

# Lessons from the life history of natural fertility societies on child growth and maturation

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### Summary

During the evolution of hominids, childhood and adolescence have been added as new life-history phases. The transition from infancy to childhood (ICT) confers a predictive adaptive response to energetic cues that strongly influence adult height, whereas the transition from juvenility to adolescence establishes longevity and the age of fertility. Evolutionary short-term adaptations to energy crises apparently use epigenetic mechanisms that defer the ICT, culminating in short stature. The study of hunter-gatherers gives us an indication of pre-demographic transition populations and their life style that prevailed for 99% of homo's evolution. The secular trend for receding age of pubertal development has been an adaptive response to positive environmental cues in terms of energy balance. In natural fertility preindustrial societies with limited access to modern contraception and health care, and whose economies are primarily subsistence-based, most resources are invested as somatic capital in human body size and fertility. Here we review results from databases for natural fertility societies, with the information on life history, population density, height and body mass, indices of adolescence and fertility. By using them it was possible to verify the ICT model as well as to explore pubertal parameters that are related to evolutionary fitness. They confirmed that body size was adaptively smaller in hostile environments, and was tightly associated with reproductive fitness.

#### Abbreviations:

BMI	Body mass index
IBI	Interbirth interval
ICT	Infancy-childhood transition
DICT	Delay in ICT
JAT	Juvenility-adolescence transition
L15	Survivorship to age 15
TFR	Total fertility rate

**Key words:** life history; evolution; natural-fertility societies; breast feeding; child growth; infancy; childhood; puberty; menarche

### Theory of human's life history

Why are we small or large and why do we mature early or late? Why do we have few or many offspring? Why do we have a short or a long lifespan? Life history has been defined as the strategic allocation of an organism's energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death [1–3]. It is, among others, the strategy of when to be born, when to be weaned, when to stop growing, when to reproduce, and when to die in the best way as to increase fitness [4]. In the case of humans, life-history evolutionary theory is best understood in the context of biological rationale and cultural expressions as a solution to an ecological problem posed by the environment and subject to phenotypic constraints intrinsic to the organism [1–3, 5–9].

### Human's life-history phases

The transition from one life-history phase to the next requires a mechanism for the onset of the latter [10]. Thus, the transition from infancy to childhood (traditionally defined by weaning from breastfeeding) is associated with the setting in of the dominance of the GH–insulin-like growth factor 1 (IGF1) axis. The transition into juvenility (independence for provision and protection) requires the development of androgen-generating adrenal reticularis – the so-called adrenarche. The beginning of adolescent-related puberty is a neuroendocrine event of the hypothalamic–pituitary–gonadal axis maturation.

During the evolution of hominids, childhood and adolescence have been added as new life-history phases [1] (fig. 1). Bogin and Smith [1, 2] have previously reported that *Homo habilis* (1.9 mya) had a shorter period of infancy than his predecessors, introducing a new strategic life-history phase: childhood, characterised by initial acceleration then stabilisation of growth velocity, dependence on the family and tribe beyond his mother for food provision

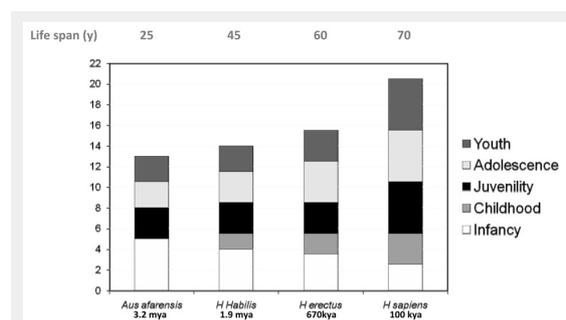
and protection, with the first molar erupting at its end [3]. Adolescence, as reconstructions suggest, came about as a distinct life-history phase as late as 100000 years ago, with the typical pubertal growth spurt and rapid sexual puberty, deferring the assumption of adulthood beyond «Youth» in a species that lives longer [3].

Thus, *Homo sapiens* have five prolonged and pronounced postnatal pre-adult life-history phases (fig. 1); infancy, which lasts for 30–36 months; childhood, which lasts for an additional 2–4 years, a juvenile stage of 3–4 years that concludes with the readiness for final sexual maturation [8]; adolescence, which lasts for 3–5 years, and youth – some four years of pre-adult stage, culminating in fecundity at an average age of 20 in females and 24 in males [3].

### Plasticity and adaptation of human's phenotype

The ability of the genotype to produce different phenotypes in response to different environments is termed “plasticity” [11]. Humans live under a variety of environmental conditions unprecedented in nature, including the entire range of geographical latitudes and altitudes, as well as extremely diverse weather conditions. Whereas the above vary slowly, nutritional conditions change more rapidly, and evolution has provided for mechanisms to adapt to these extremes; socio-cultural adjustments filled the remaining gaps when changes were faster than the evolutionary time scale. The secular trend in child growth and puberty (getting bigger and earlier in the past 150 years) is an evident example of such an adaptation [10].

As a consequence of life conditions under changing environments, a ‘predictive adaptive response’ renders children stunted for shorter or longer periods, being underweight or overweight, and at risk of disease [12]. Under adverse conditions trade-offs result in reduced survival, poor growth, constraints on physical activity, and poor reproductive outcomes [7].



**Figure 1**

The evolution of hominid life history during the first 20 years of life. The existence time is given below (kya – thousands years ago, mya – millions years ago) and the longevity – above. During the evolution of the hominids, childhood and adolescence have been added as new life-history stages as compared with apes and the presumably the early hominid *Australopithecus afarensis*. The chimpanzee serves as a living representative of the assumed *Australopithecus afarensis* life history. As childhood emerged and prolonged, infancy has gradually cut shorter, and the latest introduced adolescence came at the expense of a shorter juvenility [3].

### Infancy-childhood transition (ICT) – determination of adult body size

The transition from infancy to childhood (ICT) is marked by a growth acceleration, followed by growth stabilisation: after gradual deceleration of postnatal infantile growth, the growth rate abruptly increases between 6 and 12 mo of age as a consequence of the transition to childhood. This defines the ICT [13, 14]. A delay in ICT (DICT), has a lifelong impact on stature and is responsible for as many as 50% of children with a normal birth weight and no endocrine disease, who are referred to pediatric endocrine clinics as suffering from idiopathic short stature [5]. It has been shown that each month of delay in ICT results in a growth deficit of 0.4 cm in boys and 0.5 cm in girls at age 5 [15].

There is an evolutionary adaptive strategy of plasticity in the ICT age to match environmental cues and energy supply. Humans evolved to withstand energy crises by decreasing their body size, and evolutionary short-term adaptations to energy crises [5] apparently using epigenetic mechanisms that modify the ICT, culminating in short stature. Environmental influences during embryonic and early life development can permanently alter epigenetic gene regulation, which in turn can result in imprinting and reprogramming of the epigenome and influence growth, maturation, development as well as body composition in later life-history stages. The mechanisms by which cues about nutrient availability in utero and postnatal environment are transmitted to the offspring and by which different stable phenotypes are induced are still unknown.

For the IC growth transition to occur, the child must have a positive energy balance. The age when the IC growth transition occurs is influenced and delayed by disease [16], when energy consumption increases rapidly, and by undernutrition, gastrointestinal infection, and socioeconomic impediments [15, 17], with insufficient energy supplies. Thus, DICT is the main mechanism resulting in adaptive short stature in children living in poor areas of developing countries. In a community-based longitudinal study in Lahore, Pakistan, the median ages of the ICT were 15, 13, 10, and 9 mo in the suburban, village, urban, and Swedish control groups, respectively [17]. Among the poorest suburban children of Lahore, who suffer frequent infections and undernutrition, 35% had DICT, and among the poor children of Malawi, Africa, as many as 60% have DICT [17]. Many of them have an ICT that occurs at 3–4 y of age, in accordance with their weaning age. DICT compromises their prepubertal height by 15–20 cm, culminating in an adaptive mean adult male and female heights of 162.5 and 155 cm, respectively [18].

### Lessons from natural fertility societies on child growth

The study of natural fertility societies, mostly hunter gatherers, provides us with a glimpse into the Pleistocene, the epoch from 1800000 to 12000 years before present. Isolated tribes adjusted their life style and genes to their respective environment. It provides us with a model to verify the life history theory for stature at the population level rather than the individual level. We focused on natural fertility preindustrial societies, with limited access to modern contraception and health care and whose economies are primarily subsistence-based, 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. Information on these mostly tropical foragers, horticulturalists and pastoralists from Africa, South America, Australia and Southeast Asia, their indices of life history, population density and anthropometric data are pooled by Robert A Walker at <http://anthropology.missouri.edu/people/walker.html> [19].

In subsistence-based human societies, when no longitudinal growth data are available, the ICT is defined by weaning from breastfeeding and the mother's next pregnancy [20]. As the weaning age is often unknown, the interbirth interval (IBI; ranged from 28 to 45 months) provides a surrogate for the ICT and infancy duration; the IBI and the average weaning age when known correlated strongly ( $r = 0.75$ ;  $p = 0.002$ ) in 14 tribes.

Blurton Jones showed for the !Kung bushman of the Kalahari Desert that IBI is variable; the first IBI being generally shorter; IBI lengthen as the number of surviving children increased (until the 4<sup>th</sup> child); after the fourth child, IBI does not differ although it tends to be shorter [21]. Even though the IBI remains a valid parameter for predicting life history [19].

The ICT theory predicted that with diminishing availability of critical resources, such as energy and nutrients, a trade-off for their costly allocation would result in investment in a longer duration of breastfeeding, such as is associated with the typical decelerating growth at infancy and DICT

[10]. It predicted that DICT would be associated with smaller adult size and that the IBI will negatively correlate with body size.

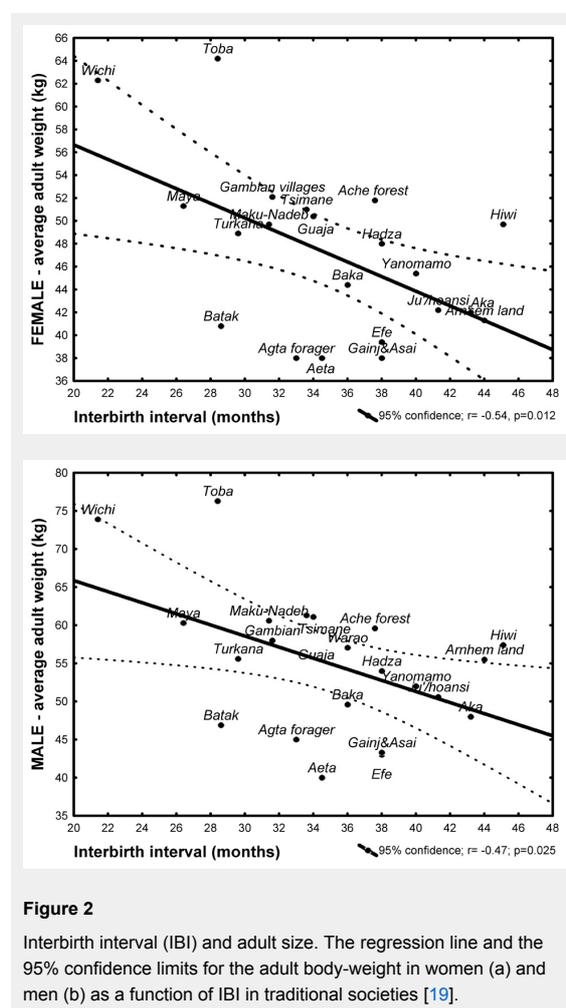
Observation of subsistence-based human societies confirmed these predictions; the IBI, as a surrogate for the ICT and infancy duration, correlated negatively with adult bodyweight in both women and men (fig. 2a & b, respectively) [19]. Moreover, considering life history and growth, after correction for 'pubertal spurt takeoff' and 'weight at age 5' as a measure at transition to juvenility [8], the IBI explained 81% of the variation between populations in average adult weight [19]. A similar relationship between weaning age and maternal bodyweight was previously reported for primates ( $r = 0.91$ ) [22]. 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 [23, 24].

In modern societies, the opposite has occurred; the secular trend for greater size has been an adaptive response to an affluent environment. While the fossil record of early hominids suggests that their stature and weight had a tendency to increase in deep time [25], environmental factors to consider in an inter-population study include variables that change more rapidly: 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) [26].

Walker and Hamilton suggested that the evolution of small body size in human hunter-gatherer societies reflects a comprehensive life-history consequence of density dependence [27]. 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 [26–28]. Data from natural-fertility societies confirmed that for the less resilient men, but not for women [29], the BMI correlated negatively with density. The finding that the IBI correlates negatively with population density implicates the duration of infancy as a tool in the density-dependent control of body size [19].

The IBI, as a surrogate of infancy length, seems to be adaptive to the tribes by economy but not their ecology. The longer IBI in foragers, with a mean 38 months, seems best explained by their low population density. The IBI is shorter among mixed peasants as well as farming-foraging economies [19]. The !Kung study revealed increased mortality to be closely related to mother's backloads entailed by decreased IBI [21, 30].

Two archetype societies at two ends of the sample size spectrum illustrate the ICT theory at the population level. The Wichi 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 average BMI of 27 kg/m<sup>2</sup> for both men and women. Their mean bodyweight is 10 kg at age 1 year. This is associated



with the lowest investment in breastfeeding (12 months) – 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/km<sup>2</sup>, mean bodyweights are merely 40 and 38 kg for adult men and women, respectively, and low mean adult female and male BMI of 19 and 18 kg/m<sup>2</sup> respectively [31]. The corresponding IBI of 35 months supports the trade-off prediction of long infancy against small body size.

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 [32]. 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 [33]. 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.

### Juvenility-adolescence transition (JAT) – determination of reproductive fitness

The secular trend for receding age of pubertal development in affluent societies has been an adaptive response to positive environmental cues in terms of energy balance [34]. The ever-younger age of girls' thelarche and menarche may have more than a single justification. In the last decade, the popular explanation has involved environmental exposure to endocrine disruptors, such as derivatives of dichloro-diphenyl-trichloroethane, thus accelerating hypothalamic maturation [35]. Whereas it may explain the earlier age of thelarche, which is a recent trend, it can hardly explain the secular trend in the age of menarche over the last 150 years. The age at menarche is linked weakly to genetic variations [7], nevertheless the time course of the secular trend suggests strong environmental influence [36].

The environmental cues for the transition into adolescence vary with species and gender, and it may be related to altitude, temperature, humidity, and lighting, but mostly it relates to energy balance. Sensors in the hypothalamus

and hindbrain monitor these signals and permit high-frequency GnRH1 release when the signals reach appropriate levels [37]. The consequences of puberty and adulthood that follow, such as the defense of territory or mate, pregnancy, and care of the young, are energetically expensive. The individual must sense whether he/she has grown sufficiently (through metabolic cues), what his/her relationship is to other individuals (through social cues), and whether conditions are optimal to begin the final leap toward reproductive maturation (through environmental cues) [38]. These factors are further explored through human rational decision for the length of youth [3].

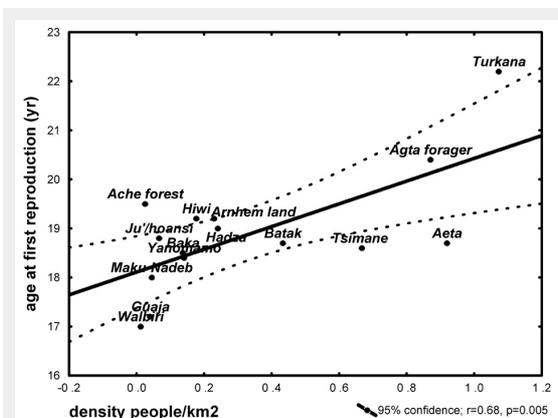
There is considerable public and medical interest in the secular trend for early onset of puberty and this reflects an increasing awareness of the consequences of the psychosocial 'mismatch' which arises from early biological reproductive competence in societies in which young women and men do not reach psychosocial maturity until the third decade of their life [35, 39].

This secular trend was recently examined from a life-history evolutionary perspective, and it was suggested that transition from juvenility to adolescence is yet another transition period of adaptive plasticity [8, 10, 34].

Two models have been proposed to explain this adaptation. In the first one Gluckman and Hanson suggested that life-history strategies for greater reproductive fitness (a product of the fertility rate and survivorship) could account for the current early onset of puberty [34]. The declining age of pubertal development has been proposed as an adaptive response to positive environmental cues in terms of energy balance [10]. The assumption is that the reproductive system maximises the number of offspring by balancing the benefit of more births against decreasing maternal mortality. With respect to puberty, women face a trade-off between spending a long time accumulating resources through childhood growth and weight gain in order to improve the likelihood for successful pregnancy, against an early-age reproduction in order to increase the number of reproductive cycles.

A different evolutionary trade-off was suggested by Migliano et al. [31]. Based on analysis of the stature, growth, and reproductive fitness in several Pygmy tribes, they argued that their small body size is an adaptation that evolved as the result of a life history trade-off between the fertility benefits of a large body size against the risk of late growth in societies where longevity is severely compromised by a hostile environment. They constructed their theory by observation of the Aeta and the Batak pygmy from the Philippines and showed that the small pygmy body size evolved through the early onset of juvenility and adolescence. They suggested that early cessation of growth is a trade-off for short lifespan and reduced resource availability [31]. Thus, short life expectancy provides a strong selective pressure for early puberty and the latter is associated with short stature.

Heavy women in pre-industrial societies are more fertile, and both increased body weight and fertility are correlated with high birth rates [40]. This trade-off model has been used to predict that 18 years is the optimal age for first birth, which is near the observed average 17.5 years in pre-industrial societies [41].



**Figure 3**

The regression line and the 95% confidence limits for the age of first reproduction as a function of density in traditional societies [26].

A recent study of natural-fertility societies investigated the age of menarche, the pattern and timing of the adolescent growth spurt, body size, and the determinants of reproductive fitness in terms of the age of the first reproduction, the IBI, the number of progeny, and mortality risk. The predictions were that early adolescence would be associated with greater reproductive fitness or with greater mortality risk and that the age at menarche and indices of adolescence growth will negatively correlate with fertility rate or positively correlate with survivorship [36]. Although the reproductive and life history strategies of males and females are quite distinct in these societies, similar considerations might apply to the males, for which indices of adolescent growth spurt were added. Indices of fertility in each society were determined from the average age at first reproduction, IBI, and the total fertility rate (TFR). It was confirmed that the age at first reproduction among natural fertility societies strongly correlated with menarche [36]. The two models have to be modified [36]: the age at menarche did not correlate with either the TFR or reproductive fitness. Whereas reproduction starts early in societies in which puberty occurs early, in the context of high population density [27], their reproductive fitness did not increase. Dwellers of the neotropical forests had a high TFR, but given their mortality risk, they had comparable reproductive fitness to other ecology groups [36]. Yet, each population maximises fitness according to population densities.

The study confirmed a previous assertion for greater reproductive fitness among heavier, better-nourished traditional societies [40, 42]. When considered as a whole, we found that the average adult body weight, but not height, correlated negatively with age at menarche ( $r = -0.60$ ) and the age at first reproduction ( $r = -0.45$ ), and positively with reproductive fitness. The BMI may not work as well in the extremes of size; in very small or very tall populations the BMI was not as accurate as were average size populations [36]. Among contemporary girls in developing countries, the age at menarche among the prosperous is earlier than that of the underprivileged [35], lending indirect support to the assertion that early puberty among girls who live in affluent and developed countries is a adaptive to a supportive environment.

However, analysis of 22 subsistence-based societies data did not confirm the fast life history theory; there were no correlation between adult size or the age of menarche with survivorship. In the cited database [36] there were two African pygmy groups – the Baka (West pygmy) and the Efe (East pygmy), both of whom had average age of menarche at 14.5 and 15.5 and age at first reproduction at 18.5 and 19, – similar to the average of the other studied societies [28].

Population density, correlating with the age of first reproduction ( $r = 0.68$ , fig. 3), was suggested to act through two pathways – nutritional constraints and juvenile mortality – at varying intensities [27].

### Conclusions

Although many questions remain to be answered, the concept of a delay in the childhood growth transition, with its evolutionary development biology (evo-devo) implications, provides a new direction for research into child

growth. The 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 [3].

The study of subsistence-based human societies show that the trait selected for such adaptation is the trade-off of infancy length against adult size, as previously demonstrated in intra-population studies [5]. In effect, the current model now provides support for the ICT model. Whereas body mass as a measure of resources is tightly associated with reproductive fitness in these traditional societies, the age of menarche is not. Thus, it may be that women's physiology tracks its own condition in such a way as to maximise their individual fitness.

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Figures (large format)

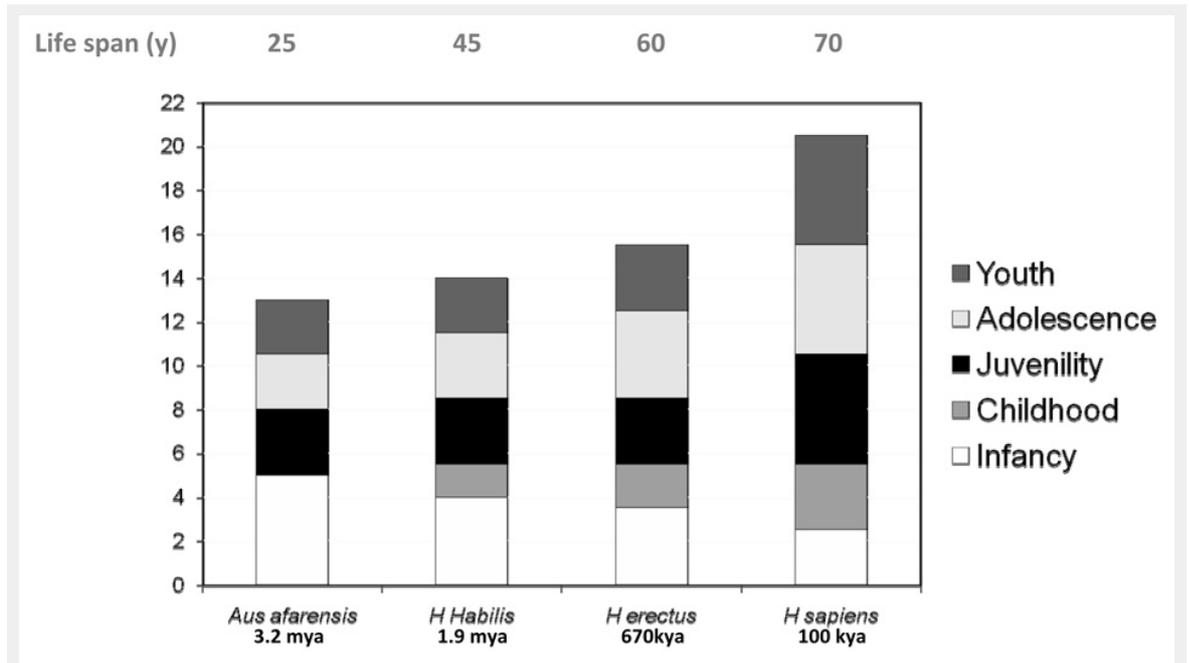


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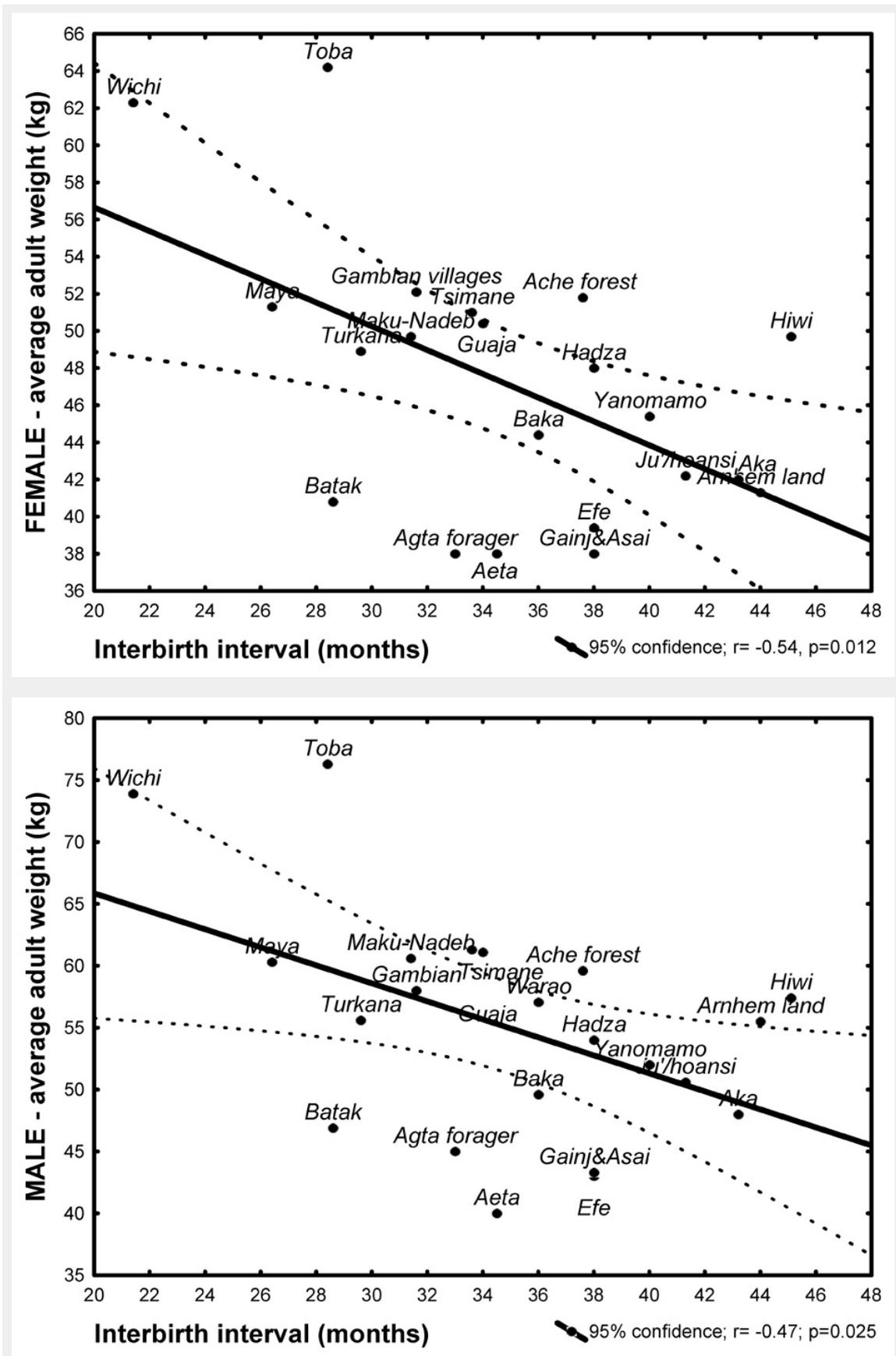


Figure 2

Interbirth interval (IBI) and adult size. The regression line and the 95% confidence limits for the adult body-weight in women (a) and men (b) as a function of IBI in traditional societies.

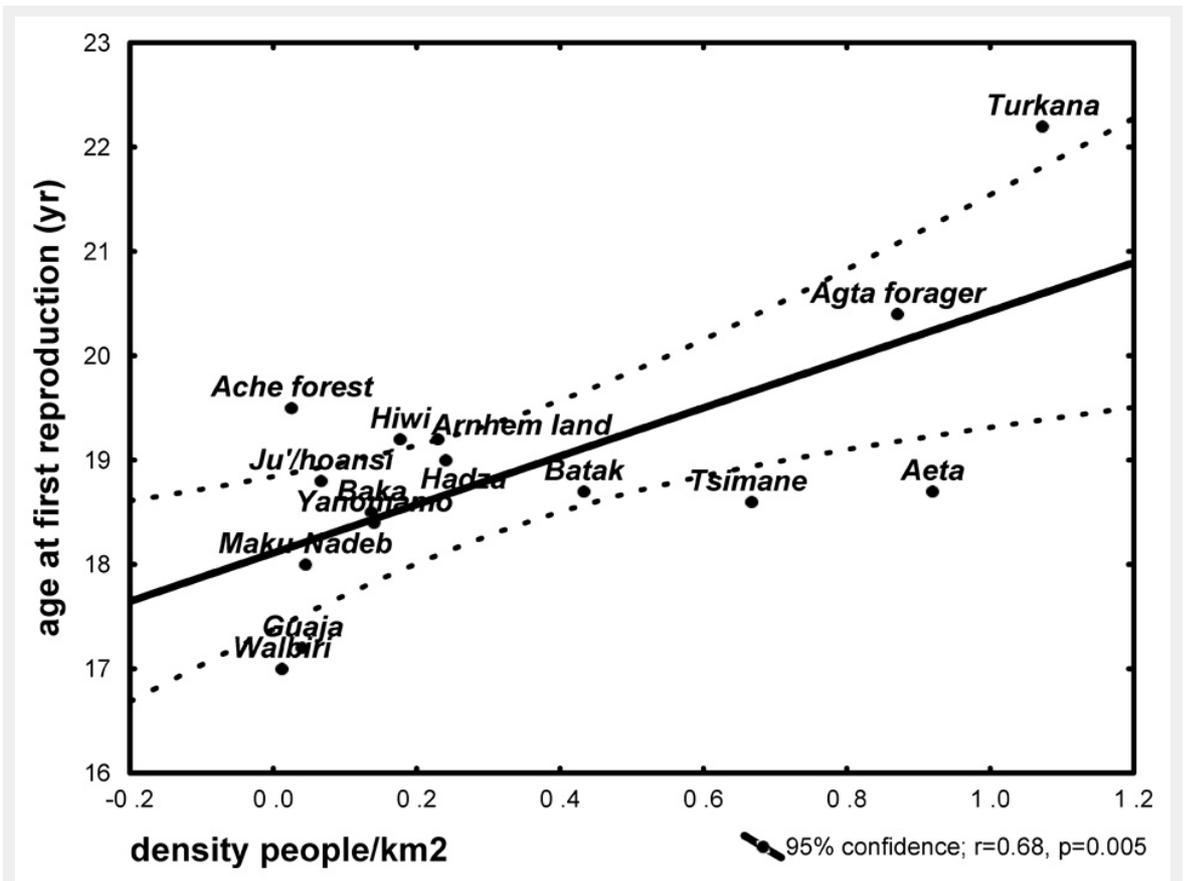


Figure 3

The regression line and the 95% confidence limits for the age of first reproduction as a function of density in traditional societies.