

Evolution of the human pygmy phenotype

George H. Perry¹ and Nathaniel J. Dominy²

¹ Department of Human Genetics, University of Chicago, 920 E. 58th Street, Chicago, IL 60637, USA

² Department of Anthropology and Department of Ecology and Evolutionary Biology, University of California, 1156 High Street, Santa Cruz, CA 95064, USA

Small human body size, or the ‘pygmy’ phenotype, is characteristic of certain African, Southeast Asian and South American populations. The convergent evolution of this phenotype, and its strong association with tropical rainforests, have motivated adaptive hypotheses that stress the advantages of small size for coping with food limitation, warm, humid conditions and dense forest undergrowth. Most recently, a life-history model has been used to suggest that the human pygmy phenotype is a consequence of early growth cessation that evolved to facilitate early reproductive onset amid conditions of high adult mortality. As we discuss here, these adaptive scenarios are not mutually exclusive and should be evaluated in consort. Findings from this area of research are expected to inform interpretations of diversity in the hominin fossil record, including the purported small-bodied species *Homo floresiensis*.

The human pygmy phenotype

Body size is central to the biology of all living organisms, affecting basic caloric requirements, basal metabolism, foraging opportunities and the risk of predation [1]. Among humans, there exists considerable intra- and interpopulation variation in body size, an important component of which can be attributed to genetic factors [2]. Although the evolutionary ecology of human body-size diversity has long intrigued anthropologists, the recent discovery of ~18 000-year-old skeletal remains of an individual purported to be ~106 cm tall and representative of a new hominin species, *Homo floresiensis* [3], has intensified the collective interest in this topic [4–6].

Of modern human populations, Efe hunter-gatherers in the Ituri rainforest (Democratic Republic of Congo) are the shortest on record, with mean adult female and male statures of 136 and 143 cm, respectively [7]. Historically, the Efe and other populations with mean adult male statures of <150, 155 or 160 cm have been termed ‘pygmies’ [6,8]. Such a broad classification tends to de-emphasize the genetic, geographic and cultural distinctiveness of these populations and, thus, might obscure the potential ecological significance of small body-size evolution in humans. On these grounds, it might be more appropriate to limit the use of the term ‘pygmy’ to discussions of the small body-size phenotype.

With few exceptions, the human pygmy phenotype is associated with populations that traditionally hunted and gathered food in tropical rainforest environments (Figure 1). An understanding of how these challenging habitats might have influenced the origins of this phenotype could shed light on the evolutionary implications of body-size diversity not only among modern humans but also potentially of that within the hominin fossil record. With this goal in mind, here we examine recent findings that inform both classic and modern hypotheses of pygmy phenotype evolution.

Genetics or growth stunting?

The small body sizes of rainforest hunter-gatherers might partly reflect stunted growth from poor childhood nutrition [9]; however, three lines of evidence suggest that this phenotype is determined principally by genetic, rather than environmental, factors. First, although the specific DNA mutations have not yet been identified, genetic disruptions of the growth hormone (GH) and insulin-like growth factor I (IGF1) pathway are likely to have etiological roles (Box 1). Second, the childhood growth rates of some rainforest hunter-gatherer populations are surprisingly fast; for example, growth rates for 3- to 10-year-old Biaka (Cameroon) girls might even exceed those for USA children (7.1 cm y⁻¹ versus 6.5 cm y⁻¹, respectively) [10]. Therefore, for at least some populations, small adult body sizes are a reflection of relatively slow growth in adolescence rather than childhood [8,10], which is inconsistent with a simple model of stunted growth from poor nutrition. Indeed, other populations that also endure frequent episodes of nutritional stress still achieve adult heights that are greater than those of rainforest hunter-gatherers [8]. Third, the offspring of Efe mothers and Lese (agriculturalist) fathers have statures intermediate to those of the two parental populations [11].

Evolutionary theories

It is important to consider whether the genetically determined component of the pygmy phenotype reflects adaptation by natural selection or by neutral evolution (i.e. genetic drift) [12]. Based on mitochondrial DNA (mtDNA) and Y chromosome haplotype data, African, Southeast Asian and South American rainforest hunter-gatherers are more closely related to other populations from their respective continents than they are to each other [13]. Therefore, it is likely that genetic mutations for the pygmy

Corresponding authors: Perry, G.H. (gperry@uchicago.edu); Dominy, N.J. (njdominy@ucsc.edu).

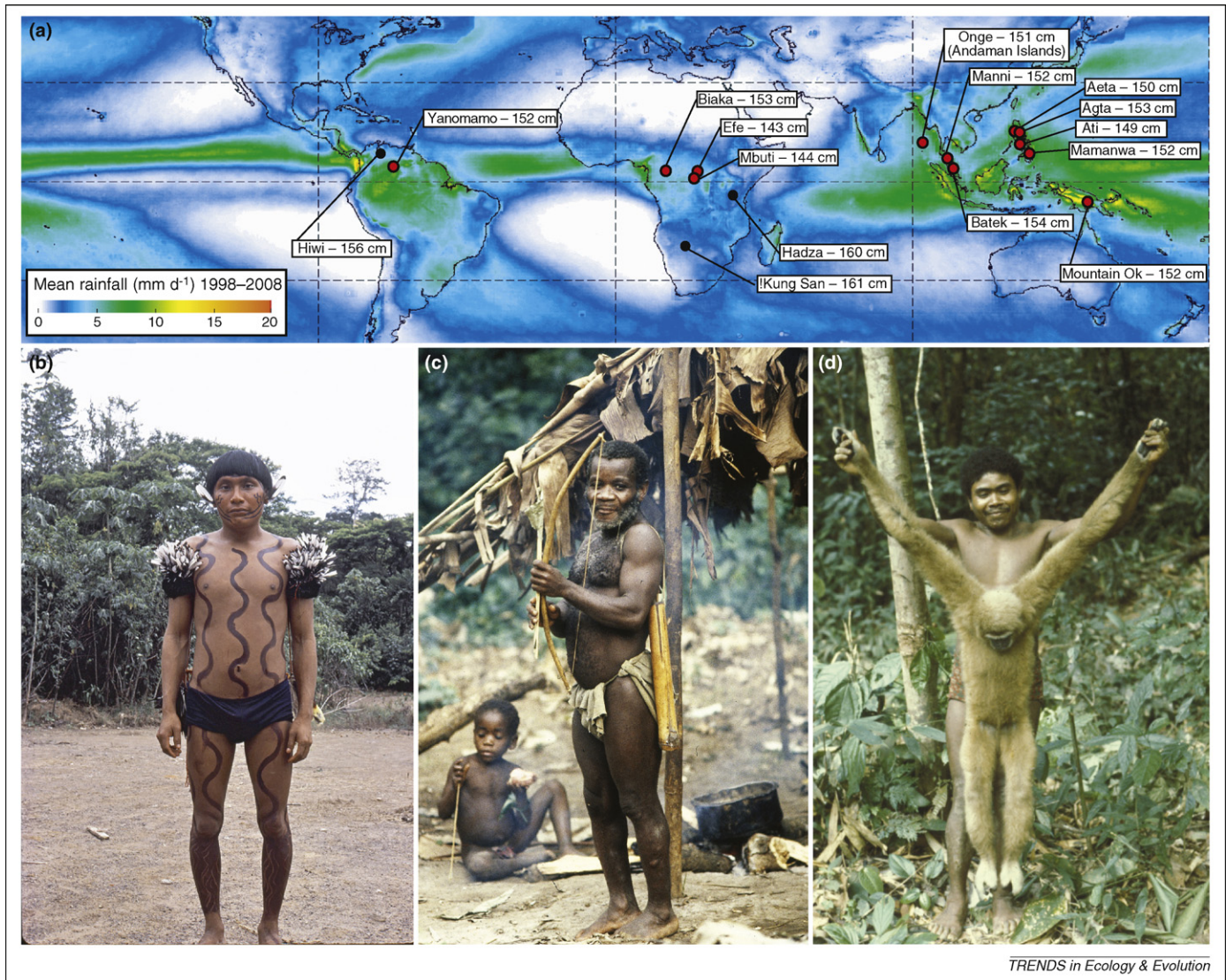


Figure 1. Association of the human pygmy phenotype with tropical rainforest habitats. (a) Approximate locations of small-bodied hunter-gatherer populations discussed in this article, with mean adult male stature estimates [6,10,65,78,79]. The smallest modern human statures (mean adult male height < 155 cm) are always associated with tropical rainforests (red circles). Some hunter-gatherer populations occupying savanna-woodlands (black circles) are also relatively small, such as the Hiwi of the Venezuelan llanos, the Hadza of Tanzania and the !Kung San of Botswana and Namibia. Precipitation data are from the Tropical Rainfall Measuring Mission (Goddard Space Flight Center, National Aeronautics and Space Administration; <http://trmm.gsfc.nasa.gov>). (b) Yanomamö male, Venezuela (photograph by Raymond Hames, with permission). (c) Efe male, Democratic Republic of Congo (photograph by William Wheeler, with permission from the National Anthropological Archives, Smithsonian Institution). (d) Batek male, Malaysia, with white-handed gibbon (*Hylobates lar*) hunted by blowdart (photograph by Kirk Endicott, with permission).

phenotype occurred and have been maintained at least three times in humans. The convergent evolution of this phenotype in generally similar environments suggests that it has been favored by natural selection, and several hypotheses have been proposed to explain the mechanisms under which this might have occurred. Here we present the four hypotheses that, in our view, remain most tenable in light of recent research.

When evaluating these (nonmutually exclusive) hypotheses, it is crucial to consider the likelihood that at least some of these populations have migrated or were displaced from the environments in which the pygmy phenotype evolved. Caution is therefore advised before rejecting a hypothesis simply because it does not apply to the ecologies of all modern small-bodied populations. Moreover, we should not necessarily expect exactly the same scenarios for each independent origin of the pygmy phenotype. This

notion might be especially relevant for those few smaller-bodied populations that inhabit savanna-woodlands rather than tropical rainforests (Figure 1).

Food limitation

Rainforests are food-limited environments for human hunter-gatherers. For example, substantive plant foods are scarce for nearly half of each year in the Ituri forest, leaving only small game (including fish), honey and insect resources of a combined marginal nutritional and caloric value [14]. Small body size might have conferred a selective advantage to hunter-gatherers in these habitats by reducing the total caloric intake necessary for survival [12]. In effect, this model considers rainforests as ‘ecological islands,’ and there are numerous examples of rapid size decreases of larger land mammals following their appearance on resource-limited islands (Box 2).

Box 1. The GH1-IGF1 pathway and the pygmy phenotype

As one of three endocrine systems regulating somatic growth and stature, the GH1-IGF1 pathway has been an attractive candidate for understanding the underlying physiological mechanisms of the pygmy phenotype. Perturbations of this pathway have been reported in rainforest hunter-gatherer populations from both Africa (Biaka, Efe and Mbuti) and Southeast Asia (Aeta, Ati, Mamanwa, Manni and Mountain Ok) [65–68].

Whereas GH1 plasma concentrations are normal in individuals from each of these populations compared to controls, downstream metabolic responses to GH1 are low. This GH1 resistance could be mediated at the level of the GH1 receptor (GHR) or its ectodomain, the GH binding protein (GHBP) [66]. Indeed, low circulating levels of GHBP have been reported for individuals from each population. Interestingly, with few exceptions, serum concentrations of IGF1 are relatively low in rainforest hunter-gatherers from Africa, Thailand and the Philippines, but not in the Mountain Ok from Papua New Guinea, suggesting differences in underlying genetic mechanisms [65–68]. Given that height is a complex trait influenced by many genes, such differences are not unexpected. Such a finding would follow examples of phenotypic convergence in other organisms that are driven by different genetic mechanisms, such as the light coat colors of beach mice from the Florida Atlantic and Gulf coasts [69] and pigmentation changes among *Drosophila* species [70]. Relatively decreased expression of the IGF1 receptor (IGF1R) has also been observed in Efe-derived immortalized cell lines [66], but, to our knowledge, this experiment has not been conducted for any other population.

Because chronic undernutrition can lead to low concentrations of GHR, GHBP and IGF1 [9], it is important to assess whether the biochemical profiles linked to pygmy size are genetic in origin, or the result of epigenetic effects. General health measurements and plasma-based nutritional indices (e.g. albumin, prealbumin, zinc, iron, etc.) are germane to this issue. For example, despite differences in adult stature, the average skinfold thickness (a measure of fatness) of Efe and taller Lese (agriculturalist) women did not differ, indicating a comparable level of nutritional health in the two populations [71]. Among the Ati (Philippines), plasma-based indices revealed some minor nutrient deficiencies, but no energy restriction overall [67]. Similarly, the serum proteins of the Mountain Ok (Papua New Guinea) showed no evidence of chronic or acute malnutrition [66]. As discussed above, levels of IGF1 among Mountain Ok are similar to taller controls, in contrast to the low levels of IGF1 reported in the Aeta, Ati, Efe, Manni and Mamanwa [65–68]. This finding argues against a shared etiology for the pygmy phenotype, further suggesting that the observed perturbations of the GH1-IGF1 pathway are largely genetically determined. However, until the specific mutations involved (probably regulatory ones) are identified, the specific detailed mechanisms underlying the pygmy phenotype will remain unknown.

Cavalli-Sforza [11] rejected this hypothesis based on the observation that African rainforest hunter-gatherers spend only approximately half of each day obtaining and cooking food, suggesting a surfeit of adequate resources. However, this activity distribution might not reflect that under which the pygmy phenotype evolved. Today, these African groups exchange hunted forest game for cultivated foods with neighboring agriculturalists, as do Southeast Asian rainforest hunter-gatherers [15]. In fact, there is the open question of whether full-time occupation of the rainforest is even possible for independent hunter-gatherers (i.e. without trade for cultivated goods), given the food limitations discussed above [14–17]. If not, then these groups might have originally inhabited rainforest-edge environments, where food resources are generally more stable, before being displaced to deeper forest habitats by the farming populations with whom they now trade [14,15].

Box 2. Foster's Island Rule: insular dwarfism

Foster's Island Rule is the phenomenon of miniaturization of large animals (insular dwarfism) and gigantism of small animals on oceanic islands and near-shore archipelagos. This rule applies to a range of vertebrate lineages in the fossil and modern records, including tortoises, lizards, birds, bats and non-volant mammals such as primates, sloths and mammoths [72,73], although by no means is it universal for even these taxa [74]. The strength of the Island Rule tends to vary as a function of island size and isolation, and among mammals it is greatest in herbivores and weakest in terrestrial carnivores [72,75]. Several mechanisms (mainly competitive release, resource limitation, dispersal ability and lighter predation pressure on islands, as well as a general physiological advantage of modal size) have been advanced to explain this pattern. Recent life-history models of island ecology have stressed the combined effects of decreased extrinsic mortality and competition for resources on individual growth rates and body size [75,76].

The extent to which the mechanisms driving insular dwarfism are also applicable to humans in tropical rainforests is unknown. Similar to small islands, rainforests (for humans) can be considered food-limited environments; but given that insular dwarfism has little or no effect on mammalian carnivores, it is valid to consider whether the same exception applies to humans, who can hunt for food by both land and water.

Insular dwarfism might still be the most appropriate model to explain the extremely small body size of *Homo floresiensis* (stature ~106 cm; mass ~16–36 kg) [3,51]). However, insular dwarfism normally results in a proportional reduction in brain size [50]. The diminutive cranial capacity of *H. floresiensis* (~417 cm³; at least as measured from the holotype specimen, LB1) is substantially smaller than expected given its body size [53]. This scaling discrepancy could be associated with ecological differences between Flores and other islands. Specifically, it has been suggested that Flores cannot support a mammalian predator larger than 5 kg [77]. Intriguingly, the cranial capacity of *H. floresiensis* scales to a hominin with a body mass near this theoretical limit, ~6 kg [50]. It is plausible that selection for dwarfism on an island the size of Flores favored the peculiar decoupling of brain size and body size in a species that was both predator and herbivore.

However, some archaeological evidence does support human occupation of African and Asian rainforest environments long before the spread of agriculture in these regions [16,18]. In this event, any early rainforest inhabitants (perhaps at lower population densities than today) are likely to have experienced severe nutritional and caloric stress, which in turn could explain the adaptive evolution of the pygmy phenotype.

Thermoregulation

For humans, sweat production and evaporation is a crucial component of thermoregulation. However, this mechanism is inefficient in tropical rainforests, where small differences between air and skin relative humidities are combined with little air movement. Cavalli-Sforza [11] suggested that, in the absence of effective evaporative cooling, smaller bodies (potentially including relatively decreased muscle masses, as suggested by calf circumference measurements [11]) would benefit thermoregulation by generating less internal heat during activity (Figure 2). Interestingly, Biaka men (from Cameroon) were unexpectedly efficient energetically relative to taller European men when running under rainforest conditions (temperature = 28.7 °C; relative humidity = 70%) [19]. Although the European men had lower energetic costs at walking speeds [19], the Biaka might have benefited from relatively



Figure 2. Thermographic image of Batek hunter-gatherers after a 1 h hike in their rainforest habitat (Taman Negara National Park, Malaysia). Internal and external body temperatures can be estimated using a thermographic camera. Analysis of pixels from the open mouth provides a good estimate of core body temperature. The open-mouth pixels of the taller man (a) (~164 cm) show an elevated core temperature of 38.0 °C, whereas those of the shorter man (b) (~156 cm) show a normal core temperature of 36.9 °C. An estimate of the skin surface temperature based on facial pixels excluding the open mouth did not differ substantially between them (mean values of 36.1 °C and 36.4 °C, respectively). Although not representing a formal test of the thermoregulatory hypothesis as an explanation for pygmy phenotype evolution, the higher core body temperature of the taller man following physical activity illustrates the plausibility of its underlying premise—that in tropical rainforests, where the thermoregulatory mechanism of sweat production and evaporation is inefficient, smaller bodies might confer a fitness advantage by generating less internal heat during activity. Images were captured with a ThermoCAM SC640 (FLIR Systems, Boston, MA, USA) under photographic license number 395108 issued by the Department of Wildlife and National Parks, Malaysia.

better thermoregulation during more rigorous exercise. Therefore, the pygmy phenotype could confer a selective advantage in tropical rainforest habitats by mitigating the fitness-reducing effects of heat stress [11].

This hypothesis might fail, however, to explain the variation in height among all small-bodied rainforest hunter-gatherer populations, at least in terms of levels of humidity and heat in their contemporary environments [20]. In particular, humidity and body size are not clearly negatively correlated; the Efe (the shortest population in the world) inhabit one of the least wet tropical rainforests (Figure 1), although the Ituri forest might have been more humid 10 000 years ago [21]. In addition, other small-bodied populations live in higher-elevation rainforests that are relatively cool (although still very wet; e.g. the Mountain Ok in Papua New Guinea). This hypothesis also has little relevance for the few relatively small bodied populations living outside rainforests.

Mobility

In open environments, longer limb lengths significantly reduce the metabolic cost of locomotion [22,23]. This is unlikely to be true in dense forests if taller individuals are regularly forced into bent or crouched postures that markedly increase energy expenditure [24]. The frequent use of such postures would also inhibit rapid travel. Accordingly, Diamond [20] hypothesized that the pygmy phenotype

might have adaptively improved mobility and increased foraging efficiency. Although the appeal of this hypothesis is readily grasped during an off-trail hike in the rainforest, at present there are only anecdotal observations regarding the density of understorey vegetation or other impediments faced by human hunter-gatherers.

The ability to climb trees of incredible height for food gathering (e.g. for honey, the Efe climbed as high as 51.8 m; mean 19.1 m; SD = 9.7 m; $n = 34$ [25]) is another potential mobility-related adaptive benefit of the pygmy phenotype [20]. These food resources, especially honey, are crucial nutritional components for African, Southeast Asian and South American rainforest hunter-gatherers [14,16,26], but their collection represents considerable energetic cost to larger-bodied foragers [27,28]. Additionally, owing to the possibility of falls, the overall fitness risk of tree climbing for larger-bodied primates is expected to be high [29]; this risk is likely to be positively correlated with body size. Even among contemporary small-bodied rainforest hunter-gatherers, accidents during the course of tree climbing for honey and palm products (e.g. pith and cabbage [16]) remain a significant cause of mortality; 7 of the 106 (7%) deaths recorded for young adult and adult Biaka males were the result of such falls [30].

We note the potential relevance of this hypothesis to the few non-rainforest small-bodied populations. Specifically, the Hiwi (Colombia and Venezuela), Hadza (Tanzania) and !Kung San (Botswana and Namibia) all rely heavily on tubers and small- to medium-sized animal prey in dense bush-land portions of their savanna-woodland habitats. Recent reports of !Kung San persistence hunts (chasing an animal to its exhaustion) emphasize the importance of locomotor efficiency amid dense vegetation [31]. It is therefore conceivable that smaller body sizes conferred a mobility-related selective advantage in both savanna-woodlands and rainforests [20], even if the habitats and specific activities invoking selection were quite different.

Life history

By analyzing detailed growth, fertility and mortality data in a life-history framework, Walker *et al.* [10] and Migliano *et al.* [8] have formulated a simple yet elegant hypothesis to explain the evolution of the pygmy phenotype. Specifically, to maximize fitness under conditions of limited lifespan, small-bodied populations have an early cessation of growth or a diminished growth spurt to facilitate a relatively early age of first reproduction. In effect, this hypothesis predicts an indirect relationship between adult life expectancy and body size (Figure 3).

Tropical rainforests are challenging habitats for humans, not only in terms of foraging, mobility and thermoregulation but also because these environments harbor many parasites and infectious disease pathogens [32]. Perhaps as a consequence, infant and child mortality rates among these groups are high relative to those of other human populations; for example, rates for African rainforest hunter-gatherers are ~20% for infants and 27–40% for children less than 5 years old, approximately twice the regional rates [33]. This pattern extends into adulthood: among six rainforest hunter-gatherer populations from Africa and Southeast Asia, the chances of surviving to

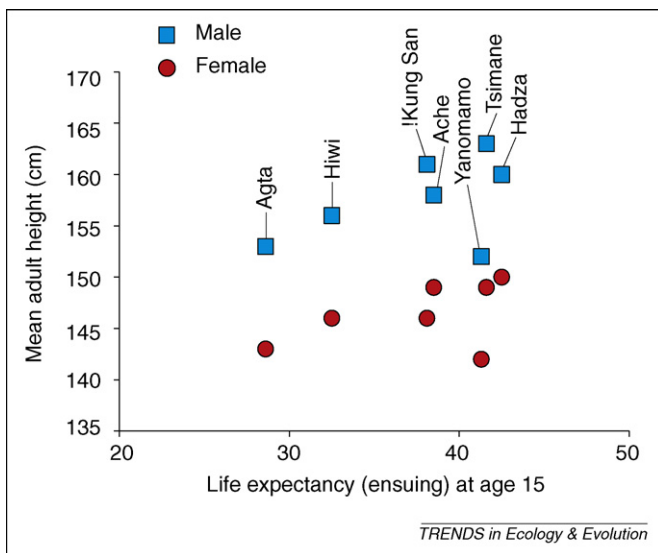


Figure 3. Relationship between adult mortality and body size. The life-history hypothesis of human pygmy phenotype evolution predicts an indirect relationship between adult mortality and body size; that is, small stature might be a morphological consequence of selection for early cessation of growth and early reproduction to offset limited adult lifespan under conditions of high adult mortality. The predicted relationship between stature and adult life expectancy (ensuing lifespan for individuals reaching 15 years of age) is generally observed, at least for the few small-scale societies for whom relatively high quality mortality data are available and have been standardized [37]. Male and female stature estimates are from Ref. [10] (populations are labeled at the male values; female values are directly below). It is not possible to control for all confounding variables; for example, poor nutritional availability could negatively affect both stature (via stunted childhood growth) and adult life expectancy. As a result, the observed relationship is consistent with but does not prove a selection-driven effect. The Yanomamö are unexpectedly short (mean adult heights: male = 152 cm; female = 142 cm) given the reported adult life expectancy (Yanomamö Mucajai, Brazil, 41.3 years), which could partly reflect variation that exists among different Yanomamö groups with respect to both stature (e.g. mean adult male statures range from 147 to 157 cm among Venezuelan Yanomamö communities [80]) and potentially adult mortality (e.g. adult life expectancy for the Brazilian Yanomamö Xiliana is only 28.3 years, albeit based on more limited data [37]).

age 15 are 30–51%, versus 59–76% for one pastoralist and two non-rainforest hunter-gatherer populations [8]. Once reaching 15 years of age, ensuing life expectancy estimates for these groups are 20–32.5 and 41.5–46.6 years, respectively [8].

Under these circumstances of high adult mortality, any widening of the otherwise small reproductive window (thereby increasing the number of opportunities to raise offspring that reach adulthood) is expected to be adaptive. Rainforest hunter-gatherers might have maximized their fitness in this respect with earlier menarche and ages of first reproduction relative to other populations [8,10,34]. In the proposed life-history model of pygmy phenotype evolution [8,10], early maturation is achieved at the expense of body size. Indeed, growth curves level off for rainforest hunter-gatherer females at around age 12, when for other populations the adolescent growth spurt is just beginning [8,10]. In an extension of this model, Walker and Hamilton [34] also consider the effects of population density on human body-size variation, because at least within similar environments (e.g. across tropical rainforests) population density might be positively correlated with both resource constraint and mortality. These observations are concordant with recent life-history theory and research on other organisms [35,36].

Based on their data, Migliano *et al.* [8] concluded that early growth cessation is the primary (although not necess-

arily exclusive) mechanistic cause of the human pygmy phenotype. This result seems somewhat discordant with analyses of detailed growth data from the Efe which showed increasing stature differences between this population and neighboring agriculturalists from birth to age 5 [7]. It is possible that the Efe achieve small body size via a different mechanism from other small-bodied populations (i.e. a change in growth rate rather than timing). Alternatively, growth might be both slow in childhood and stop early in the Efe. Because longitudinal data were not collected into adulthood for this population [7], such a possibility cannot yet be evaluated.

Migliano *et al.* [8] reasoned that life-history factors alone probably explain the evolutionary origins of the human pygmy phenotype, to the exclusion of direct selection for small body size itself under the food limitation-, thermoregulation- and mobility-associated adaptive scenarios discussed above (beyond what they might contribute to high mortality). However, given that early growth cessation could be a mechanism of small body-size evolution regardless of the ultimate evolutionary pressures, it might be too soon to distinguish among these hypotheses. Although the observation that the pygmy phenotype is often associated with unusually high adult mortality [8] is certainly a promising line of evidence in support of the life-history hypothesis, mortality rates can be difficult to estimate accurately depending on the underlying data source [37] and detailed mortality rates have thus far been examined for only a few populations. It is not yet clear the extent to which these mortality rates are representative of those for other rainforest hunter-gatherers, or even whether they appropriately reflect those from the same populations in pre-modern times. For example, one of the populations examined by Migliano *et al.* [8], the Agta, have experienced considerable cultural change in the past 50 years [38] that corresponds to a marked increase in adult mortality [37]. Moreover, the life-history hypothesis does not explain the relatively small body sizes of all the savanna-woodland populations mentioned previously: whereas the Hiwi experience high adult mortality [39] comparable to that of the small-bodied rainforest hunter-gatherers studied by Migliano *et al.* [8], the Hadza and !Kung San do not [8,39].

It could be beneficial to consider the combined effects of habitat-specific ecology and high adult mortality on pygmy phenotype evolution. For example, in open environments, the locomotor efficiency of taller statures could partly offset any life-history pressures favoring early growth cessation. By contrast, the strongest directional selection for the pygmy phenotype might have been driven by high adult mortality in habitats absent of such advantages for larger body sizes or in which small body sizes are even beneficial (Figure 4). Detailed growth and mortality data from the Efe might be germane to this issue, given the evidence that small stature in this population is not entirely due to early growth cessation [7].

Antiquity of the pygmy phenotype

Although we must be careful not to confuse entirely population histories with the issue of pygmy phenotype evolution, insights from one might inform the other. Among

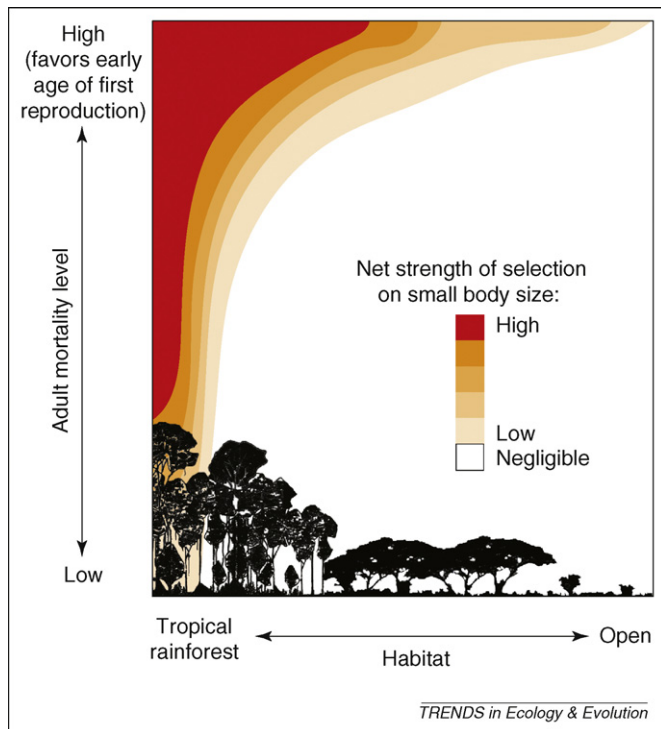


Figure 4. Integrated model of pygmy phenotype evolution. This model proposes that the overall strength of selection on small body size in humans might be driven by the combination of habitat- and adult mortality-level variables. Specifically, the intensity of selection for small body size might be highest for tropical rainforest populations that also experience high adult mortality, in which case the pygmy phenotype might confer fitness benefits related to both ecology (e.g. food limitations, high temperature and humidity, dense forest undergrowth) and life history (i.e. early growth cessation could facilitate an early age of first reproduction). Otherwise, selection coefficients for small body size might be lower or negligible. For example, the life-history-related benefits of early growth cessation could be mitigated by the locomotor advantages of larger body sizes in open environments.

African rainforest hunter-gatherers, mtDNA haplotype profiles of the Mbuti (Democratic Republic of Congo) and populations from Western Africa (Cameroon, Gabon and the Central African Republic, including the Biaka) have little overlap [40,41]. This level of differentiation (although partly reflecting genetic drift) exceeds that observed between Western African rainforest hunter-gatherers and Bantu agriculturalist populations, which itself is thought to represent a divergence of 30 000–70 000 years and only limited gene flow [41,42]. The Mbuti and Biaka are also readily distinguished in analyses of nuclear DNA single-nucleotide polymorphism genotypes [43,44].

Together, these data suggest a relatively ancient population divergence between rainforest hunter-gatherers from the two African regions (Western and more Eastern). If the pygmy phenotype pre-dates this divergence, then it could be old, certainly older than the emergence and spread of agriculture in Africa ~5000 years ago [41]. Alternatively, the introgression of any more recent, highly advantageous, mutations might have required only limited gene flow between these groups. Finally, there could have been multiple, independent origins of the pygmy phenotype even within Africa.

Ultimately, identification of the specific causative mutations for the pygmy phenotype (Box 1) will help us to distinguish among these scenarios, and potentially to estimate the ages of the mutations themselves. Similar

analyses will also be important for studying the evolutionary ecology of Southeast Asian rainforest hunter-gatherers for whom, interestingly, similar issues exist. Specifically, the mtDNA profiles of Malaysian and Andaman Island populations do not overlap, and each of these different sets of haplotypes was estimated to have diverged >50 000 years ago from other populations in Asia [13,45–47].

Paleoanthropological relevance

Knowledge of the adaptive basis of modern human body-size variation, including the pygmy phenotype, could benefit interpretations of the hominin fossil record. Currently, the evolution of major shifts in body sizes is poorly understood. Moreover, as discussed earlier, recent analyses have shown that distinct modern populations achieve small body sizes by the early cessation of growth; thus, it now seems clear that life history can evolve surprisingly rapidly in humans (i.e. within the last 30 000–50 000 years and perhaps considerably more recently). Extending this notion to a broader view of human evolution, we should anticipate the possibility of considerable life-history diversity among fossil hominins.

Flores

The description in 2004 of ~18 000-year-old skeletal remains of a ~106 cm tall hominin from the island of Flores, Indonesia [3], generated considerable excitement and debate [5,6,48,49]. In particular, the designation of *Homo floresiensis* as a new species that is more closely related to *Homo erectus* than to *Homo sapiens* has been criticized on the grounds that pathologies could account for distinctive traits such as a relatively small cranial capacity [50,51]. Although not all questions of pathology and taxonomy have been resolved, long bone skeletal material from a second Flores individual suggests that small stature, at least, was characteristic of the population, rather than restricted to the holotype specimen, LB1 [52]. If *H. floresiensis* does prove to be distinct from modern humans, then it would represent another independent origin of the pygmy phenotype in recent hominin evolution.

Several studies on the taxonomic validity and other aspects of *H. floresiensis* have used modern human rainforest hunter-gatherers as a referential model [4–6,52–55]. However, such a model should be applied with some caution. Specifically, *H. floresiensis* (as presently construed) is characterized by diminutive cranial capacity [53], which represents a marked departure from the overall phenotype of modern small-bodied rainforest hunter-gatherers [50].

The extremely small body size of *H. floresiensis* was perhaps driven largely by a special case of insular dwarfism (Box 2), although Jacob *et al.* [5] emphasize the high humidity and dense vegetation of Flores. Therefore, the adaptive advantages of improved thermoregulation and mobility of small body size that were potentially involved in the evolution of the modern human pygmy phenotype should also be considered for *H. floresiensis*.

Based on a new appreciation of life-history diversity among modern humans and the apparent association of this diversity with body size [8], it becomes reasonable to ask whether the life-history pattern of *H. floresiensis* was relatively accelerated compared to *H. erectus* and other fossil

hominins. Such a question could be answered with microscopic analyses of fossil teeth. Specifically, enamel is secreted in a circadian manner and contains short- and long-period incremental features that enable reconstructions of dental growth rates and molar eruption schedules [56]. Additionally, the timing of major life events, such as birth, weaning and illness, manifest as discrete disruptions in enamel deposition; as a result, the overall pace of dental growth can be compared to somatic growth schedules [57]. These techniques have been used to describe dental development rates or life-history profiles for australopithecines, *H. erectus*, Neandertals (*Homo neanderthalensis*) and anatomically modern humans dated to as early as 160 000 years ago [57–62]. We hope that similar analyses can eventually be performed on the remains of *H. floresiensis*.

Palau

Other potentially interesting skeletal remains were recently recovered from small islands in the Republic of Palau. These remains, with estimated adult body sizes similar to, or smaller than, those of modern Onge (Andaman Islands), have been dated to ~1000–3000 years ago and attributed to *H. sapiens* [63]. If these body-size estimates are confirmed (for a critical view, see Ref. [64]), then it will be important to test whether this Palauan population was closely related to extant Southeast Asian rainforest hunter-gatherers and thus was probably small bodied before arriving on Palau, or whether they independently evolved small body size by insular dwarfism.

Concluding remarks

Small body size is a characteristic that is shared among multiple human populations that hunt and gather food in tropical rainforests. The convergent origins of this phenotype in Africa, Southeast Asia and South America can probably be explained as an adaptive response to the similar challenges posed by rainforest or rainforest-edge habitats, whether those challenges were related to food limitation, high temperature and humidity, structural properties of the forest itself, unusually high adult mortality or some combination thereof.

Future research on this topic might benefit from the detailed study of rainforest hunter-gatherer behavioral ecology and non-body-size physiology. Specifically, these populations might have numerous cultural and genetic adaptations to the tropical rainforest that are not yet described or considered in this framework. By understanding the evolutionary context of such adaptations, and thereby isolating features of rainforest habitats that have strongly affected fitness in the histories of these populations, we will be better positioned to identify the evolutionary pressures that favored the pygmy phenotype. Ultimately, by considering modern human and broader hominin body-size diversity in the context of life-history, mortality, habitat and other measured and reconstructed ecological variables, we stand to shed considerable light on our evolutionary history.

Acknowledgements

We thank Nurul Fatanah, Zanisha Man and the Batek for their hospitality, and Luis Barreiro, Geoffrey Benjamin, John Hart, Kim Hill,

Kirk Endicott, Raymond Hames, Tuck-Po Lye, Edith Mirante, Etienne Patin, Gary Schwartz, Paul Verdu and Robert Walker for helpful comments and discussions. This work was supported by a grant to N.J.D. from the Packard Foundation. G.H.P. is supported by NIH fellowship F32GM085998.

References

- Blankenhorn, W.U. (2000) The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* 75, 385–407
- Visscher, P.M. (2008) Sizing up human height variation. *Nat. Genet.* 40, 489–490
- Brown, P. *et al.* (2004) A new small-bodied hominin from the late Pleistocene of Flores, Indonesia. *Nature* 431, 1055–1061
- Argue, D. *et al.* (2006) *Homo floresiensis*: microcephalic, pygmoid, *Australopithecus*, or *Homo*? *J. Hum. Evol.* 51, 360–374
- Jacob, T. *et al.* (2006) Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalities. *Proc. Natl. Acad. Sci. U. S. A.* 103, 13421–13426
- Richards, G.D. (2006) Genetic, physiologic and ecogeographic factors contributing to variation in *Homo sapiens*: *Homo floresiensis* reconsidered. *J. Evol. Biol.* 19, 1744–1767
- Bailey, R.C. (1991) The comparative growth of Efe pygmies and African farmers from birth to age 5 years. *Ann. Hum. Biol.* 18, 113–120
- Migliano, A.B. *et al.* (2007) Life history trade-offs explain the evolution of human pygmies. *Proc. Natl. Acad. Sci. U. S. A.* 104, 20216–20219
- De Souza, R.G. (2006) Body size and growth: the significance of chronic malnutrition among the Casiguran Agta. *Ann. Hum. Biol.* 33, 604–619
- Walker, R. *et al.* (2006) Growth rates and life histories in twenty-two small-scale societies. *Am. J. Hum. Biol.* 18, 295–311
- Cavalli-Sforza, L.L. (1986) African pygmies: an evaluation of the state of research. In *African Pygmies* (Cavalli-Sforza, L.L., ed.), pp. 361–426, Academic Press
- Shea, B.T. and Bailey, R.C. (1996) Allometry and adaptation of body proportions and stature in African pygmies. *Am. J. Phys. Anthropol.* 100, 311–340
- Thangaraj, K. *et al.* (2003) Genetic affinities of the Andaman Islanders, a vanishing human population. *Curr. Biol.* 13, 86–93
- Hart, T.B. and Hart, J.A. (1986) The ecological basis of hunter-gatherer subsistence in African rain forests: the Mbuti of Eastern Zaire. *Hum. Ecol.* 14, 29–55
- Bailey, R.C. *et al.* (1989) Hunting and gathering in tropical rain forest: is it possible? *Am. Anthropol.* 91, 59–82
- Endicott, K. and Bellwood, P. (1991) The possibility of independent foraging in the rain forest of peninsular Malaysia. *Hum. Ecol.* 19, 151–185
- Headland, T.N. and Bailey, R.C. (1991) Introduction: have hunter-gatherers ever lived in tropical rain forest independently of agriculture? *Hum. Ecol.* 19, 115–122
- Mercader, J. (2002) Forest people: the role of African rainforests in human evolution and dispersal. *Evol. Anthropol.* 11, 117–124
- Minetti, A.E. *et al.* (1994) Pygmy locomotion. *Eur. J. Appl. Physiol. Occup. Physiol.* 68, 285–290
- Diamond, J.M. (1991) Why are pygmies small? *Nature* 354, 111–112
- Weijers, J.W. *et al.* (2007) Coupled thermal and hydrological evolution of tropical Africa over the last deglaciation. *Science* 315, 1701–1704
- Bramble, D.M. and Lieberman, D.E. (2004) Endurance running and the evolution of *Homo*. *Nature* 432, 345–352
- Pontzer, H. (2005) A new model predicting locomotor cost from limb length via force production. *J. Exp. Biol.* 208, 1513–1524
- Carey, T.S. and Crompton, R.H. (2005) The metabolic costs of bent-hip, bent-knee walking in humans. *J. Hum. Evol.* 48, 25–44
- Bailey, R.C. (1991) *The Behavioral Ecology of Efe Pygmy Men in the Ituri Forest, Zaire*. Museum of Anthropology, University of Michigan
- Chagnon, N.A. (1997) *Yanomamo*. Harcourt Brace
- Elton, S. *et al.* (1998) Habitual energy expenditure of human climbing and clambering. *Ann. Hum. Biol.* 25, 523–531
- Hanna, J.B. *et al.* (2008) The energetic cost of climbing in primates. *Science* 320, 898
- Pontzer, H. and Wrangham, R.W. (2004) Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J. Hum. Evol.* 46, 317–335
- Hewlett, B.S. *et al.* (1986) Causes of death among Aka pygmies of the Central African Republic. In *African Pygmies* (Cavalli-Sforza, L.L., ed.), pp. 45–63, Academic Press

- 31 Liebenberg, L. (2006) Persistence hunting by modern hunter-gatherers. *Curr. Anthropol.* 47, 1017–1026
- 32 Guernier, V. *et al.* (2004) Ecology drives the worldwide distribution of human diseases. *PLoS Biol.* 2, e141
- 33 Ohenjo, N. *et al.* (2006) Health of indigenous people in Africa. *Lancet* 367, 1937–1946
- 34 Walker, R.S. and Hamilton, M.J. (2008) Life-history consequences of density dependence and the evolution of human body size. *Curr. Anthropol.* 49, 115–122
- 35 Stearns, S.C. *et al.* (2000) Experimental evolution of aging, growth, and reproduction in fruitflies. *Proc. Natl. Acad. Sci. U. S. A.* 97, 3309–3313
- 36 Reznick, D. *et al.* (2001) Life history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *Am. Nat.* 157, 126–140
- 37 Gurven, M. and Kaplan, H. (2007) Longevity among hunter-gatherers: a cross-cultural examination. *Popul. Dev. Rev.* 33, 321–365
- 38 Early, J.D. and Headland, T.N. (1998) *Population Dynamics of a Phillipine Rain Forest People: The San Ildefonso Agta*. University Press of Florida
- 39 Hill, K. *et al.* (2007) High adult mortality among Hiwi hunter-gatherers: implications for human evolution. *J. Hum. Evol.* 52, 443–454
- 40 Destro-Bisol, G. *et al.* (2004) The analysis of variation of mtDNA hypervariable region 1 suggests that eastern and western pygmies diverged before the Bantu expansion. *Am. Nat.* 163, 212–226
- 41 Quintana-Murci, L. *et al.* (2008) Maternal traces of deep common ancestry and asymmetric gene flow between pygmy hunter-gatherers and Bantu-speaking farmers. *Proc. Natl. Acad. Sci. U. S. A.* 105, 1596–1601
- 42 Batini, C. *et al.* (2007) Phylogeography of the human mitochondrial L1c haplogroup: genetic signatures of the prehistory of Central Africa. *Mol. Phylogenet. Evol.* 43, 635–644
- 43 Jakobsson, M. *et al.* (2008) Genotype, haplotype and copy-number variation in worldwide human populations. *Nature* 451, 998–1003
- 44 Li, J.Z. *et al.* (2008) Worldwide human relationships inferred from genome-wide patterns of variation. *Science* 319, 1100–1104
- 45 Macaulay, V. *et al.* (2005) Single, rapid coastal settlement of Asia revealed by analysis of complete mitochondrial genomes. *Science* 308, 1034–1036
- 46 Thangaraj, K. *et al.* (2005) Reconstructing the origin of Andaman Islanders. *Science* 308, 996
- 47 Hill, C. *et al.* (2006) Phylogeography and ethnogenesis of aboriginal Southeast Asians. *Mol. Biol. Evol.* 23, 2480–2491
- 48 Diamond, J. (2004) The astonishing micropygmies. *Science* 306, 2047–2048
- 49 Tocheri, M.W. *et al.* (2007) The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317, 1743–1745
- 50 Martin, R.D. *et al.* (2006) Flores hominid: new species or microcephalic dwarf? *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* 288, 1123–1145
- 51 Niven, J.E. (2007) Brains, islands and evolution: breaking all the rules. *Trends Ecol. Evol.* 22, 57–59
- 52 Morwood, M.J. *et al.* (2005) Further evidence for small-bodied hominins from the Late Pleistocene of Flores. *Indonesia. Nature* 437, 1012–1017
- 53 Falk, D. *et al.* (2005) The brain of LB1, *Homo floresiensis*. *Science* 308, 242–245
- 54 Larson, S.G. *et al.* (2007) *Homo floresiensis* and the evolution of the hominin shoulder. *J. Hum. Evol.* 53, 718–731
- 55 Gordon, A.D. *et al.* (2008) The *Homo floresiensis* cranium (LB1): size, scaling, and early *Homo* affinities. *Proc. Natl. Acad. Sci. U. S. A.* 105, 4650–4655
- 56 Smith, T.M. (2008) Incremental dental development: methods and applications in hominoid evolutionary studies. *J. Hum. Evol.* 54, 205–224
- 57 Dean, M.C. (2006) Tooth microstructure tracks the pace of human life-history evolution. *Proc. R. Soc. Lond. B Biol. Sci.* 273, 2799–2808
- 58 Macchiarelli, R. *et al.* (2006) How Neanderthal molar teeth grew. *Nature* 444, 748–751
- 59 Smith, T.M. *et al.* (2007) Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proc. Natl. Acad. Sci. U. S. A.* 104, 6128–6133
- 60 Smith, T.M. *et al.* (2007) Rapid dental development in a Middle Paleolithic Belgian Neanderthal. *Proc. Natl. Acad. Sci. U. S. A.* 104, 20220–20225
- 61 Guatelli-Steinberg, D. and Reid, D.J. (2008) What molars contribute to an emerging understanding of lateral enamel formation in Neandertals vs. modern humans. *J. Hum. Evol.* 54, 236–250
- 62 Robson, S.L. and Wood, B. (2008) Hominin life history: reconstruction and evolution. *J. Anat.* 212, 394–425
- 63 Berger, L.R. *et al.* (2008) Small-bodied humans from Palau. *Micronesia. PLoS ONE* 3, e1780
- 64 Fitzpatrick, S.M. *et al.* (2008) Small scattered fragments do not a dwarf make: biological and archaeological data indicate that prehistoric inhabitants of Palau were normal sized. *PLoS ONE* 3, e3015
- 65 Ishida, T. *et al.* (1998) Preliminary report on the short stature of Southeast Asian forest dwellers, the Manni, in southern Thailand: lack of an adolescent spurt in plasma IGF-I concentration. *Southeast Asian J. Trop. Med. Public Health* 29, 62–65
- 66 Jain, S. *et al.* (1998) Insulin-like growth factor-I resistance. *Endocr. Rev.* 19, 625–646
- 67 Clavano-Harding, A.B. *et al.* (1999) Initial characterization of the GH-IGF axis and nutritional status of the Ati Negritos of the Philippines. *Clin. Endocrinol. (Oxf.)* 51, 741–747
- 68 Davila, N. *et al.* (2002) Growth hormone binding protein, insulin-like growth factor-I and short stature in two pygmy populations from the Philippines. *J. Pediatr. Endocrinol. Metab.* 15, 269–276
- 69 Steiner, C.C. *et al.* (2009) The genetic basis of phenotypic convergence in beach mice: similar pigment patterns but different genes. *Mol. Biol. Evol.* 26, 35–45
- 70 Wittkopp, P.J. *et al.* (2003) *Drosophila* pigmentation evolution: divergent genotypes underlying convergent phenotypes. *Proc. Natl. Acad. Sci. U. S. A.* 100, 1808–1813
- 71 Dietz, W.H. *et al.* (1989) Nutritional status of Efe pygmies and Lese horticulturists. *Am. J. Phys. Anthropol.* 78, 509–518
- 72 Lomolino, M.V. (2005) Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* 32, 1683–1699
- 73 Bromham, L. and Cardillo, M. (2007) Primates follow the ‘island rule’: implications for interpreting *Homo floresiensis*. *Biol. Lett.* 3, 398–400
- 74 Meiri, S. *et al.* (2008) The island rule: made to be broken? *Proc. Biol. Sci.* 275, 141–148
- 75 Raia, P. and Meiri, S. (2006) The island rule in large mammals: paleontology meets ecology. *Evolution Int. J. Org. Evolution* 60, 1731–1742
- 76 Palkovacs, E.P. (2003) Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* 103, 37–44
- 77 Burness, G.P. *et al.* (2001) Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proc. Natl. Acad. Sci. U. S. A.* 98, 14518–14523
- 78 Schebesta, P. and Lebzelter, V. (1928) Anthropological measurements in Semangs and Sakais in Malaya (Malacca). *Anthropologie* 6, 183–251
- 79 Pandey, A.K. (2004) Anthropometry of male Onges of Little Andaman. *South Asian Anthropol.* 4, 135–140
- 80 Hames, R. and Kuzara, J. (2004) The nexus of Yanomamo growth, health, and demography. In *Lost Paradises and the Ethics of Research and Publication* (Salzano, F.M. and Hurtado, A.M., eds), pp. 110–145, Oxford University Press