

REGULAR ARTICLE

Impact of infancy duration on adult size in 22 subsistence-based societies

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ABSTRACT

Aim: Humans evolved to withstand harsh environments by adaptively decreasing their body size. Thus, adaptation to a hostile environment defers the infancy-childhood transition age (ICT), culminating in short stature. In natural-fertility human societies, this transition is associated with weaning from breastfeeding and the mother's new pregnancy. We therefore used the interbirth interval (IBI) as a surrogate for the ICT.

Methods: We hypothesized that long IBI will be associated with smaller body size. The sample used is 22 subsistence-based societies of foragers, horticulturalists and pastorals from Africa, South America, Australia and Southeast Asia.

Results: The IBI correlated negatively with the average adult bodyweight but not height. After correction for 'pubertal spurt takeoff' and 'weight at age 5', the IBI explains 81% of 'average adult weight' variability.

Conclusions: This inter-population study confirms that body weight is adaptively smaller in hostile environments and suggests that the selected trait for this adaptation is the ICT age.

INTRODUCTION

The concept of the developmental origins of adult diseases emphasizes the importance of intrauterine and early life events in the aetiology of human diseases. There is evidence to suggest that a critical 'window of opportunity' may exist in the human infant before and during pregnancy and up to 24 months of age (1). Growth during this window of opportunity is a major determinant of height in later childhood and adulthood. We have previously shown that the transition age from infancy (I) to childhood (C) at age 6–12 months in affluent societies is strongly associated with adult height (2,3). Based on the above, we previously formulated the ICT theory (2,3): (i) The ICT is assigned with the determination of final adult height. (ii) This is a period of predictive adaptive plasticity in growth that has evolved to adjust an individual's size to environmental cues (4). (iii) It is transmitted trans-generations but is not genetic. It was shown that the age when this transition occurs may be delayed by disease (5), by decreases in energy consumption, by gastrointestinal infection and by socioeconomic impediments (6,7).

Several within-population studies have shown that a delay in ICT, which we refer to as delayed ICT (DICT), has a lifelong impact on stature (2,3). DICT is responsible for the referral to paediatric endocrine clinics of as many as 44–50% of children with normal birth weight and no endocrine disease – the so-called idiopathic short stature (2,3). This effect is time dependent, with a longer delay resulting in shorter stature (7).

Here, we take an evolutionary approach using a comparison between populations, each in its particular environment. Because humans lived as foragers for 95% of our species' history, we analysed growth patterns among 22 present-day foraging societies. In subsistence-based human societies, when no longitudinal growth data are available,

Abbreviations

BMI, body mass index; DICT, delayed ICT; IBI, interbirth interval; ICT, infancy to childhood transition.

Key notes

- Adaptation to a hostile environment defers the infancy-childhood transition (ICT) age, culminating in short stature. This study of 22 subsistence-based societies of foragers, horticulturalists and pastorals shows a negative correlation of the interbirth interval (IBI), as a surrogate for the ICT, with adult bodyweight. The IBI explains 81% of 'average adult weight' variability. Thus, weight is adaptively smaller in hostile environments; the selected trait for this adaptation is the ICT age.

the ICT is defined by weaning from breastfeeding and the mother's new pregnancy (8). We therefore used the IBI as a surrogate for the ICT. In a sample of 113 non-industrial, traditional societies, the duration of breastfeeding was reported to have a wide variation of 29 ± 10 months, concord with those at which key weaning transitions are biologically optimal for most normal healthy children (8).

Breastfeeding controls ovulation through bursts of prolactin into the mother's body; mother's return of ovulation is suppressed until lactation becomes less frequent. This sequence of events is called 'the baby in the driving seat' (9), envisioning the baby as having taken control of the mother's hormonal balance while he or she needs the supply of breast milk to maximize his/her survival throughout infancy.

Building on earlier work (10), the sample used here is 22 subsistence-based societies of mostly tropical foragers, horticulturalists and pastoralists from Africa, South America, Australia and Southeast Asia. We focus in this study on subsistence-based societies, in which most resources are invested as somatic capital in human bodies (i.e. body size and fertility) in contrast to industrial societies, who possess more stored, inherited wealth. We hypothesized that late ICT would be associated with smaller adult size and predicted that the IBI will negatively correlate with body size.

METHODS

Subsistence-based human societies

We analysed data collected from published literature and unpublished field notes for 22 subsistence-based societies and the demographic characteristics of each society (10) (Table S1). Information on the life history and population density of these societies and their average IBI, height, body weight and body mass index (BMI) is available at <http://anthropology.missouri.edu/people/walker.html> as compiled by one of us (RSW) from previous reports (10,11) and sources therein. In these societies, the IBI ranged from 21 to 45 months. By nature of this approach, comparing population level averages and attributing differences to reported data, analyses depend on the availability of specific parameters, and hence, important ones such as heights were available only in a small fraction of the societies and not included here. At the time of data collection, ethical approval was considered not required, and the authors had no access to individuals' data.

Statistical analyses

Linear regressions with 95% confidence intervals of outcome as a function of the variables were performed using Statistica 6.0. One-way ANOVA and Kruskal-Wallis ANOVA were used to test the differences between means. To search for a formula that can describe life-history elements in a vector of variables, we utilized multivariate regression analysis for IBI as a dimension for the ICT, 'size at age 5' as a dimension towards the end of childhood and transition to juvenility and 'pubertal spurt takeoff' as a dimension for the juvenility-adolescence transition. Statistical significance was defined with a probability of $<5\%$.

RESULTS

IBI as a surrogate for infancy

For 14 societies where the 'average weaning age' was available (range 19.6–42 months), the IBI (range 28.6–45.1 months) correlated positively ($r = 0.755$, $p = 0.002$) with weaning age.

IBI and adult size and BMI

The IBI correlated negatively with average adult bodyweight (kg) for women $r = -0.537$, $p = 0.012$, and men, $r = -0.475$, $p = 0.025$ and with adult BMI for women ($r = -0.467$, $p = 0.033$) but not for men ($r = -0.387$, $p = 0.075$, Fig. S1). The IBI did not correlate with adult height in either men or women.

IBI and child growth

Interbirth interval correlated negatively with '1-year-old bodyweight' and with 'gestation to 1-year weight gain' for men ($r = -0.678$, $p = 0.015$; $r = -0.694$, $p = 0.018$, respectively, Fig. S2) but not for women ($r = -0.473$, $p = 0.088$; $r = -0.473$, $p = 0.088$, respectively) and positively with the 'age 3 mass as percent of adult mass' for both women ($r = 0.695$, $p = 0.008$) and men ($r = 0.662$, $p = 0.014$, Fig. S2). Attempt to determine a formula that can describe life-history growth stages in a vector of variables by multivariate regression analysis used IBI as a dimension for the ICT, 'size at age 5' as a dimension towards the end of childhood and 'pubertal spurt takeoff' as a dimension for the juvenility-adolescence transition. It reveals significant influence of IBI on the dependent variable 'adult weight'.

Equation: 'Adult weight'

$$= 85.00 (\pm 28.69) - 0.60 (\pm 1.61) \times \text{'pubertal spurt takeoff'} \\ - 0.96 (\pm 0.20) \times \text{IBI} + 0.35 (\pm 0.89) \times \text{'weight at age 5'} \pm 3.65$$

$$\text{Adjusted } \tilde{R}^2 = 0.792, p = 0.0057$$

After correction for 'pubertal spurt takeoff' and 'weight at age 5', the IBI explains 81.0% of the 'average adult weight' variability (partial correlation coefficient = -0.900). The influence of the 'pubertal spurt takeoff' and 'weight at age 5' is not significant.

Density, BMI and IBI

Interbirth interval correlated negatively with the population density ($r = -0.526$, $p = 0.044$, Fig. S3). For men, less so for women, BMI correlated negatively with population density ($r = -0.636$, $p = 0.011$; $r = -0.512$, $p = 0.051$, respectively; Fig. S3).

Phylogenetic correlates

When categorizing societies by ecology, IBI was comparable for inhabitants of tropical forest, neotropical forest or the savanna. When categorizing societies by economy type, the IBI was longest in foragers, with a mean 38 mo, and shortest in mixed peasant economies with a mean IBI of 28 mo, $p < 0.001$ (Table S2).

DISCUSSION

The approach to human life history adopted here is a biological and behavioural model, with consideration of anthropology and human evolutionary history (12). The evolutionary advantage of childhood as a unique human life-history stage lies in the mother's ability to discontinue breastfeeding her 3-year-old infant to initiate a new pregnancy, increasing her fertility fitness, while the child is cared for by the extended family (13). Thus, the duration of infancy is part of the evolutionary 'design' in a population evolutionary strategy. The IBI demonstrates effectiveness as a surrogate for the ICT age, with the average weaning age correlating strongly with the IBI. In traditional societies, some mothers wean after the next pregnancy is established and are both lactating and pregnant for a month, while very few have several months of periods between breastfeeding and pregnancy.

Even though the IBI is variable according to birth order, as shown for the Kalahari Desert's !Kung bushman, the first IBI being generally shorter than later IBI (14), it remains a valid parameter for predicting life history. The IBI lengthens as the number of surviving children increases, until the fourth child, after which it does not vary significantly, although tends to become shorter (14). For IBI subsequent to the first, mortality increased markedly as IBI decreased (14). Thus, the fitness benefit accruing from more births will be balanced against the costs of caring for more children (14). Whereas very long (>60 months) or short IBI were shown to be associated with prematurity and small newborns, the intervals utilized by the study societies are not correlated with intrauterine adversity (15).

We previously demonstrated within a population, the ICT to be a major determinant of adult body height (3). The current results confirm the predicted trade-off between the length of infancy and adult weight; the IBI, as a measure of the ICT, correlated negatively with adult bodyweight in both women and men. Considering life history and growth, we now show that after correction for 'pubertal spurt take-off' and 'weight at age 5' as a measure at transition to juvenility (16), the IBI explains 81.0% of 'average adult weight' variability. A similar relationship between weaning age and maternal bodyweight was previously reported for primates ($r = 0.91$) (17). However, these authors proposed an opposite perspective of cause and effect – weaning age decreased because of the inability of a mother's metabolism to support the energetic needs of her infant that quadrupled its birth weight (18,19).

We propose that with diminishing availability of critical resources, such as energy and nutrients, a trade-off for their costly allocation results in investment in a longer duration of breastfeeding, such as is associated with the typical decelerating growth at infancy (2). Small body size is a plastic response to disease and malnutrition (12,20). The plasticity of ICT and prospective size in response to energetic cues was demonstrated in a community-based longitudinal within-population study in Lahore, Pakistan, where the median ages of the ICT were 15, 13, 10 and 9 months for infants of the suburban, village, urban and Swedish control

groups, respectively (7). Among the poorest suburban children of Lahore, who suffered frequent infections and under-nutrition, 35% were of short stature in association with delayed ICT (7). Here, the IBI was long when weight gain in infancy was low. In modern societies, the opposite has occurred; the secular trend for greater size has been an adaptive response to an affluent environment. For the purpose of understanding the adaptive response to environmental cues, the present study utilized an inter-population approach. While the fossil record of early hominids suggests that their stature and weight had a tendency to increase (21), environmental factors to consider in an inter-population study include the physical environment (e.g. population density), the biological environment (e.g. food availability, disease and other mortality risks) and social behaviours (e.g. age at marriage) (10).

Several limitations of this approach require consideration. Comparing population level averages and attributing differences to ecological differences may not be straightforward. It assumes that the relationships observed would be the same if examined at an individual level, as discussed by others (22). In this report, Greenland and Robin constructed several epidemiological examples that show that data at the ecologic level can be misinterpreted if nonlinear effects at the individual level and other confounders are not accounted for. Such data for the individual level were not available to us. Comparative studies across societies may also suffer from problems of phylogenetic non-independence. This was addressed for these data previously by adjusting for geographical location (Africa, South America, Australia and Southeast Asia), but the effect was very weak and not significant in any of the multiple regressions (23). Some parameters, such as height, were available only for a small number of the study societies. In a population with high childhood mortality, it has to be realized that the IBI is shorter when the earlier child dies (depending upon the age at death) (24). Despite all these limitations, it was shown time and again that hunter-gatherer cultural patterns are critical for assessing models of cultural evolution (25).

We previously suggested that the evolution of small body size in human hunter-gatherer societies does not reflect direct selection of body size per se, a comprehensive life-history consequence of density dependence (26). Density-dependent life histories are a ubiquitous feature of naturally occurring biological populations owing to finite availability of resources. Other things being equal, increased density in energy-limited populations implies, by definition, increased competition for resources, resulting in reduced birth rates and increased mortality rates (10,23,26). We now show that for the less resilient men, but not for women (27), the BMI correlated negatively with density. The finding that the IBI correlates negatively with population density implicates the ICT as a tool in the density-dependent control of body weight.

The IBI, as a surrogate of infancy length, seems to be adaptive to the tribes by economy. The longer IBI in foragers seems best explained by their low population density. The IBI is shorter among mixed peasants, farmers and

foragers. Indeed, a study of the Kung bushman revealed increased mortality to be closely related to mother's backloads entailed by decreased IBI (14). The IBI did not segregate by the tribes' ecology.

Two archetype societies at two ends of the sample size spectrum illustrate the ICT model. The Wichí from the headwaters of the Bermejo River and the Pilcomayo River in Argentina and Bolivia are an isolated indigenous people with relative economic self-sufficiency. Known also as 'the river people', their body shape is bulky, with mean male and female bodyweight, at the time of data collection, 74 and 62 kg, respectively, and a high mean BMI of 27 kg/m² for both men and women. Their mean bodyweight is 10 kg at age 1 year. This is associated with smallest low investment in infancy – an average IBI of 21 months. In contrast, the Aeta negritos, who live in scattered, isolated mountainous regions of Luzon, Philippines, with a high population density of 0.9 people/km², mean bodyweights are merely 40 and 38 kg for adult men and women, respectively, and very low mean adult female and male BMI of 19 and 18 kg/m² respectively. The corresponding IBI of 35 months supports the trade-off prediction of long infancy against small weight.

Among people of industrial nations, growth stunting in height is associated with worse indicators of adult well-being. But in traditional societies, no such association was found between well-being and stunting (28). The reason for this discrepancy can only be speculated. In industrial societies, height bears a positive association with well-being in part because it is associated with greater human-capital accumulation, such as intergenerational transmission of social status, education and income (29). In a traditional rural society without much schooling and pay-offs to academic skills, height might have no pathway through which to influence socioeconomic indicators of well-being.

Our ICT model provides a framework for understanding the life-history consequences of resources and density dependence in the evolution of body size changes in humans. From this inter-population study, we concluded that among subsistence-based human societies, population density correlates negatively with bodyweight and BMI. The trait selected for this adaptation is the trade-off of infancy length against adult weight, as previously demonstrated in intra-population studies (3). In effect, the current model now provides support for the ICT theory.

CONFLICT OF INTEREST

The authors have no conflict of interest to disclose.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Interbirth interval (IBI) and adult size and BMI. Regression and 95% confidence limits for adult size as a function of IBI (left panel) and the BMI (right panel).

Figure S2 IBI and child growth. Regression and 95% confidence limits for the IBI as a function of gestation to 1-year growth rate (upper panels) 1-year-old mass (middle panel)

and weight at age 3 as percent of adult weight (lower panels) for women (left panels) and men (right panels).

Figure S3 Density BMI and IBI. Regression and 95% confidence limits for the BMI as a function population density in women (upper panels) and men (middle panel) and for the IBI as a function of density in both sexes (lower panels).

Table S1 Ecology and economy type of the 22 tribes comprising the study populations.

Table S2 Sorting IBI of 22 societies by economy-type.

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