

ORIGINAL  
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## Mammals of Borneo – small size on a large island

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### ABSTRACT

**Aim** Island mammals have featured prominently in models of the evolution of body size. Most of these models examine size evolution across a wide range of islands in order to test which island characteristics influence evolutionary pathways. Here, we examine the mammalian fauna of a single island, Borneo, where previous work has detected that some mammal species have evolved a relatively small size. We test whether Borneo is characterized by smaller mammals than adjacent areas, and examine possible causes for the different trajectories of size evolution between different Bornean species.

**Location** Sundaland: Borneo, Sumatra, Java and the Malay/Thai Peninsula.

**Methods** We compared the mammalian body size frequency distributions in the four areas to examine whether the large mammal fauna of Borneo is more depauperate than elsewhere. We measured specimens belonging to 54 mammal species that are shared between Borneo and any of the other areas in order to determine whether there is an intraspecific tendency for Bornean mammals to evolve small body size. Using data on diet, body size and geographical ranges we examine factors that are thought to influence body size.

**Results** Borneo has fewer large mammals than the other areas, but this is not statistically significant. Large Bornean mammals are significantly smaller than their conspecifics in the other regions, while there are no differences between the body sizes of mammals on Sumatra, Java and the Malay/Thai Peninsula. The finding that large mammals show the greatest size difference between Borneo and elsewhere contrasts with some models of size evolution on islands of different areas. Diet does not correlate with the degree of size reduction. Sunda region endemics show a weaker tendency to be small on Borneo than do widespread species.

**Main conclusions** We suggest that soil quality may drive size evolution by affecting primary productivity. On Borneo, where soils are generally poor in nutrients, this may both limit biomass and cause mammals to be reduced in body size. We hypothesize that widespread species respond to low resource abundance by reducing in size, while endemic elements of the fauna have had longer to adjust to local conditions by altering their behaviour, physiology and/or ecology, and are thus similar in size across the region.

### Keywords

Body size, Borneo, distribution, dwarfism, island rule, Java, Malay Peninsula, productivity, Sumatra.

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## INTRODUCTION

Island mammals often differ strikingly in size from their mainland relatives (Hooijer, 1949; Kurten, 1953). Much research effort has concentrated on quantifying size evolution over a large array of islands to examine whether attributes of the colonizing species (e.g. phylogenetic affinity, body size, diet) result in predictable patterns of size evolution (Foster, 1964; Lomolino, 1985; Raia & Meiri, 2006; Meiri *et al.*, 2008). Island attributes such as area, isolation and latitude have been widely studied (Heaney, 1978; Clegg & Owens, 2002; Lomolino, 2005; Meiri *et al.*, 2005a; Meiri, 2007).

Other attributes of islands are often harder to quantify, and are thus more seldom studied. Some attributes, however, may have important and island-specific consequences for size evolution. Recent work suggests that Borneo, the world's third largest island (743,000 km<sup>2</sup>), may be an island where evolution usually favours small size: Meijaard (2004a) found that Bornean sun bears (*Helarctos malayanus*) were significantly smaller than mainland Asian and Sumatran specimens. Similar size trends were found for the greater chevrotain (*Tragulus napu*) (Meijaard & Groves, 2004b) and sambar (*Cervus unicolor*) (Meijaard & Groves, 2004a), with Bornean specimens being much smaller than their conspecifics on Sumatra. Meiri *et al.* (2004) found that among carnivores in general, Bornean forms were smaller than their mainland conspecifics (six species). Still, these size relationships are not consistent across all taxa; for instance the lesser chevrotain (*Tragulus kanchil*) is larger on Borneo than elsewhere (Meijaard & Groves, 2004b).

Available data suggest that Borneo has lower primary productivity and soil nutrient levels than Java and Sumatra (Payne, 1990; Meijaard *et al.*, 2005; Marshall *et al.*, in press; S. A. Wich, A.J. Marshall, G. Fredriksson, N. Ghaffar, M. Leighton, C.P. Yeager, F.Q. Brearley, J. Proctor, M. Heydon & C.P. Van Schaik, unpublished data). Between Borneo and Peninsular Malaysia, which share a similar geological history (Hall, 1998), the differences in productivity are less clear, but may still be substantial, with soils on Peninsular Malaysia being more fertile than those on Borneo and leaf digestibility likewise being greater on the mainland (Waterman *et al.*, 1988).

Perhaps because of these differences in soil quality, Borneo seems to support generally lower population densities and lower biomass per unit area than the adjacent mainland, Sumatra and Java, in diverse vertebrate groups (Waterman *et al.*, 1988; Payne, 1990; Meijaard, 2004b; Wong *et al.*, 2005). Lower population densities may reflect, in part, greater hunting pressure (e.g. Marshall *et al.*, 2006), but comparative resource limitation on Borneo could also limit population densities and body size relative to areas with higher productivity more typical of Java and Sumatra. Although Peninsular Malaysia is similar to Borneo in some geological attributes (Hall & Holloway, 1998), it is connected to the Asian mainland and generally supports higher population densities (Payne, 1990; Meijaard, 2004b).

Here, we test whether Borneo is characterized not only by low population densities but also by smaller numbers of large mammal species, and if body sizes of Bornean mammals are

lower than those on the other large landmasses of the Sunda area. We start by comparing interspecific body size frequency distributions to examine whether Borneo has fewer large species than its near neighbours. We also compare body sizes within species (or species-groups, since some Bornean mammals have recently been classified as distinct species from their closest relatives elsewhere) to see whether Bornean mammals are generally smaller than their conspecifics on the adjacent mainland and nearby large islands (Java and Sumatra).

Specifically, we examine predictions regarding size evolution that will arise if primary production is indeed lower on Borneo. We then test the following predictions regarding the roles of body size and diet in driving the observed patterns of size variation:

- (1) Larger-bodied species may suffer less from resource scarcity since their lower mass-specific metabolic requirements and higher energy reserves allow them to survive periods of reduced food availability (Wheatley, 1982; Lindstedt & Boyce, 1985). Thus, we hypothesize that larger-bodied species will be less affected by the relatively low productivity of Borneo than smaller-bodied species, and therefore that small species will differ more in size between Borneo and adjacent areas whereas large species will be more similar in size. This is consistent with models of size evolution in relation to island area (Heaney, 1978; Lomolino, 1985) that would predict that the largest mammals on Borneo will be larger than those on the smaller islands of Java and Sumatra, and that small-bodied species will be smaller there (the Malay Peninsula may function either as an island or a mainland, and hence predictions are more difficult).
- (2) We hypothesize that body size of species with higher-quality diets would be most affected by resource scarcity and therefore show a more drastic reduction in size on Borneo compared with species with lower-quality diets.

## METHODS

We compared the body size frequency distribution of mammal faunas from Borneo, the Malay Peninsula (south of the Isthmus of Kra), Sumatra and Java, using distribution data from Corbet & Hill (1992), Wilson & Reeder (2005), other literature sources and data from museum specimens. We omitted species that probably represent human introductions (*Lepus nigricollis*, *Mus caroli*, *Mus musculus*, *Mus terricolor*, *Rattus exulans*, *Rattus rattus*, *Rattus norvegicus* and *Bandicota* spp.; Wilson & Reeder, 2005). We used body masses from the literature (mostly from Smith *et al.*, 2003; see Appendix S1 in Supplementary Material). For some species, we were unable to obtain body mass data. For these, we use the average of the log-transformed body masses of all species of a known mass in their genus.

We compared body sizes using the condylobasal lengths (CBL) of skulls from all species that we measured in natural history museums and that were represented both on Borneo and on Sumatra, Java or the Malay Peninsula. Condylobasal length is commonly employed as an index of mammalian body

size, and is known to be measured with little error (Dayan *et al.*, 2002; Meiri *et al.*, 2005b). Because sexual size dimorphism is substantial in some species, we calculated the mean CBL for each gender and then averaged these values, regardless of within-gender sample size. For sexually dimorphic species for which we had measurements for only one gender from a particular region we restricted our inter-regional comparisons to data for that gender only. Sample sizes for different species range from 3 to 170 (mean 39).

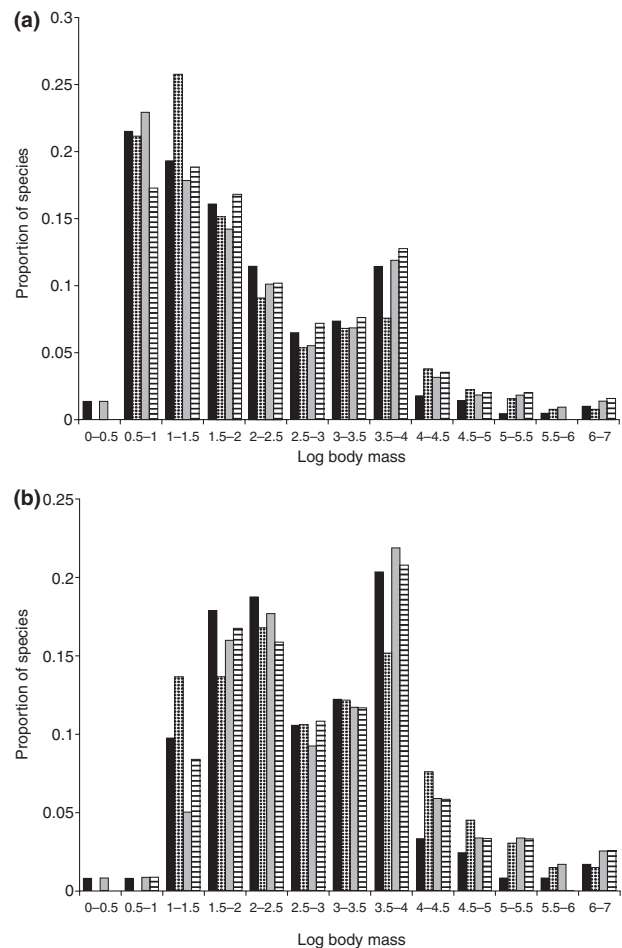
We used two methods to test for size differences between Borneo and other regions. First, for each species (or sister-species pair) we averaged CBL values for all populations outside of Borneo (Java, the Malay Peninsula and Sumatra) from which we had measurements, and then compared these averages with the average CBL on Borneo using a paired *t*-test. In a separate analysis, we calculated the ratio of each population relative to the one with the largest CBL for each species (so where a species was largest the index is 100%). We then compared the relative sizes across all species using a one-way ANOVA.

To explore the role of different biological attributes in promoting size change on Borneo, we used the ratio of CBL on Borneo to CBL where a species is largest as the response variable, and examined whether the degree of size reduction is related to body mass and feeding habits. Body-mass data were taken from the literature (see Appendix S2). We used quantitative data on diets (Payne & Francis 1985; Meijaard *et al.*, 2008) to score, for each species, a 'dietary quality' index as follows:

quality = proportion of leaves in the diet + 2 × proportion of fruit in the diet + 3.5 × proportion of animal food in the diet (Sailer *et al.*, 1985; Leonard & Robertson, 1994). All analyses were conducted using R (R Development Core Team, 2006).

## RESULTS

Our data set included 218 species from Borneo, 218 from the Malay Peninsula, 196 from Sumatra and 132 from Java (see Appendix S1). Average (log-transformed) body mass was lower on Borneo (108 g), than on the Malay Peninsula (144 g) and Sumatra (184 g) but no lower than on Java (106 g). However, these differences were not statistically significant (one-way ANOVA,  $F_{3,760} = 1.42$ ,  $P = 0.23$ ). Results were qualitatively similar when we omitted bats from the analysis (Borneo, 124 species, 551 g; Malay Peninsula, 119 species, 1120 g; Sumatra, 120 species, 885 g; Java, 66 species, 799 g;  $F_{3,425} = 1.39$ ,  $P = 0.24$ ). Examining only the highest quartile of body masses (excluding bats) to see whether Borneo has fewer large mammals yielded no significant results ( $F_{3,105} = 1.43$ ,  $P = 0.24$ ), although Borneo had the lowest mass for this subset (16,600 g vs. 28,300 g on Sumatra, 32,200 g on Java and 42,400 g on the Malay Peninsula). Comparing the body size frequency distribution of mammal species on Borneo with other regions similarly revealed no significant differences (Kolmogorov–Smirnov tests; all mammals: Sumatra,  $d = 0.08$ ,  $P = 0.48$ ; Java,  $d = 0.06$ ,  $P = 0.94$ ; Malay Peninsula,  $d = 0.06$ ,



**Figure 1** Body size distribution of mammalian masses on Borneo, Java, Sumatra and the Malay Peninsula: (a) all mammals, (b) non-volant mammals (excluding bats). The x-axis on a base-10 logarithmic scale (0–0.5 = < 3.1 g; 0.5–1 = 3.1–10 g; 1–1.5 = 10–31 g; 1.5–2 = 32–100 g etc.). The y-axis is the proportion of species in each size class of the total mammalian species in an area (i.e. the number of species in the size class divided by the total number of species). Filled bars, Borneo; squares, Java; grey, Malay Peninsula; stripes, Sumatra. Sample sizes: all mammals, Borneo,  $n = 218$ ; Java,  $n = 132$ ; Sumatra,  $n = 196$ ; Malay Peninsula,  $n = 218$ . Terrestrial mammals, Borneo,  $n = 123$ ; Java,  $n = 66$ ; Sumatra,  $n = 120$ ; Malay Peninsula,  $n = 119$ .

$P = 0.83$ ; terrestrial mammals only: Sumatra,  $d = 0.09$ ,  $P = 0.66$ ; Java,  $d = 0.09$ ,  $P = 0.85$ ; Malay Peninsula,  $d = 0.13$ ,  $P = 0.23$ ; Fig. 1).

### Intraspecific comparisons

Borneo shares 87 mammal species with Java, 142 with Sumatra and 154 with the Malay Peninsula (Appendix S1). Skull measurements of 54 species that are shared between Borneo and at least one of these regions are presented in Appendix S2.

Bornean mammals were significantly smaller than their conspecifics elsewhere, both when we averaged the skull lengths of non-Bornean species (paired *t*-test,  $n = 53$  pairs;

mean difference = 4.97 mm,  $t = 2.84$ ,  $P = 0.006$ ) and when we divided the CBL of each population by the value of the largest population of their species (one-way ANOVA,  $F_{3,158} = 4.58$ ,  $P = 0.004$ ). A *post hoc* Tukey honestly significant difference (HSD) test revealed significant differences between Borneo and Java, and between Borneo and the Malay Peninsula, but not in other comparisons (Table 1).

### Correlates of size differences

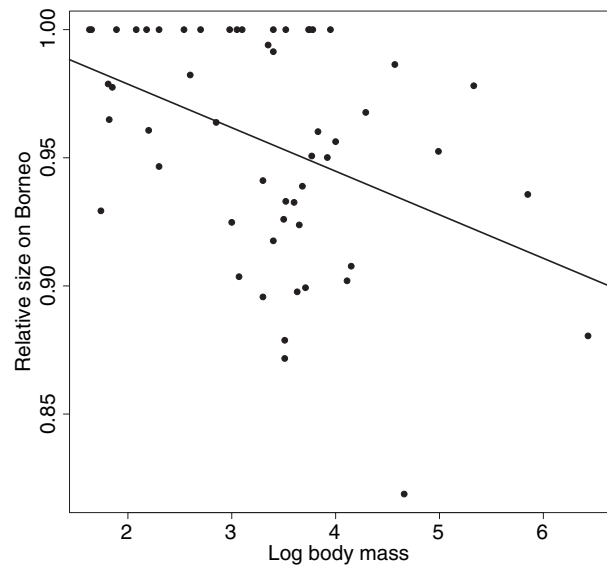
We examined several predictors of body size in Bornean mammals relative to the size of the largest-bodied population on the Sunda Shelf. Body mass was negatively correlated with relative size on Borneo, i.e. larger taxa tend to be relatively smaller there ( $n = 54$ ,  $r = -0.40$ ,  $P = 0.003$ ; Fig. 2), contradicting our first prediction. In fact, small (< 1 kg) mammals are not, on average, smaller on Borneo than elsewhere (controlling for species identity,  $F_{3,31} = 0.26$ ,  $P = 0.86$ ).

Correlations between body mass and relative size for the other regions are all positive but non-significant (Malay Peninsula,  $n = 43$ ,  $r = 0.14$ ,  $P = 0.368$ ; Sumatra,  $n = 45$ ,  $r = 0.07$ ,  $P = 0.631$ ; Java,  $n = 20$ ,  $r = 0.32$ ,  $P = 0.16$ ). Diet is unrelated to the degree of size reduction on Borneo ( $F_{2,51} = 1.20$ ,  $P = 0.31$ ), and dietary index does not correlate with the degree of size reduction ( $n = 51$ ,  $r^2 = 0.006$ ,  $P = 0.59$ ), contradicting our second prediction.

We note an additional pattern that emerged from our analyses: mammals endemic to the Sundaic region are, on average, 97.7% of the maximum size in the region ( $n = 27$ ). However, Bornean populations of mammals with wider distribution in the Oriental Realm are on average relatively smaller: 93.5% of the maximum size ( $n = 27$ ,  $t = 3.96$ ,  $P = 0.0003$ ). When we compare relative sizes of wide-ranging species, we find significant differences between the four areas ( $F_{3,81} = 9.21$ ,  $P < 0.0001$ , mean relative size = 93.5% on Borneo vs. 96.0% on Sumatra, 98.2% on the mainland and 98.3% on Java). A Tukey HSD test found no significant differences between Sumatra, Java and the mainland, but comparisons involving Borneo are nearly (vs. Sumatra,  $P = 0.083$ ) or highly significantly (Borneo vs. the mainland,  $P = 0.0001$ , vs. Java,  $P = 0.0004$ ) different. Comparing endemic Sundaic species in the four areas, however, no significant differences between relative sizes were found ( $F_{3,73} = 0.07$ ,  $P = 0.98$ , mean relative sizes all between 97.3% and 97.8%).

**Table 1** Results of a *post hoc* Tukey honestly significant difference (HSD) test for intraspecific differences in condylobasal length (CBL) between mammals on Borneo, Java, the Malay Peninsula and Sumatra.

Comparison	Difference	Lower 95% confidence limit	Upper 95% confidence limit	<i>P</i>
Java–Borneo	0.025	0.001	0.048	0.034
Malaya–Borneo	0.023	0.005	0.042	0.007
Sumatra–Borneo	0.014	−0.004	0.032	0.198
Malaya–Java	−0.002	−0.026	0.023	0.998
Sumatra–Java	−0.011	−0.035	0.013	0.639
Sumatra–Malaya	−0.009	−0.028	0.010	0.585



**Figure 2** The relative skull size of Bornean mammals (Borneo condylobasal lengths (CBL)/largest CBL in the region) vs. the base-10 logarithm of their body mass (in grams, species-specific data from the literature). Sample sizes: Borneo,  $n = 53$  species; Java,  $n = 20$  species; Sumatra,  $n = 44$  species; Malay Peninsula,  $n = 43$  species.

### DISCUSSION

There is strong evidence that large terrestrial mammals on Borneo are, in general, smaller than their closest relatives on Java, Sumatra and the Malay Peninsula. These latter three areas, on the other hand, show few consistent patterns of size differences between them. Borneo also has fewer species of large mammals than these other regions (Fig. 1), although this is not statistically significant, and its largest mammals are smaller. Neither of the hypotheses we set out to explain this pattern are supported by our data: size reduction is most prominent in large, not small, mammals, and diet does not seem to influence the degree of size difference between Borneo and adjacent regions.

Current theory regarding change in size on islands (e.g. Lomolino, 2005) would not identify Borneo as an island where considerable size evolution would be expected. One of the largest islands in the world, Borneo lies on the Asian continental shelf, maintained a continuous land-bridge connection with the Asian mainland until the Middle Pliocene and

an intermittent connection that subsequently did not disappear until the Late Pleistocene (Meijaard, 2003), and supports a rich and diverse mammalian fauna. It is thus reasonable to expect that similar trophic structuring and competition regimes should characterize the mammalian faunas of Borneo and the mainland. However, one major difference between the two areas is the lack of large predators on Borneo today, which probably means that large mammals on Borneo face lower rates of predation than on Sumatra, Java and Peninsular Malaysia. These latter regions are all inhabited today, or were until recent centuries, by tigers, leopards (absent from Sumatra) and Asian wild dogs – all of which are missing from Borneo (Meijaard, 2004b). Past land connections to Java, Sumatra and the Asian mainland would have provided access to Borneo for any of the large predator species that existed in the region during the Pleistocene (e.g. *Panthera tigris*, *Panthera pardus*, *Hyaena brevirostris*, Merriam's dog *Megacyon merriami*, the dirk-toothed cat *Megantereon* sp., the sabre-toothed cat *Hemimachairodus zwierzyckii* and the scimitar-toothed cat *Homotherium ultimum*). Tigers inhabited Borneo until the Holocene (Piper *et al.*, 2007), but because of Borneo's poor fossil record, it is unclear whether and when other large predators existed there. The evidence suggests that none of the other large predators have survived on Borneo since the Last Glacial Maximum. Release from predation could thus be one factor implicated in dimensional size reduction in Borneo, especially for large species (Heaney, 1978; Raia & Meiri, 2006). The largest carnivore on Borneo is the 20 kg clouded leopard *Neofelis nebulosa* (the sun bear feeds mostly on fruit and insects: Fitzgerald & Krausman, 2002; Fredriksson *et al.*, 2006). Nevertheless, emerging evidence suggests that until the late Pleistocene and, to a lesser extent, until at least the mid Holocene, Borneo's large mammal fauna was considerably richer than it is today (Cranbrook & Piper, 2007; Louys *et al.*, 2007; Piper *et al.*, 2007). To what extent palaeoenvironmental changes, or over-hunting and habitat modification by humans played a role in the extinctions of Borneo's mammals remains unclear. Firmer understanding of ecological mechanisms underlying the relatively small size of mammals in Borneo may help to explain why extinctions of large mammals during the Holocene have been more severe on Borneo relative to smaller landmasses such as Sumatra and Java (Louys *et al.*, 2007).

The Sunda Shelf, of which Borneo, Java and Sumatra are a part, is geologically very active. The land areas of Sumatra and Java on the region's volcanic arc are relatively new, but Borneo is part of the old geological core of the Sunda Shelf, which once connected it to the Thai/Malay Peninsula (Meijaard, 2003). Bornean soils are generally much less fertile than the rich volcanic soils of large parts of neighbouring Java and Sumatra (MacKinnon *et al.*, 1996). Deep complete weathering, combined with leaching, results in soils of low fertility in many of the lowland areas surrounding the central mountain chain in Borneo. The more frequent soil renewal around the active volcanoes of Java and Sumatra results in more productive soils. This is indicated in the predominant agricultural systems. On

Borneo, low soil fertility has predominantly resulted in shifting cultivation with short cropping regimes and long fallows, nomadic hunter-gatherer systems and permanent agriculture in only a few of the most fertile areas, while these permanent systems are much more common in Sumatra, and are the norm on Java. The general productivity of Kalimantan (the Indonesian part of Borneo), Sumatra and Java is reflected in the percentage of total land area suitable for agricultural development, which is respectively 45%, 55% and 93% (Land Resources Department/Bina Program, 1990). It may also affect human population densities which, historically, were much lower on Borneo than on either Sumatra or Java (Mohr, 1938). Clearly, there is within-island variation in the overall productivity patterns, with areas of low productivity on Java and Sumatra, such as the south-eastern limestone of the former and the extensive coastal peat swamps in the latter. Locally poor soils may reduce productivity even in well-watered high-energy regions. It has been hypothesized that overall forest productivity in Borneo is lower than on the mainland (Waterman *et al.*, 1988), and lower than typical of Sumatra and Java, because extensive tectonic activity and volcanism generated more fertile soils on Sumatra and Java (MacKinnon *et al.*, 1996; Delgado & van Schaik, 2000). Although a detailed analysis of overall forest productivity across the Sunda Shelf remains to be conducted, recent multi-site comparisons indicate that forest fruit production is higher on Sumatra than on Borneo (Marshall *et al.*, in press; S. A. Wich *et al.*, unpublished data). The biomass of leaf-eating monkeys (*Presbytis*) is lower on Borneo than on Sumatra, Java and Peninsular Malaysia (Waterman *et al.*, 1988), even though their diversity is higher (Meijaard & Groves, 2004c), further supporting a hypothesis of lower productivity on Borneo (Waterman *et al.*, 1988; Payne, 1990). Furthermore, Borneo lacks three species of common and widespread fruit bats that otherwise occur widely on the Sunda Shelf (*Rousettus leschenaultii*, *Cynopterus titthaechilus* and *Macroglossus sobrinus*), perhaps indicating lower fruit production. Waterman *et al.* (1988) reported lower digestibility of leaves on Borneo relative to that on Peninsular Malaysia, which again may promote size differences. If these findings are indicative of overall forest productivity, this could be an important factor explaining smaller body sizes on Borneo. Overall poor soil productivity may have resulted in low prey biomass (Waterman *et al.*, 1988; Wong *et al.*, 2005), in turn affecting the diversity and abundance of large predators (Meijaard, 2004a,b). This may have resulted in herbivores growing smaller in the face of reduced mortality, causing the remaining predators to grow smaller in turn (Raia & Meiri, 2006, and see Appendix S2 for, e.g., *Neofelis*).

Wong *et al.* (2005) hypothesized that frequent starvation of large Bornean mammals, and overall low large mammal densities on the island may result from high inter-annual variation in fruit abundance. High intra-annual variation in productivity (i.e. high seasonality) has been thought to promote size increase (Lindsey, 1966; Calder, 1974; cf. Meiri *et al.*, 2005c), because large size is associated with a longer time

to starvation. It may be, however, that this mechanism leads to large size where food availability varies between seasons, but that when food availability varies over a longer time-scale (between years) large mammals are at a disadvantage, because of their high overall food requirements (McNab, 1971). Thus, the fact that Java is more seasonal than Borneo (Regional Physical Planning Programme for Transmigration, 1991) but inter-annual variability is higher on Borneo (Wong *et al.*, 2005) may explain why Javan mammals are larger.

Our finding that mammals endemic to the Sundaic region differ less in size between Borneo and other areas, but that mammals with wider distribution in Southeast Asia are smaller on Borneo, provides a possible hint towards a role for resource limitation in size evolution. Most species widely distributed in the Southeast Asian region arrived later on Borneo compared with Sundaic endemics (some of which may have evolved on Borneo; Meijaard, 2003). These widely distributed species also tend to be more ecologically versatile than regionally endemic taxa, usually occurring across a greater range of habitats than Sundaic endemics, which tend to be closely associated with forests (Meijaard *et al.*, 2008). We suggest that this relative ecological flexibility coincides with a tendency towards greater morphological lability (Meiri *et al.*, 2007), and that widespread taxa quickly adapt to the resource-poor local environment of Borneo by reducing their size. Longer-established Sundaic endemics may have adapted to Bornean environmental conditions through trenchant changes in ecology and behaviour (such as diet, physiology or habitat specialization), not just via size change. In other words, size change might be a first step in the adaptation process, followed and tempered by ecological or behavioural change. This suggests that time since isolation should be taken into account when predicting patterns of body size evolution on islands.

In conclusion, while we have shown that large Bornean mammals are smaller than conspecifics elsewhere, the actual mechanism or mechanisms underlying this phenomenon remain speculative. It is also not yet clear whether relatively small body size characterizes other groups of Bornean vertebrates (e.g. birds, reptiles), though sufficient resources to evaluate this point are probably available in museum collections. Continuing examinations of such patterns have a high potential to further our understanding of the reasons for change in mammal size on Borneo, and the mechanisms that promote body size evolution in general.

## ACKNOWLEDGEMENTS

We thank Tamar Dayan and Daniel Simberloff for their support, help and advice. We thank Robert Asher (Museum für Naturkunde, Humboldt Universität zu Berlin), Yang Chang Man and Norman Lim (Raffles Museum of Biodiversity Research), Judith Chupasko (Museum of Comparative Zoology), Judith Eger (Royal Ontario Museum), Thor Holmes (Museum of Natural History, University of Kansas), Paula Jenkins and Daphne Hills (Natural History Museum,

London), Richard Kraft (Zoologische Staatssammlung München), Georges Lenglet (Institut Royal des Sciences Naturelles de Belgique), Suzanne McLaren (Carnegie Museum of Natural History), Adri Rol (University of Amsterdam Zoological Museum), Byrdena Shepherd, Linda Gordon, Don Wilson, and Lauren Helgen (National Museum of Natural History, Smithsonian Institution), Chris Smeenk (National Museum of Natural History 'Naturalis'), William Stanley (Field Museum), Clara Stefen (Staatliche Naturhistorische Sammlungen, Dresden), Ray Symonds (Zoology Museum, Cambridge University), Géraldine Veron (Muséum National d'Histoire Naturelle, Paris) and Darrin Lunde, Nancy Simmons and Eileen Westwig (American Museum of Natural History) for their invaluable help during data collection. We thank Gavin Thomas and Ally Phillimore for advice and discussion. We are grateful to Alison Boyer, Joaquín Hortal and an anonymous referee for important comments on an earlier version of this paper.

## REFERENCES

- Calder, W.A. (1974) Consequences of body size for avian energetics. *Avian energetics* (ed. by R.A. Paynter), pp. 86–151. Nuttall Ornithological Club, Cambridge, MA.
- Clegg, S.M. & Owens, I.P.F. (2002) The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1359–1365.
- Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region*. Oxford University Press, Oxford.
- Cranbrook, Earl of. & Piper, P.J. (2007) The Javan rhinoceros *Rhinoceros sondaicus* in Borneo. *Raffles Bulletin of Zoology*, **55**, 217–220.
- Dayan, T., Wool, D. & Simberloff, D. (2002) Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology*, **28**, 508–526.
- Delgado, R.A. & van Schaik, C.P. (2000) The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. *Evolutionary Anthropology*, **9**, 201–218.
- Fitzgerald, C.S. & Krausman, P.R. (2002) *Helarctos malayanus*. *Mammalian Species*, **696**, 1–5.
- Foster, J.B. (1964) Evolution of mammals on islands. *Nature*, **202**, 234–235.
- Fredriksson, G.M., Wich, S.A. & Trisno (2006) Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. *Biological Journal of the Linnean Society*, **89**, 489–508.
- Hall, R. (1998) The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 99–125. Backhuys Publishers, Leiden.
- Hall, R. & Holloway, J.D. (eds) (1998) *Biogeography and geological evolution of SE Asia*. Backhuys Publishers, Leiden.

- Heaney, L.R. (1978) Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, **32**, 29–44.
- Hooijer, D.A. (1949) Mammalian evolution in the Quaternary of Southern and Eastern Asia. *Evolution*, **3**, 125–128.
- Kurten, B. (1953) On the variation and population dynamics of fossil and recent mammal populations. *Acta Zoologica Fennica*, **76**, 1–122.
- Land Resources Department/Bina Program (1990) *The land resources of Indonesia: a national overview from Regional Planning Programme for Transmigration (RePPPProT)*. Land Resources Department, Natural Resources Institute, Overseas Development Administration, London, UK and Direktorat Bina Program, Direktorat Jenderal Penyiapan Pemukiman, Departemen Transmigrasi, Jakarta, Indonesia.
- Leonard, W.R. & Robertson, M.L. (1994) Evolutionary perspectives on human nutrition: the influence of brain and body size on diet and metabolism. *American Journal of Human Biology*, **6**, 77–88.
- Lindsey, C.C. (1966) Body sizes of poikilotherm vertebrates at different latitudes. *Evolution*, **20**, 456–465.
- Lindstedt, S.L. & Boyce, M.S. (1985) Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, **125**, 873–878.
- Lomolino, M.V. (1985) Body size of mammals on islands: the island rule re-examined. *The American Naturalist*, **125**, 310–316.
- Lomolino, M.V. (2005) Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**, 1683–1699.
- Louys, J., Curnoe, D. & Tong, H. (2007) Characteristics of Pleistocene megafauna extinctions in Southeast Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **243**, 152–173.
- MacKinnon, K., Hatta, G., Halim, H. & Mangalik, A. (1996) *The ecology of Kalimantan*. Periplus Editions Ltd, Hong Kong.
- Marshall, A.J., Nardiyono, Engström, L.M., Pamungkas, B., Palapa, J., Meijaard, E. & Stanley, S.A. (2006) The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. *Biological Conservation*, **129**, 566–578.
- Marshall, A.J., Ancrenaz, M., Brearley, F.Q., Fredriksson, G.M., Ghaffar, N., Heydon, M., Husson, S., Leighton, M., McConkey, K.R., Morrogh-Bernard, H., Proctor, J., van Schaik, C.P., Yaeger, C.P. & Wich, S.A. (in press) The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans: are Sumatran forests better orangutan habitat than Bornean forests? *Orangutans: geographic variation in behavioural ecology* (ed. by S.A. Wich, S.S. Utami Atmoko, T. Mitra Setia and C.P. van Schaik), Oxford University Press, Oxford.
- McNab, B.K. (1971) On the ecological significance of Bergmann's rule. *Ecology*, **52**, 845–854.
- Meijaard, E. (2003) *Solving mammalian riddles. A reconstruction of the Tertiary and Quaternary distribution of mammals and their palaeoenvironments in island South-East Asia*. PhD thesis, Department of Anthropology and Archaeology, Australian National University, Canberra, Australia.
- Meijaard, E. (2004a) Craniometric differences among Malayan sun bears (*Ursus malayanus*); evolutionary and taxonomic implications. *Raffles Bulletin of Zoology*, **52**, 665–672.
- Meijaard, E. (2004b) Biogeographic history of the Javan leopard *Panthera pardus* based on a craniometric analysis. *Journal of Mammalogy*, **85**, 302–310.
- Meijaard, E. & Groves, C.P. (2004a) Morphometrical relationships between South-East Asian Cervinae: evolutionary and biogeographic implications. *Journal of Zoology*, **263**, 179–196.
- Meijaard, E. & Groves, C.P. (2004b) A taxonomic revision of the *Tragulus* mouse-deer (*Artiodactyla*). *Zoological Journal of the Linnean Society*, **140**, 63–102.
- Meijaard, E. & Groves, C.P. (2004c) The biogeographical evolution and phylogeny of the genus *Presbytis*. *Primate Report*, **68**, 71–89.
- Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M.J., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S. & O'Brien, T. (2005) *Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo*. CIFOR, WCS and UNESCO, Bogor Indonesia.
- Meijaard, E., Sheil, D., Marshall, A.J. & Nasi, R. (2008) Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica*, **40**, 76–85.
- Meiri, S. (2007) Size evolution in island lizards. *Global Ecology and Biogeography*, **16**, 702–708.
- Meiri, S., Dayan, T. & Simberloff, D. (2004) Body size of insular carnivores: little support for the island rule. *The American Naturalist*, **163**, 469–479.
- Meiri, S., Dayan, T. & Simberloff, D. (2005a) Area, isolation, and size evolution in insular carnivores. *Ecology Letters*, **8**, 1211–1217.
- Meiri, S., Dayan, T. & Simberloff, D. (2005b) Variability and correlations in carnivore crania and dentition. *Functional Ecology*, **19**, 337–343.
- Meiri, S., Dayan, T. & Simberloff, D. (2005c) Biogeographic patterns in the Western Palearctic: the fasting-endurance hypothesis and the status of Murphy's rule. *Journal of Biogeography*, **32**, 369–375.
- Meiri, S., Yom-Tov, Y. & Geffen, E. (2007) What determines conformity to Bergmann's rule? *Global Ecology and Biogeography*, **16**, 788–794.
- Meiri, S., Cooper, N. & Purvis, A. (2008) The island rule: made to be broken? *Proceedings of the Royal Society B: Biological Sciences*, **275**, 141–148.
- Mohr, E.C.J. (1938) The relation between soil and population density in the Netherlands Indies. *Comptes Rendus du Congrès International du Géographie, Amsterdam, Tome Deuxieme*, **IIIc**, 478–493.

- Payne, J. (1990) Rarity and extinctions of large mammals in Malaysian rainforests. *In harmony with nature* (ed. by Y.S. Kheong and L.S. Win), pp. 310–320. Kuala Lumpur, Malaysia.
- Payne, J. & Francis, C.M. (1985) *A field guide to the mammals of Borneo*. The Sabah Society, World Wildlife Fund Malaysia, Kuala Lumpur.
- Piper, P.J., Cranbrook, Earl of & Rabbet, R.J. (2007) Confirmation of the presence of the tiger *Panthera tigris* (L.) in late Pleistocene and Holocene Borneo. *Malayan Nature Journal*, **59**, 257–265.
- R Development Core Team (2006) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raia, P. & Meiri, S. (2006) The island rule in large mammals: paleontology meets ecology. *Evolution*, **60**, 1731–1742.
- Regional Physical Planning Programme for Transmigration (1991) *Review of Phase 1*. Main report. Land Resources Department ODNRI, Overseas Development Administrator, London, UK and Departemen Transmigrasi, Jakarta, Indonesia.
- Sailer, L.D., Gaulin, S.J., Boster, J.S. & Kurland, J.A. (1985) Measuring the relationship between dietary quality and body size in primates. *Primates*, **26**, 14–27.
- Smith, F.A., Lyons, S.K., Morgan Ernest, S.K., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. & Haskell, J.P. (2003) Body mass of late Quaternary mammals. *Ecology*, **84**, 3403.
- Waterman, P.G., Ross, J.A.M., Bennett, E.L. & Davies, A.G. (1988) A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rainforests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biological Journal of the Linnean Society*, **34**, 1–32.
- Wheatley, B.P. (1982) Energetics of foraging in *Macaca fascicularis* and *Pongo pygmaeus* and a selective advantage of large body size in the orang-utan. *Primates*, **23**, 348–363.
- Wilson, D.E. & Reeder, D.M. (eds) (2005) *Mammal species of the world*, 3rd edn. Johns Hopkins University Press, Baltimore.
- Wong, S.T., Servheen, C., Ambu, L. & Norhayati, A. (2005) Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology*, **21**, 627–639.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Body masses and mammal distribution.

**Appendix S2** Mammal measurements, dietary data and geographical distributions.

This material is available as part of the online article from: <http://www.blackwellsynergy.com/10.1111/j.1365-2699.2008.01897.x> (This link will take you to the article abstract).

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## BIOSKETCH

**Shai Meiri** is interested in the evolution of body size and its implications, biogeographical correlates of morphology and the morphological signatures of speciation and community composition.

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Editor: Lawrence Heaney

## Appendix S1 Body masses and mammal distribution

Order	Family	Species	Log mass	Borneo	Malaya	Sumatra	Java
Artiodactyla	Bovidae	<i>Bos gaurus</i>	5.90		x		
Artiodactyla	Bovidae	<i>Bos javanicus</i>	5.85	x	x		x
Artiodactyla	Bovidae	<i>Naemorhedus sumatraensis</i>	4.94		x	x	
Artiodactyla	Cervidae	<i>Cervus timorensis</i>	4.80				x
Artiodactyla	Cervidae	<i>Cervus unicolor</i>	5.33	x	x	x	
Artiodactyla	Cervidae	<i>Muntiacus atherodes</i>	4.19	x			
Artiodactyla	Cervidae	<i>Muntiacus muntjak</i>	4.15	x	x	x	x
Artiodactyla	Suidae	<i>Sus barbatus</i>	4.99	x	x	x	
Artiodactyla	Suidae	<i>Sus scrofa</i>	5.07		x	x	x
Artiodactyla	Suidae	<i>Sus verrucosus</i>	4.91				x
Artiodactyla	Tragulidae	<i>Tragulus javanicus/kanchil</i>	3.52	x	x	x	x
Artiodactyla	Tragulidae	<i>Tragulus napu</i>	3.77	x	x	x	
Carnivora	Canidae	<i>Cuon alpinus</i>	4.11		x	x	x
Carnivora	Felidae	<i>Catopuma badia</i>	3.40	x			
Carnivora	Felidae	<i>Catopuma temminckii</i>	4.06		x	x	
Carnivora	Felidae	<i>Panthera pardus</i>	4.66		x		x
Carnivora	Felidae	<i>Panthera tigris/sumatrae/sondaica</i>	5.21		x	x	x
Carnivora	Felidae	<i>Pardofelis marmorata</i>	3.51	x	x	x	
Carnivora	Felidae	<i>Neofelis nebulosa/diardi</i>	4.29	x	x	x	
Carnivora	Felidae	<i>Prionailurus bengalensis</i>	3.52	x	x	x	x
Carnivora	Felidae	<i>Prionailurus planiceps</i>	3.83	x	x	x	
Carnivora	Felidae	<i>Prionailurus viverrinus</i>	4.04		x	x	x
Carnivora	Herpestidae	<i>Herpestes brachyurus</i>	3.30	x	x	x	
Carnivora	Herpestidae	<i>Herpestes javanicus</i>	2.88		x		x
Carnivora	Herpestidae	<i>Herpestes semitorquatus</i> <sup>10</sup>	3.50	x		x	
Carnivora	Herpestidae	<i>Herpestes urva</i>	3.27		x		
Carnivora	Mustelidae	<i>Aonyx cinerea</i>	3.60	x	x	x	x
Carnivora	Mustelidae	<i>Arctonyx collaris</i>	3.80		x	x	
Carnivora	Mustelidae	<i>Lutra lutra</i>	4.04		x	x	
Carnivora	Mustelidae	<i>Lutra sumatrana</i>	3.74	x	x	x	
Carnivora	Mustelidae	<i>Lutrogale perspicillata</i>	3.95	x	x	x	x
Carnivora	Mustelidae	<i>Martes flavigula</i>	3.40	x	x	x	x
Carnivora	Mustelidae	<i>Melogale everetti</i> <sup>10</sup>	3.30	x			
Carnivora	Mustelidae	<i>Melogale orientalis</i>	3.30				x
Carnivora	Mustelidae	<i>Mustela lutreolina</i>	2.85			x	x
Carnivora	Mustelidae	<i>Mustela nudipes</i>	2.70	x	x	x	
Carnivora	Mustelidae	<i>Mydaus javanensis</i>	3.40	x		x	x
Carnivora	Ursidae	<i>Helarctos malayanus</i>	4.66	x	x	x	
Carnivora	Viverridae	<i>Arctictis binturong</i>	4.11	x	x	x	x
Carnivora	Viverridae	<i>Arctogalidia trivirgata</i>	3.35	x	x	x	x
Carnivora	Viverridae	<i>Cynogale bennetti</i>	3.65	x	x	x	
Carnivora	Viverridae	<i>Diplogale hosei</i> <sup>10</sup>	3.38	x			
Carnivora	Viverridae	<i>Hemigalus derbyanus</i>	3.40	x	x	x	
Carnivora	Viverridae	<i>Paguma larvata</i>	3.63	x	x	x	
Carnivora	Viverridae	<i>Paradoxurus hermaphroditus</i>	3.51	x	x	x	x
Carnivora	Viverridae	<i>Prionodon linsang</i>	2.85	x	x	x	x
Carnivora	Viverridae	<i>Viverra megaspila</i>	3.97		x		
Carnivora	Viverridae	<i>Viverra tangalunga</i>	4.00	x	x	x	
Carnivora	Viverridae	<i>Viverra zibetha</i>	3.95		x		
Carnivora	Viverridae	<i>Viverricula indica</i>	3.47		x	x	x
Chiroptera	Emballonuridae	<i>Emballonura alecto</i>	0.72	x			
Chiroptera	Emballonuridae	<i>Emballonura monticola</i>	0.73	x	x	x	x
Chiroptera	Emballonuridae	<i>Taphozous longimanus</i>	1.43	x	x	x	x
Chiroptera	Emballonuridae	<i>Taphozous melanopogon</i>	1.44	x	x	x	x
Chiroptera	Emballonuridae	<i>Taphozous saccolaimus</i>	1.64	x	x	x	x

Chiroptera	Emballonuridae	<i>Taphozous theobaldi</i>	1.60	x				x
Chiroptera	Hipposideridae	<i>Aselliscus stoliczkanus</i>	0.69			x		
Chiroptera	Hipposideridae	<i>Coelops frithi</i>	0.87			x	x	x
Chiroptera	Hipposideridae	<i>Coelops robinsoni</i>	0.81	x		x		
Chiroptera	Hipposideridae	<i>Hipposideros armiger</i>	1.72			x		
Chiroptera	Hipposideridae	<i>Hipposideros ater</i>	0.77	x		x	x	x
Chiroptera	Hipposideridae	<i>Hipposideros bicolor</i>	0.88	x		x	x	x
Chiroptera	Hipposideridae	<i>Hipposideros cervinus</i>	0.97	x		x	x	
Chiroptera	Hipposideridae	<i>Hipposideros cineraceus</i>	0.61	x		x	x	
Chiroptera	Hipposideridae	<i>Hipposideros diadema</i>	1.64	x		x	x	x
Chiroptera	Hipposideridae	<i>Hipposideros dyacorum</i> <sup>14</sup>	0.78	x		x		
Chiroptera	Hipposideridae	<i>Hipposideros galeritus</i>	0.95	x		x	x	x
Chiroptera	Hipposideridae	<i>Hipposideros larvatus</i>	1.30	x		x	x	x
Chiroptera	Hipposideridae	<i>Hipposideros lekaguli</i>	1.49			x		
Chiroptera	Hipposideridae	<i>Hipposideros nequam</i> <sup>16</sup>	1.09			x		
Chiroptera	Hipposideridae	<i>Hipposideros pomona</i>	0.79			x		
Chiroptera	Hipposideridae	<i>Hipposideros ridleyi</i>	0.98	x		x		
Chiroptera	Hipposideridae	<i>Hipposideros doriae/ sabanus</i>	0.62	x		x	x	
Chiroptera	Megadermatidae	<i>Megaderma lyra</i>	1.66			x		
Chiroptera	Megadermatidae	<i>Megaderma spasma</i>	1.39	x		x	x	x
Chiroptera	Molossidae	<i>Chaerephon plicata</i>	1.30	x		x	x	x
Chiroptera	Molossidae	<i>Cheiromeles torquatus</i>	2.21	x		x	x	x
Chiroptera	Molossidae	<i>Mops mops</i>	1.49	x		x	x	x
Chiroptera	Molossidae	<i>Mormopterus doriae</i> <sup>16</sup>	0.92				x	
Chiroptera	Molossidae	<i>Otomops formosus</i> <sup>16</sup>	1.54					x
Chiroptera	Molossidae	<i>Tadarida johorensis</i> <sup>8</sup>	1.35			x	x	
Chiroptera	Nycteridae	<i>Nycteris javanica</i>	1.25					x
Chiroptera	Nycteridae	<i>Nycteris tragata</i>	1.16	x		x	x	
Chiroptera	Pteropodidae	<i>Aethalops alecto/aequalis</i>	1.18	x		x	x	x
Chiroptera	Pteropodidae	<i>Balionycteris maculata</i>	1.15	x		x	x	
Chiroptera	Pteropodidae	<i>Chironax melanocephalus</i>	1.25	x		x	x	x
Chiroptera	Pteropodidae	<i>Cynopterus brachyotis</i>	1.50	x		x	x	x
Chiroptera	Pteropodidae	<i>Cynopterus horsfieldi</i>	1.74	x		x	x	x
Chiroptera	Pteropodidae	<i>Cynopterus sphinx</i>	1.64	x		x	x	x
Chiroptera	Pteropodidae	<i>Cynopterus titthaechelus</i>	1.75				x	x
Chiroptera	Pteropodidae	<i>Dyacopterus brooksi</i> <sup>5</sup>	1.95	x			x	
Chiroptera	Pteropodidae	<i>Dyacopterus spadiceus</i> *	1.89	x		x	x	
Chiroptera	Pteropodidae	<i>Eonycteris major</i>	1.86	x				
Chiroptera	Pteropodidae	<i>Eonycteris spelaea</i>	1.75	x		x	x	x
Chiroptera	Pteropodidae	<i>Macroglossus minimus</i>	1.20	x		x	x	x
Chiroptera	Pteropodidae	<i>Macroglossus sobrinus</i>	1.35			x	x	x
Chiroptera	Pteropodidae	<i>Megaerops ecaudatus</i>	1.39	x		x	x	
Chiroptera	Pteropodidae	<i>Megaerops kusnoto</i> <sup>16</sup>	1.39					x
Chiroptera	Pteropodidae	<i>Megaerops wetmorei</i>	1.27	x		x	x	
Chiroptera	Pteropodidae	<i>Penthetor lucasi</i>	1.58	x		x	x	
Chiroptera	Pteropodidae	<i>Pteropus hypomelanus</i>	2.63	x		x	x	
Chiroptera	Pteropodidae	<i>Pteropus vampyrus</i>	3.02	x		x	x	x
Chiroptera	Pteropodidae	<i>Rousettus amplexicaudatus</i>	1.90	x		x	x	x
Chiroptera	Pteropodidae	<i>Rousettus leschenaultii</i>	1.99			x	x	x
Chiroptera	Pteropodidae	<i>Rousettus spinalatus</i>	1.96	x			x	
Chiroptera	Rhinolophidae	<i>Rhinolophus acuminatus</i>	1.07	x		x	x	x
Chiroptera	Rhinolophidae	<i>Rhinolophus affinis</i>	1.15	x		x	x	x
Chiroptera	Rhinolophidae	<i>Rhinolophus arcuatus</i>	0.94	x			x	
Chiroptera	Rhinolophidae	<i>Rhinolophus borneensis</i> <sup>14</sup>	0.90	x		x		x
Chiroptera	Rhinolophidae	<i>Rhinolophus canuti</i> <sup>16</sup>	1.01					x
Chiroptera	Rhinolophidae	<i>Rhinolophus celebensis</i> <sup>16</sup>	1.01					x
Chiroptera	Rhinolophidae	<i>Rhinolophus coelophyllus</i>	0.85			x		
Chiroptera	Rhinolophidae	<i>Rhinolophus creaghi</i> <sup>14</sup>	1.08	x				
Chiroptera	Rhinolophidae	<i>Rhinolophus lepidus</i>	0.76			x	x	
Chiroptera	Rhinolophidae	<i>Rhinolophus luctus</i>	1.53	x		x	x	x

Chiroptera	Rhinolophidae	<i>Rhinolophus macrotis</i>	0.79		x	x		
Chiroptera	Rhinolophidae	<i>Rhinolophus malayanus</i>	0.83		x			
Chiroptera	Rhinolophidae	<i>Rhinolophus marshalli</i>	0.70		x			
Chiroptera	Rhinolophidae	<i>Rhinolophus megaphyllus</i>	1.00		x			
Chiroptera	Rhinolophidae	<i>Rhinolophus pearsonii</i>	1.07		x			
Chiroptera	Rhinolophidae	<i>Rhinolophus philippinensis</i>	1.03	x				
Chiroptera	Rhinolophidae	<i>Rhinolophus pusillus</i>	0.71	x	x	x	x	x
Chiroptera	Rhinolophidae	<i>Rhinolophus stheno</i>	0.90		x	x	x	x
Chiroptera	Rhinolophidae	<i>Rhinolophus trifolius</i>	1.17	x	x	x	x	x
Chiroptera	Rhinopomatidae	<i>Rhinopoma microphyllum</i>	1.45				x	
Chiroptera	Vespertilionidae	<i>Glischropus javanus</i> <sup>16</sup>	0.65					x
Chiroptera	Vespertilionidae	<i>Glischropus tylopus</i>	0.65	x	x	x		
Chiroptera	Vespertilionidae	<i>Harpiocephalus harpia/mordax</i>	1.13	x	x	x		x
Chiroptera	Vespertilionidae	<i>Hesperoptenus blanfordi</i>	0.83	x	x			
Chiroptera	Vespertilionidae	<i>Hesperoptenus doriae</i> <sup>16</sup>	1.18	x	x			
Chiroptera	Vespertilionidae	<i>Hesperoptenus tomesi</i>	1.49	x	x			
Chiroptera	Vespertilionidae	<i>Phoniscus / Kerivoula atrox</i>	0.68	x	x	x		x
Chiroptera	Vespertilionidae	<i>Kerivoula flora</i>	0.77	x				
Chiroptera	Vespertilionidae	<i>Kerivoula hardwickei</i>	0.66	x	x	x		x
Chiroptera	Vespertilionidae	<i>Kerivoula intermedia</i> <sup>14</sup>	0.54	x	x			
Chiroptera	Vespertilionidae	<i>Phoniscus / Kerivoula jagorii</i>	0.67	x	x			x
Chiroptera	Vespertilionidae	<i>Kerivoula minuta</i>	0.31	x	x			
Chiroptera	Vespertilionidae	<i>Kerivoula papillosa</i>	1.00	x	x	x		x
Chiroptera	Vespertilionidae	<i>Kerivoula pellucida</i>	0.61	x	x	x		x
Chiroptera	Vespertilionidae	<i>Kerivoula picta</i>	0.65	x	x	x		x
Chiroptera	Vespertilionidae	<i>Kerivoula whiteheadi</i>	0.52	x	x			
Chiroptera	Vespertilionidae	<i>Miniopterus australis</i>	0.86	x				x
Chiroptera	Vespertilionidae	<i>Miniopterus magnater</i>	1.15	x	x	x		x
Chiroptera	Vespertilionidae	<i>Miniopterus medius</i>	1.03	x	x			x
Chiroptera	Vespertilionidae	<i>Miniopterus pusillus</i>	0.94	x	x	x		x
Chiroptera	Vespertilionidae	<i>Miniopterus schreibersii</i>	1.06	x	x	x		x
Chiroptera	Vespertilionidae	<i>Murina aenea</i>	0.88	x	x			
Chiroptera	Vespertilionidae	<i>Murina cyclotis</i>	0.96	x	x	x		
Chiroptera	Vespertilionidae	<i>Murina rozendaali</i> <sup>14</sup>	0.65	x	x			
Chiroptera	Vespertilionidae	<i>Murina suilla</i>	0.60	x	x	x		x
Chiroptera	Vespertilionidae	<i>Myotis adversus</i>	1.02	x	x	x		x
Chiroptera	Vespertilionidae	<i>Myotis formosus</i>	0.85		x	x		x
Chiroptera	Vespertilionidae	<i>Myotis hasseltii</i>	0.94	x	x	x		x
Chiroptera	Vespertilionidae	<i>Myotis hermani</i>	0.85			x		
Chiroptera	Vespertilionidae	<i>Myotis horsfieldii</i>	0.78	x	x			x
Chiroptera	Vespertilionidae	<i>Myotis macrotarsus</i>	1.10	x				
Chiroptera	Vespertilionidae	<i>Myotis montivagus</i>	0.92	x	x			
Chiroptera	Vespertilionidae	<i>Myotis muricola</i>	0.65	x	x	x		x
Chiroptera	Vespertilionidae	<i>Myotis ridleyi</i>	0.60	x	x	x		
Chiroptera	Vespertilionidae	<i>Myotis siligorensis</i>	0.47	x	x			
Chiroptera	Vespertilionidae	<i>Philetor brachypterus</i>	1.06	x	x	x		
Chiroptera	Vespertilionidae	<i>Pipistrellus ceylonicus</i>	0.92	x				
Chiroptera	Vespertilionidae	<i>Pipistrellus / Arielulus circumdatus</i>	1.02		x			x
Chiroptera	Vespertilionidae	<i>Pipistrellus cuprosus</i>	0.74	x				
Chiroptera	Vespertilionidae	<i>Pipistrellus/Hypsugo imbricatus</i>	0.75	x				x
Chiroptera	Vespertilionidae	<i>Pipistrellus javanicus</i>	0.72	x	x	x		x
Chiroptera	Vespertilionidae	<i>Pipistrellus/Hypsugo kitcheneri</i> <sup>16</sup>	0.76	x				
Chiroptera	Vespertilionidae	<i>Pipistrellus/Hypsugo macrotis</i> <sup>16</sup>	0.76		x	x		
Chiroptera	Vespertilionidae	<i>Pipistrellus/Falsistrellus mordax</i> <sup>16</sup>	0.76					x

Chiroptera	Vespertilionidae	<i>Pipistrellus petersi</i> <sup>14</sup>	0.81	x				
Chiroptera	Vespertilionidae	<i>Pipistrellus / Arielulus societatis</i> <sup>16</sup>	0.76			x		
Chiroptera	Vespertilionidae	<i>Pipistrellus stenopterus</i>	1.18	x	x		x	
Chiroptera	Vespertilionidae	<i>Pipistrellus tenuis</i>	0.67	x	x		x	x
Chiroptera	Vespertilionidae	<i>Pipistrellus /Hypsugo vordermanni</i> <sup>14</sup>	0.78	x				
Chiroptera	Vespertilionidae	<i>Scotophilus kuhlii</i>	1.36	x	x		x	x
Chiroptera	Vespertilionidae	<i>Tylonycteris pachypus</i>	0.55	x	x		x	x
Chiroptera	Vespertilionidae	<i>Tylonycteris robustula</i>	0.89	x	x		x	x
Dermoptera	Cynocephalidae	<i>Galeopterus / Cynocephalus variegatus</i>	3.00	x	x		x	x
Insectivora/Erinaceomorpha	Erinacidae	<i>Echinosorex gymnurus</i>	2.98	x	x		x	
Insectivora/Erinaceomorpha	Erinacidae	<i>Hylomys parvus</i> <sup>24</sup>	1.63				x	
Insectivora/Erinaceomorpha	Erinacidae	<i>Hylomys suillus</i>	1.81	x	x		x	x
Insectivora/ Soricomorpha	Soricidae	<i>Chimarrogale phaeura / hantu/sumatrana</i> <sup>16</sup>	1.61	x	x		x	
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura attenuata</i> <sup>6</sup>	0.87			x		x
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura beccarii</i> <sup>16</sup>	1.02				x	
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura fuliginosa/baluensis/orientalis</i>	1.08	x	x		x	x
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura foetida</i> <sup>16</sup>	1.02	x				
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura hutani</i> <sup>16</sup>	1.02				x	
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura malayana</i> <sup>16</sup>	1.02			x		
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura maxi</i> <sup>16</sup>	1.02					x
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura monticola</i> <sup>16</sup>	1.02	x	x			x
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura neglecta</i> <sup>16</sup>	1.02				x	x
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura negligens</i> <sup>16</sup>	1.02			x		
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura paradoxura</i> <sup>16</sup>	1.02				x	x
Insectivora/ Soricomorpha	Soricidae	<i>Crocidura vosmaeri</i> <sup>16</sup>	1.02				x	
Insectivora/ Soricomorpha	Soricidae	<i>Suncus ater</i> <sup>16</sup>	0.80	x				
Insectivora/ Soricomorpha	Soricidae	<i>Suncus etruscus</i>	0.37	x	x			
Insectivora/ Soricomorpha	Soricidae	<i>Suncus murinus</i>	1.83	x	x		x	x
Insectivora/ Soricomorpha	Talpidae	<i>Talpa/ Euroscaptor micrura</i>	1.78			x		
Lagomorpha	Leporidae	<i>Nesolagus netscheri</i>	3.18				x	
Perissodactyla	Rhinocerotidae	<i>Dicerorhinus sumatrensis</i>	6.10	x	x		x	
Perissodactyla	Rhinocerotidae	<i>Rhinoceros sondaicus</i>	6.24			x	x	x
Perissodactyla	Tapiridae	<i>Tapirus indicus</i>	5.47			x	x	
Pholidota	Manidae	<i>Manis javanica</i>	3.71	x	x		x	x
Primates	Cercopithecidae	<i>Macaca arctoides</i>	3.70			x		
Primates	Cercopithecidae	<i>Macaca fascicularis</i>	3.68	x	x		x	x
Primates	Cercopithecidae	<i>Macaca nemestrina</i>	3.78	x	x		x	
Primates	Cercopithecidae	<i>Nasalis larvatus</i>	3.95	x				
Primates	Cercopithecidae	<i>Presbytis comata</i>	3.80					x
Primates	Cercopithecidae	<i>Presbytis femoralis/ chrysomelas/siamensis</i>	3.85	x	x		x	
Primates	Cercopithecidae	<i>Presbytis frontata</i>	3.78	x				
Primates	Cercopithecidae	<i>Presbytis hosei</i>	3.81	x				
Primates	Cercopithecidae	<i>Presbytis melalophos</i>	3.80				x	
Primates	Cercopithecidae	<i>Presbytis rubicunda</i>	3.80	x				
Primates	Cercopithecidae	<i>Presbytis thomasi</i>	3.83				x	
Primates	Cercopithecidae	<i>Trachypithecus auratus</i>	3.85					x
Primates	Cercopithecidae	<i>Trachypithecus cristatus</i>	3.92	x	x		x	
Primates	Cercopithecidae	<i>Trachypithecus obscurus</i>	3.81			x		
Primates	Hominidae	<i>Pongo pygmaeus/abelii</i>	4.57	x			x	
Primates	Hylobatidae	<i>Hylobates agilis/albibarbis</i>	3.75	x	x		x	
Primates	Hylobatidae	<i>Hylobates lar</i>	3.69			x	x	
Primates	Hylobatidae	<i>Hylobates moloch</i>	3.81					x
Primates	Hylobatidae	<i>Hylobates muelleri</i>	3.74	x				

Primates	Hylobatidae	<i>Hylobates / Symphalangus syndactylus</i>	4.00		x		x	
Primates	Lorisidae	<i>Nycticebus coucang/ javanicus/menagensis</i>	3.07	x		x		x
Primates	Tarsiidae	<i>Tarsius bancanus</i>	1.89	x			x	
Proboscidea	Elephantidae	<i>Elephas maximus</i>	6.43	x		x		x
Rodentia	Hystricidae	<i>Atherurus macrourus</i>	3.30			x		
Rodentia	Hystricidae	<i>Hystrix brachyura</i>	3.90	x		x		x
Rodentia	Hystricidae	<i>Hystrix crassispinis</i>	3.90	x				
Rodentia	Hystricidae	<i>Hystrix javanica</i>	4.36					x
Rodentia	Hystricidae	<i>Hystrix sumatrae</i> <sup>15</sup>	3.66				x	
Rodentia	Hystricidae	<i>Trichys fasciculata</i>	3.19	x		x		x
Rodentia	Muridae	<i>Berylmys bowersi</i>	2.48			x		x
Rodentia	Muridae	<i>Chiropodomys gliroides/pusillus</i>	1.40	x		x		x
Rodentia	Muridae	<i>Chiropodomys major</i> <sup>13</sup>	1.60	x				
Rodentia	Muridae	<i>Chiropodomys muroides</i> <sup>12</sup>	1.21	x				
Rodentia	Muridae	<i>Haeromys margaretae</i> <sup>12</sup>	1.10	x				
Rodentia	Muridae	<i>Haeromys pusillus</i>	1.02	x				
Rodentia	Muridae	<i>Hapalomys longicaudatus</i>	1.85			x		
Rodentia	Muridae	<i>Kadarsanomys sodyi</i> <sup>12</sup>	2.30					x
Rodentia	Muridae	<i>Lenothrix canus</i>	2.08	x		x		
Rodentia	Muridae	<i>Leopoldamys edwardsi/ciliatus</i>	2.48			x		x
Rodentia	Muridae	<i>Leopoldamys sabanus</i>	2.54	x		x		x
Rodentia	Muridae	<i>Maxomys alticola</i> <sup>14</sup>	1.95	x				
Rodentia	Muridae	<i>Maxomys baeodon</i> <sup>17</sup>	1.85	x				
Rodentia	Muridae	<i>Maxomys bartelsii</i> <sup>2</sup>	1.97					x
Rodentia	Muridae	<i>Maxomys hylomyoides</i> <sup>16</sup>	2.02				x	
Rodentia	Muridae	<i>Maxomys inas</i>	1.95			x		
Rodentia	Muridae	<i>Maxomys inflatus</i>	1.95				x	
Rodentia	Muridae	<i>Maxomys ochraceiventer</i> <sup>14</sup>	1.99	x				
Rodentia	Muridae	<i>Maxomys rajah</i>	2.18	x		x		x
Rodentia	Muridae	<i>Maxomys surifer</i>	2.14	x		x		x
Rodentia	Muridae	<i>Maxomys whiteheadi</i>	1.74	x		x		x
Rodentia	Muridae	<i>Mus cervicolor</i> <sup>1</sup>	1.23				x	x
Rodentia	Muridae	<i>Mus crociduroides</i> <sup>18</sup>	1.30				x	
Rodentia	Muridae	<i>Mus vulcani</i> <sup>9</sup>	1.31					x
Rodentia	Muridae	<i>Niviventer cremoriventer</i>	1.82	x		x		x
Rodentia	Muridae	<i>Niviventer fulvescens</i>	1.90			x		x
Rodentia	Muridae	<i>Niviventer lepturus</i> <sup>16</sup>	1.93					x
Rodentia	Muridae	<i>Niviventer rapit//cameroni/fraternus</i> <sup>16</sup>	1.93	x		x		x
Rodentia	Muridae	<i>Pithecheir melanurus</i> <sup>12</sup>	2.03					x
Rodentia	Muridae	<i>Pithecheir parvus</i> <sup>12</sup>	2.03			x		
Rodentia	Muridae	<i>Pithecheirops otion</i> <sup>22</sup>	2.03	x				
Rodentia	Muridae	<i>Rattus annandalei</i>	2.30			x		x
Rodentia	Muridae	<i>Rattus argentiventer</i>	2.12	x		x		x
Rodentia	Muridae	<i>Rattus baluensis</i>	2.03	x				
Rodentia	Muridae	<i>Rattus blangorum</i> <sup>23</sup>	2.06				x	
Rodentia	Muridae	<i>Rattus hoogerwerfi</i> <sup>16</sup>	2.16				x	
Rodentia	Muridae	<i>Rattus korinchi</i> <sup>21</sup>	2.00				x	
Rodentia	Muridae	<i>Rattus tiomanicus</i>	2.11	x		x		x
Rodentia	Muridae	<i>Sundamys infraluteus</i>	2.62	x			x	
Rodentia	Muridae	<i>Sundamys maxi</i> <sup>16</sup>	2.57					x
Rodentia	Muridae	<i>Sundamys muelleri</i>	2.52	x		x		x
Rodentia	Sciuridae	<i>Aeromys tephromelas</i>	3.10	x		x		x
Rodentia	Sciuridae	<i>Callosciurus adamsi</i>	2.13	x				
Rodentia	Sciuridae	<i>Callosciurus baluensis</i> <sup>12</sup>	2.55	x				
Rodentia	Sciuridae	<i>Callosciurus caniceps</i>	2.38			x		

Rodentia	Sciuridae	<i>Callosciurus erythraeus</i>	2.45		x			
Rodentia	Sciuridae	<i>Callosciurus nigrovittatus</i>	2.31		x		x	x
Rodentia	Sciuridae	<i>Callosciurus notatus</i>	2.31	x	x		x	x
Rodentia	Sciuridae	<i>Callosciurus orestes</i> <sup>12</sup>	2.44	x				
Rodentia	Sciuridae	<i>Callosciurus prevostii</i>	2.60	x	x		x	
Rodentia	Sciuridae	<i>Dremomys everetti</i>	2.11	x				
Rodentia	Sciuridae	<i>Dremomys rufigenis</i>	2.30			x		
Rodentia	Sciuridae	<i>Exilisciurus exilis</i>	1.28	x				
Rodentia	Sciuridae	<i>Exilisciurus whiteheadi</i>	1.30	x				
Rodentia	Sciuridae	<i>Glyphotes simus</i> <sup>21</sup>	1.71	x				
Rodentia	Sciuridae	<i>Hylopetes bartelsi</i> <sup>7</sup>	1.94					x
Rodentia	Sciuridae	<i>Hylopetes lepidus</i>	1.70	x	x		x	x
Rodentia	Sciuridae	<i>Hylopetes spadiceus</i>	1.70	x	x		x	
Rodentia	Sciuridae	<i>Hylopetes winstoni</i> <sup>12</sup>	1.97				x	
Rodentia	Sciuridae	<i>Iomys horsfieldii</i>	2.08	x	x		x	x
Rodentia	Sciuridae	<i>Lariscus hosei</i>	2.26	x				
Rodentia	Sciuridae	<i>Lariscus insignis</i>	2.30	x	x		x	x
Rodentia	Sciuridae	<i>Menetes berdmorei</i> <sup>11</sup>	2.29			x		
Rodentia	Sciuridae	<i>Nannosciurus melanotis</i> <sup>14</sup>	1.30	x			x	x
Rodentia	Sciuridae	<i>Petaurillus emiliae</i> <sup>7</sup>	1.13	x				
Rodentia	Sciuridae	<i>Petaurillus hosei</i> <sup>7</sup>	1.32	x	x			
Rodentia	Sciuridae	<i>Petaurista elegans</i>	2.98	x	x		x	x
Rodentia	Sciuridae	<i>Petaurista petaurista</i>	3.13	x	x		x	x
Rodentia	Sciuridae	<i>Petinomys genibarbis</i>	2.04	x	x		x	x
Rodentia	Sciuridae	<i>Petinomys hageni</i> <sup>7</sup>	2.59	x			x	
Rodentia	Sciuridae	<i>Petinomys setosus</i> <sup>7</sup>	1.65	x	x		x	
Rodentia	Sciuridae	<i>Petinomys vordermanni</i> <sup>7</sup>	1.63	x	x			
Rodentia	Sciuridae	<i>Pteromyscus pulverulentus</i>	2.60	x	x		x	
Rodentia	Sciuridae	<i>Ratufa affinis</i>	3.05	x	x		x	
Rodentia	Sciuridae	<i>Ratufa bicolor</i>	3.31			x	x	x
Rodentia	Sciuridae	<i>Rheithrosciurus macrotis</i>	3.09	x				
Rodentia	Sciuridae	<i>Rhinosciurus laticaudatus</i>	2.34	x	x		x	
Rodentia	Sciuridae	<i>Sundasciurus brookei</i>	2.06	x				
Rodentia	Sciuridae	<i>Sundasciurus hippurus</i>	2.70	x	x		x	
Rodentia	Sciuridae	<i>Sundasciurus jentinki</i> <sup>16</sup>	2.19	x				
Rodentia	Sciuridae	<i>Sundasciurus lowei</i>	1.95	x	x		x	
Rodentia	Sciuridae	<i>Sundasciurus tenuis</i>	1.88	x	x		x	
Rodentia	Sciuridae	<i>Tamiops mccllellandii</i>	1.74			x		
Rodentia	Spalacidae	<i>Rhizomys pruinosus</i>	3.39			x		
Rodentia	Spalacidae	<i>Rhizomys sumatrensis</i>	2.40			x		x
Scandentia	Tupaiaidae	<i>Dendrogale melanura</i>	1.78	x				
Scandentia	Tupaiaidae	<i>Ptilocercus lowii</i>	1.63	x	x		x	
Scandentia	Tupaiaidae	<i>Tupaia dorsalis</i> <sup>16</sup>	2.15	x				
Scandentia	Tupaiaidae	<i>Tupaia glis/longipes/hypochrysa</i>	2.20	x	x		x	x
Scandentia	Tupaiaidae	<i>Tupaia gracilis</i>	1.87	x				
Scandentia	Tupaiaidae	<i>Tupaia javanica</i> <sup>4</sup>	1.78				x	x
Scandentia	Tupaiaidae	<i>Tupaia minor</i>	1.85	x	x		x	
Scandentia	Tupaiaidae	<i>Tupaia montana</i>	2.45	x				
Scandentia	Tupaiaidae	<i>Tupaia picta</i> <sup>14</sup>	2.17	x				
Scandentia	Tupaiaidae	<i>Tupaia splendidula</i> <sup>14</sup>	2.20	x				
Scandentia	Tupaiaidae	<i>Tupaia tana</i>	2.30	x			x	

### Region and body mass data

Mass data are from Smith *et al.*, 2003 (Smith, F. A., Lyons, S. K., Morgan Ernest, S. K.,

Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H. & Haskell, J. P.

(2003) Body mass of late Quaternary mammals. *Ecology*, **84**, 3403) unless otherwise indicated, and are not necessarily based upon Bornean specimens.

x = species present.

Log mass: log 10 of body mass in grams.

average genus mass: mean of log transformed data of congenics with known mass (mostly from Smith *et al.*, 2003).

\* Distribution and taxonomy of *Dyacopterus* after Helgen *et al.* (2007).

#### Additional mass sources

1. Auffray, J. C., Orth, A., Catalan, J., Gonzalez, J-P., Desmarais, E. & Bonhomme, F. (2003) Phylogenetic position and description of a new species of subgenus *Mus* (Rodentia, Mammalia) from Thailand. *Zoologica Scripta*, **32**, 119–127.
2. Breed, W. G. (2004) The spermatozoon of Eurasian murine rodents: Its morphological diversity and evolution. *Journal of Morphology*, **261**, 52- 69.
3. Breed, W. G. & Taylor, J. (2000) Body mass, testes mass and sperm size in murine rodents. *Journal of Mammalogy*, **81**, 758-768.
4. Campbell, C. B. G. (1966) The relationships of the tree shrews: the evidence of the nervous system. *Evolution*, **20**, 276-281.
5. Helgen, K. M., Kock, D., Gomez, R. K. S. C., Ingle, N. R. & Sinaga, M. H. (2007) Taxonomy and natural history of the Southeast Asian fruit-bat genus *Dyacopterus*. *Journal of Mammalogy*, **88**, 302–318.
6. Innes D. G. L. (1994) Life histories of the Soricidae: a review. *Advances in the biology of shrews, special publication no. 18* (ed. by J.F. Merritt, G.L. Kirkland, G. L. and R.K. Rose), pp. 111-136. Carnegie Museum of Natural History, Pittsburgh.

7. Jackson, S. M. (1999) Glide angle in the genus *Petaurus* and a review of gliding in mammals. *Mammal Review*, **30**, 9-30.
8. Kingston, T., Francis, C. M., Akbar, Z. & Kunz, T. H. (2003) Species richness in an insectivorous bat assemblage from Malaysia. *Journal of Tropical Ecology*, **19**, 67–79.
9. Marshall, J. T. (1977) A synopsis of Asian species of *Mus* (Rodentia, Muridae). *Bulletin of the American Museum of Natural History*, **158**, 173-220.
10. Meiri, S., Simberloff, D. & Dayan, T. (2005) Insular carnivore biogeography: Island area and mammalian optimal body size. *American Naturalist*, **165**, 505-514.
11. Nowak, R. M. (1999) *Walker's "Mammals of the world"*, 6<sup>th</sup> edn. Johns Hopkins University Press, Baltimore.
12. Soligo, C. & Martin, R. D. 2006. Adaptive origins of primates revisited. *Journal of Human Evolution*, **50**, 414-430.
13. Wells, K., Pfeiffer, M., Lakim, M. B. & Linsenmair, K. E. (2004) Arboreal spacing patterns of the Large pencil-tailed tree mouse *Chiropodomys major* in a rainforest in Sabah, Malaysia. *Ecotropica*, **10**, 15-22.
14. Yasuma, S., Andau, M., Apin, L., Yu, F. T. Y. & Kimsui, L. (2003) *Identification keys to the mammals of Borneo. Insectivora, Scandentia, Rodentia Chiroptera*. BBEC, Kota Kinabalu, Sabah.
15. [www.answers.com](http://www.answers.com)
16. average genus mass (see text)
17. Meijaard, unpublished
18. Similar to *M. vulcani*, E. Meijaard, unpublished
19. [http://www.aciar.gov.au/web.nsf/att/JFRN-6BN9BN/\\$file/mn100-part3.pdf](http://www.aciar.gov.au/web.nsf/att/JFRN-6BN9BN/$file/mn100-part3.pdf)
20. Similar to *R. tiomanicus*, E. Meijaard, unpublished

21. Bornean Biodiversity & Ecosystems Conservation.  
[www.bbec.sabah.gov.my/overall/bbec25/page%2038-139.pdf](http://www.bbec.sabah.gov.my/overall/bbec25/page%2038-139.pdf)
22. Similar to *Pithecheir parvus*, K. Helgen, unpublished
23. About 10% smaller than *Rattus tiomanicus*, K. Helgen, unpublished
24. <http://www.indonesianfauna.com/dwarfgymnure.php>

## Appendix S2 Mammal measurements, dietary data and geographic distributions

Order	Species	sex	Borneo	Malaya	Sumatra	Java	diet	% leaves in diet	% fruit in diet	% animal in diet	distribution
Artiodactyla	<i>Bos javanicus</i>	male	429.35	ns	ns	458.85	herbivore	100	0	0	SE Asia
Artiodactyla	<i>Muntiacus muntjak</i>	female	176.29	ns	184.28	194.21	herbivore	50	50	0	SE Asia
Artiodactyla	<i>Rusa (Cervus) unicolor</i>	both	332.75	ns	340.19	ns	herbivore	80	20	0	SE Asia
Artiodactyla	<i>Sus barbatus</i>	male	406.87	415.67	427.14	ns	herbivore	35	30	35	Sundaland
Artiodactyla	<i>Tragulus javanicus/kanchil</i>	both	90.16	87.98	89.54	89.44	frugivore	20	80	0	SE Asia
Artiodactyla	<i>Tragulus napu</i>	female	103.58	108.95	104.5	107.75	frugivore	20	80	0	Sundaland
Carnivora	<i>Aonyx cinerea</i>	male	83.54	83.37	86.74	89.58	carnivore	0	0	100	SE Asia
Carnivora	<i>Arctictis binturong</i>	male	129.47	139.83	137.86	143.54	frugivore	5	90	5	SE Asia
Carnivora	<i>Arctogalidia trivirgata</i>	both	105.06	105.69	104.86	99.66	carnivore	5	40	55	SE Asia
Carnivora	<i>Cynogale bennettii</i>	male	119.01	128.82	116.75	ns	carnivore	0	0	100	SE Asia
Carnivora	<i>Helarctos malayanus</i>	male	205.1	250.5	234.55	ns	frugivore	20	40	40	SE Asia
Carnivora	<i>Hemigalus derbyanus</i>	both	100.63	101.5	101.03	ns	carnivore	3	3	95	Sundaland
Carnivora	<i>Herpestes brachyurus</i>	both	86.31	91.71	90.98	ns	carnivore	0	0	100	Sundaland
Carnivora	<i>Herpestes semitorquatus</i>	female	80.46	ns	86.89	ns	carnivore	0	0	100	Sundaland
Carnivora	<i>Lutra sumatrana</i>	female	99.82	98.89	ns	ns	carnivore	0	0	100	SE Asia
Carnivora	<i>Lutrogale perspicillata</i>	both	119.76	118.7	ns	115.35	carnivore	0	0	100	SE Asia
Carnivora	<i>Martes flavigula</i>	both	84.27	91.84	89.13	91.67	carnivore	5	5	90	SE Asia
Carnivora	<i>Melogale everetti/orientalis</i>	both	65.81	ns	ns	73.47	carnivore	0	0	100	SE Asia
Carnivora	<i>Mustela nudipes</i>	male	60.14	58.51	59.81	ns	carnivore	0	0	100	Sundaland
Carnivora	<i>Mydaus javanensis</i>	both	89.32	ns	86.78	83.16	carnivore	0	0	100	Sundaland
Carnivora	<i>Neofelis nebulosa/N. diardi</i>	both	140.64	ns	145.33	ns	carnivore	0	0	100	SE Asia
Carnivora	<i>Paguma larvata</i>	both	118.49	132	129.23	ns	carnivore	0	25	75	SE Asia
Carnivora	<i>Paradoxurus hermaphroditus</i>	both	97.71	103.94	104.89	112.09	frugivore	10	70	20	SE Asia
Carnivora	<i>Pardofelis marmorata</i>	male	80.55	88.66	91.66	ns	carnivore	0	0	100	SE Asia
Carnivora	<i>Prionailurus bengalensis</i>	both	78.09	83.7	80.68	78.31	carnivore	0	0	100	SE Asia
Carnivora	<i>Prionailurus planiceps</i>	both	89.48	90.27	93.19	ns	carnivore	0	0	100	Sundaland
Carnivora	<i>Prionodon linsang</i>	female	68.1	70.66	69	ns	carnivore	0	0	100	SE Asia

Order	Species	sex	Borneo	Malaya	Sumatra	Java	diet	% leaves in diet	% fruit in diet	% animal in diet	distribution
Carnivora	<i>Viverra zangalunga</i>	male	113.6	118.79	114.5	ns	carnivore	5	15	80	Sundaland
Chiroptera	<i>Dyacopterus spadiceus</i>	both	35.2	ns	34.9	ns	frugivore	0	100	0	Sundaland
	<i>Galeopterus (Cynocephalus)</i>										
Dermoptera	<i>variegatus</i>	both	66.8	71.33	68.92	72.23	herbivore	100	0	0	SE Asia
Insectivora	<i>Echinosorex gymnurus</i>	male	84.05	78.6	81.57	ns	carnivore	0	0	100	Sundaland
Pholidota	<i>Manis javanica</i>	both	92.93	103.34	ns	ns	carnivore	0	0	100	SE Asia
Primates	<i>Hylobates agilis/albibarbis</i>	female	87.98	80.57	84.44	ns	frugivore	28	70	2	Sundaland
Primates	<i>Macaca fascicularis</i>	male	93.19	92.61	87.78	99.25	frugivore	30	65	5	SE Asia
Primates	<i>Macaca nemestrina</i>	both	110.96	109.62	109.84	ns	frugivore	10	80	10	Sundaland
Primates	<i>Nycticebus coucang</i>	female	52.1	56.16	56.55	57.66	frugivore	25	50	35	SE Asia
Primates	<i>Pongo pygmaeus/abelii</i>	both	217.25	ns	220.25	ns	frugivore	50	50	0	Sundaland
Primates	<i>Trachypithecus cristatus</i>	both	74.96	78.9	76.57	ns	frugivore				Sundaland
Proboscidea	<i>Elephas maximus</i>	both	787.58	894.5	845.05	ns	herbivore	95	5	0	SE Asia
Rodentia	<i>Aeromys tephromelas</i>	female	62.77	62.53	60.77	ns	frugivore	25	75	0	Sundaland
Rodentia	<i>Callosciurus prevosti</i>	both	51.51	ns	52.44	ns	frugivore	40	40	20	Sundaland
Rodentia	<i>Hylomys suillus</i>	both	35.5	36.27	33.14	33.36	carnivore	0	0	100	SE Asia
Rodentia	<i>Iomys horsfieldi</i>	both	42.04	41.59	ns	ns	frugivore				Sundaland
Rodentia	<i>Lariscus insignis</i>	both	44.11	44.64	46.6	44.78	frugivore	35	35	30	Sundaland
Rodentia	<i>Leopoldamys sabanus</i>	both	52.06	51.23	ns	ns	carnivore	20	30	60	SE Asia
Rodentia	<i>Maxomys rajah</i>	both	42.96	40.49	38.78	ns	carnivore	0	20	80	Sundaland
Rodentia	<i>Maxomys whiteheadi</i>	both	29.03	29.57	31.24	ns	carnivore	0	10	90	Sundaland
Rodentia	<i>Niviventer cremoriventer</i>	both	31.34	32.48	ns	31.91	frugivore	30	40	30	Sundaland
Rodentia	<i>Petinomys setosus</i>	male	29.37	28.26	25.59	ns	frugivore				Sundaland
Rodentia	<i>Ratufa affinis</i>	both	60.64	59.24	58.01	ns	frugivore	20	80	0	SE Asia
Scandentia	<i>Ptilocercus lowii</i>	male	36.66	36.03	ns	ns	carnivore	0	0	100	Sundaland
Scandentia	<i>Tupaia glis</i>	male	48.62	49.02	49.61	50.61	carnivore	0	25	75	Sundaland
Scandentia	<i>Tupaia minor</i>	both	33.48	33.98	34.25	ns	carnivore	0	15	85	Sundaland
Scandentia	<i>Tupaia tana</i>	male	54.62	ns	54.33	ns	carnivore	0	3	97	Sundaland

Borneo, Malaya, Sumatra & Java: mean CBL (condylobasal length, in mm) of measured specimens.

Sex: gender measured

Both: average of mean male and mean female CBL

ns: no specimens measured (either the species doesn't occur there or we obtained no specimens).