What Was Human Birth Weight in the Past? Simulations Based on Data on Stature from the Palaeolithic to the Present

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ABSTRACT Human populations are well known to have undergone secular trends in height. Due to the sensitivity of stature to nutrition in early life, these trends in height imply complementary trends in birth weight, albeit displaced in time by a few generations. This article presents a simulation of birth weight in past populations, based on the assumption of an inherent association between birth weight and adult height. These simulations suggest a substantial decrease in birth weight between the Palaeolithic and Neolithic periods, followed by more modest trends within the historical era. Whilst birth weight clearly responds to other environmental factors, these findings give some indication of the magnitude of plasticity in birth weight across time, and have implications for our understanding of the energy costs of reproduction and the likely survival of infants across different periods of human evolution.

INTRODUCTION

Anthropologists have long been interested in the relationship between body size and ecological conditions (Roberts 1953; Katzmarzyk and Leonard 1998). By definition, associations between adult size and ecological factors can be attributed to differential growth rates, however these may occur either by alterations in the rate of growth, or in the duration of growth (Bogin 1999). Recent interest in the contribution of developmental plasticity to adult phenotype has focused attention on the importance of fetal and infant growth rates (Wells 2003; Wells and Stock 2007; Wells 2007).

The traditional view has seen adaptation to varying climatic or ecological conditions as primarily a genetic process, requiring the natural selection of particular traits in response to their capacity to improve fitness in any given environment. For example, Holliday considered slow changes in body proportions in early European populations as evidence of such genetic adaptation (Holliday 1997). Contrary to that view, biomedical studies have recently emphasised that growth in early life is highly plastic (Clausson et al. 2000; Baird et al. 2001), with fetal life and infancy representing the periods of growth most sensitive to environmental factors, though growth rate during adolescence can also respond (Satyanarayana et al. 1989). However, the period of developmental plasticity is located within the period of maternal physiological provisioning (placental nutrition and lactation) (Wells 2003;

2007). Thus, during early life, human off-spring adapt not to the local environment per se, but to maternal phenotype (Wells 2007).

Birth weight has long attracted interest as a component of human phenotype. From an evolutionary perspective, birth weight represents the magnitude of maternal investment during fetal life, negotiated through dynamic hormonal interactions between mother and fetus (Haig 1993). From a biomedical perspective, birth weight is strongly predictive of morbidity and mortality during early life (Kramer 1987), as well as being associated with a wide variety of traits in adulthood (Barker 1998). In particular, birth weight within populations is strongly associated with adult height, as shown in numerous populations (Li et al. 2003; Sayer et al. 2004; Euser et al. 2005).

This association between birth weight and adult height also holds across populations. In a previous analysis of the association between birth weight and heat stress, maternal height was found to be a strong predictor of birth weight across populations (Wells and Cole 2002). This association is demonstrated in Figure 1, and is characterised by the regression equation (extracted from these published data for the present analysis) as follows:

Birth weight (g) = -2720 (SE 950) + [37 (SE 6) * maternal height (cm)]

where mean population birth weight is the average for males and females combined. Maternal height is a highly significant predictor of birth weight in this equation ($p < 0.0001$), and accounts for 36.9% of the variance (Wells and Cole 2002).

In that analysis, other factors were also significant predictors of birth weight variability across populations, the most notable being heat stress. However, this paper will focus on the association between maternal height and birth weight in order to keep this initial investigation simple.

Within the last 20 years, our understanding of body size in the past has improved substantially, through two related developments. First, an expanding fossil record has clarified broad trends in body size characterising hominins during long-term human evolution. Second, data either from skeletal material or actual measurements of living individuals has provided considerable information on variability in height within the last few thousand years. Collectively, these data indicate upward and downward secular trends in height occurring across time, continents, habitats, populations and their subdivisions (Komlos 1991, 1994; Steckel 1995, 1998). Because of the sensitivity of adult height to nutrition during early life, these secular trends in adult height to give some clue as to changes in nutritional supply during early development (Steckel 1995).

In this paper, I use the above equation linking maternal height to offspring birth weight in order to simulate secular trends in birth weight, using the assumption that fetal growth makes a key contribution to adult stature. In reality, it is well

known that adult stature reflects the quality of nutrition not only during fetal life, but also during infancy and early childhood. However, in order to identify broader trends, I consider it realistic to use adult height as a predictor of birth weight, and thereby to discern broad trends in birth weight across time and space.

METHODS

Data on secular trends in height were obtained from the literature for several populations or geographical regions: Western Europe (Formicola and Giannecchini 1999), the eastern Mediterranean (Boix and Rosenbluth 2004), Portugal (Cardoso and Gomes 2008), Latvia (Gerhards 2005), and South America (Bogin and Keep 1999). These data sets are constructed from combinations of skeletal analyses and actual height measurements. The limitations of these approaches are discussed in these original articles, and are therefore not addressed here.

Data from multigenerational studies of primates have elegantly illustrated a time lag in the effect of increasing maternal size on size of the offspring. In rhesus macaques, it took five generations for increases in maternal size to drive increasing birth weight of the offspring (Price et al. 1999). Thus, in any simulation of birth weight based on adult stature, this time lag should ideally

Fig. 1. Association between maternal height in birth weight across populations, using data presented previously (Wells and Cole, 2002).

be taken into account. In this preliminary analysis, no such an adjustment was made, on the grounds that the timescale over which birth weight is being investigated is likely largely to resolve the issue. This is because over time, birth weight is assumed to reflect uterine size (Kramer 1987), which will likewise track adult stature with a time lag. The time lag between offspring birth weight and maternal size across generations is shown schematically in Figure 2.

Fig. 2. Schematic diagram illustrating the time lag by which birth weight is assumed to track secular trends in female stature.

The equation presented above was therefore used to predict sex-averaged birth weight from values for female adult height in the five populations, which were selected on account of their wide time spans.

RESULTS

Figure 3 illustrates the long-term trend in birth weight illustrated by data from Palaeolithic, Mesolithic and Neolithic populations. There is a substantial decline from around 3300 - 3500 g, to around 2900 - 3000 g at the period of the origins of agriculture. In each of the two populations, the total decline appears to have exceeded 400 g, and was almost 600 g in the eastern Mediterranean. The wide disparity between the two populations at around 15,000 years BP is likely to reflect both geographic differences between the samples, and the approximation of the mean date in grouping these data for graphic presentation.

Figure 4 illustrates equivalent shorter-term trends in birth weight since the origins of agriculture. Amongst the four populations considered, there was a modest secular decline in the eastern Mediterranean, little systematic change in Latvia and South America, and a modest increase in Portugal. These fluctuations

Fig. 3. Secular trends in birth weight, predicted from trends in adult female stature, from the Palaeolithic to the Neolithic, based on data from western Europe and the Eastern Mediterranean.

Fig. 4. Secular trends in birth weight, predicted from trends in adult female stature, from the Neolithic to the present, based on data from Portugal, Latvia, the eastern Mediterranean and South America.

resulted in birth weight values between 2700 and 3200 g. All populations show a trend towards increasing birth weight in the 20th century, reflecting the impact of industrialisation.

DISCUSSION

This preliminary simulation, based on the assumption that variability in adult height has a predictable association with variability in birth weight, has indicated a significant secular decline in birth weight from the Palaeolithic into the Neolithic. This decline, of around 400 - 600g, is probably attributable to changes in subsistence practices impacting on the availability of food, which characterised the transition to agriculture (Cohen 1977; Cohen and Armelagos 1984; Starling and Stock 2007). There is now substantial evidence that the emergence of agriculture did not improve dietary supply, but rather induced dietary stress due to a narrower range of foods being available, the greater risk of famine, and the loss of nutritional quality of food stored following harvest. The imputed values of 3300 to 3500 g in the early Palaeolithic are certainly not implausible, and fall within the upper part of the range of the 20th century data reviewed previously (Wells and Cole 2002).

Following this systematic decline, subsequent oscillations in height in the populations

available for this analysis suggest more moderate impact on birth weight, and trends within populations are considerably more modest than average differences between populations. In the four regional populations providing data, the secular trends in height are equivalent to gains or losses in birth weight of around 300 g over 8000 years. Again, the typical values of 2700 to 3200 g are not implausible, and are similar to the range reported in developing countries in the 20th century (Wells and Cole 2002).

There are obvious limitations to this analysis. First, the notion that there is a simple linear relationship between adult height and birth weight is simplistic, due to the influence of numerous other environmental factors which are not addressed here. Amongst the important factors are maternal energy supply prior to and during pregnancy, maternal disease load, interbirth interval, altitude and the thermal environment (Wells and Cole 2002; Wells 2002). More sophisticated simulations are therefore recommended, attempting to incorporate information on these variables, to define the magnitude of effect with lower error. Second, growth is sensitive to nutrition during other periods of development, particularly infancy but also adolescence (Wells et al. 2005; Sachdev et al. 2005; Chomtho et al. 2008; Ekelund et al. 2006; Satyanarayana et al. 1989). Therefore, not all of the effect of variability

in adult stature may be immediately attributable to trans-generational influences on birth weight, and the magnitude of birth weight variability may be smaller than the magnitude of height variability. Furthermore, whilst there is a substantial fossil evidence base for adult stature from the Palaeolithic onwards, very little is known about birth size and early growth patterns.

Nevertheless, there is a broad dose response association between maternal height and birth weight across populations, as shown in Figure 1, and it is understood to be driven in large part by the association between maternal height and maternal uterine size. Indeed, it is precisely the plasticity of fetal and infant growth in relation to uterine size as well as other factors that makes possible secular trends in human growth. Over generations, birth weight is predicted to track trends in stature, but with a time lag. In contemporary humans, secular trends in birth weight have been discerned both in industrialised populations (Kramer et al. 2002) and also in modernising populations such as India (Agnihotri et al. 2008; Satpathy et al. 1990), following or accompanying trends in height. Hence, the broad patterns reported here, which consider all of the variability in stature to be attributable to birth weight variability, are likely to be robust, and are suggestive of significant variability in birth weight across time within and between populations.

These findings have implications for several aspects of human biology. Given the strong association between lower birth weight and risk of morbidity and mortality during early life (Kramer 1987), the apparent decline in birth weight between the Palaeolithic and Neolithic aids understanding the deterioration of health during this period of human evolution (Cohen and Armelagos 1984). Many infectious diseases impact disproportionately on individuals during early life, and reduced birth weight increases susceptibility to such diseases. Such diseases are now considered to have proliferated following the domestication of animals, such that a variety of pathogens jumped the species barrier to humans (Diamond 1998).

Maternal height is likewise well established to represent an adaptation to local ecological conditions, including effects such as food supply and thermal load (Roberts 1953; Katzmarzyk and Leonard 1998). A previous analysis already indicated a strong association between birth weight and thermal load, even after maternal height

was taken into account (Wells and Cole 2002). Thus, variable fetal growth has already been demonstrated to one of the ways in which contemporary populations tailor adult stature to local ecological conditions across generations.

Variability in birth weight also has implications for the energetic costs of reproduction in females (Aiello and Key 2002; Aiello and Wells 2002). However, these costs are complex, because lower birth weight tends to predispose to catch up growth (Ong et al. 2000). Of the two periods of maternal provisioning, lactation is substantially more expensive for the maternal energy budget than gestation (Clutton-Brock et al. 1989). Thus, whilst a small baby imposes a reduced cost of gestation, this reduction may be relatively small, and may be partially offset by an increased cost of lactation for funding catch-up growth. For these reasons, trends in birth weight imply knock-on effects on other components of reproduction, such as birth spacing, and for maternal-offspring conflict over the optimum transfer of resources during parental care.

CONCLUSION

In summary, this analysis has used secular trends in adult height to propose complementary trends in birth weight, which have implications for our understanding of changes in mortality patterns and reproductive costs across time and populations. The analysis presented is necessarily preliminary, but indicates the likely patterns and estimates the approximate magnitude of effect. It is hoped this analysis may prove the basis for more sophisticated modelling in the future.

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