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.
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 km²), 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 nigricolis, 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:

\[
\text{Quality} = \text{proportion of leaves in the diet} + 2 \times \text{proportion of fruit in the diet} + 3.5 \times \text{proportion of animal food in the diet}
\]

(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, \(F_{1,769} = 1.42, P = 0.23\)). 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 (\(F_{1,103} = 1.43, P = 0.24\)), 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, \(d = 0.06, P = 0.83\); 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;
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 \((n = 54, r = -0.40, P = 0.003; \text{Fig. 2})\), contradicting our first prediction. In fact, small (< 1 kg) mammals are not, on average, smaller on Borneo than elsewhere (controlling for species identity, \(F_{3,51} = 0.26, P = 0.86\)).

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 \((F_{3,51} = 1.20, P = 0.31)\), 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 \((F_{3,81} = 9.21, P < 0.0001, \text{mean relative size} = 93.5\% \text{on Borneo vs.} 96.0\% \text{on Sumatra, 98.2}\% \text{on the mainland and} 98.3\% \text{on Java})\). A Tukey HSD test found no significant differences between Sumatra, Java and the mainland, but comparisons involving Borneo are nearly \((vs. \text{Sumatra}, P = 0.083)\) or highly significantly \((\text{vs. Java}, P = 0.0001)\) different. Comparing endemic Sundaic species in the four areas, however, no significant differences between relative sizes were found \((F_{3,73} = 0.07, P = 0.98, \text{mean relative sizes all between} 97.3\% \text{and} 97.8\%)\).

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.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Difference</th>
<th>Lower 95% confidence limit</th>
<th>Upper 95% confidence limit</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Java–Borneo</td>
<td>0.025</td>
<td>0.001</td>
<td>0.048</td>
<td>0.034</td>
</tr>
<tr>
<td>Malaya–Borneo</td>
<td>0.023</td>
<td>0.005</td>
<td>0.042</td>
<td>0.007</td>
</tr>
<tr>
<td>Sumatra–Borneo</td>
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<td>-0.004</td>
<td>0.032</td>
<td>0.198</td>
</tr>
<tr>
<td>Malaya–Java</td>
<td>-0.002</td>
<td>-0.026</td>
<td>0.023</td>
<td>0.998</td>
</tr>
<tr>
<td>Sumatra–Java</td>
<td>-0.011</td>
<td>-0.035</td>
<td>0.013</td>
<td>0.639</td>
</tr>
<tr>
<td>Sumatra–Malaya</td>
<td>-0.009</td>
<td>-0.028</td>
<td>0.010</td>
<td>0.585</td>
</tr>
</tbody>
</table>

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...
Bornean soils are generally much less fertile than the rich connected it to the Thai/Malay Peninsula (Meijaard, 2003). Java on the region's volcanic arc are relatively new, but Borneo part, is geologically very active. The land areas of Sumatra and the Holocene have been more severe on Borneo relative to 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 titthaceiulus 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.

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REFERENCES


**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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