individual identification, and recaptures were excluded from the abundance estimates.

Since species richness is a function of the number of individuals sampled, we generated rarefaction curves in EcoSim (Gotelli & Entsminger 1999) to compare species richness across samples (1995–1997 vs. 1999). For each sample, rarefaction algorithms generate expected species richness based on random subsamples of individuals at each abundance level. Iteration generates a mean and variance of species richness for each abundance, allowing a statistical comparison of expected species richness of two or more samples that differ in abundance of individuals (Gotelli & Entsminger 1999, Gotelli & Graves 1996, Heck *et al.* 1975, Sanders 1968).

RESULTS

We caught 2560 individuals of 45 insectivorous species (Appendix 1, size measurements given in Appendix 2), 18 of which were additions to the published Kuala Lompat list (Heller & Volleth 1995). Twenty-three species were captured in mist nets and four (out of five) of the open-space bats were only caught by this means (see Appendix 1). Thirty-eight species were captured in harp traps, of which 22 were taken exclusively by this method (Table 1).

The 1995–1999 harp-trap survey resulted in 1789 captures of 33 species over 723 harp-trap nights in the 1995–1997 season, and 114 harp-trap nights in 1999. Cumulative species curves based on sampling effort and individual abundance both reached an asymptote (Figure 1), strongly suggesting that most understorey species that could be captured with harp traps in this area had been caught. Despite a lower sampling effort and a 2-y interlude, the 1999 sample fell within the 95% confidence interval of the rarefaction curve of the 1995–1997 sample, suggesting that species richness across years did not differ (Figure 1b). *Murina rozendaali* was the only species captured in 1999 that was not represented in the 1995–1997 survey, but *M. rozendaali* and an additional five species were captured in harp traps by CMF between 1991–1993 (*Rhinolophus robinsoni*, *Hipposideros galeritus*, *Myotis siligorensis*, *Hesperotenus blanfordi*, *Miniopterus medius*).

Some species were more commonly caught than others in harp traps (Appendix 1, Figure 2). The four most abundant species (*Hipposideros cervinus*, *Rhinolophus stheno*, *Kerivoula intermedia* and *R. refulgens*) accounted for 54% of the 2374 harp-trap captures and were represented by more than 300 individuals each. At the other extreme, many species were captured in very low numbers. Ten species were represented by less than 5 captures,

Table 1. Numbers of individuals and bat species captured with mist nets and harp traps for each family at Kuala Lompat, Krau Wildlife Reserve, 1991–1999. N_{bats} , number of individuals; N_{sp} , number of species; $N_{\text{sp excl.}}$, number of species caught exclusively by that capture method. Excludes captures by other means.

Family (N_{sp})	Bats captured in mist nets		Bats captured in harp traps	
	N_{bats}	N_{sp} ($N_{\text{sp excl.}}$)	N_{bats}	N_{sp} ($N_{\text{sp excl.}}$)
Emballonuridae (1)	3	1	5	1
Nycteridae (1)	1	1	24	1
Megadermatidae (1)	2	1	9	1
Rhinolophidae (8)	35	6	864	8 (2)
Hipposideridae (10)	21	2 (1)	677	9 (8)
Vespertilionidae (10)	16	6 (3)	83	7 (4)
Murinae (4)	1	1	153	4 (3)
Kerivoulinae (7)	2	2	723	7 (5)
Molossidae (3)	46	3 (3)	–	–
Total	127	23 (7)	2538	38 (22)

19 species were represented by less than 10 individuals, and 25 species by less than 20 captures.

Three taxa dominated the assemblage of 38 species captured by harp traps set in the forest interior, both in terms of the numbers of species and numbers of individuals captured, with 36% *Rhinolophus* (8 species), 29% *Hipposideros* (10 species), and 24% *Kerivoula* and *Phoniscus* (subfamily Kerivoulinae) (7 species).

DISCUSSION

The present study was limited to < 3 km² of relatively homogeneous habitat; thus the 45 species we captured can be fairly legitimately considered to represent a community. Together with previously published records (Heller & Volleth 1995, Zubaid 1993), this brings the cumulative species list for Kuala Lompat to 51 insectivorous species. This greatly surpasses anything previously reported for a single site in the Palaeotropics. Only Paracou with 50 species comes close in the Neotropics (Heller & Volleth 1995, Simmons & Voss 1998). Although 55 insectivorous species have been listed for the Iwokrama forest in Guyana, this was achieved by geographically extensive sampling (13 sites within the 3600 km² reserve, and all except the base camp for less than 2 wk), and the local maximum reported was 26 species (Lim *et al.* 2000). Paracou is a more appropriate comparison as the trapping was restricted to approximately 3 km². Not only are insectivorous bat species more numerous in the Old World, but also their contribution to the overall bat diversity is much greater. Insectivorous and animal-eating bats constitute between 30% and 66% of recorded neotropical assemblages (Lim & Engstrom 2001, Simmons & Voss 1998), but comprise 82% of the bat fauna at Kuala Lompat where 11 species of Megachiroptera are known (Francis 1994, R. Hodgkison, pers. comm.). Including the Megachiroptera, the currently known list of 62 species at Kuala Lompat is comparable with the overall bat diversity in many neotropical sites (reviewed in Voss & Emmons

1996), and greatly exceeds all African sites studied to date.

That 18 species were added to a relatively well-known bat fauna in the present study suggests that the diversity of insectivorous palaeotropical bat communities has likely been greatly underestimated in most published studies as a result of incomplete sampling. Moreover, five of the additions were new records for Peninsular Malaysia, including three range extensions (*Phoniscus jagorii*, Kingston *et al.* 1997; *Myotis ater*, Francis & Hill 1998; *Murina rozendaali*, Francis 1997); a previously undescribed species of *Kerivoula* (Francis *et al.*, unpubl. data); and the discovery that bats identified as *Hipposideros 'bicolor'* include two morphologically similar species that could only be separated by acoustic and genetic means (Kingston *et al.* 2001). Given the relatively limited area in which we worked, it thus seems likely that even at regional or national levels, the species lists for most countries in South-East Asia are still incomplete. Given our findings, it would also be interesting to determine whether species richness in the lowland equatorial rain forests of Central and West Africa is as low as is currently believed. The record of 27 species of insectivorous bats is held by Makokou, Gabon (Happold 1996, D. C. D. Happold, pers. comm.), but only a limited range of sampling methods were used in that area, and in particular no harp trapping had been carried out.

Despite the intensity of the trapping effort at Kuala Lompat, and the large number of species recorded, the species list is unlikely to be complete. The species discovery curves for the forest-interior species captured by harp traps (Figure 1) suggest that the species list for this guild may be nearly complete. However, *Murina rozendaali* was first caught by TK in 1999, and a further five species were captured in harp traps by CMF and not TK. Many of the latter were caught in traps set over small streams or in a separate grid of trails adjacent to the area surveyed by TK, although with essentially similar habitat. This indicates that even small changes in the placement of traps

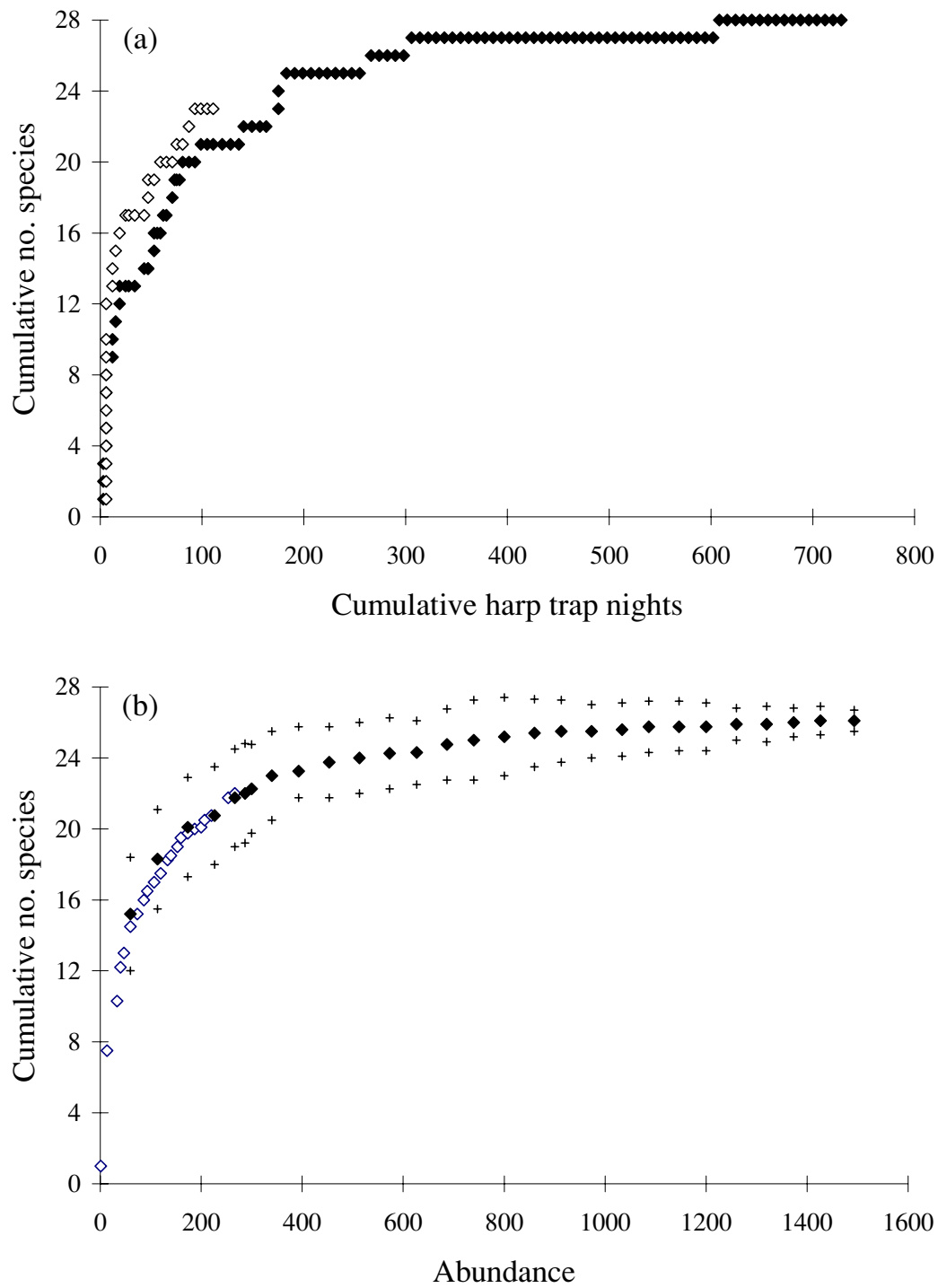


Figure 1. (a) Species discovery curve for all insectivorous bats captured by harp traps in the forest interior of Kuala Lompat, 1995–1997 (closed symbols) and 1999 (open symbols). (b) Rarefaction curves for narrow-space insectivorous bats captured in harp traps in 1995–1997 (closed symbols) and 1999 (open symbols). The crosses represent the 95% confidence interval for the larger 1995–1997 sample. Despite a lower sampling effort, the abundance curve from 1999 falls within the 95% confidence interval for the 1995–1997 sample – the two sampling periods did not differ in estimated species richness. Rarefaction conducted using EcoSim (Gotelli & Entsminger 1999).

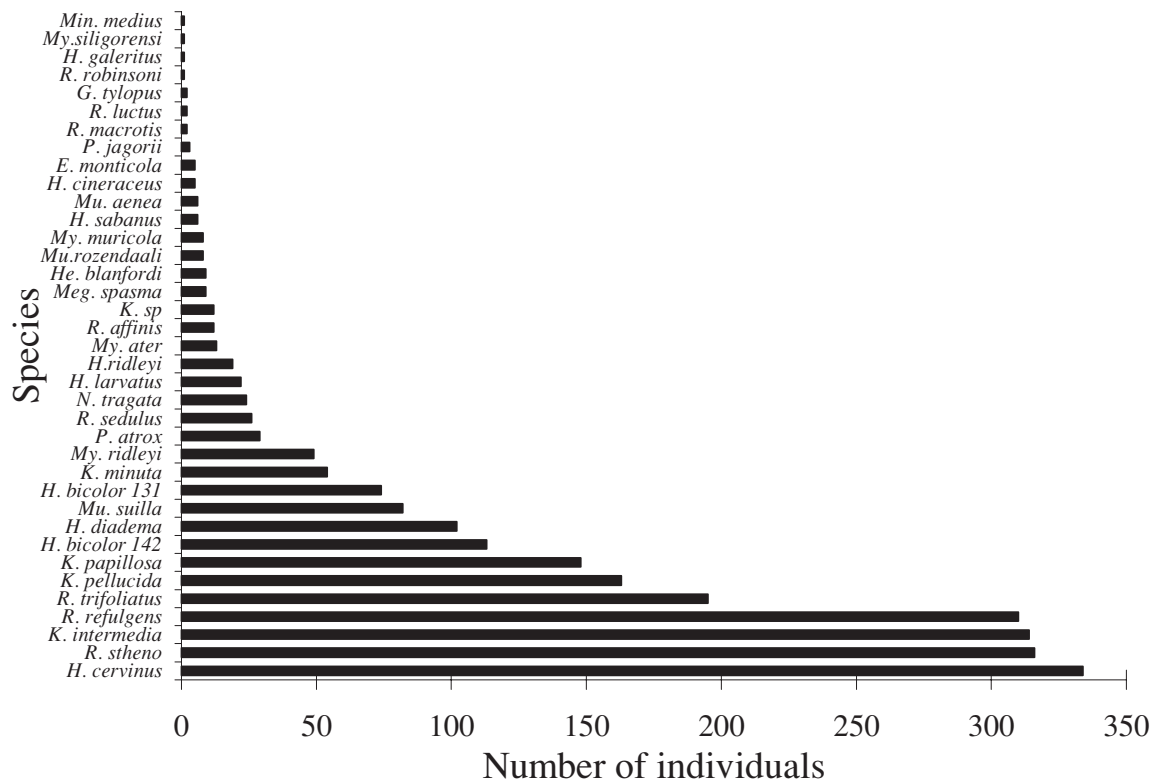


Figure 2. Relative abundance of insectivorous bat species captured with harp traps in the forest interior of Kuala Lompat. *H.*, *Hipposideros*; *He.*, *Hesperoptenus*; *K.*, *Kerivoula*; *Meg.*, *Megaderma*; *Min.*, *Miniopterus*; *Mu.*, *Murina*; *My.*, *Myotis*; *N.*, *Nycteris*; *P.*, *Phoniscus*; *R.*, *Rhinolophus*.

can affect the species caught. Thus, despite the apparent asymptote of species discoveries (Figure 1) the sample by TK was not complete, and it is likely that there are still further unrecorded forest interior species.

Our species list for the open-space and edge/gap foraging insectivorous species was clearly incomplete, as indicated by several bat species, most of which forage in open areas, that have been reported in previous studies at this site, but were not captured by us (*Scotophilus kuhlii*, Heller & Volleth 1995; *Tylonycteris pachypus*, *T. robustula*, *Pipistrellus javanicus*, *Taphozous melanopogon*, Zubaid 1993; *Hipposideros armiger*, Medway & Wells 1971). *Tylonycteris* spp. roost in the culms of large bamboos which occur in the forest understorey around Kuala Lompat, but were absent from the immediate vicinity of our harp traps. The previous records of these species were of specimens captured by hand while roosting in bamboo (ZA, pers. obs.). *Taphozous* spp. typically forage in open spaces above the canopy (TK, pers. obs.), and the individual netted at Lompat may have come from a roost in a house in a neighbouring village (ZA, pers. obs.).

Species that forage primarily in open areas or over the canopy can occasionally be captured near ground level when commuting from roosts or coming down to drink, but reliance on this approach for sampling is unlikely to yield a complete list. It thus seems unlikely, even includ-

ing the published records, that this guild is completely represented. Alternative sampling methods may be more appropriate for this group. Most species that forage over the forest canopy, or in other open areas, use relatively high-intensity echolocation calls (Neuweiler 1990) that can be detected fairly readily by acoustic monitoring (unlike the calls of many of the narrow-space species that are of short effective range). Future efforts that focus on developing an echolocation call library and surveying these guilds remotely could be valuable in expanding our knowledge of this guild.

We may also have undersampled species that forage or roost primarily within the forest canopy, because our harp-trapping was largely restricted to the understorey. Vertical stratification is evident in Old World fruit bat communities (Francis 1994, Ingle 1993), and some neotropical phyllostomids (Bonaccorso 1979, Brosset & Charles-Dominique 1990, Handley 1967). Edge/gap insectivores were caught more commonly in elevated nets than ground-level nets in Brazil (Kalko & Handley 2001). A preliminary attempt to evaluate this effect in the present study was unsuccessful; mist nets placed in the canopy and subcanopy were seen to be avoided by insectivorous bats.

Species richness tends to increase with spatial scale in other taxa (Robinson *et al.* 2000), as more habitats and

patchily distributed species are encompassed. Given the small scale of the present study, the methods deployed, and the great diversity of bats known for Malaysia (> 100 species), we predict that total bat diversity for Krau Wildlife Reserve, which encompasses 530 km² and an altitudinal gradient of 2100 m, is likely considerably higher than the 62 species so far known from Kuala Lompat, probably totalling at least 70–80 species. Inspection of range maps (Corbet & Hill 1992) suggests that approximately 57 insectivorous species might be expected to occur in the reserve. Although the cumulative list of Kuala Lompat is 51 species, this includes species not listed by Corbet & Hill (1992) (undescribed species and range extensions), and thus our list currently omits 14 species predicted to be present. Similarly, Simmons & Voss (1998) estimated that another 20 insectivorous species might be plausibly present in the vicinity of Paracou. Apart from the likelihood that we have overlooked species that occur at Kuala Lompat, as described above, additional species may occur elsewhere in the reserve that require factors, such as particular roost sites or foraging habitats, that are not present in the immediate vicinity of Kuala Lompat. *Pipistrellus societus* is known from the northern end of the reserve, on the lower slopes of Gunung Benom (Hill 1972), and at least three of the expected species have been reported from similar lowland rain forest in the large national park (Taman Negara) approximately 70 km north of Krau Wildlife Reserve (*Kerivoula hardwickii* (TK, pers. obs.), *Pipistrellus tenuis* and *Hipposideros ater* (Yeap Chin Aik, pers. comm.). No large cave systems are known in the immediate vicinity of Kuala Lompat, and this may account for the omission of several more of the expected species (*Taphozous longimanus*, *T. saccolaimus*, *Megaderma lyra*, *Miniopterus schreibersii*, *M. magnater*), all of which tend to roost in caves or boulder crevices.

Additional surveys are required to learn more about spatial diversity in bat distributions within Malaysia. As yet, very little is known about the specific factors that limit the distribution of individual bat species and such information is particularly important in light of the continued loss of pristine habitats, and the need to ensure that designated reserve systems encompass the requirements of all species.

Our surveys indicate, as with many other tropical species (Robinson *et al.* 2000), that there is a highly uneven distribution of species abundances, with many relatively rare species (Figure 2). Capture rarity may be a consequence of a bias in the trapping method or sample design, or a true reflection of local abundance. As discussed above, some species may be more common in subhabitats under-represented by the present study (canopy, subcanopy, streams, bamboo groves), or may be relatively adept at avoiding capture in harp traps. Other species may be commuting from roosting sites such as caves outside the trapping area and might be expected to be more

common in sites nearer to the roost (potentially including several of the *Hipposideros* and *Rhinolophus*; Medway 1982). For some species, however, apparent rarity may be a true reflection of low population densities, possibly related to specific roosting (e.g. *Nycteris tragata*) or habitat requirements that can lead to widely dispersed and in some cases patchy distributions (Kingston 2000). Patchily distributed species may appear rare if sampling fails, by chance or as a consequence of the scale of the study, to include a cluster of individuals (Robinson *et al.* 2000). Differentiating between these possibilities requires further information on the ecology of each species.

The present study indicates that palaeotropical insectivorous bat communities at least match and may exceed the species richness of their neotropical counterparts. The intensive harp-trapping protocol suggests that this is primarily due to the great numbers and diversity of insectivorous species in the forest interior. Of the 38 species captured with harp traps in the forest interior, we classified 27 as strict or predominantly narrow-space insectivores with a further seven representing a mix of narrow-space and edge/gap characteristics (Kingston *et al.*, unpubl. data). In contrast, the narrow-space insectivorous/animalivorous guild in the neotropics has not been found to exceed the 22 species at Paracou, where habitat heterogeneity was an important contributing factor (Simmons & Voss 1998), and assemblages of *c.* 10 species are more typical (Kalko *et al.* 1996, Simmons & Voss 1998). Bats in the forest interior are an extremely diverse group in Peninsular Malaysia and as a consequence are of intrinsic conservation value and ecological importance. However, they are particularly susceptible to the effects of habitat disruption, as they are likely to experience both quantitative loss of habitat and qualitative changes as edge effects alter the forest microclimate (Kapos 1989, Saunders *et al.* 1991), and impact insect availability (Johns 1997).

The susceptibility of many forest-interior bats to disturbance events is further heightened by specializations of wing morphology and echolocation signal design that equip them to forage in the dense clutter of the forest understorey, but greatly constrain their ecological flexibility. Clutter-tolerant echolocation (that enables the bat to distinguish echoes from prey from those returning from the background vegetation) and manoeuvrable flight are characteristic of many species that forage in dense stands of vegetation (Fenton 1990), but they come at a price. The operating range of signals may be limited and manoeuvrable flight is energetically expensive (Norberg & Rayner 1987, Schnitzler & Kalko 1998), leaving bats ill-suited for prey detection and capture in more open habitats where dispersed, low-density prey distribution necessitates long-range detection capabilities and fast, efficient, agile flight (Neuweiler 1990, Neuweiler & Fenton 1988, Norberg & Rayner 1987, Schnitzler & Kalko 1998). Thus, insectivorous bats of the forest interior are entirely dependent upon

intact expanses of forest and are likely to experience a severe decline in diversity as forest habitats are lost and fragmented. Empirical data support this prediction. Zubaid (1993) reported a greater loss of insectivorous than of frugivorous bat species in a fragmented secondary forest, and species richness of insectivorous bats is similarly impacted by logging in Sumatra and Australia (Danielsen & Heegaard 1995, Law 1996). Pottie (1996) was only able to locate four species of forest-interior bats in Singapore, where extensive urbanization has reduced the remaining forest to fragments (although sampling effort was dominated by the use of mist nets and acoustic monitoring which can result in undersampling of high-frequency Rhinolophoidea and the Kerivoulinae and Murinae). Future work is clearly desirable to provide ecological information necessary to protect this diverse yet vulnerable ensemble of bats.

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Appendix 1. Numbers of individuals captured using various sampling methods for all species of insectivorous bats captured at Kuala Lompat, Krau Wildlife Reserve, 1991–1999. Nomenclature and order of species according to Corbet & Hill (1992), except as indicated in the footnotes. Additions to the species list for Kuala Lompat in Heller & Volleth (1995) are marked with §. TK, captures by T. Kingston; CMF, captures by C. M. Francis; FS, foraging strategy; M, male; F, female.

	Number of captures					
	Capture method			Sex		Foraging strategy ²
	Harp traps		Other ¹	M	F	
	TK	CMF				
Emballonuridae						
<i>Emballonura monticola</i>	4	1	3(m)	3	5	E
Nycteridae						
<i>Nycteris tragata</i> ³	20	4	1(m)	12	13	N
Megadermatidae						
<i>Megaderma spasma</i>	7	2	1(m)1(s)1(h)	6	5	N
Rhinolophidae						
<i>Rhinolophus sedulus</i> §	20	6	1(m)	19	18	N
<i>Rhinolophus trifoliatus</i>	145	50	20(m)1(s)1(v)	114	102	N
<i>Rhinolophus luctus</i>	1	1	2(m)	3	1	N
<i>Rhinolophus macrotis</i>	2				2	N
<i>Rhinolophus refulgens</i> ⁴	256	54	1(m)1(v)	124	187	N
<i>Rhinolophus robinsoni</i> ^{4§}		1			1	N
<i>Rhinolophus stheno</i>	244	72	1(m)2(s)4(v)	140	182	N
<i>Rhinolophus affinis</i>	11	1	1(m)	9	4	N/E
Hipposideridae						
<i>Hipposideros 'bicolor'</i> 131-kHz ^{5§}	21			9	12	N
<i>Hipposideros 'bicolor'</i> 142-kHz	32			5	27	N
<i>Hipposideros 'bicolor'</i> sp. ⁵	83	52		42	91	
<i>Hipposideros cineraceus</i> §	4	1	5(r)	5	5	N
<i>Hipposideros ridleyi</i>	15	4		10	9	N
<i>Hipposideros sabanus</i>	4	2		2	4	N
<i>Hipposideros galeritus</i> §		1			1	
<i>Hipposideros cervinus</i>	208	126		92	242	E/N
<i>Hipposideros lylei</i> §			1(c)			
<i>Hipposideros larvatus</i> §	14	8		2	20	E/N
<i>Hipposideros diadema</i>	55	47	8(m)6(s)1(c)5(v)	83	39	E/N
Vespertilionidae						
<i>Myotis siligorensis</i>		1	1(m)1(h)	2	1	E
<i>Myotis ridleyi</i>	20	29		25	24	E/N
<i>Myotis ater</i> §	9	4		6	7	E/N
<i>Myotis muricola</i> ⁶	2	6		3	5	E/N
<i>Myotis horsfieldii</i> §			1(w)		1	
<i>Myotis hasseltii</i> ^{7§}			2(w)	2		E
<i>Pipistrellus stenopterus</i>			7(w)	2	5	O/E
<i>Glischropus tylopus</i> §	2		2(w)1(f)	1	4	N/E
<i>Hesperotenus blanfordi</i>		9	1(w)	5	5	O
<i>Miniopterus medius</i> §		1		1		
<i>Murina suilla</i>	75	7	1(m)	33	50	N
<i>Murina rozendaali</i> §	1	7		7	1	
<i>Murina aenea</i> §	4	2		3	3	N
<i>Murina cyclotis</i>	46	11		36	21	N
<i>Kerivoula minuta</i> ^{8§}	11	43		46	8	N
<i>Kerivoula intermedia</i>	241	73		134	180	N
<i>Kerivoula pellucida</i> §	136	27	1(m)	74	89	N
<i>Kerivoula papillosa</i>	95	53	1(m)	73	76	N
<i>Kerivoula</i> sp. ^{9§}	10	2		1	11	N
<i>Phoniscus atrox</i>	25	4		16	13	N
<i>Phoniscus jagorii</i> §	3				3	N
Molossidae						
<i>Tadarida mops</i>			4(w)	1	2	O
<i>Tadarida johorensis</i>			2(c) 34(w)	17	19	O
<i>Cheiromeles torquatus</i>			6(w)	2	4	O

¹ Letters refer to capture methods: m, mist nets set at ground level; w, mist nets placed over rivers; s, stacked nets; c, canopy nets; v, vertical nets; f, flicked nets; h, hand net; r, captured at a roost.

² Foraging strategies (N, narrow-space insectivores; E, edge and gap insectivores; O, open-space insectivores) were assigned based on cluster analysis of aspect ratio and relative wing loading (T. Kingston, unpubl. data).

³ Listed as *Nycteris javanica* in Medway (1982) and Heller & Volleth (1995), but assigned to *N. tragata* following Corbet & Hill (1992).

⁴ *Rhinolophus refulgens* and *R. robinsoni* were treated as subspecies of *R. lepidus* and *R. megaphyllus* respectively by Corbet & Hill (1992), but recent genetic analyses (A. Guillén *et al.*, unpubl. data) suggest that they are probably both distinct species, so we have retained the current names which have, in any case, been used in Medway (1982) and other sources.

⁵ Individuals identified externally as *Hipposideros 'bicolor'* comprised two phonic types. These morphologically cryptic, but acoustically divergent species are virtually indistinguishable in the hand, but differ genetically and in echolocation call frequencies (mean values 131 kHz and 142 kHz) (Kingston *et al.* 2001). Individuals for which no echolocation recordings were made are listed as *Hipposideros 'bicolor'* sp.

⁶ *Myotis muricola* was distinguished from *Myotis ater* by smaller size (FA < 36.0 mm, BM < 5.5 g) and/or position of the 2nd upper premolar which is smaller and displaced inwards in *M. ater* such that the 1st and 3rd premolar touch (Francis & Hill 1998).

⁷ *Myotis hasseltii* was differentiated from *Myotis horsfieldii* by the attachment of the wing membrane to the ankle rather than the side of the foot, the presence of a small pad at the base of the thumb, and a small, inwardly displaced second upper premolar. However, no voucher specimens were collected for *M. hasseltii*.

⁸ *Kerivoula intermedia* and *K. minuta* are difficult to differentiate based on external characters, and were separated mainly by body mass (*K. intermedia* > 2.5 g (range: 2.5–5.0 g); *K. minuta* < or = 2.5 g (range: 2.0–2.5 g)).

⁹ *Kerivoula* sp. Represents an undescribed species (Francis *et al.*, unpubl. data).

Appendix 2. Measurements of species of insectivorous bats captured at Kuala Lumpur. See Appendix 1 for notes on nomenclature and taxonomy.

	Measurements ¹			
	Length of forearm (mm)		Body mass (g)	
	M	F	M	F
Emballonuridae				
<i>Emballonura monticola</i>	43.9 (1)	44.2 ± 1.10 42.3–45.5 (5)	5.7 (1)	5.1 ± 0.39 4.7–5.8 (4)
Nycteridae				
<i>Nycteris tragata</i>	49.8 ± 0.96 48.4–51.2 (8)	51.4 ± 1.60 49.0–54.5 (9)	15.4 ± 1.51 12.6–17.0 (8)	17.4 ± 2.08 15.0–22.5 (9)
Megadermatidae				
<i>Megaderma spasma</i>	57.5 ± 1.13 56.2–58.8 (5)	60.5 ± 1.60 57.3–61.7 (5)	23.5 ± 1.21 22.0–25.0 (5)	26.9 ± 3.70 22.0–32.5 (5)
Rhinolophidae				
<i>Rhinolophus sedulus</i>	39.7 ± 1.27 37.6–42.8 (16)	40.8 ± 0.80 39.8–42.2 (6)	7.5 ± 0.38 6.8–8.0 (16)	8.7 ± 0.80 7.5–9.6 (6)
<i>Rhinolophus trifoliatus</i>	50.1 ± 1.61 45.8–53.1 (64)	52.2 ± 1.76 48.1–55.7 (57)	12.6 ± 0.92 10.7–14.5 (63)	14.7 ± 1.20 11.5–18.5 (55)
<i>Rhinolophus luctus</i>	63.4 (1)		26.3 (1)	
<i>Rhinolophus macrotis</i>		46.0 ± 0.50 45.5–46.5 (2)		7.5 ± 0.00 7.5–7.5 (2)
<i>Rhinolophus refulgens</i>	40.3 ± 1.00 38.6–42.8 (70)	40.6 ± 0.90 38.7–43.0 (98)	6.3 ± 0.50* 5.5–7.2 (67)	6.2 ± 0.61 5.0–8.5 (84)
<i>Rhinolophus robinsoni</i>		44.0 (1)		8.7 (1)
<i>Rhinolophus stheno</i>	45.9 ± 1.00** 43.4–48.5 (116)	45.7 ± 0.90 43.4–47.5 (135)	8.7 ± 0.68*** 6.0–10.5 (114)	8.6 ± 0.75 6.5–12.0 (127)
<i>Rhinolophus affinis</i>	49.5 ± 0.88 48.3–51.1 (9)	50.7 ± 0.60 49.9–51.5 (4)	14.1 ± 1.78 11.5–17.0 (9)	13.9 ± 1.11 12.5–15.5 (4)
Hipposideridae				
<i>Hipposideros 'bicolor'</i> 131-kHz	45.2 ± 1.00 43.9–46.9 (9)	45.5 ± 1.00 44.0–47.2 (12)	7.9 ± 0.52 7.0–8.5 (9)	8.2 ± 0.70 7.0–9.0 (12)
<i>Hipposideros 'bicolor'</i> 142-kHz	42.6 ± 0.69 41.3–43.2 (5)	43.5 ± 0.70*** 42.0–45.1 (26)	7.9 ± 0.72 7.3–9.3 (5)	8.0 ± 0.8 6.5–9.5 (24)
<i>Hipposideros cineraceus</i>	38.3 ± 0.97 36.8–39.3 (4)	40.0 ± 0.70 38.9–40.6 (4)	5.6 ± 0.22 5.5–6.0 (4)	5.8 ± 0.3 5.3–6.0 (4)
<i>Hipposideros ridleyi</i>	48.3 ± 0.86 47.4–49.5 (6)	48.6 ± 0.90 47.0–50.2 (7)	9.2 ± 0.9 7.5–10.3 (6)	8.9 ± 0.40 8.5–9.5 (7)
<i>Hipposideros sabanus</i>	33.9 ± 0.30 33.6–34.2 (2)	36.6 ± 0.81 35.6–37.7 (4)	4.0 (1)	4.9 ± 0.36 4.4–5.3 (3)
<i>Hipposideros galeritus</i>		47.4 (1)		7.7 (1)
<i>Hipposideros cervinus</i>	49.0 ± 0.75 47.4–50.6 (32)	49.6 ± 0.80** 47.5–51.9 (83)	9.6 ± 0.93 7.5–11.5 (32)	9.5 ± 1.01 7.8–12.8 (75)
<i>Hipposideros larvatus</i>	58.2 ± 1.20 57.0–59.4 (2)	58.1 ± 1.16 55.6–60.0 (20)	15.5 ± 0.50 15.0–16.0 (2)	16.8 ± 1.19 14.6–19.0 (19)
<i>Hipposideros diadema</i>	84.7 ± 2.28 79.0–89.2 (47)	84.2 ± 2.94 79.5–89.8 (18)	46.9 ± 6.89 30.7–63.7 (47)	42.3 ± 2.90 36.9–47.4 (18)
Vespertilionidae				
<i>Myotis siligorensis</i>	29.3 ± 1.30 28.0–30.6 (2)	31.6 (1)	2.9 ± 0.10 2.8–3.0 (2)	3.3 (1)
<i>Myotis ridleyi</i>	29.6 ± 1.78 27.7–35.0 (20)	29.8 ± 1.30 28.5–34.7 (22)	4.9 ± 0.41* 4.3–5.7 (21)	4.8 ± 0.42 4.2–5.6 (20)
<i>Myotis ater</i>	37.5 ± 0.75 36.2–38.7 (6)	37.4 ± 1.18 35.6–39.4 (7)	6.7 ± 0.80 5.0–7.5 (6)	6.0 ± 0.35 5.5–6.5 (7)
<i>Myotis horsfieldii</i>		37.0 (1)		6.0 (1)
<i>Myotis hasseltii</i>	35.9 ± 1.00 34.9–36.9 (2)		7.4 ± 0.38 7.0–7.8 (2)	
<i>Pipistrellus stenopterus</i>	39.4 ± 0.85 38.5–40.2 (2)	39.4 ± 1.30 37.3–40.9 (5)	19.6 ± 0.88 18.8–20.5 (2)	15.8 ± 0.91 14.3–16.8 (2)
<i>Glischropus tylopus</i>		30.0 ± 0.15 29.8–30.1 (4)		4.8 ± 0.25 4.5–5.0 (4)
<i>Hesperotenus blanfordi</i>	25.9 ± 0.54 25.3–26.8 (5)	26.0 ± 0.30 25.6–26.5 (5)	6.0 ± 0.38 5.5–6.5 (5)	6.6 ± 0.51 6.0–7.4 (3)
<i>Miniopterus medius</i>	43.2 (1)		8.7 (1)	
<i>Murina suilla</i>	29.3 ± 0.70 27.7–31.0(32)	29.8 ± 0.70 28.3–31.0 (21)	3.8 ± 0.50 3.0–5.0 (32)	4.1 ± 0.47 3.0–5.0 (19)
<i>Murina rozendaali</i>	30.1 ± 1.0 28.7–31.7 (7)	30.6 (1)	4.1 ± 0.21 3.8–4.5 (7)	4.8 (1)
<i>Murina aenea</i>	34.6 ± 0.37 34.1–35.0 (3)	36.2 ± 0.54 35.6–36.9 (3)	7.0 ± 0.82 6.0–8.0 (3)	7.2 ± 0.88 6.0–8.0 (3)

Appendix 2. Continued.

	Measurements ¹			
	Length of forearm (mm)		Body mass (g)	
	M	F	M	F
<i>Murina cyclotis</i>	34.8 ± 0.62 33.6–35.9 (28)	37.4 ± 0.88** 35.5–38.7 (20)	7.9 ± 0.57 7.0–9.5 (27)	9.3 ± 0.57*** 8.1–10.5 (20)
<i>Kerivoula minuta</i>	27.2 ± 0.78 25.5–29.6 (46)	27.9 ± 1.64 23.9–28.8 (7)	2.3 ± 0.19 2.0–2.5 (46)	2.4 ± 0.86 2.2–2.5 (7)
<i>Kerivoula intermedia</i>	28.5 ± 0.69 26.6–30.3 (81)	29.8 ± 0.82 28.0–31.7 (118)	3.2 ± 0.33 2.5–4.0 (87)	3.5 ± 0.41 2.5–5.0 (103)
<i>Kerivoula pellucida</i>	30.1 ± 0.70 28.7–31.8 (47)	31.5 ± 0.60* 30.2–32.8 (62)	4.4 ± 0.60 3.0–5.5 (47)	4.6 ± 0.40*** 4.0–5.5 (43)
<i>Kerivoula papillosa</i>	41.0 ± 1.28 37.8–43.6 (62)	41.7 ± 1.59 38.6–44.7 (57)	8.8 ± 1.07 5.6–10.7 (61)	8.8 ± 1.10 6.0–10.7 (52)
<i>Kerivoula</i> sp.	28.7 (1)	30.6 ± 0.54 30.0–31.7 (8)	2.5 (1)	2.9 ± 0.20 2.5–3.0 (5)
<i>Phoniscus atrox</i>	33.1 ± 1.0 30.7–35.7 (15)	34.0 ± 1.17 32.4–35.9 (10)	4.5 ± 0.32 4.0–5.3 (15)	4.9 ± 0.34 4.3–5.3 (9)
<i>Phoniscus jagorii</i>		40.4 ± 1.52 39.1–42.5 (3)		9.6 ± 0.31 9.3–10.0 (3)
Molossidae				
<i>Tadarida mops</i>	43.2 (1)	42.7 ± 1.24 41.0–43.9 (3)	26.7 (1)	24.0 ± 0.82 23.0–25.0 (3)
<i>Tadarida johorensis</i>	45.2 ± 1.02 42.6–46.6 (13)	45.1 ± 2.31 41.5–48.4 (14)	21.5 ± 3.46 16.6–28.8 (13)	23.3 ± 4.55 15.4–28.0 (11)
<i>Cheiromeles torquatus</i>	86.2 (1)	79.4 ± 0.94 78.1–80.1 (3)	185.0 (1)	171.0 ± 16.0 155.0–187.0 (2)

¹ Results of tests that sexes are monomorphic in forearm length and body weight are indicated as: * P < 0.05; ** P < 0.01; *** P < 0.001 and denote the larger sex (tests conducted on all species with a minimum of five individuals of each sex).