

Can life history trade-offs explain the evolution of short stature in human pygmies? A response to Migliano and colleagues

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Abstract

Walker et al. (2006) used life-history theory to develop an innovative explanation for human diversity in stature. Short stature could have been selected for in some human populations due to the advantage of an earlier growth cessation and earlier reproduction in a context of high mortality. Migliano et al. (PNAS 2007) recently published an important article that tested this hypothesis to explain short stature in human pygmy populations. However innovative this work may be, we felt that some data and results presented herein were controversial if not questionable: using an arbitrary threshold of height (155cm) to categorize populations into pygmies and non-pygmies is problematic; the use of demographic data from Philippine pygmy groups is an issue because they have experienced dramatic cultural and environmental changes in the last 20 years and demographic data on African pygmy groups is also problematic because good systematic data on these groups do not exist; and finally we find mathematical errors and loopholes in the optimisation model developed by the authors. We propose alternative trade-offs that could be considered to precise the authors' results.

Raymond Pearl, the founder of Human Biology, was concerned throughout his career with the proper measure of Man (Sokal 2004), probably his main legacy to Anthropological Sciences. Thus, we thought that Human Biology was an appropriate place to publish a commentary on a research article (Migliano, Vinicius and Lahr 2007), which proposed to interpret human diversity in stature and the human pygmy phenotype in the light of life history theory. However innovative and challenging this work may be, some features and results presented by its authors seemed controversial. Here, we aimed to stimulate the growing debate raised by this article since its publication (Perry and Dominy 2009), in order to improve potential future work in this promising line of research.

The question of small stature in human pygmy populations has been extensively debated in the anthropological literature. Several hypotheses propose that pygmy's stature is an adaptation to environmental pressures (e.g., nutritional, thermoregulatory, metabolic or energetic) (Perry and Dominy 2009). Following precursor works of Hill and Hurtado (1996), Walker et al. (Walker et al. 2006) used life history theory to develop an alternative explanation. They hypothesize that short stature in pygmies is a consequence of high mortality rates: in contexts of high mortality, earlier growth cessation and reproduction onset may be adaptive. Migliano et al. (Migliano, Vinicius and Lahr 2007) published an important paper to test this hypothesis. The authors explored two questions: 1) Do pygmy growth rates and final stature reflect nutritional stress? and 2) Is earlier onset of reproduction (associated with growth cessation) optimal in pygmies due to higher mortality, thus explaining the pygmies' shorter stature ?

Migliano et al. (2007) compared growth curves of pygmy and U.S. women, and found that pygmies grew faster than under-nourished U.S. citizens, but ceased to grow earlier. They concluded that small stature in pygmies was due to a shorter duration of growth rather than to

a lower growth rate, and that nutritional stress was not a likely explanation for pygmy short stature.

Migliano et al. (2007) further presented data on survival and fertility in pygmy and non-pygmy populations. First, they found a lower survivorship and an earlier age-specific fertility in pygmy populations. Second, they found a positive correlation between height and fertility in pygmy women. Third, they incorporated age-trajectories of survival and fertility and correlation between height and fertility into a life history model. In this model, growth cessation at maturity was the key factor regulating the trade-off between risk of death before first reproduction and fertility after maturity. The authors thus tested if earlier growth cessation was selected for in pygmies in order to decrease the risk of dying before reproduction. The lower height at maturity however came at the cost of a loss in fertility. The authors calculated the optimal age at maturity for the Aeta pygmies from the Philippines and three non-pygmy populations using previously published data: the South American Ache (Hill and Hurtado 1996), the Namibian !Kung (Howell 1979) and Gambian rural women (Allal et al. 2004). The authors found an earlier optimal age at first reproduction in the Aeta (15 years) than in the non-pygmy groups (18-19 years). They concluded that an early onset of reproduction was optimal in pygmies even if the resulting smaller adult size induced a reduction of fertility.

Life history theory has been successfully used to explore reproductive scheduling in human populations, as the optimal age at first and last reproduction (Shanley and Kirkwood 2001, Allal et al. 2004) and the optimal reproduction rate (Mace 1998). The riddle of pygmy stature being unsolved (Perry and Dominy 2009), it was promising to test whether a trade-off between timing in growth and reproductive outcome could explain pygmies' stature (Hill and Hurtado 1996).

Although we are fully aware of the challenges encountered by Migliano et al. (2007), we think that the data and model are insufficient to support their conclusions. Rather, we consider Migliano et al.'s study as a promising first step for testing life history hypothesis in pygmy populations. First, issues arise when an arbitrary height threshold is used to categorise human populations into pygmies and non-pygmies. Second, we question the pygmy demographic data: 1) Philippine pygmies' demography is influenced by recent forces of acculturation (e.g. tuberculosis, alcoholism, forced resettlement) and 2) African pygmy data are still insufficient to construct age-specific survivorship or age-specific fertility schedules. Third, mathematical errors and loopholes were found in the optimisation models and other relevant trade-offs could be considered.

1. A Height Threshold to Categorise Human Populations into Pygmies and Non-Pygmies

The Greek word “pygmy” is a measure of size (“a cubit”). Applied to various animal species, it refers to populations showing a reduction in stature as compared to the average size of the same specie. In human populations, there is no gap in size between pygmy and non-pygmy populations, although populations designated as pygmies are found in the lowest extreme of the worldwide variability of stature (Froment 1993). If life history hypothesis explored by Migliano et al. (2007) was true, a continuous positive correlation should exist between adult height and mortality rates. Problems inevitably arise when an arbitrary threshold on height is established to distinguish pygmy and non-pygmy populations. If we define the human pygmy phenotype by an average adult male height shorter than 1.50m, then the Efé from Eastern Democratic Republic of Congo are the only pygmy population (Schmidt 1905, Schreider 1968). If 1.60m is considered (Cavalli-Sforza 1986), more than 200 populations worldwide could be categorised as pygmies (Hiernaux 1974, Froment 1993).

The arbitrary choice of 1.55m as the size threshold (Migliano, Vinicius and Lahr 2007) included the Namibian !Kung in the non-pygmy category. Migliano et al. (2007) found an optimal age at first reproduction for the !Kung of 19.5 years. Setting the threshold at 1.60m following Cavalli-Sforza (1986) would have however classified the !Kung as pygmies and therefore jeopardised Migliano et al. (2007)’s conclusions. Similarly, the Ache were considered as non-pygmies by Migliano et al. (2007), but could be divided in two subpopulations: the Northern Ache pygmies (1.53m on average) and the Southern Ache non-pygmies (1.60m on average) (K. Hill, personal communication).

In Central Africa, cultural criteria, such as the way of life, identity with forest, language, music, or social interactions are often utilized to distinguish pygmies from non-

pygmies (Bahuchet 1992b, Bahuchet 1993a, Bahuchet 1993b, Froment 1993). By doing so, some populations taller than 1.55m are designated as pygmies. For instance, the Twa (literal translation from Bantu languages is “Pygmy”) of the Western Democratic Republic of Congo are 1.61 m tall on average but are nevertheless designated as pygmies (Pagezy 1988, Froment 1993). Such complex cultural categorisation has recently been explored from a genetics perspective in nine Western Central African pygmy populations and their respective non-pygmy neighbours (Verdu et al. 2009). These authors found strong genetic evidences for a very recent common origin (about 2,800 years ago) of nine Western Central African populations categorised as pygmies following numerous cultural criteria. Among them were populations taller than 1.55m (Froment 1993, Verdu 2009, Verdu et al. 2009).

2. Issues with Demographic Data

The demographic data collected by Migliano et al. (2007) on Aeta and Batak pygmies are an important contribution to anthropological demography. However, the demographic data of the Batak, Agta and Aeta populations should be used carefully when testing long-term evolutionary processes since recent sociocultural changes may have strongly affected their mortality and fertility.

For the Batak, Migliano constructed mortality and fertility schedules using Eder's data (Eder 1987, Migliano 2005). However, Eder (1987) indicated that Batak's high mortality and low fertility, resulting in a strong population decline since 1981, were in fact due to intermarriages with lowlanders, land loss and decline in cultural identity. Similar issues arise with the Agta demographic data used by Migliano and researched by Earle and Headland (Earle and Headland 1998). The high adult mortality rates in Casiguran Agta were due to tuberculosis, malnutrition and alcohol-related deaths and homicides (Headland 1989). Tuberculosis was the single biggest killer among Agta adults, and 6% of all adult deaths and 20% of adult male deaths were alcohol related (Headland 1989). The demographic data for the Philippines Aeta were collected and presented for the first time by Migliano (Migliano 2005). These Aeta were removed from their traditional lands in 1991 and moved to urban settlements near cities. Since then, they could not hunt and gather and had access to Western medicines (Migliano 2005). Living for nearly 20 years in forced urban resettlements likely influenced the demography of the Aeta originally living in forest areas. The higher mortality currently observed in these three populations may not reflect their past demography, when short stature evolved. Past demography of these populations may be extrapolated by removing recent causes of death within a competitive risk modelling.

On the other hand, African pygmy populations, Aka (often called Biaka), Mbuti and Efé, are particularly relevant for testing long term evolutionary hypotheses. Ethnographers and biological anthropologists do not characterise African pygmies as being near extinction, do not identify alcoholism and tuberculosis as primary causes of death (Cavalli-Sforza 1986, Bahuchet 1992b, Bahuchet 1993a, Hewlett 1996, Joiris 2003) and do not suggest that malnutrition is common (Pagezy 1988, Bahuchet, Hladik and de Garine 1989, Bahuchet, McKey and de Garine 1991, Koppert et al. 1993, Froment 2001). However, African demographic data suffers from another issue: focused and systematic studies have not been conducted for these populations (Cavalli-Sforza 1986, Bahuchet 1992a).

Efé and Mbuti pygmies, grouped as a single “Eastern African pygmy” population by Migliano et al. (2007) in Figure 2 (but reported separately in the text), are linguistically, culturally and demographically very different (Hewlett 1996). The data for these two groups were extracted from Schebesta’s (Schebesta 1938) general census data. However, Migliano et al. (2007) could have used Bailey’s (Bailey 1985) more recent demographic data on this Eastern African pygmy group, leading to very different conclusions. Indeed, Bailey (1985) estimated an infant mortality rate of 14.0 and child mortality of 22.0, substantially lower than those for all other pygmy and non-pygmy groups in Migliano et al. (2007). Furthermore, survivorship to age 15 among the Efé is 78% (Bailey 1985), but 44% considering Schebesta’s older census data (1938) used by Migliano et al. (2007).

Migliano et al. (2007) refer respectively to Migliano (Migliano 2005) and Weiss (Weiss 1973a) for the Efé and the Mbuti life expectancies. In fact, life tables based on actual data do not exist for either one of these populations. Migliano et al. (2007) reconstructed the life tables using Weiss’ theoretical demographic models (Weiss 1973a, Weiss 1973b) based on census data (e.g., number of children and adults in camps) collected by ethnographers. Unfortunately, these models assume stable age-specific mortality and a stable age structure in

the population which is unlikely for African pygmies. These model-based life tables were built using the African demographic data on “Western pygmies” (including the Aka) from Cavalli-Sforza (1986) and on “Eastern pygmies” both from Turnbull (Turnbull 1986) on the Mbuti and from Schebesta (1938) on the Efé (Migliano 2005). None of these ethnographers or anthropologists recorded birthdates over time, tried to rank individuals by age or collected detailed reproductive histories from a large number of individuals. Moreover, Cavalli-Sforza was clear about the quality of his demographic data: “We have no totally satisfactory estimates of mortality rates in pygmies” (1986:376) and “the analysis of fertility, like that of mortality, suffers greatly from the difficulty of knowing ages reliably, and therefore one is unable to compute age-specific fertilities (1986:39)”. Froment (1993) also highlighted the challenges of building reliable growth curves for African pygmy populations in the absence of precise age estimates. The actual data on pygmy growth are indeed contradictory as Bailey’s study (Bailey 1991) showed that growth was slower in Efe pygmy children from birth to age five than in farmers whereas this pattern was not evident among Aka (Van de Koppel and Hewlett 1986).

On an ethnographic note, most Central African non-pygmy farmers view pygmies as being incredibly fertile and their infants as healthier than their own (Turnbull 1965, Kazadi 1981). One might suggest that if child mortality was in fact higher in pygmies, farmers would have had the opposite cultural representation of pygmies’ fertility. Anyway, the demographic reality of such cultural representation could only be assessed using quality demographic data.

3. Critics on the Optimisation Models

Migliano et al. found a positive correlation between fertility and height for the Efé and the Aeta pygmies. However, it is the relationship between weight and fertility that has been largely theorised through models incorporating allometric production function and that holds in most mammal species (Charnov 1991, Charnov 1993). The authors failed to estimate such correlation for Aeta (see Supporting Material). For the Ache population, a positive correlation was found between fertility and weight rather than height (Hill and Hurtado 1996) and in the case of Gambian women, no significant effect of height on fertility has been identified (Sear et al. 2004). The authors thus incorporated indifferently trade-offs considering height for the non-pygmy populations (Ache and Gambia) and weight for the unique pygmy population (Aeta). This can be a problem knowing that 1) the allometric relationship between height and weight is complex and their age-trajectories are different (Howell 1979) and 2) the relationship between height and fertility is still inductive and may vary widely between populations.

We wonder whether the conclusions drawn by Migliano et al. (2007) would still hold if the authors had incorporated additional well known correlations between fertility and mortality, enhancing the advantage of delaying growth cessation and age at first reproduction: 1) Young primipara have more risk of both mother and child death due to pregnancy complications than older primipara (Makinson 1985, Friede et al. 1987, Zabin and Kigaru 1998, Rush 2000) and 2) Taller Gambian women have fewer stillbirths and reduced infant mortality showing that height is positively correlated with offspring survival (Sear et al. 2004).

Following Hill and Hurtado (Hill and Hurtado 1996), Migliano et al. (2007) extended the Lotka-Volterra model (Lotka 1925, Volterra 1926) by incorporating a non negative multiplier $H(\alpha)$ on fertility rates m_x into the Euler-Lotka equation (Euler 1760, Lotka 1925), where α was the age at maturity. The magnitude of $H(\alpha)$ depended on individuals' height at maturity. Fertility as a function of height at maturity $m_x H(\alpha)$ was therefore a monotonic positive function of height at age α . This equation (equation [1] in Migliano et al. 2007, reproduced below) allowed numerical calculation of the intrinsic rate of population increase r (also called Malthusian parameter):

$$1 = \sum_{x=0}^{\infty} l_x m_x H_{\alpha} e^{-r(x-\alpha+1)} \quad [1]$$

Malthusian parameter r (taken as a measure of population fitness) was then calculated for an age at maturity α taken between 12 and 30 years and the optimal age at maturity was the value of α for which r was maximal. Unfortunately, equation [1] in Migliano et al. (2007) is wrong. First, it accepts negative ages when $x < (\alpha-1)$. Second, r is rate sensitive, i.e. it captures the importance of the relative timing of life history events: the age $x-\alpha$ in equation [1] by which r is multiplied within the exponential component (the +1 being here to set the first age-class to 0) must be similar to the corresponding age used for fertility rates and age-specific survival (the age x in m_x and l_x respectively, equation [1]). If not, stable population growth rates (intrinsic or finite) and stable population structure are not correctly estimated. Rather than [1], we believe that the correct equation should be:

$$1 = \sum_{x=0}^{\infty} l_x m_x H_{\alpha} e^{-r(x+1)} \quad , \quad [2]$$

with m_x equals 0 for $x < \alpha$ (because H_α is positive for $\alpha > 0$; equation [4] in Migliano et al. 2007).

Such an error may be due to mistyping. However, if the authors applied equation [1], this strongly overestimated population growth or decline, individuals producing offspring sooner in [1] than in [2]. This may explain why the intrinsic rates of population increase r calculated by Migliano et al. (2007) were widely inconsistent with those previously estimated and even unreasonable for some populations. For instance in the Ache population, r as a function of α was found between 0.32 and 0.36 (Migliano et al. 2007). Such values correspond to finite rates of population increases λ between $e^{0.32}=1.38$ and $e^{0.36}=1.43$. No human population increases by 38 to 43% per year. These estimates are 10-folds higher than previous estimates (3.6% of increase per year; Hill and Hurtado 1996 pp 101). Similarly, for the !Kung, Migliano et al. (2007) estimated r values (i.e., between 0.015 and 0.023) 10 times larger than Howell's (1979, i.e. $r=0.0026$).

We were also concerned about potential loopholes in the optimisation framework. First, the Aeta population being in decline, r corresponding to the optimal age at maturity α was negative (Figure 3, Migliano et al. 2007). From an evolutionary perspective, one may be sceptical about considering a strategy leading to population extinction as optimal. As discussed above (Part 2), the decline in the Aeta is likely due to recent life-style changes. The Aeta could not have exhibited such a 3% decline in population size per year for a long period of time: within the last 100 years (~ 4-5 generations), they would have fallen in size by 95%.

Rather than comparing strategies optimised for populations exhibiting different demographic regimes, adaptive landscape could be analysed for variations in parameters "everything else being equal" (Lande 1982). Indeed, no population can grow or decline indefinitely. Ideally, survival and fertility parameters should have been incorporated to obtain a continuum of optimal strategies (from very small to very tall) for a large range of

demographic scenarios. Finally, the curve of r as a function of height presented for the Aeta (Figure 3, Migliano et al. 2007) is rather flat around the optimal α . From $\alpha = 14$ to $\alpha = 18$, magnitude of variation in r is roughly between 0.001 and 0.005. Long-term evolution should be advocated for such small effect leading to evolutionary outcomes (and therefore a constant past demographic regime), as well as accurate demographic estimates (optimum α values being more sensitive to small changes in demographic parameters). Because $\alpha = 18$ falls within the range of optimal α values calculated for non-pygmy populations (18 for the Ache, 19.5 for the !Kung and 18 for the Gambian population), one can therefore wonder if the authors really succeed to bring to light a significant difference in reproductive strategies between populations categorised as pygmies and non-pygmies. To evaluate the significance of such difference, the robustness of the optimums could be analysed by calculating the secondary derivative $\partial^2 r / \partial \alpha^2$ of r with respect to α .

Conclusion

Migliano et al. (2007) explored whether pygmy's stature is a biological adaptation resulting from the advantage of reproducing early in a context of high mortality, at the cost of a shorter adult height that entails future fertility. Within a model incorporating this trade-off, the authors calculated an earlier optimal age at first reproduction for the Aeta pygmies (15 years old), than for the three non-pygmy populations: the Ache, the !Kung and the Gambian rural women (18-19.5 years old).

However, we showed that categorising populations between pygmies and non-pygmies differentiated only by an arbitrary threshold of height can be problematic: 1) it leads to group populations with different demographic features; 2) the populations hereby clustered do not necessarily share recent common ancestry and 3) it fails to explain variation in stature throughout the continuum of height observed in humans.

Migliano has collected important demographic data on Aeta and Batak populations to test Walker's hypothesis. However the Philippine pygmies are in decline because of recent forces of acculturation. As a consequence, the author compared populations exhibiting very different demographic regimes: from a population growing very fast, the Ache, to a population in dramatic decline, the Aeta. In the case of the Aeta, this also led to consider as optimal a life history strategy leading to population extinction.

Concerning African pygmy populations, demographic data are inaccurate largely due to the lack of longitudinal studies and the absence of precise age estimates. In turn, such inaccuracies may have large effect on the estimated optimum, which makes analyses of the robustness of the optimum essential.

A mathematical mistake has been found in Migliano et al.'s modelling framework and problems may arise by considering that height and weight at maturity impact on fertility in a

similar way. In future studies, other well-known trade-offs (e.g. a trade-off resulting from maternal mortality) should be taken into account since they could highly influence the optimal age at first reproduction.

The application of Charnov's life history theory to explain short stature in humans is innovative and provocative (Walker et al. 2006). Migliano's attempt to test it in pygmies is a promising research angle, although we doubt that the study succeeded in demonstrating the role played by life history trade-offs in the evolution of human morphological diversity. We nevertheless hope that this first attempt will encourage further researches on the potential implication of life history theory in pygmies' stature. This will require the enrichment of demographic data on pygmy populations, especially from Africa, including values of age-specific survival and fertility as well as growth patterns.

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