Reports

Life-History Consequences of Density Dependence and the Evolution of Human Body Size

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Previous attempts to explain variation in human growth and development emphasize the energetic constraints imposed by malnutrition and disease. However, this approach does not address the evolutionary effects of mortality risk on ontogenetic variation, a common theme in life-history studies. The conventional approach can be reconciled with life-history theory by considering the effect of mortality on the rates and timing of maturity in subsistence-based human populations. Humans slow down growth and development and demonstrate smaller adult body sizes in high-population-density contexts, presumably because of increased nutritional constraints and disease loads. In addition, there is evidence of mortality-based selection for relatively *faster/earlier* ontogeny in small-bodied hunter-gatherers living at high densities. This finding may be interpreted as an evolved reaction norm for earlier reproductive maturity and consequent smaller adult body size in high-mortality regimes. In sum, comparative results support density-dependent effects on body size that act through two pathways—nutritional constraints and juvenile mortality—at varying intensities, contributing to a nearly twofold range in body size across human societies.

The evolution of body size is a prominent topic in evolutionary biology (Sibly, Calow, and Nichols 1985; Stearns and Koella 1986; Stearns 1992; Berrigan and Koella 1994). Dwarfism and gigantism on islands present an opportunity to test the evolutionary mechanisms of body-size change (Foster 1964; Brown 1995; Brown and Lomolino 1998). Some of the world's smallest humans are hunter-gatherers living on islands (e.g., Philippine "Negritos" and Andaman Islanders) and in island-like ecologies (e.g., African "Pygmies" in circumscribed rain forests), with mean adult female body sizes of 34–43 kg. Palkovacs (2003) integrates insular biogeography into a life-history framework by suggesting that less extrinsic mortality (e.g., low predation) increases body size in smaller animals, while resource scarcity reduces body size in larger animals. We follow this approach by focusing on two concurrent pathways leading to human body size reduction: density-dependent responses to resource scarcity and selection for rapid development in the face of high extrinsic mortality rates.

Some have interpreted small body size in tropical foraging populations as an adaptation to hot and humid rain forests (Roberts 1953, 1978; Cavalli-Sforza 1986) and efficient foraging (Tobias 1964; Lee 1979). We examine the evolution of small body size in human hunter-gatherers not as direct selection on body size per se but as a generalized life-history consequence of density dependence. Density-dependent life histories are a ubiquitous feature of naturally occurring biological populations because of the finite availability of resources (Malthus 1798; Murdoch 1994; Sibly, Calow, and Nichols 2005) but have previously received little attention in humans (but see Waguespack 2002; Wood and Smouse 1982). Other things being equal, increased density in energy-limited populations implies, by definition, increased competition among conspecifics for resources, resulting in reduced birth rates and increased mortality rates. In effect, as a population approaches its carrying capacity, per capita resource availability diminishes monotonically. If foraging populations are at equilibrium and distributed in an ideal-free manner, the null expectation is no relationship between body size and population density across hunter-gatherer societies. However, if a negative density-dependent relationship emerges, then this suggests that populations are in different states of expansion and implies differential mortality rates and per capita resource availability.

Small body size is a plastic response to disease and malnutrition (Stini 1969; Wilbur 1977; Levitan 1988; Holmes 1995) that is likely exacerbated by high population density. In addition, small body size may be a life-history consequence of relatively faster/earlier ontogeny in high-mortality regimes (Migliano 2005). The conventional anthropological approach tends to consider growth and developmental rates to be primarily driven by energetic/disease constraints (Bogin 1999; Ulijaszek, Johnston, and Preece 1998; Eveleth and Tanner 1990). Life-history models incorporate these constraints but also predict that a delay in age at first reproduction will be more costly when the probability of survival to that age is low, other things being equal (Stearns and Koella 1986; Stearns 1992; Berrigan and Koella 1994; Charnov 1993). Mortality-induced increases in growth and early reproducZtion have likely evolved in other species when a size or developmental threshold had to be quickly reached (Arendt 1997). Size-specific mortality leading to faster growth has been proposed to explain why human neonates are larger than expected in countries with high risk of parasitic and infectious diseases (Thomas et al. 2004). Increases in height and weight between the ages of 3 and 10 are relatively faster in human societies with high juvenile mortality if nutritional considerations are held mostly constant by including adult body size

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in the regressions (Walker et al. 2006). An interpretation of these results is that at the population level selection promotes faster and earlier maturation in high-mortality regimes but at the individual level resource scarcity prevents an optimal allocation from being expressed (Pettay et al. 2007). Energetic constraints and mortality-based selection are two important components of a comprehensive life-history model for the evolution of body size in humans, and both can be related to population density, considered here to be a prime mover of variation in human life histories.

Combining data on human body size and shape (Eveleth and Tanner 1990) with data on demographic variation in fertility and mortality (Wood 1994; Pennington 2001) can help uncover important relationships among growth and development, resource availability, and population dynamics. For example, studies among the Ache (Hill and Hurtado 1996), Gambian villagers (Sear, Mace, and McGregor 2003), and New Guinea Highlanders (Brush, Boyce, and Harrison 1983) show a positive effect of body size on fertility rates. These results support the hypothesis that "bigger is better" when it comes to fertility in small-scale societies and that selection should act to increase body size when more resources are available. However, larger body size incurs higher maintenance costs (Gurven and Walker 2006), and therefore we expect individuals to settle near optimal body sizes, with size being driven up by the benefits of higher fertility but driven down by the energetic costs of maintenance and the reproductive opportunity costs of more time spent growing. With less available nutrition, the costs of maintaining a larger body increase proportionally. With higher mortality, the opportunity costs of forgone reproduction increase. As a result, smaller adult body size is likely to follow in both scenarios even if it comes at the expense of the fertility that would have accrued with larger body size.

We hypothesize that body size will show negative density dependence across hunter-gatherer societies. In addition, we evaluate the hypothesis of density-dependent increases in juvenile mortality that prompt earlier menarche and reproduction and consequently smaller adult body size in hunter-gatherers that are near or above carrying capacity. Finally, we provide a model that incorporates these relationships and illustrates the evolution of human body size as a generalized life-history consequence of increasing population density.

Methods

The hunter-gatherer sample used to assess density-dependent body size consists of populations characterized by mostly foraging economies that exhibit near-natural fertility and have little access to modern health care. Table 1 provides descriptive information, latitude, female adult mass, and population density for a worldwide sample of 32 hunter-gatherer societies. While we focus on foraging populations because agro-pastoralism tends to support more people per unit area, we also utilize life-history data for other small-scale societies (including Yanomamo, Gainj, and Tsimane horticulturists and Turkana pastoralists) to bolster our small sample, which is limited by reliable estimates of juvenile mortality (before age 15). We include these well-studied nonforagers in analyses of age at menarche and first reproduction because they meet the criteria of subsistence-based economy and natural fertility with little access to health care. We feel justified in doing so because similar cost/benefit structures of energy, reproduction, and survival are likely acting on rates of development in these societies. Data are compiled from Binford (2001), Walker et al. (2006), and sources therein.

Adult female body sizes are generally calculated as the mean of all available individuals from their mid-20s to their mid-50s. Population density is estimated as the total population size divided by land use area and is $\log_{10}$-transformed in analyses because this normalizes the distribution. We also used effective temperature in place of latitude, although the relationship between latitude and body size is slightly stronger. We use ordinary-least-squares regression to estimate the parameters of our models and resampling to test the significance of the regressions with small sample sizes. The strength of this procedure lies in the fact that resampling is less sensitive to the assumptions of normality and has more power than parametric tests when samples are so small that distributions may be nonnormal (Manly 1991).

Results

Across hunter-gatherers, body size is density-dependent ($B = -8.39$ for body mass by $\log_{10}$-population density, $p < 0.0001$, $R^2 = 0.44$, $n = 29$). Small-bodied foragers tend to live at population densities greater than 0.1 km^{-2}, whereas larger-bodied foragers tend to live at lower densities. However, this relationship is confounded by latitude because body size tends to increase with colder temperatures (Bergmann 1847; Katzmarzyk and Leonard 1998). Given that Arctic foragers tend to live at low population densities, latitudinal effects can obscure the true relationship between population density and body size. We addressed this issue by regressing both body size and $\log_{10}$-population density on latitude and analyzing the relationship between the unstandardized residuals, thereby partially controlling for variation in environmental quality. The negative density-dependent relationship of body size remains ($B = -4.78$, $p = 0.011$, $R^2 = 0.22$, $n = 29$; fig. 1). This relationship is probably an underestimate, since we have two outlying societies with considerable leverage. One is the coastal Asmat, who despite their high density have a large body size for their latitude. The other is the desert Walbiri, who are small given their low population density. Omitting these two societies yields a stronger negative density dependence in body size ($B = -7.91$, $p < 0.0001$, $R^2 = 0.46$, $n = 27$).

A multiple regression of body size as a function of latitudinal gradient ($p = 0.0009$) and population density ($p = 0.0127$) explains 63% of the variation in global hunter-gath-

Table 1. Group-Level Data for Hunter-Gatherers in This Study

Society	Country	Latitude (degrees)	Ecology	Population Density (people/km^2)	Female Adult Body Size (kg)
Ache	Paraguay	25.7	Neotropical forest	0.03	51.8
Aeta	Philippines	15	Tropical forest	0.92	–[a]
Agta (Casiguran)	Philippines	17.3	Tropical forest	0.87	38
Agta (Isabela)	Philippines	17.5	Tropical forest	0.42	34
Aka	Congo/C.A.R.	2	Tropical forest	0.09	42
Asmat	Irian Jaya	6	Coastal	1.80	50
Batak	Philippines	10	Tropical forest	0.43	40.8
Chenchu	India	17	Scrub forest	1.25	–[a]
Gidjingali	Australia	12.2	Coast/savanna	0.73	41.3
Groote-eylandt	Australia	14	Coast/savanna	0.23	42
Guaja	Brazil	3	Neotropical forest	0.03	50.4
Gunwinggu	Australia	12.4	Savanna	0.18	46.1
G/wi	Botswana	22.5	Desert	0.03	49.6
Hadza	Tanzania	3.8	Savanna	0.24	48
Hiwi	Venezuela	5.4	Savanna	0.18	49.7
Jarwa	Andaman Islands	12.2	Tropical forest	0.45	42.3
Ju/'hoansi	Botswana/Namibia	20	Desert	0.07	42.2
Kadar	India	10.3	Savanna	0.50	37.1
Kutchin	United States (Alaska)	65.9	Boreal forest	0.02	55
Mirrngadja	Australia	12.3	Desert	0.39	43.1
Nunamiut	United States (Alaska)	68.2	Polar tundra	0.01	65.7
Onge	Andaman Islands	10.7	Tropical forest	0.40	39.5
Pume	Venezuela	6.9	Savanna	0.20	45.6
Punan	Indonesia	3	Tropical forest	0.12	37.9
Pygmy (East Africa)	Democratic Repuplic of Congo	2.7	Tropical forest	0.56	39.4
Pygmy (West Africa)	Cameroon/Congo/C.A.R.	2	Tropical forest	0.14	42.7
Seri	Mexico	32	Coastal/desert	0.25	–[a]
Shompen	Nicobar Islands	7	Tropical forest	0.40	47.1
Sivokamiut	United States (Alaska)	63.5	Polar tundra	0.15	56.5
Tareumiut	United States (Alaska)	71.3	Polar tundra	0.04	61.2
Walbiri	Australia	20	Desert	0.01	45.4
Yavapai	United States (Arizona)	33.4	Shrub forest	0.01	63

[a] Aetu, Chenchu, and Seri lack body-mass data that are contemporaneous with population-density estimates.

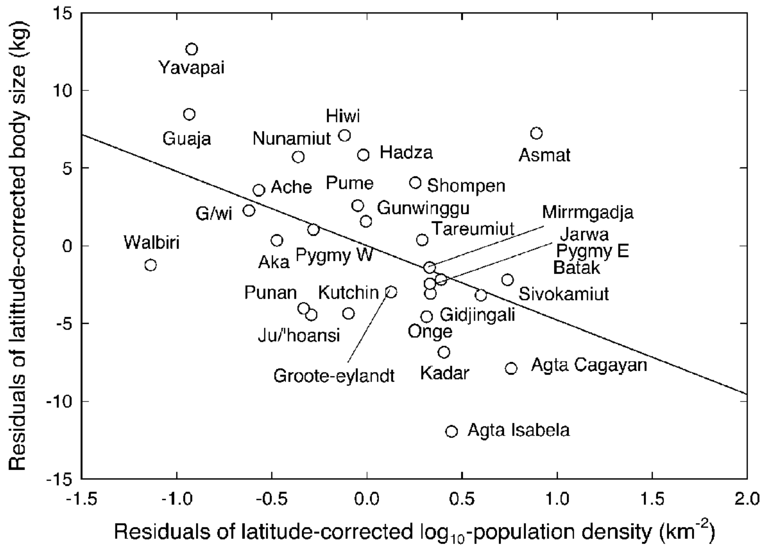

Figure 1. Residuals of adult female body size by latitude against the residuals of $\log_{10}$-population density by latitude. Undoubtedly, the residuals of this regression are associated with local resource availability.

erer body size (mass $= 38.5 - 4.8 * \log_{10}$-population density $+0.2 *$ latitude). Remarkably, the average female body size at a density of 0.1 km^{-2} is about 5 kg heavier than at a density of 1 km^{-2}, a decrease of approximately one-eighth of total adult female body mass per order-of-magnitude increase in population density. In addition, every 5° increase in latitude corresponds to 1 extra kg of body mass. We also examined whether habitat type was related to body size in hunter-gatherers. Tropical forest groups appear to be slightly smaller than groups living in open habitats (tundra, savanna, and desert). However, the difference is small, about 1 kg on average, and is not statistically significant when latitude and population density are included in the regression. Some tropical forest foragers like the Guaja and Ache demonstrate fairly robust body sizes that seem best explained by their low population density.

Juvenile mortality in humans is a trait that has been shown to correlate more closely with rates and timing of development

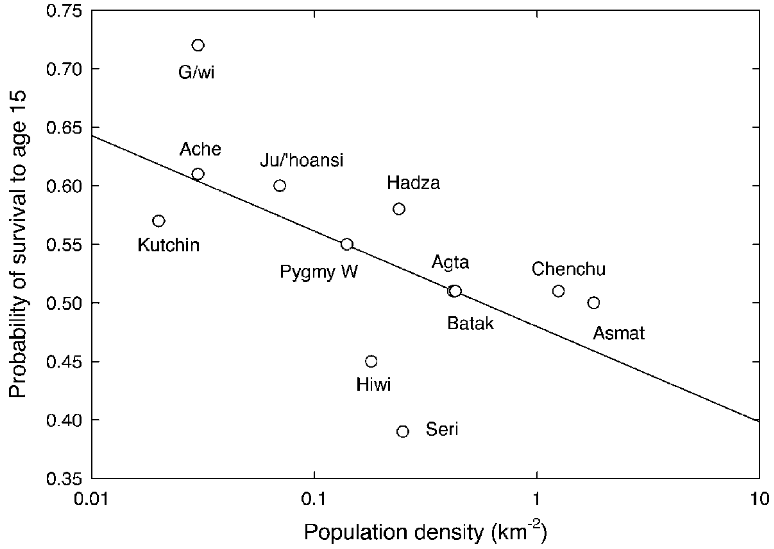

Figure 2. Density-dependent juvenile survival to age 15 (x-axis is $\log_{10}$).

than adult mortality (Walker et al. 2006). Figure 2 shows that juvenile survival decreases with increasing population density ($B = -0.082$, $p = 0.037$, p(resampling) $= 0.006$, $R^2 = 0.37$, $n = 12$), a conclusion also reached by Waguespack (2002) with a similar sample and by Wood and Smouse (1982) for the Gainj of highland Papua New Guinea. Here survival prospects for juveniles drop by around 8% per order-of-magnitude increase in population density. There is no latitudinal effect on juvenile mortality in this mostly tropical sample.

Two pathways seem to link body size to population density. First, higher population density likely increases nutritional constraints because of increased competition for limited resources, which should slow down the rate of growth and development and may increase juvenile mortality risk. Second, density-dependent (extrinsic) juvenile mortality may prompt a relatively earlier age of reproductive maturity. Both pathways lead to smaller body sizes but with different mechanisms and different developmental outcomes. Ideally, we would model adult body size as a function of food intake and extrinsic mortality. Unfortunately, the only available proxy variable for nutrition is adult body size itself. One solution is to remove the positive statistical effects of adult body size on age at menarche and first reproduction and then plot these residuals as a function of juvenile survival. The goal is to isolate the effect of survival on reproductive timing while attempting to control for the opposing effects of nutritional constraints. The available number of foraging societies with life-table information is small, and we include the well-studied Turkana pastoralists and the Yanomamo, Gainj, and Tsimane horticulturists, all of which are also natural-fertility, subsistence-level societies, to bolster the sample. Body-size-adjusted age at menarche (fig. 3) is indeed positively related to juvenile survival ($B = 7.91$, $p = 0.038$, p(resampling) $= 0.010$, $R^2 = 0.44$, $n = 10$, no datum for Yanomamo). In addition, relative age at first reproduction (fig. 4) is higher when juvenile survival is high ($B = 9.34$, $p = 0.031$, p(resampling) $= 0.004$, $R^2 = 0.39$, $n = 12$). While the sample size is regrettably small, both slopes are significant, and therefore the pattern would seem to support the proposition that high-mortality environments favor investments in current over future reproduction, resulting in attenuated growth periods and consequently smaller adult body sizes. In fact, the regression coefficients for this sample suggest that for each 10% decline in survival prospects, menarche and reproduction commence about 10–11 months earlier.

Discussion

Our results demonstrate negative density dependence in both hunter-gatherer body size and juvenile mortality. Population density and latitudinal gradient explain two-thirds of the variance in global hunter-gatherer body sizes. In our model, population density is treated as the extrinsic impetus for changes in hunter-gatherer body size (fig. 5). One could interpret much of modern human variation as being driven mostly by resource availability—higher malnutrition and disease leading to smaller body size, lower juvenile survival, and later age at menarche and first reproduction. This interpretation would be in concert with conventional anthropological wisdom that poor environmental conditions lead to poor growth and life-history outcomes as a result of less nutrition and higher disease in human and nonhuman studies alike (Bogin 1999; Eveleth and Tanner 1990; Hill and Hurtado 1996). However, an important and only recently recognized

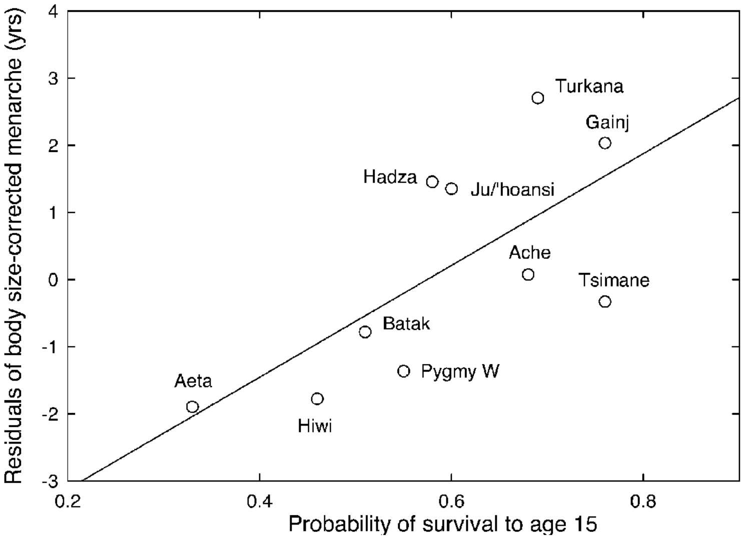

Figure 3. Residuals of age at menarche by body size as a function of survival to age 15. Data are a mixed set of small-scale economies.

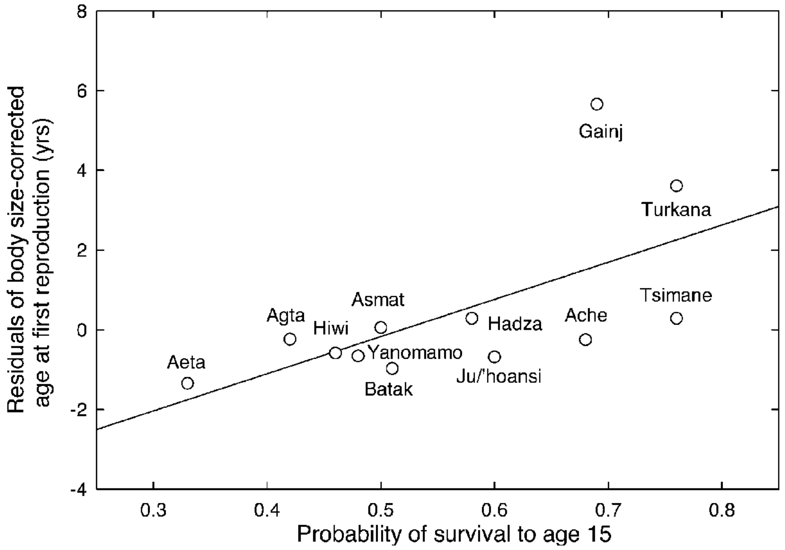

Figure 4. Residuals of age at first reproduction by body size as a function of survival to age 15. The slope decreases considerably but the positive correlation holds when Gainj and Turkana are removed. Data are a mixed set of small-scale economies.

corollary to this position is that human body growth and developmental rates increase with juvenile mortality after adjusting for female body size (Walker et al. 2006; see also Migliano 2005). Our interpretation is that life history speeds up in the face of high mortality, leading to relatively earlier reproduction as expected from life-history theory (Stearns 1992). The physiological mechanism is unknown but likely involves the neuroendocrine stress axis relaying information about the current mortality context and affecting growth and development appropriately (Crespi and Denver 2005).

Higher population density leads to higher juvenile mortality in hunter-gatherer societies, probably because of increased violence, infanticide, and epidemics, and may select for relatively earlier growth and development to pass more quickly into safer adulthood. The prediction is that extrinsic mortality risks that are (by definition) largely unavoidable should prompt a faster life history, while general resource scarcity will likely slow down rates of growth and development. Both pathways likely lead to smaller body size; increased growth rates do not fully compensate for shortened growth periods in the face of high mortality, and lengthened growth periods do not fully compensate for slower growth rates under resource scarcity.

Life-history theory, with its emphasis on delineating fitness costs and benefits, provides a powerful framework for human growth and development studies. Traditionally, bioanthropological studies have focused mostly on the energetic constraints imposed by malnutrition, disease, and the synergism between them. Life-history theory firmly addresses these constraints but also considers that optimal allocations to growth

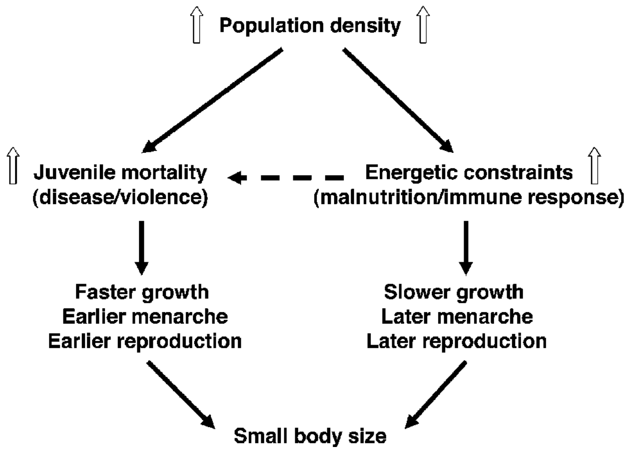

Figure 5. The evolution of human body size as a life-history consequence of population density acting through energetic constraints and juvenile mortality. The left-hand pathway captures the extrinsic mortality risks (e.g., violence, predation, and epidemics) that are expected to speed up life histories, while the right-hand pathway captures the energetic constraints and energetic allocations (e.g., immune response) that slow down ontogeny. Undoubtedly, the relative importance of one or the other of these pathways will be specific to particular socioecological circumstances. While death from malnutrition is probably rare in most traditional populations, energetic constraints may increase juvenile mortality (*dotted arrow*).

and reproduction are likely to vary systematically with relevant mortality risks. What we suggest is not that energetic constraints are not important to understanding delayed growth and development but that the life-history approach provides a more satisfactory and inclusive explanation of modern human variation. In our view, smaller body size likely results from a combination of decreases in growth rate due to resource scarcity and a downshift in the reaction norm leading to a younger age and smaller size at maturity due to the evolutionary effects of increased mortality.

Our model provides a general framework for understanding the life-history consequences of density dependence in the evolution of body size changes in humans and perhaps other animals. In effect, the model predicts that during periods of population expansion, the negative effects of density dependence are low, resulting in bottom-heavy age-structured populations and large adult body size. As population density increases, competition for limited resources increases, leading to reduced per capita consumption and slower population growth rates. In addition, our model predicts that human insular(-like) dwarfism results from selection favoring a fast life history in response to increased rates of density-dependent juvenile mortality. A high-mortality fast life history may best characterize the Hiwi (Hill, Hurtado, and Walker 2007), "Pygmies," and "Negritos" (Migliano 2005), while a resource-limited slow life history may best characterize the Gainj and the Ju/'hoansi, whose survival prospects are comparatively better (Walker et al. 2006).

Climate change, nutritional constraints, and mortality risks are potentially important components of an understanding of the evolution of smaller body size in humans in the last 50,000 years (Ruff, Trinkaus, and Holliday 1997; Ruff 2002), including apparent size reductions in Holocene populations (e.g., Australia [Brown 1987]). We suggest that density-dependent insular dwarfism may help explain the evolution of 1-m-tall *Homo floresiensis* on the Indonesian island of Flores (Brown et al. 2004; Morwood et al. 2005). An important caveat is that the model presented here may be complicated by strong selection acting directly on body size that may swamp mortality-driven effects on earlier development (Palkovacs 2003). However, we expect that while direct selection for body size may be relaxed in tool-using modern humans, allowing us to demonstrate density-dependent effects on body size, this is not necessarily the case when looking across hominin species. For example, the large body size of Neanderthals is consistent with (presumably) low population densities, but we cannot rule out selection on body size due to climatic conditions, size-dependent mortality, and/or foraging-niche considerations (Finlayson 2004). We hope that future research will address the general implications of density-dependent life histories in the evolution of body size across and within species and that more attention will be paid to the effects of mortality risks on the rates and timing of human ontogeny.

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