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Primate brains, the ‘island rule’ and the evolution of *Homo floresiensis*

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ABSTRACT

The taxonomic status of the small bodied hominin, *Homo floresiensis*, remains controversial. One contentious aspect of the debate concerns the small brain size estimated for specimen LB1 (Liang Bua 1). Based on intraspecific mammalian allometric relationships between brain and body size, it has been argued that the brain of LB1 is too small for its body mass and is therefore likely to be pathological. The relevance and general applicability of these scaling rules has, however, been challenged, and it is not known whether highly encephalized primates adapt to insular habitats in a consistent manner. Here, an analysis of brain and body size evolution in seven extant insular primates reveals that although insular primates follow the ‘island rule’, having consistently reduced body masses compared with their mainland relatives, neither brain mass nor relative brain size follow similar patterns, contrary to expectations that energetic constraints will favour decreased relative brain size. Brain:body scaling relationships previously used to assess the plausibility of dwarfism in *H. floresiensis* tend to underestimate body masses of insular primates. In contrast, under a number of phylogenetic scenarios, the evolution of brain and body mass in *H. floresiensis* is consistent with patterns observed in other insular primates.

Introduction

A decade on from their discovery the remains of a small brained, small-bodied hominin from the Indonesian island of Flores (Brown et al., 2004) are still cause for much debate. Attributed to a new species of *Homo*, *Homo floresiensis*, the findings raise questions about the timing of early human migrations, how early human species co-existed, and the cognitive significance of brain size (Brown et al., 2004; Falk et al., 2005; Aiello, 2010; Wood, 2011). However, their status as a new species remains controversial with several studies reporting to show similarities between *H. floresiensis* and various pathological disorders in modern humans (Jacob et al., 2006; Martin et al., 2006; Hershkovitz et al., 2008; Oxnard et al., 2010). These suggestions have been consistently refuted (e.g., Martinez and Hamsici, 2008; Falk et al., 2009a,b; Brown, 2012) and no proposed pathology encompasses the full range of phenotypes observed in *H. floresiensis*, or satisfactorily explains how a diseased population could persist for over 50,000 years (Brown et al., 2004; Morwood et al., 2005). In a recent review of these arguments, Aiello (2010) concluded that, although the debate can only be settled with the discovery of new specimens, the current level of evidence supporting a pathological explanation is not convincing. If not pathological, the small brain and body size of *H. floresiensis* requires an evolutionary explanation.

Two evolutionary hypotheses have been proposed to explain the origins of *H. floresiensis*. Either the small body (16–41 kg, Brown et al., 2004; Aiello, 2010) or small brain (417 cc, Falk et al., 2005; 426 cc, Kubo et al., 2013) of *H. floresiensis* is a product of insular dwarfism from a larger bodied ancestor, perhaps *Homo erectus* (Brown et al., 2004; Kubo et al., 2013), or *H. floresiensis* is a descendent of an earlier, small bodied hominin that left Africa before *H. erectus* (Brown et al., 2004; Brown and Maeda, 2009). The latter hypothesis is controversial as the long supported ‘Out of Africa 1’ model posits that *Homo ergaster/erectus* was the earliest hominin to leave Africa (Wood, 2011). This model has, however, been challenged by recent palaeontological discoveries (Dennell and Roebroeks, 2005; Ferring et al., 2011) and a number of morphometric and cladistic analyses have suggested that *H. floresiensis* bears most similarity to early African hominins, such as *Homo habilis*, or the hominins discovered at Dmanisi, Georgia (Tocheri et al., 2007; Gordon et al., 2008; Argue et al., 2009; Baab and McNulty, 2009; Brown and Maeda, 2009). Not all studies agree, with some providing evidence for morphological affinities with early Javanese *H. erectus* (Kaifu et al., 2011).

Although descent from an unknown, similarly sized hominin remains possible, the insular dwarfism hypothesis attracted the most attention immediately after the description of the remains (Falk et al., 2006; Martin et al., 2006; Bromham and Cardillo, 2007) and continues to be discussed in both the academic and popular press (e.g., Weston and Lister, 2009; Baab, 2012; Kubo et al., 2013). This is in spite of the generality of the ‘island rule’ being strongly

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disputed (Meiri et al., 2006, 2008, 2011). The ‘island rule’ suggests that large vertebrates generally experience a reduction in body size on islands perhaps due to energetic constraints or changes in predation rates (Foster, 1964; Van Valen, 1973). Dwarfism on islands is not a general trend found across mammals but has occurred in a limited number of groups (Meiri et al., 2006, 2008), dependent upon the species’ ecology and evolutionary history (McClain et al., 2013). One order where the island rule may hold is primates (Bromham and Cardillo, 2007; Welch, 2009). Support for the island rule is found using interspecific datasets (Bromham and Cardillo, 2007; Welch, 2009), but not with intraspecific datasets (Meiri et al., 2008; Schillaci et al., 2009) raising the possibility that dwarfism in primates develops over longer time frames (Meiri et al., 2008).

Which of the two evolutionary hypotheses is correct has implications for interpreting the small brain size of *H. floresiensis*. Brain:body allometry between closely related species closely follows intraspecific scaling relationships (Lande, 1979). Hence, if *H. floresiensis* descended from a small-bodied hominin it is reasonable to expect that its brain size would be predictable based on the degree of body size change and intraspecific allometry. However, several notable examples suggest that during episodes of insular dwarfism, selection can dramatically reduce brain size in a non-allometric manner, both in absolute mass and relative to body size (Roth, 1992; Köhler and Moyá-Solá, 2004; Weston and Lister, 2009). One suggested explanation for this has been that in an environment with limited resources, energetically expensive tissues, such as the brain (Aiello and Wheeler, 1995), are decreased in size in order to balance energy expenditure (Köhler and Moyá-Solá, 2004). Hence, if *H. floresiensis* evolved from a larger bodied ancestor in a resource-limited environment, additional selective pressures may have driven the evolution of its small brain.

However, using both intraspecific scaling relationships between brain and body mass in humans and other mammals, and an example of insular dwarfism, Martin et al. (2006) argued that the estimated brain size for LB1 (*H. floresiensis*) is too small for its body mass. They suggest this departure from expected patterns of brain:body allometry points towards a pathological origin for the specimens (Jacob et al., 2006; Martin et al., 2006). The relevance of these scaling relationships has, however, been questioned (Falk et al., 2006; Niven, 2007; Kaifu et al., 2011) and some alternative scaling relationships are more accommodating of *H. floresiensis*’ small brain (Weston and Lister, 2009; Montgomery et al., 2010). Weston and Lister (2009), for example, showed that the predicted decrease in *H. floresiensis*’ brain size during descent from African *H. erectus* is within the range observed in dwarfed hippos, whilst Montgomery et al. (2010) found it was within the range observed in primate genera in which body mass decreased, if *H. floresiensis* was a descendent of either *H. habilis* or Dmanisi hominins. These studies show that major phenotypic changes in brain size can occur during episodes of dwarfism. However, comparisons with *H. floresiensis* are not entirely straight forward. Comparing *H. floresiensis* with particular non-primate dwarfs assumes conservation in the genetic, developmental, physiological and behavioural constraints acting on brain size across large phylogenetic distances. The use of these examples to assert that extensive dwarfism and brain reduction is ‘mechanistically possible’ (Weston and Lister, 2009; Kubo et al., 2013) in hominins therefore has limitations. Likewise, comparing intergeneric patterns in non-insular primates assumes conservation in allometry between taxonomic scales and ecological niches.

Unfortunately our expectations of patterns of brain evolution on islands are based on only a handful of examples, and it remains unclear if there is a consistent pattern among insular dwarfs. Assessing whether or not *H. floresiensis* departs from expected evolutionary patterns of brain:body allometry relies on choosing taxa with which to compare the evolution of *H. floresiensis* to in a biologically meaningful way. In this respect, a comparison with other insular primates is of direct relevance (Bromham and Cardillo, 2007). If primates follow the island rule for body mass (Bromham and Cardillo, 2007; Welch, 2009), examining how brain size evolved in these insular species arguably provides the best reference for contextualizing the small brain of *H. floresiensis* and assessing the arguments put forward against its taxonomic status, and different evolutionary hypotheses.

Based on a thorough analysis of seven mainland/island pairs of extant primates, the present study examines patterns of brain evolution in insular primates and re-analyses predicted patterns of brain evolution during the origin of *H. floresiensis*. I first test whether or not there is an ‘island rule’ for brain size and then examine whether the patterns of brain:body allometry in extant insular primates are in line with scaling models previously used to assess the plausibility of the dwarfism hypothesis for *H. floresiensis*. Finally I examine predicted patterns of brain evolution during the descent of *H. floresiensis* using both the observed allometric scaling among extant insular primates and typical intraspecific mammalian scaling. By doing so, I aim to identify the phylogenetic scenarios under which the brain and body size of *H. floresiensis* is acceptable under either, or both, of the hypotheses that it descended through insular dwarfism, or from a similarly sized hominin. These results are discussed in the context of morphological similarities between *H. floresiensis* and other hominins.

Materials and methods

Mainland/island pairs

This study makes use of the dataset of mainland/island taxon pairs compiled by Bromham and Cardillo (2007) that was used to test the island rule for primate body size. Endocranial volume (ECV) and body mass data from wild individuals are available for seven mainland/island primate pairs; all are catarrhines (Table 1; Isler et al., 2008). Although ECV is an indirect measure of brain size, it is a more readily measurable trait and scales isometrically with brain mass (Isler et al., 2008). Data on cranial capacities were converted to brain mass by multiplication by the density of fresh brain tissue (1.036 g/cc) (Isler et al., 2008). Of the 14 species included in the analysis, three were classed as ‘data deficient’ by the original authors (Isler et al., 2008) and are based on less than three individuals. Whilst poor sampling of intraspecific variation may introduce error in these cases, the data are included in the analysis in order to maximize an already small sample size. Comparisons involving these species are not outliers and the conclusions are robust to their exclusion.

Isler et al.’s (2008) data on species means are used throughout, but analyses using data from each sex separately are also presented in the Supplementary Online Material (SOM) and lead to the same conclusions. In addition to low intraspecific sampling, variation in the sex ratios of the data and the geographic distribution of the mainland species could introduce error into the analyses. However, I assume this error affects both brain and body mass equally and would not bias the results towards finding differences in the patterns of evolution between the two traits, or bias estimates of brain:body scaling in any particular direction. Isler et al. (2008) suggest that sample size has a more important effect on parameter estimation than data quality so it is likely that the size of the dataset is the most limiting factor of this study.

Identifying the true ancestor of insular populations/species is challenging, and a potential source of error in this study. For their study on primate body size, Bromham and Cardillo (2007) selected