

Physiological Constraints and Comparative Economic Development*

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Abstract. It is a well known fact that economic development and distance to the equator are positively correlated variables in the world today. It is perhaps less well known that as recently as 1500 C.E. it was the other way around. The present paper provides a theory of why the “latitude gradient” seemingly changed sign in the course of the last half millennium. In particular, we develop a dynamic model of economic and physiological development in which households decide upon the number and nutrition of their offspring. In this setting we demonstrate that relatively high metabolic costs of fertility, which may have emerged due to positive selection towards greater cold tolerance in locations away from the equator, would work to stifle economic development during pre-industrial times, yet allow for an early onset of sustained growth. As a result, the theory suggests a reversal of fortune whereby economic activity gradually shifts away from the equator in the process of long-term economic development.

Keywords: long-run growth, evolution, nutrition, fertility, education, comparative development.

JEL: O11, I12, J13.

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1. INTRODUCTION

It is a well known regularity that economic development tends to increase as one moves away from the equator. Figure 1 provides one particular illustration, which employs the urbanization rate as a proxy for development, but similar patterns emerge if one were to consider other indicators such as GDP per capita. The strong “latitude gradient” emerges across the world at large, and even within Europe.

Strikingly, however, this state of affairs is of relatively recent origin as evidenced by Figure 2. As is visually obvious, economic development (measured by population density; Acemoglu et al., 2002; Ashraf and Galor, 2011) was negatively correlated with absolute latitude at the eve of the Age of Discovery. Again, this association is found both across the world at large and within Europe. The fundamental objective of the present paper is to provide a theory, which can account for this remarkable “reversal of fortune”.¹

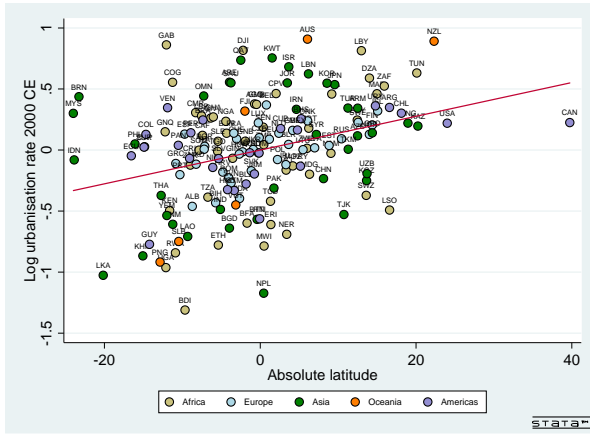
This paper proposes that the intertemporally shifting latitude gradient is a consequence of differences in the physiological constraints faced by individuals at different geographical locations. The argument is anchored in an important fact from the fields of biology and physical anthropology: Individuals are inherently physically bigger in locations further away from the equator. This phenomenon is labeled “Bergmann’s rule” in the relevant literatures, after Bergmann (1847). Bergmann’s rule is possibly a consequence of positive selection towards greater cold tolerance in the aftermath of the exodus from Africa some 50,000 years ago, but it could potentially have other roots as well (see discussion below). The substantive implication of this “latitude gradient in body size” is that individuals living in colder climate zones would end up facing higher metabolic costs of fertility, on purely physiological grounds, since these costs are increasing in the body mass of the individual. As a consequence, during pre-industrial times one would expect to see progressively lower levels of population density as one moves away from the equator (see Dalgaard and Strulik, 2015). Moreover, if, in the pre-industrial era, technological change was positively influenced by population size, societies where citizens were larger but less numerous would tend to be less technologically sophisticated, reinforcing the physiologically founded reason for low economic development.²

¹As far as we know, the negative link between absolute latitude and population density was noticed first in Ashraf and Galor (2011).

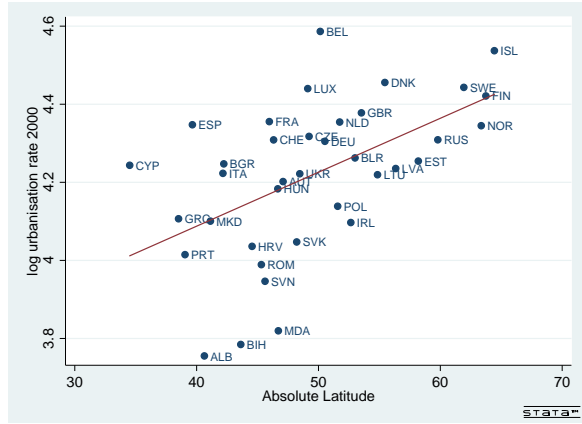
²For a formal discussion of the link between population density and technological change in a pre-industrial environment, see Aiyar et al. (2008) and Ashraf and Galor (2011).

FIGURE 1: CONTEMPORANEOUS LATITUDE GRADIENT

A: World



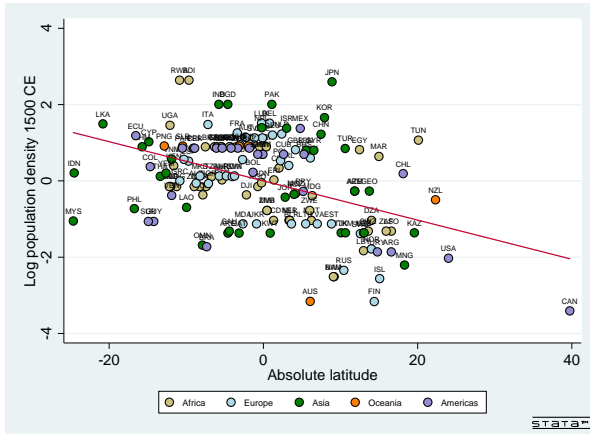
B: Europe



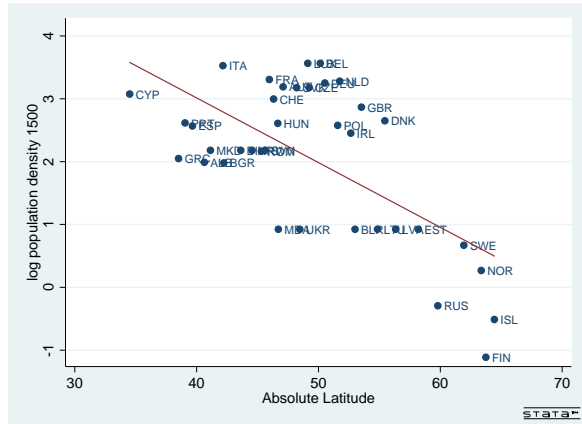
The figures show the correlation between absolute latitude and urbanization rates in the year 2000 across the world and in Europe. Continental fixed effects have been partialled out in Panel A. The depicted line is estimated by OLS.

FIGURE 2: PRE-INDUSTRIAL LATITUDE GRADIENT

A: World



B: Europe



The figures show the correlation between absolute latitude and population density in 1500 C.E. across the world and in Europe. Continental fixed effects have been partialled out in Panel A. The depicted line is estimated by OLS.

However, as technological change makes formal education more attractive it is likely to be adopted sooner in societies where the (relative) cost of child quantity are greater; places inhabited by bigger individuals, further away from the equator. This is where the latitude-productivity nexus gradually begins its turnaround: as educational investments are undertaken, fertility declines and economic growth takes off. Consequently, the currently observed positive correlation between absolute latitude and development outcomes may be the product of a differentiated

timing of the take-off, which has provided places further away from the equator with a developmental head start in the modern growth regime.

In support of this hypothesis we develop a unified growth model. The model features overlapping generations of children and adults. Adults are the economically active agents and decide on family size, the level of nutrition and schooling of the offspring as well as own (luxury) consumption. Following Dalgaard and Strulik (2015, 2016) parents are subject to the physiological constraint that they have to cover their basal metabolic needs, which depend on their own body mass as well as the level of fertility. Moreover, body mass is transmitted via an intergenerational law of motion. Finally, a unique output good is produced using body size augmented labor, human capital, land, and technology.

Aside from these features the theory builds on three key elements. First, utility of parents is increasing in the quality and quantity of offspring as well as own consumption. There are two dimensions to child quality, which are assumed to be imperfect substitutes: nutrition and skill formation. Moreover, preferences are assumed to fulfill a “hierarchy of needs” principle: in a time of crisis parents will tend to adjust own (luxury) consumption more strongly than child quantity and quality. Second, the return to skill formation is increasing in the level of technological sophistication and human capital production features a non-convexity. The latter element involves the assumption that parents costlessly transmit a minimum amount of skills to the next generation, which permits a corner solution in terms of skill investments when the level of technology is sufficiently low. Third, technology evolves endogenously and depends on human capital augmented population size.

These elements interact in the following way. At early stages of development the economy finds itself in a “subsistence regime” featuring low income and a relatively poor state of technology. Consequently, parents only invest in child quantity and the nutrition-based quality component. As technology slowly advances, however, income rises gradually despite the resource diluting influence from population. Eventually, the economy transits into a “pre-modern regime”. The higher level of income entices the parents to start spending resources on themselves; i.e. above and beyond subsistence requirements. In addition, parents choose to increase the size of the family further. Nutritional investments also rise, but not on a per child basis. Consequently average body mass is not increasing despite a higher level of income. Yet as technology continues to advance, now at a higher speed, the economy ultimately moves into the “modern growth

regime”, where human capital investments are deemed optimal. As quality investments are intensified, individuals respond by lowering fertility, which also allows nutritional spending per child to increase. Consequently, growth takes off: economically, and physiologically in the sense of increasing body mass. In the long-run the economy converges to a steady state where fertility is at replacement level, average body mass and human capital investments are constant, and economic growth occurs at a constant exponential rate.

With this model in hand we conduct experiments in order to examine the causes of the shifting latitude gradient, described above. Specifically, we compare societies where individuals are inherently (i.e., for given food intake) of different body size, which potentially could have been due to e.g. selection. The question is then whether societies in cold locations, where people tend to be bigger are likely to take off sooner, yet be less developed early on.

We consider several scenarios. The simplest scenario, which we can deal with analytically, assumes instantaneous diffusion of ideas across societies. That is, all societies share the same pool of knowledge. In this setting the result is unambiguous: societies inhabited by larger individuals feature lower population densities early on, but will transit to the modern growth regime relatively sooner. The intuition is simple. The transition to modern growth arises when a critical level of technological sophistication is attained enticing individuals to commence human capital investments. This critical level of technology is declining in the average body size of individuals, since families with higher metabolic cost of fertility (child quantity) requires less of an inducement to investment in child quality in the sense of human capital. If the level of technology evolves at the same pace everywhere, societies where people are physiologically bigger will therefore unambiguously take-off sooner, which creates the reversal. The model thus rationalizes the regularities depicted in Figure 1 and 2.

The assumption of instantaneous knowledge sharing is admittedly extreme and tends to bias the results in favor of an earlier transition for societies inhabited by larger individuals. If bigger populations produce more ideas it is possible that the “small but many” society, close to equator, could transit to modern growth earlier despite being somewhat more reluctant to invest in quality, on physiological grounds.

We therefore further scrutinize the predictions of the model, by way of numerical experiments, in more realistic settings where knowledge diffusion is gradual and possibly incomplete. We show, for instance, that if societies asymptotically share all knowledge, then places further away

from the equator (featuring bigger people) will transit to the modern growth regime relatively earlier unless the diffusion lag in the transmission of ideas is more than 12 generations, which in our calibrations means 360 years. We examine other scenarios as well, some of which involve imperfect knowledge sharing (i.e., some ideas are *never* diffused). Overall, we find for a range of settings, featuring both gradual diffusion and imperfect sharing of ideas, that societies featuring citizens of larger body mass are predicted to take off sooner. Hence, our analytical results, which require instantaneous and perfect knowledge sharing, are fairly robust.

This paper is related to several strands of literature. On the theoretical side, the paper belongs to the literature on growth in the very long run (e.g. Galor and Weil, 2000; Galor and Moav, 2002; Lucas, 2002; Cervellati and Sunde, 2005; Strulik and Weisdorf, 2008; de la Croix and Licandro, 2013). In particular, the model developed below borrows elements from Dalgaard and Strulik (2015, 2016), in regards to the physiological constraints, and from Strulik and Weisdorf (2008) and Dalgaard and Strulik (2016) on the preference side. The contribution of the present paper lies in showing how differences in initial conditions with respect to underlying physiological constraints may have affected comparative development in general, and led to the reversal depicted in Figure 1 and 2 in particular.³

The paper is also related to existing contributions that have aimed to explain observed “reversals of fortune” (Acemoglu et al. 2002; Olsson and Paik, 2016a,b; Litina, 2016; Dalgaard et al., 2016). The present study differs from previous contributions on two fronts: (i) In our focus on the role played by absolute latitude, rather than other structural characteristics, and, (ii) in the mechanism responsible for the reversal. Whereas previous work, in the latter context, has focused on either institutional or cultural drivers, the present study proposes a physiological mechanism. We elaborate on the value added of the present work in the next section.

The paper proceeds as follows. In the next section we document a series of stylized facts, regarding the interrelationship between geography, body mass and economic activity, which we require the model to be able to account for. Section 3 develops the model, and Section 4 describes the development trajectory implied by the model. Section 5 discusses the model’s predictions regarding comparative development whereas Section 6 concludes.

³On the potential predictive power of unified growth theory with respect to comparative development, see Galor (2010) and Cervellati and Sunde (2015).

2. MOTIVATING EVIDENCE

This section falls in three subsections. We begin by examining the reversal with more detailed data, which allows us to gauge whether the “latitude reversal” has already been accounted for by previous work. Subsequently, we turn to the link between geography and physiology in Section 2.2 after which we turn to the link between physiology and comparative development in Section 2.3.

2.1. The reversal re-examined. In gauging “initial conditions” we rely on the HYDE database version 3.1., which provides grid-level estimates of population size in 1500 C.E. (Goldewijk et al., 2010, 2011). In particular, we employ a one degree latitude by one degree longitude resolution. Similarly, when we examine the current latitude gradient, where economic activity is measured by gross cell product (GCP) per capita from the Yale GECON database version 4.0, the unit of analysis is also a pixel of size 1x1 degree latitude/longitude.

Accordingly, column 1 of Tables 1 and 2 examines the link between absolute latitude and population density in 1500 CE and GCP per capita in 2000, respectively, across the world. In keeping with the message from Figures 1 and 2 we observe a negative correlation between absolute latitude and population density in pre-industrial times, both across the world and within Europe, whereas economic activity appears to rise as one moves away from the equator today. When distance to the equator increases by one degree latitude income rises today by about three percent, whereas population density declines by about nine percent in 1500 C.E.

Table 1 and 2 about here

As noted in the Introduction several previous studies have observed important instances of “reversals”. Perhaps most famously, Acemoglu et al. (2002) observe a reversal of fortune across former colonies, arguing in favor of an institutional explanation. The argument is that places that initially were successful (measured by population density or urbanization rates) were more likely to be “treated” by extractive institutions by the colonial powers, leading to a reversal in relative prosperity among former colonies. A natural question is whether institutions are implicitly responsible for the reversal of the latitude gradient. To address this question, Column 2 of Table 1 and column 3 of Table 2 control for a full set of country fixed effects.⁴ Insofar as

⁴The country fixed effects refer to contemporary country borders, which is a poor guide to country borders in 1500 C.E. Nevertheless, if geographical areas that ex post became part of the same nation features certain commonalities the country fixed effects is a convenient way to control for unobserved heterogeneity.

institutions mainly vary across countries, the results informs us whether the latitude reversal is – implicitly – accounted for by institutional developments. This does not seem to be the case. Furthermore, to our knowledge there is no institutional theory, which can explain the reversal of the latitude gradient *within* Europe.

More recent work by Olsson and Paik (2016a,b) draws attention to a reversal involving the timing of the Neolithic revolution, whereas Litina (2016) and Dalgaard et al. (2016) observe a similar phenomenon related to soil suitability for agricultural production. Olsson and Paik argue that countries that underwent the Neolithic revolution relatively early developed extractive institutions and norms emphasizing obedience to the detriment of long-run growth. While an early Neolithic revolution allowed for a developmental head start, the cultural and institutional side effects eventually stifled development, allowing latecomers to sedentary agriculture to overtake. Litina (2016) argues that the reversal in soil quality can be explained by cultural change in favor of cooperative behavior in geographically “challenged” nations, eventually allowing them to industrialize comparatively early. Finally, Dalgaard et al. (2016) argue that rich inland soil productivity, relative to the productivity of the nearby ocean, lead to less coastal orientation of economic activity early on, and thereby to the accumulation of capabilities that were less favorable to industrialization. Accordingly, the common feature of this group of studies is a reliance on mechanisms that involve cultural change or an institutional mechanism.

While some (or most) of the variation in cultural values likely is controlled for by the country fixed effects, a compelling argument can be made that cultural values exhibit important within country variations (e.g., Tabellini, 2010; Michalopoulos and Papaioannou, 2013). In order to gauge if the latitude gradient can be accounted for by cultural adaptation, Table 2 therefore studies the link between absolute latitude and current economic activity, when the data has been pruned for cultural differences to the extent possible. Following Andersen et al. (2016) we employ a full set of language fixed effects to proxy world wide variations in cultural values, under the assumption that differences in local languages represents a meaningful proxy for cultural differences. Controlling for “culture” in this manner means adding in excess of 1000 fixed effects to the regression model.⁵ As seen from Columns 4 and 5 of Table 2, when both country and language fixed effects are in the control set the positive link between absolute latitude and economic activity still obtains. This provides some assurance that the “latitude

⁵See Andersen et al. (2016) for details on the construction of the language fixed effects.

reversal”, which is the focus of the present study, has not already been accounted for by previous work on the general topic that involve cultural or institutional mechanisms.

Finally, Andersen et al. (2016) provide evidence that the level of ultraviolet radiation (UV-R) has left a mark on current income differences. A potential explanation is that UV-R captures disease ecology in regards to eye disease, which influences the return to investments in skill and may have worked to delay the take-off to sustained growth. Since UV-R and absolute latitude are very strongly correlated, Column 2 of Table 2 introduces UV-R as a separate control.⁶ Consistent with the results in Andersen et al. (2016), UV-R is negatively correlated with economic activity, even controlling for country and language fixed effects.⁷ At the same time absolute latitude remains positively correlated with economic activity. The overall impression is that the reversal of the latitude gradient appears to require further explanations, aside from those already (albeit implicitly) provided in the literature.

Before we turn to the link between geography and physiology, it is worth reflecting on the fact that the latitude gradient obtains *within* countries. A natural question is if it is plausible that within country variations in body size (implicitly captured by absolute latitude) could be believed to influence within country long-run developments.

In a recent study, Kelly, O’Grada and Mokyr (2015) provide a fresh look at the determinants of the Industrial Revolution within two prominent European countries: England and France. In the case of England, the Industrial Revolution took hold first in the North, leading to a reversal of fortune since the South historically had access to richer agricultural lands. Empirically, the authors document that individuals in the North were physiologically relatively bigger than in the South. Kelly et al. explain the latter fact by persistent differences in the organization of production and a more nutritious diet. In the case of France the authors also detect a significant link between body size and the timing of the Industrial Revolution. Moreover, people are indeed bigger on average in the Northern part of France. Hence, in case of these forerunner countries of the Industrial Revolution one observes differences in physiological development, prior to the take-off, which hold predictive power vis-a-vis subsequent comparative regional development.

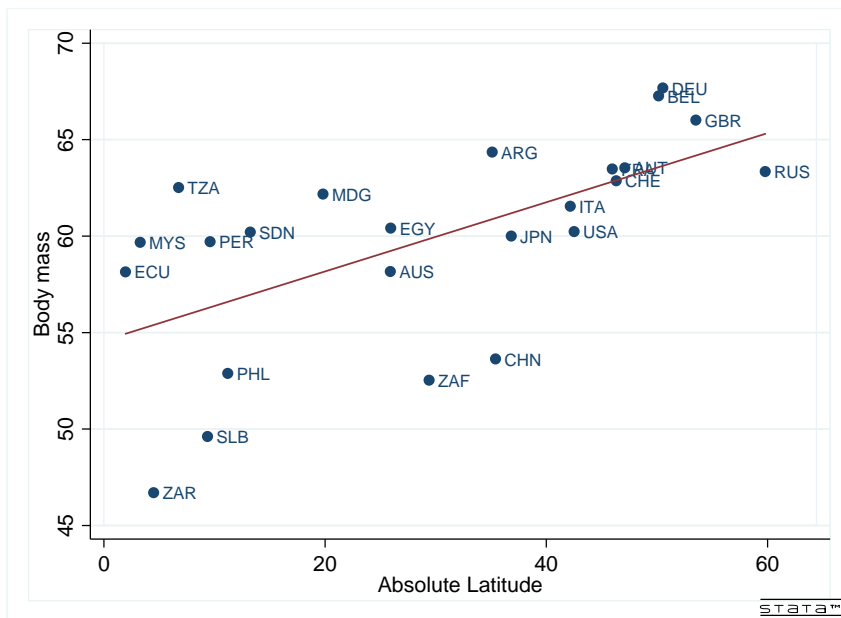
⁶UV-R is not added as a control in Table 1 since Andersen et al. (2016) show that its influence on economic activity only emerges in the 19th and early 20th century.

⁷In the European sample, where the variation in UV-R is more limited, UV-R does become imprecisely estimated. Since UV is not significant in column 2 of Table 2B we omit it in column 5. Adding UV-R to this specification does not overturn the significance of absolute latitude.

2.2. **Geography and Physiology.** In biology, Bergmann’s rule (Bergmann, 1847) is a well established regularity with bearing on body size for (most) mammalian species. The rule states that average body mass (kg) of individuals is increasing in the distance to the equator; in the context of the human species, support is found in Roberts (1978), Ruff (1994), Katzmarzyk and Leonard (1998), and Gustavson & Lindenfors (2009). However, to have bearing on the reversal documented above, the latitude gradient needs to be apparent across *countries* and not just across indigenous societies, which has been the favored unit of analysis in the relevant empirical literature within physical anthropology.

To begin an exploration of Bergman’s rule at the country level, Figure 3 illustrates the correlation between absolute latitude and a measure of average body mass, which derives from the so-called “Goldman data set” (Auerbach and Ruff, 2004). More specifically, average body mass is calibrated using skeletal remains from the Holocene period up until about ca. 1500 C.E.⁸ We view this small sample of observations as reasonable indicators of (pre-industrial) initial condi-

Figure 3: Bergmann’s Rule



The figure shows the bivariate association between body mass and absolute latitude, across pre-industrial societies. The data on body mass derives from the Goldman data set (Auerbach and Ruff, 2004), which comprises morphological observations from skeletons dating from 1500 C.E. or earlier. The depicted line is estimated by OLS and is statistical significant at the 1% level of significance.

⁸See the appendix for details on this data and the calibration.

tions with respect to body mass characteristics.⁹ As is visually obvious, Bergmann’s rule holds up in this sample.

Table 3 about here

More formally, Table 3 reports the results from regressing absolute latitude on body size. In the first two columns we employ the Goldman data set; both body mass (weight, column 1) and body size (height, column 2) are positively correlated with absolute latitude. While geographically diverse (see Appendix), the sample is of modest size. Accordingly, to further examine the cross-country viability of Bergmann’s rule we employ data constructed by the NCD Risk Factor Collaboration (2016), which covers a much larger cross-section of countries. In this data set we rely on height estimates for cohorts born in 1900 and 1995, respectively. Admittedly, data on body weight would be a more ideal measure but does not appear to be available for this early period. Hence, we use height as a proxy for body weight. In Column 3 and 4 we study the world wide link between latitude and height in 1900, with and without continental fixed effects. In either case absolute latitude is strongly and positively correlated with body size. But if the link between body size and latitude is generated by way of natural selection (see below), it is not obvious that these tests are ideal, since the post-Colombian period witnessed considerable international migration (Putterman and Weil, 2010). As a result, the geographical location of people today does not necessarily identify the geographical location of their ancestors. Hence, in order to control for the potential influence from post 1500 people flows, column 5 explores the latitude-height nexus within a sample of countries that were only affected by immigration to a limited extent over the past 500 years; that is, countries where less than 10% of the current population are ancestors of people who immigrated since 1500 C.E. As seen, the latitude gradient carries over. Finally, Column 6 examines whether average body size varies with distance from the equator within Europe, around the turn of the 20th century. Again, the answer appears to be in the affirmative. The last five columns in Table 3 show that the findings for the 1900 cohorts carry over to cohorts born in 1995. Quantitatively our estimates suggest that in areas separated by 10 degrees of latitude, within any given continent, people differ on average by 1.6 cm in height in 1900 (column 4) and 1.8 cm in 1995 (column 8).

⁹Based on a similar presumption, previous research in human biology has employed the Goldman data set in order to examine the viability of the out-of-Africa hypothesis with regard to height. That is, whether the variability in height within population groups declines with migratory distance to east Africa, consistent with the serial founder effect; see Betti et al. (2009).

Overall the results reported in Table 3 complement the findings of Ruff (1994) and Gustavson and Lindenfors (2009) of a positive latitude gradient in body size, in keeping with Bergmann’s rule. The most commonly cited interpretation of this latitude gradient is that it emerged due to selective pressure whereby individuals with body characteristics that ensure greater cold tolerance have been positively selected in colder locations, in the aftermath of the exodus from Africa (e.g., Ruff, 1994; Katzmarzyk and Leonard, 1998). The logic is, as a matter of geometric fact, that the surface area to volume ratio declines as body mass increases, which serves to limit heat loss (see Ruff, 1994). Evidence of recent (i.e., over the last 50,000 years) genetic selection towards greater cold tolerance in human populations is found in Hancock et al. (2010).

While a genetic interpretation of Bergmann’s rule appears viable other possibilities exist. In particular, since the process of human growth is subject to some degree of plasticity, adjustment of body mass and proportions may be viewed as a form of acclimatization, which thus may arise without genetic change (see James, 2010). In addition, it is also possible that disease could be an intervening factor, if Northern regions were less prone to disease, which works to stifle body growth during childhood.

It is worth emphasizing that our proposed theory does not hinge critically on any particular origin of a latitude gradient in body size. The theory remains relevant as long as absolute latitude predicts body size variation *regardless* of the exact underlying the reason. For example, if Bergmann’s rule turns out to be caused by variation in disease load rather than evolutionary forces, this would not undermine the proposed physiological theory for the reversal of the latitude gradient.

2.3. Physiology and Comparative Development. The issue to which we now turn is how body size appears to correlate with economic outcomes of interest. In the present context we are particularly interested in the potential link between body size and, respectively, the timing of the fertility transition and current economic development.¹⁰

Table 4 about here

Table 4 reports on what the stylized facts are with respect to the former outcome. In panel A we rely on the estimates of the “year” of the transition derived in Reher (2004), whereas panel

¹⁰The key reason why the fertility transition is a particular object of interest is that many unified growth models assign a decisive role for this transition in admitting the take-off to sustained growth. See e.g. Galor and Weil (2000) and Galor and Moav (2002). See Dalgaard and Strulik (2013) and Andersen et al. (2016) for evidence on the impact of the fertility transition on current levels of income per capita in a cross-country setting.

B uses an alternative set of estimates due to Caldwell and Caldwell (2001). In the first two columns we ask if the timing of the fertility transition appears systematically related to initial body size, measured prior to 1500 C.E. Despite the small sample the estimates are statistically significant and indicate a negative link. Employing height data for cohorts born in 1900, similar results obtain in a full world sample (with and without continental fixed effects) as well as in the European sample. Quantitatively, the estimates imply that for each centimeter reduced height, the fertility transition is delayed by about 2-3 years, on average (Column 4 and 9).

In Table 5 we turn to economic development, which we measure in three ways: GDP per capita, urbanization, and years of schooling. As can be seen from the table we generally find that places where individuals historically were physiologically bigger are places that feature higher economic development today. The estimates are statistically strongly significant in the world wide samples, but less so in our small samples.

The preceding discussion can be summarized in five stylized facts:

- (1) In pre-industrial times, the extent of economic development varied inversely with distance to the equator, cf Figure 2, and Table 1.
- (2) Currently, the extent of economic development and distance to the equator is positively correlated, cf. Figure 1, and Table 2.
- (3) Body size, today and historically, is positively correlated with the distance from the equator (Bergmann's rule, Table 3).
- (4) Societies that were historically inhabited by physiologically bigger people underwent the fertility transition earlier (Table 4).
- (5) Societies that were historically inhabited by physiologically bigger people are more economically developed today (Table 5).

In the remainder of the paper we develop a unified growth model, which can account for this set of facts, thereby providing a potential explanation for the reversal of the latitude-development gradient.

3. THE MODEL

3.1. Preferences. Consider an economy populated by a measure L_t of adult individuals, called households or parents. We abstract from gender differences such that any per capita variable can

be thought of as being measured in per parent terms. Households derive utility from children, spending on child quality, and from consuming non-food (luxury) goods.

As Strulik and Weisdorf (2008) and Dalgaard and Strulik (2016) we assume that utility is quasi-linear. Non-food goods enter linearly, which makes them less essential and easier postponable. This creates a simple device according to which consumption is restricted to subsistence needs when income is sufficiently low. The qualitative results would not change under a more general utility function as long the intertemporal elasticity of substitution for child nutrition is smaller than for non-food (luxury) consumption.

Spending on child quality comes in two dimensions: nutrition and schooling. Following the anthropological literature (Kaplan, 1996) we assume that from the preference side there is not a big difference between both quality components. Thus both enter parental utility with the same weight. The most natural way to model this idea is to assume that both components are imperfect substitutes such that child quality (Becker, 1960) is given by the compound $c_t h_{t+1}$, in which c_t is child nutrition expenditure (approximating physiological quality) and h_{t+1} is human capital of the grown up child (approximating educational quality).

Summarizing, the simplest functional representation of utility is

$$u = \log n_t + \gamma [\log c_t h_{t+1}] + \beta x_t, \tag{1}$$

in which n_t is the number of offspring, x_t is non-food consumption, and β and γ are the relative weight of non-food consumption and child quality in utility.

Parental child expenditure is driven by (impure) altruism, the “warm glow”, i.e. it is not instrumental; parents do not calculate how expenditure improves child productivity and future wages. Moreover, notice that parents take into account how education improves human capital of their children but not how nutrition affects body size. Given that humans invested in nutrition of their offspring long before they understood human physiology, this seems to be a plausible assumption. Moreover, at the steady state, the stock variable (body mass) is proportional to nutritional investments. Accordingly, in the long-run the two formulations will lead to similar steady-state results.¹¹

¹¹In Dalgaard and Strulik (2015) we demonstrate that a “utility from body mass” and a “utility from nutrition” yield very similar results at the steady state. Yet the utility from body mass formulation is analytically considerably more cumbersome.

3.2. Technology. Following Galor and Weil (2000) and Galor and Moav (2002) we assume that production takes place according to a constant returns to scale technology using the factors land X and human capital \tilde{H}_t , such that aggregate output is

$$Y_t = A_t \tilde{H}_t^\alpha X^{1-\alpha}, \quad (2)$$

in which A_t is the endogenously determined level of technological knowledge at time t . Aggregate human capital is determined by the number of workers L_t times their human capital h_t times their physical capacity (muscle force) which scales with body mass m_t , such that $\tilde{H}_t \equiv m_t^\phi h_t L_t$. We denote human capital in the narrow sense, i.e. the aggregate productive knowledge incorporated in people, by H_t , $H_t = h_t L_t$. Following again conventional unified growth theory, we assume no property rights on land such that workers earn their average product and income per capita is given by $y_t \equiv Y_t/L_t$. Normalizing land to unity we obtain

$$y_t = A_t m_t^\phi h_t^\alpha L_t^{\alpha-1}, \quad (3)$$

in which $\phi \equiv \alpha\tilde{\phi}$. For simplicity we focus on a one-sector economy such that output can be converted without cost into food and non-food.

The main motivation for adding body mass to the production function is that body mass matters to the amount of force the individual can muster; “brawn”, in other words. Because muscle force is proportional to muscle cross-section area, measured in meters², it rises with weight as $m^{2/3}$ (e.g., Astrand and Rodahl, 1970; Markovic and Jaric, 2004). Of course not all tasks of the production processes rely on ‘brute force’ to the same extent. Theoretical reasoning and empirical estimates in sport physiology suggest that individual performance in different tasks scales with body size as m^ϕ , in which $\phi = 2/3$ for exerting force (as for example plowing and digging), $\phi = 0$ for moving and $\phi = -1/3$ for supporting body weight (Markovic and Jaric, 2004). In practise, one would then probably expect a positive exponent, which is bounded from above at $2/3$.

3.3. Human Capital. Human capital production is a positive function of parental education expenditure per child e_t and the level of knowledge that could potentially be learned at school A_t . Specifically we assume that

$$h_{t+1} = \nu A_t e_t + \bar{h}, \quad 0 < \nu \leq 1. \quad (4)$$

The parameter $\nu > 0$ controls for the productivity of the education sector (or the share of productive knowledge that can be conveyed at school): The constant \bar{h} denotes human capital picked up for free, for example, by observing parents and peers at work. The production function for human capital could be made more general at the cost of analytical inconvenience. The only crucial part is, as in Galor and Moav (2002), that the return on education is not infinite for the first unit of educational expenditure. This feature, generated by the assumption of some costless acquisition of human capital, produces a corner solution, i.e. the possibility that not investing in human capital is optimal in some environments. It allows us to capture the long epoch of stagnation where investment in formal education arguably did not take place (to a first approximation).

3.4. Physiological Constraints. Parents are assumed to experience utility from consumption above subsistence needs x_t but not from subsistence food consumption. Yet they have to eat to fuel their metabolism. The metabolic rate is endogenous and depends – as in Dalgaard and Strulik (2015, 2016) – on body size and fertility. As elaborated by Kleiber (1932) and many studies since, energy requirements of non-pregnant humans scales with body size according to $B_0 \cdot m^b$, with $b = 3/4$; this parameter value has withstood empirical falsification for decades, and is consistent with theoretical priors, see Dalgaard and Strulik (2015) for more details. Moreover, rearing up a child from conception to weaning increases the mother’s metabolic needs by a factor ρ (Prentice and Whitehead, 1987; Sadurkis et al., 1988). This means that metabolic needs of an adult with n_t children is given by $(1 + \rho \cdot n_t)B_0 m_t^b$. In order to convert energy into goods we employ the energy exchange rate ϵ , which is measured in kcal. per unit of a unique consumption good.¹² Summarizing, the parental budget constraint reads

$$y_t = x_t + (c_t + e_t)n_t + (1 + \rho n_t) \frac{B_0}{\epsilon} m_t^b. \quad (5)$$

In order to construct the intergenerational law of motion for body size we begin with the following energy conservation equation:¹³

$$E_t^c = b_c N_t + e_c (N_{t+1}' - N_t) \quad (6)$$

¹²See Dalgaard and Strulik (2015) for a more detailed elaboration of these physiological foundations.

¹³Implicitly, we draw on West, Brown, and Enquist’s (2001) model of ontogenetic growth; see also Dalgaard and Strulik (2015).

in which E_t^c is energy consumption during childhood after weaning (prior consumption is covered by adult metabolic needs), N_t denotes the number of human cells after weaning, N'_{t+1} is the number of cells of the child as a grown up, b_c is the metabolic energy a cell requires during childhood for maintenance and replacement, and e_c is the energy required to create a new cell. Hence the left hand side is energy “input” and the right hand side captures energy use.

Observe that the conservation equation does not allow for heat loss. The extent of heat loss is thus implicit in the parameters; a human who manages greater heat loss can thus be seen as one featuring greater energy costs of cell maintenance and repair, i.e. a greater parameter value for b_c . As discussed in Section 2 there is good reason to believe that humans operating under different climatic circumstances are different in terms of cold tolerance, i.e., are different in terms of how effective the body is at releasing heat. Accordingly, a simple representation of acclimatization or genetic selection toward cold resistance would be that of a *smaller* value for b_c implying less “wasted” energy expenditure due to heat loss. Less disease, which works to sap the individual of energy, would work in a similar way. Hence, in our simulations below we will allow b_c to differ across countries and study how this affects the relative timing of the take-off and thereby comparative development, economically and physiologically.

The next step involves solving (6) for N'_{t+1} so as to obtain the number of cells of an adult as a function of the number of cells of a child after weaning and energy intake during childhood, i.e. isolating N'_{t+1} in the equation above. We can further exploit the fact that the mass of a body is simply the mass of a cell \bar{m} times the number of cells. This implies for the size of an adult that $m_{t+1} = \bar{m}N'_{t+1}$. Moreover, using the fact that after weaning the size of a child equals μ times the size of the mother (Charnov, 1991, 1993) we have $\bar{m}N_t = \mu m_t$.¹⁴ This leaves us with:

$$m_{t+1} = \frac{\bar{m}}{e_c} E_t^c + \left(1 - \frac{b_c}{e_c}\right) \mu m_t. \quad (7)$$

The intergenerational law of motion for body size has a simple interpretation: The size of the adult, m_{t+1} is determined by energy consumption during childhood, E_t^c , plus initial size, μm_t , adjusted for energy needs during childhood, $-(b_c/e_c)\mu m_t$.

¹⁴A physiological justification for this assumption is that child development until weaning depends on energy consumption in utero and during the breastfeeding phase. Since larger mothers consume absolutely more energy the offspring should be larger at this point as it receives a fraction thereof. With this interpretation the linearity should be seen as a simplification. It has no substantive implications for our main results if the linearity is relaxed except for reduced tractability.

Given that c_t denotes consumption of a child in terms of goods, total energy intake during childhood is $c_t \cdot \epsilon = E_t^c$, where ϵ converts units of goods into calories. Inserting this into (7) we obtain a law of motion for body size across generations:

$$m_{t+1} = a \cdot \epsilon \cdot c_t + (1 - d) \cdot \mu \cdot m_t, \quad (8)$$

in which a and d are “deep” physiological parameters that are given at the population level and which may differ across populations, as observed above. In particular, we will allow d (implicitly, b_c) to differ: b_c will be assumed to be larger in locations closer to the equator, and smaller in places further away from to the equator where greater cold tolerance is assumed to prevail.

3.5. Individual Optimization. Parents maximize (1) subject to (4) and (5) and non-negativity constraints on all variables. In order to avoid uninteresting case differentiation we assume that $\gamma < 1/2$ such that fertility is always strictly positive (see below). Let λ denote the shadow price of income and – to save notational space let $B_t \equiv B_0 m_t^b / \epsilon$ denote the metabolic needs of a non-fertile adult in terms of goods. The first order conditions for a utility maximum are:

$$0 = (\beta - \lambda) \cdot x_t \quad (9a)$$

$$0 = 1/n_t - \lambda(c_t + e_t - \rho B_t) \quad (9b)$$

$$0 = \gamma/c_t - \lambda n_t \quad (9c)$$

$$0 = \left[\frac{\gamma \nu A_t}{\nu A_t e_t + \bar{h}} - \lambda n_t \right] \cdot e_t. \quad (9d)$$

Depending on the environment the solution is assumed at the interior or at the corner where non-negativity constraints on education or on non-food consumption are binding with equality. These solutions identify a “modern equilibrium”, a “pre-modern equilibrium”, and a “subsistence equilibrium”, respectively.

3.6. Interior Solution: The Modern Equilibrium. The interior solution of (9) is obtained as:

$$n_t = \frac{(1 - 2\gamma)\nu A_t}{\beta(\nu A_t \rho B_t - \bar{h})} \quad (10a)$$

$$c_t = \frac{\gamma(\nu A_t \rho B_t - \bar{h})}{\nu A_t(1 - 2\gamma)} \quad (10b)$$

$$e_t = \frac{\gamma\rho\nu A_t B_t - (1-\gamma)\bar{h}}{(1-2\gamma)\nu A_t} \quad (10c)$$

$$x_t = y - B_t - 1/\beta. \quad (10d)$$

PROPOSITION 1. *At the modern equilibrium, child nutrition, education, and fertility are independent from income. Education and nutrition are increasing functions of knowledge and fertility is a declining function of knowledge. With rising knowledge, education, nutrition, and fertility converge to the constants*

$$e^* = c^* = \frac{\gamma\rho B_0 (m^*)^b}{\epsilon(1-2\gamma)}, \quad n^* = \frac{\epsilon(1-2\gamma)}{\beta\rho B_0 (m^*)^b}$$

and body size converges towards the constant

$$m^* = \left(\frac{a\gamma\rho B_0}{(1-2\gamma)[1-(1-d)\mu]} \right)^{1/(1-b)}.$$

The proof begins with assuming that m_t converges towards a constant m^* and concludes that consumption converges to c^* for $A_t \rightarrow \infty$. Inserting c^* into (8) and solving for the steady state at which $m_{t+1} = m_t$ provides the solution for m^* and verifies the initial assumption that body size is constant. Inspection of (10) provides the results of comparative statics.

A key result here is that education and nutrition are positively correlated. The result is intuitive. When the return on education increases because of increasing knowledge (increasing A_t), parents prefer to spend more on education and substitute child quantity for quality. The lower number of children reduces the total cost of child nutrition, to which parents respond by spending more on nutrition for each child.

Another important result is the trade-off between fertility and body size; since bigger mothers face greater metabolic costs of child rearing, compared to smaller mothers, the result is intuitive. As seen below, this trade-off is obtained in all regimes, though the level of fertility and body size may vary. Empirically, there is strong support to be found in favor of a “size-number trade-off”. Within biology the association is documented in e.g. Charnov and Ernest (2006) and Walker et al. (2008), and in the context of human societies the inverse link between size and number of offspring is documented in e.g. Hagen et al. (2006) and Silventoinen (2003); see Dalgaard and Strulik (2015) for a fuller discussion.

3.7. Corner Solution for Education: The Pre-Modern Equilibrium. The pre-modern era is defined by the feature that there is no education but income is high enough for parents to finance consumption above subsistence level.

PROPOSITION 2. *Parents do not invest in education when the level of knowledge A_t is sufficiently low and thus the return on education is relatively low such that*

$$A_t \leq \bar{A} \equiv \frac{(1 - \gamma)\bar{h}}{\nu\gamma\rho B_t}.$$

The threshold \bar{A} is declining in the weight of child quality in utility (γ), the metabolic needs of adults ($B_t = B_0 m_t^b / \epsilon$), and the productivity of education ν .

The proof solves (10c) for $e_t = 0$. Notice that the threshold is more easily crossed when parents put more weight on child quality or when parents are heavier. The latter result occurs because children of bigger parents are more energy intensive, which causes parents to have fewer children and makes them more inclined to invest in their education.

The solution at the pre-modern equilibrium (i.e. for $x_t > 0$ and $e_t = 0$) are

$$n_t = \frac{1 - \gamma}{\beta\rho B_t} \equiv n^x \tag{11a}$$

$$c_t = \frac{\gamma\rho B_t}{1 - \gamma} \equiv c^x \tag{11b}$$

$$x_t = y - B_t - 1/\beta. \tag{11c}$$

Notice that the child quality-quantity decision is, in contrast to the modern equilibrium, independent from knowledge.

3.8. Corner Solution for Education and Parental Consumption: Subsistence Equilibrium. It seems reasonable that mankind spent most of their history at or close to subsistence.

PROPOSITION 3. *Parents do not spend on non-food (luxury) consumption when*

$$y \leq \bar{y} = B_t - 1/\beta.$$

The threshold \bar{y} is increasing in the metabolic needs of adults.

The proof solves (11c) for $y_t \leq 0$. The result becomes immediately intuitive after noting from (11a) and (11b) that total child expenditure $c_t n_t$ is simply $1/\beta$ at the pre-modern equilibrium.

The solution at the subsistence equilibrium ($e_t = x_t = 0$) is obtained as

$$n_t = \frac{(1 - \gamma)(y_t - B_t)}{\rho B_t} \equiv n^s, \quad (12)$$

and nutrition per child c_t is the same as in (11b).

PROPOSITION 4. *Fertility at the subsistence equilibrium is increasing in income and declining in body size.*

The proof follows from inspection of (12). This result was already obtained and extensively discussed by Dalgaard and Strulik (2015). We next compare fertility and body size at the three equilibria.

PROPOSITION 5. *Fertility is highest at the pre-modern equilibrium and lowest at the modern equilibrium, $n^s \leq n^x \leq n^*$. Body size is the same at the subsistence and pre-modern equilibrium and highest at the modern equilibrium.*

For the proof notice that $n^* < n^x$ because $2\gamma > \gamma$ and that $n^s \leq n^x$ when $1/\beta < y_t - B_t$, i.e. whenever the subsistence constraint binds. For body size notice that $c^* > c^x$ since $(1 - 2\gamma) < 1 - \gamma$ and that steady-state body size is a unique function of childhood nutrition.

In theory there is also the possibility that people take up education before they leave subsistence. In practice we rule this implausible case out by an appropriate choice of parameter values. This implies that there is a unique sequence of macroeconomic development, which we discuss next.

4. MACROECONOMIC DYNAMICS AND STAGES OF DEVELOPMENT

We next place the households into a macro economy. The size of the adult population evolves according to

$$L_{t+1} = n_t L_t. \quad (13)$$

Following conventional unified growth theory (Galor and Weil, 2000, and many other studies), we assume that knowledge creation is a positive function of education and population size. Denoting growth of knowledge by $g_{t+1} = (A_{t+1} - A_t)/A_t$, we thus assume

$$g_{t+1} = g(e_t, L_t) \quad (14)$$

with $\partial g/\partial e_t > 0$, $\partial g/\partial L \geq 0$, $g(0, L_t) > 0$ and $\lim_{L \rightarrow \infty} g(e_t, L_t)$ bounded from above. The assumption that there is technological progress without education, $g(0, L_t) > 0$, makes an escape from the Malthusian trap and the take-off to growth feasible. The assumption that the effect of population size on g is bounded means that there cannot be permanent long-run growth driven by population growth alone. It excludes the empirical unobserved case that technological progress generated by population growth overpowers the depressing effect of limited land such that the pre-modern economy explodes with forever rising population and rising rates of technological progress without the initiation of education.

Suppose that human history begins at a sufficiently low level of A such that both the education constraint and the subsistence constraint are binding initially. Human economic and physiological development then runs through three distinct phases: A Subsistence Regime, a Pre-Modern Era and a Modern Era.

4.1. The Subsistence Regime. When both the subsistence constraint and the education constraint are binding, there is a positive association of income and population growth, see (12). There is also a positive association with the population level and knowledge creation. Malthusian forces in production, however, keep income near the level of subsistence. The economy is at or converges towards a quasi-steady state. To see this formally, begin with inserting nutrition (11b) into (8) and compute the steady state for $m_{t+1} = m_t$:

$$m^s = \left(\frac{a\gamma\rho B_0}{(1-\gamma)[1-(1-d)\mu]} \right)^{1/(1-b)}. \quad (15)$$

Comparing (15) with m^* from Proposition 1 leads to the conclusion:

PROPOSITION 6. *During the Malthusian era, humans are smaller than at the modern steady state.*

The proof utilizes that $1-\gamma > 1-2\gamma$. Notice that the result remains true for the pre-modern era, since nutrition does not change when the economy transits from the Malthusian to the pre-modern era.

It is worth observing from (15) that a smaller value for d implies greater body mass at the steady state. Hence, if, via selection or plasticity and acclimatization, the body shape of people changes to allow for less heat loss, and thereby greater cold tolerance, then the model predicts that such societies will also feature heavier people. In this sense the model suggests that “Allen’s

rule” leads to “Bergmann’s rule”; given changes in body shape, changes in body weight follow (in the long run).

Since nutrition per child is constant during the Malthusian era and no income is spent on non-food (luxury) consumption and on education, all income gains are spent to expand fertility. Observing from (3) that income growth is fueled by knowledge growth and observing from (14) that knowledge growth is solely fueled by the expanding population verifies the following statement:

PROPOSITION 7. During the Malthusian era fertility (population growth) increases with population size, $n_t = f(L_t)$, $f' > 0$.

This phenomenon has been extensively discussed in Kremer (1993).

4.2. The Pre-Modern Era. With output per capita gradually growing the economy eventually surpasses the threshold \bar{y} and people start enjoying utility from non-food (luxury) consumption. Food provision per child remains constant but fertility rises to a higher plateau, see (11). The economy has escaped subsistence, but economic growth is still low since fertility is high and limited land depresses output per capita.

4.3. The Modern Era. With further growing knowledge the economy eventually surpasses the threshold \bar{A} and parents start investing in the education of their children. This has a double effect on economy growth. Education raises the productivity of the current worker generation as well as, through knowledge improvements, the productivity of the next worker generation, which then in turn invests even more in education such that the economy eventually converges to the steady state e^* . Along the transition to the steady state, fertility declines, which reduces the Malthusian pressure and leads to further increasing income. As a result, the economy takes off enjoying accelerating growth rates. Eventually, economic growth stabilizes at a high plateau at the end of the fertility transition when education expenditure has reached its steady state.

With respect to education and fertility the transition to the modern era is similar to the transition established in conventional unified growth theory (e.g. Galor and Weil, 2000). The present model additionally explains the physiological transformation of humans: with the take-off to growth, humans start getting bigger. As explained above, the uptake of education and the entailed reduced fertility make nutrition of children more desirable and, subsequently, the next generation of adults is bigger. The grandchildren are even bigger because there is a double

effect: grandchildren are born bigger because they are conceived by larger mothers, and their parents spend more on nutrition because increasing knowledge makes them prefer child quality in both the education and nutrition dimension. Eventually, however, nutrition and thus body size converges to constants (see Proposition 1).

5. PHYSIOLOGICAL CONSTRAINTS AND COMPARATIVE ECONOMIC DEVELOPMENT

5.1. Analytical Results. Consider a setting where all countries share the same knowledge base. That is, technology is locally determined by population size (and when relevant: education) but the produced ideas spread instantaneously.

Suppose, moreover, that two countries differ in terms of the parameter d , due to natural selection or plasticity and acclimatization. In the subsistence environment this variation will generate differences in body mass and income, as established in Dalgaard and Strulik (2015): In colder environments, average body mass is greater and population density will be lower. To see the latter result more clearly, assume that in pre-historic times the evolution of knowledge was so slow that constant knowledge is a reasonable approximation, $A_t = A$. The pseudo steady state becomes a real steady state at which, from (13), $n_t = 1$. Inserting (15) into (12) and solving $n_t = 1$ for $L_t = L^s$ provides population density

$$L^s = \left(\frac{\epsilon(1-\gamma)A\bar{h}}{B_0[\rho/(2-\gamma)]} \right)^{1-\alpha} \left(\frac{(1-\gamma)(1-d)\mu}{a\gamma\rho} \right)^{\frac{b-\phi}{1-\alpha}}, \quad (16)$$

Observe that lower d increases m^s in (15) and reduces L^s in (16), as long as $b > \phi$. The latter parameter restriction implies that when body mass goes up, subsistence requirements rise faster than food procurement. On empirical grounds $b = 3/4 > \phi < 2/3$, as discussed above. Moreover, as discussed in Dalgaard and Strulik (2015) this parameter restriction ($b > \phi$) is in fact a necessary condition for a subsistence equilibrium to be viable during pre-industrial times.

Now, for our theoretical experiment we consider countries (or areas) that share the same initial fertility and the same technology and all parameter values aside from the one for heat loss, d . We assume that d is lower in country A than in country B. Consequently, humans are bigger in country A, and initial population size (i.e., density) is lower in country A. Inspecting (16) and applying Propositions 2 and 3 then verifies the following result.

PROPOSITION 8. *Consider two countries which are identical aside of the metabolic needs of adults determined by d (heat loss). Then the country with the smaller d*

- *is inhabited by larger individuals*
- *is less densely populated*
- *creates less knowledge in the Malthusian era*
- *and enters the modern era earlier.*

These results reproduce the stylized facts listed in Section 2, when it is further recalled that an earlier take-off will yield an income gap between the two countries if observed at an appropriate point in time after the country inhabited by bigger people has taken off. Moreover, these results are quite intuitive.

Relatively higher metabolic costs of fertility will, in the Malthusian era, work to lower fertility in places inhabited by physiologically bigger people. Furthermore, low population density works to stifle technological change in keeping with the Kremer (1993)–mechanism; more people, more ideas. However, the high metabolic costs of fertility and subsequent nutrition of larger children makes the “heavier country” more inclined to invest in education, and thus to substitute child quantity with quality. As a result, a lower critical level of technology is required for the fertility transition to take place. Consequently, an income gap emerges in favor of the country inhabited by physiologically bigger people.

These results can be illustrated numerically. For that purpose we use the parameterizations suggested in Dalgaard and Strulik (2015). Specifically, we set $b = 3/4$, $B_0 = 70$, $\mu = 0.15$; $\rho = 0.2$, $\epsilon = 0.28$ and, for the benchmark run, $d = 0.5$. We set β and γ such that population growth peaks at 1.5 percent annually and fertility converges to replacement level at the modern steady state. This provides the estimates $\gamma = 0.1$ and $\beta = 0.0053$. We set a such that the body weight at Malthusian times is 60 kg. This provides the estimate $a = 1.65$. Country B (the country closer to the equator) is populated by individuals who share the same parameters except d , which is 0.8. In country B body weight is therefore 49.6 in the subsistence regime. At the economic side of the model we set $\alpha = 0.8$ and $\phi = 0.25$.

In keeping with the theoretical analysis above, we assume all ideas are shared between the two countries, A and B. Concretely, let \tilde{A}_t^j denote the knowledge that has been *created* in country j , $j = A, B$. Knowledge *available* in country j , denoted by A_t^j , is given by

$$A_t^j = \tilde{A}_t^A + \tilde{A}_t^B. \quad (17)$$

Hence, at any given point in time the two countries share ideas; or, equivalently, new ideas diffuse “instantaneously”. In order to facilitate numerical experiments we need to choose a functional form for the creation of knowledge, equation (14). Following Lagerlöf’s (2006) parametrization of the Galor and Weil (2000) model we assume knowledge created in country j grows at rate

$$g_{t+1}^j = \delta(e_t^j + \lambda) \cdot \min \left\{ (L_t^j)^\eta, \Lambda \right\}. \quad (18)$$

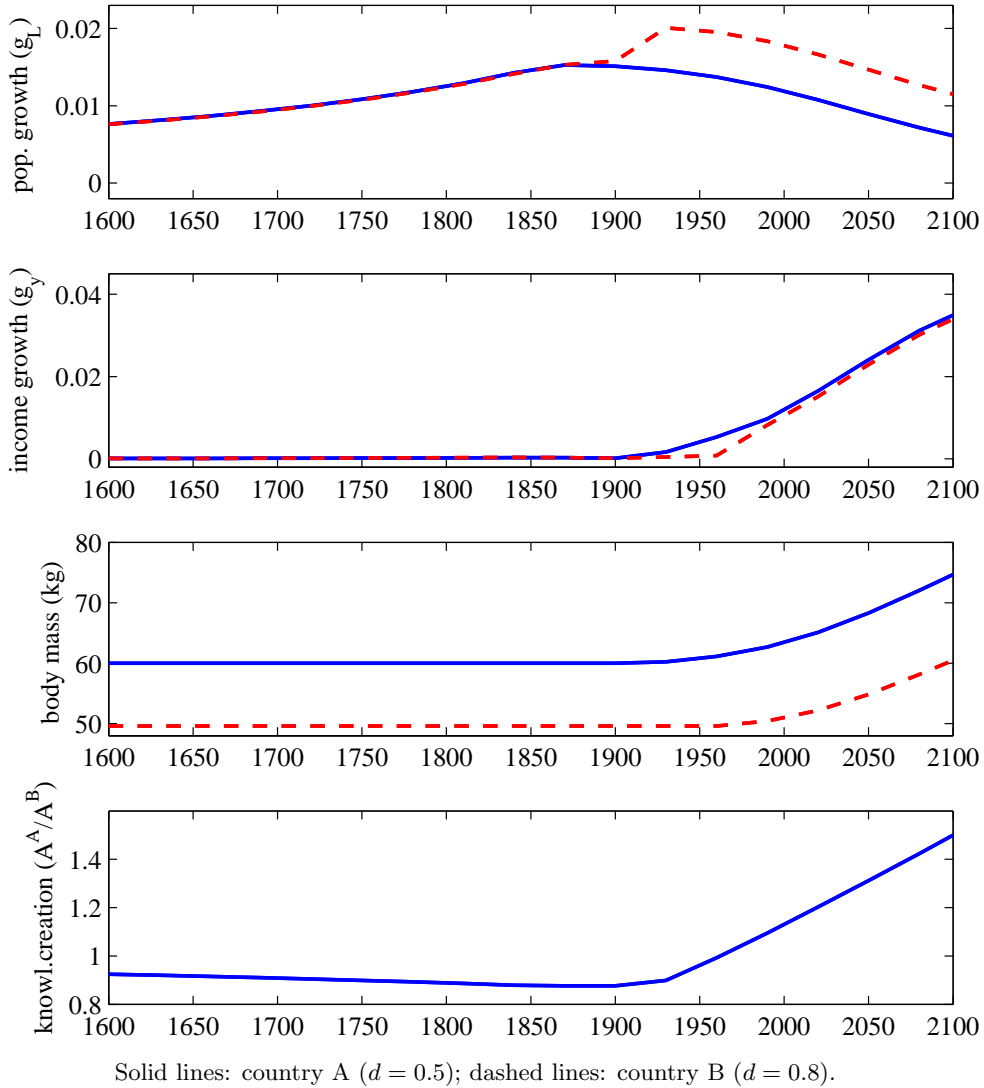
We set the productivity parameters such that the model generates plausible growth rates during the subsistence era, pre-modern era, and modern era. This leads to the estimates $\delta = 0.05$, $\lambda = 0.8$ and $\eta = 0.3$. We set $\Lambda = 2.5$.

Finally, we normalize $\nu = 1$ and $\bar{h} = 1700$ such that country A experiences a century of almost constant high fertility rates before fertility begins to decline. After running the experiment we convert all variables in units per year using a period length of 30 years. We start the economies in the year 1000 and determine the initial population size and technology level such that country A leaves the Malthusian phase in the year 1830. The implied initial fertility rate is 1.106 and the implied population growth rate is 0.34 percent. Country B shares the same initial technology and the same initial fertility rate, which means that it is more densely populated since people are smaller. The implied initial population ratio is $L^B(0)/L^A(0) = 1.42$.

Figure 4 shows the implied trajectories for population growth, income growth, and body mass. Solid lines reflect trajectories of country A and dashed lines show country B. The bottom panel shows the relative stock of technologies invented in country A. The figure starts in the year 1600 because the years before 1600 look very much like 1600 (aside from population growth which is gradually increasing). Both countries share virtually the same population growth rate during the subsistence phase, implying that country B remains more populous and poorer than country A. Because of its larger size, country B produces more innovations; the innovation ratio $A^A/A^B = (L^A/L^B)^\eta$ is around 0.9 during the Malthusian phase and mildly falling.

In the year 1870, country A starts investing in education and initiates the fertility transition. Consequently income growth takes off one period later, when the educated children enter the workforce and contribute to knowledge creation. In country B the take-off takes place two generations later. The technological leadership switches after the take-off of country A and the innovation ratio improves very quickly. In the year 1950 we observe for the first time since the year 1000 that both countries contributed the same to the worldwide stock of knowledge.

Figure 4: Long-Run Comparative Dynamics



From then on country A's relative contribution is increasing rapidly due to its better educated workforce. After the take-off, body weight is gradually increasing and reaches 65 kg in the year 2000.

Country B benefits from the take-off of country A since the newly created knowledge diffuses freely. In country B however, the resulting increasing productivity is initially used predominantly to further expand fertility because the country is still in its subsistence phase and then briefly enters the pre-modern phase. Consequently, population growth rises further and approaches a high plateau in the first half of the 20th century while income growth is improving only very little. Then, in 1930, with two generations delay, country B invests in education and in 1960

income takes off, population growth starts to decline, body size increases, and income growth converges to that of country A.

5.2. Robustness: Gradual Diffusion and Imperfect Knowledge Sharing. The assumption of instantaneous diffusion of ideas is admittedly extreme and “biases” the results in the direction of an early take-off in societies that are inhabited by larger but fewer people. In order to allow for only partial (and in any event: gradual) diffusion of ideas, we replace (17) with

$$A_t^A = \tilde{A}_t^A + \xi \tilde{A}_{t-k}^B, \quad A_t^B = \tilde{A}_t^B + \xi \tilde{A}_{t-k}^A, \quad (19)$$

In the equation above, ξ captures the fraction of ideas that (asymptotically) can be diffused. Hence, $\xi < 1$ means that some ideas are never diffused. Furthermore, the equation above captures that new ideas arrive in the non-innovating countries with a delay of k generations. Aside from these novel elements, we keep the structure of the model unchanged, along with the parameter values discussed above.

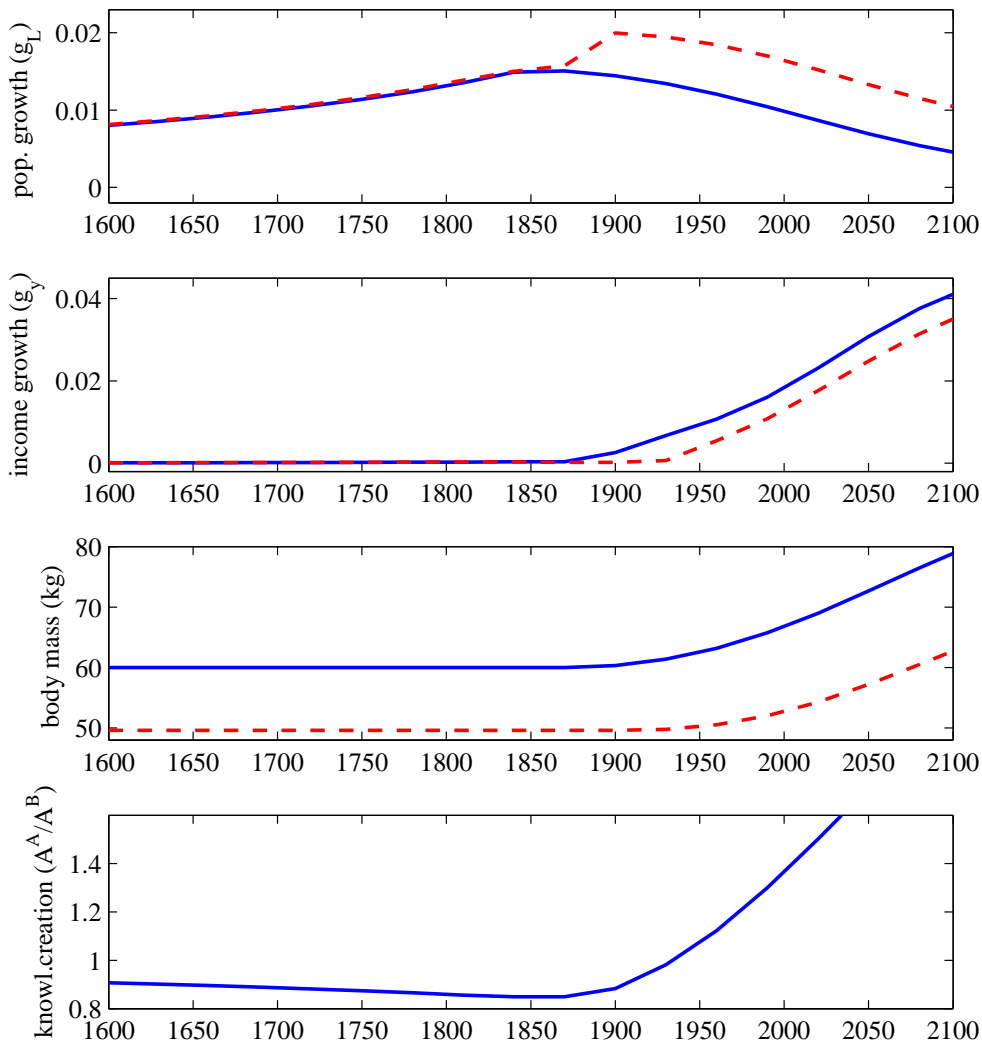
The initial value of technologies available in each country is adjusted such that both countries initially share the same fertility rate (as in the benchmark run). This implies that the initial technologies created in each country are given by $\tilde{A}_0^A = (A_0^A - \xi A_0^B)/(1 - \xi^2)$ and $\tilde{A}_0^B = (A_0^B - \xi A_0^A)/(1 - \xi^2)$. We adjust the initial value of population size such that country A experiences the take-off in 1870 and the outcome is comparable with Figure 4.

Figure 5 shows results for $\xi = 1$ and $k = 2$, i.e. for 60 years delay in international knowledge diffusion. Interestingly and, perhaps, surprisingly, the delayed knowledge flow does not delay the take-off of country B. The reason is, that imperfect knowledge flows operate also during Malthusian times, during which country B is the technological leader. It thus reduces the speed at which country A reaches the threshold \bar{A} . The difference to the development in Figure 4 is mainly that delayed knowledge flows reduce the catch up speed of country B after its take off.

More generally, we can use the model and ask the question: For which delay in international knowledge diffusion does the result of the earlier take-off of country A break down? The results are summarized in Table 4.

If all knowledge is usable in all countries ($\xi = 1$), then country A takes off first up to a diffusion lag of 12 generations (360 years). The maximum diffusion lag, naturally, decreases as we reduce the degree of international knowledge sharing. If only 60 percent of knowledge are transferable internationally, country A takes off for up to a diffusion lag of 5 generations (150 years). If 20

Figure 5: Long-Run Comparative Dynamics: Gradual diffusion of ideas



Parameters as for Figure 4 but knowledge diffuses with a lag: knowledge created in one country at time t reaches the other country at time $t - 2$.

TABLE 4. ROBUSTNESS CHECKS: KNOWLEDGE DIFFUSION

ξ	1	0.8	0.6	0.4	0.2
k	12	9	5	2	—

The table shows for alternative degrees of international knowledge sharing ξ up to which diffusion lag (in terms of generations) the result that the initially backward country A takes off first continues to hold.

percent or less of the knowledge are shared internationally, country A fails to take off earlier. We experimented with different numerical specifications of the model and found generally that country A takes off 1 to 2 generations earlier and that this result is robust against substantial impediments to knowledge diffusion; usually we can allow for 10 or more generations delay

when all knowledge is shared internationally and up to just 50 percent international knowledge sharing when the diffusion delay is 3 generations or less. The theoretical result of the geo-reversal, which we could prove only for perfect knowledge sharing, appears to be robust against substantial imperfections in international knowledge sharing.

6. CONCLUSION

In the present paper we have provided a theory designed to shed light on the remarkable shift in the “latitude gradient” with respect to economic development, which appears to have occurred over the last roughly 500 years. The reversal is observed across the world as well as within continents and even within countries.

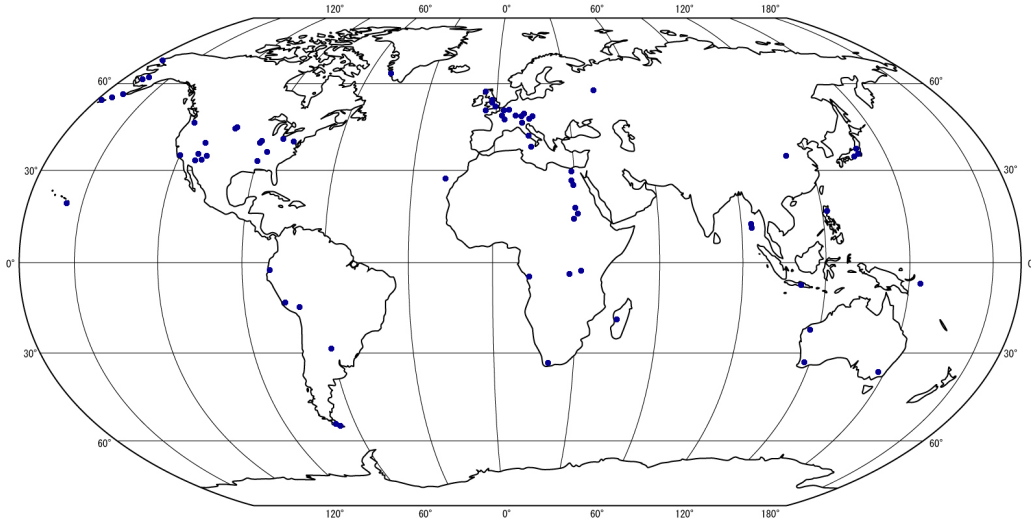
We advance the hypothesis that differences in physiological constraints faced by individuals in different geographical locations can account for the observed reversal. In places where humans were bigger historically the physiological costs of children were greater, leading to low population density early on. However, the relatively high cost of children simultaneously provided a comparative advantage in child quality investments for physiologically bigger parents, which worked to bring forth an earlier take-off. Hence, in the contemporary era historical body size should be positively correlated with economic development. Since average body mass exhibits a clear latitude gradient (Bergmann’s rule) our theory suggests that this physiological mechanism could have been responsible, at least in part, for the changing latitude gradient in the course of history: A negative link between absolute latitude and population density in 1500 C.E. but a positive correlation between distance to the equator and economic development today.

In order to substantiate this hypothesis, we have developed a unified growth model which captures the above elements. Importantly, the model allows us to examine the robustness of the highlighted explanation to an important countervailing mechanism. In historical times it is plausible that more people led to more ideas. This scale effect could work to circumvent the physiological mechanism, thereby allowing the more innovative society inhabited by more but physiologically smaller people to take off earlier. We find, however, that even if knowledge diffusion is gradual, and possibly incomplete, the physiological mechanism is likely to prevail.

In terms of possible extensions of the present study, it is worth observing that the model fully ignores the issue of obesity. While this is surely less of a problem for most of human history, it is clearly an issue for the 21st century. Hence, an interesting extension of the model above

would be to allow for obesity, and thereby potentially gain insights into the consequences of the developed theory for comparative differences in incidence of obesity across the world.

Figure A1: The Goldman data



The figure shows the approximate location of the samples included in the Goldman data set. Source: <http://web.utk.edu/~auerbach/Goldman.htm>

DATA APPENDIX

Pre-industrial body size and shape. The underlying data is taken from the so-called Goldman data set, which is available online at <http://web.utk.edu/~auerbach/GOLD.htm>. As noted above, the data derives from skeletons from different points in time during the Holocene, ranging from as early as 3500 B.C.E to as late as the early Medieval period (ca 1500 C.E.).

The samples are distributed reasonably evenly around the world; cf figure A1. In the data set individual measurements are assigned to a country, and each country observation in our regression data represents the average across available information for each country. The data we employ refers to males, as the number of observations on females in the Goldman data set is more limited.

In order to calibrate body mass (m) we employ the data on femoral head anterior-posterior breadth (FH) and the formula developed by Ruff et al. (1991) (which pertains to males):

$$m = (2.741 \cdot FH - 54.9) \cdot 0.90. \quad (20)$$

Height can also be calibrated in the historical sample by employing the Goldman data on femoral maximum length (FM) and the formula (for males) developed by Genoves (1967):

$$h = 2.26 \cdot FM + 66.379 - 2.5. \quad (21)$$

Other data.

- Country level data on population density in 1500 is taken from Ashraf and Galor (2011).
- The data on the timing of the fertility decline derives from two sources: Reher (2004) and Caldwell and Caldwell (2001).
- The data on (year 2000) urbanization rates are from World Development Indicators (<http://data.worldbank.org/data-catalog/world-development-indicators>)
- data on average years of schooling in 2000. From Barro and Lee (2013)
- Data on GDP per capita in 2000. From Ashraf and Galor (2011)
- .Body size (height) for cohorts born in 1900 and 1995, from NCD Risk Factor Collaboration (2016)
- Absolute latitude from Andersen et al. (2016).
- UV radiation. From Andersen et al. (2016)
- Pixel-level data on Gross cell product per capita: Real (PPP 1995 USD) gross product per capita, cell of 1-degree latitude by 1-degree longitude, constructed with data from GEcon Yale data version 3.4, available at <http://gecon.yale.edu>.
- Data on population density in 1500 C.E., cell of 1-degree latitude by 1-degree longitude. Based on the Hyde database, version 3.1 (Klein Goldewijk et al., 2010, 2011).
- Language fixed effects. From Andersen et al. (2016)

REFERENCES

- Acemoglu, D., S. Johnson, and J.A. Robinson, 2002. Reversal of fortune: geography and institutions in the making of the modern world income distribution. *Quarterly Journal of Economics* 117, 1231–1294.
- Aiyar S., C-J. Dalgaard and O. Moav, 2008. Technological Progress and Regress in Pre-industrial Times. *Journal of Economic Growth* 13, p. 125-44.
- Andersen, T.B., C-J. Dalgaard, and P. Selaya, 2016. Climate and the Emergence of Global Income differences. *Review of Economic Studies* 83, p. 1334–63.
- Ashraf, Q, and O. Galor, 2011. Dynamics and stagnation in the Malthusian epoch. *American Economic Review* 101, 2003-2041.
- Astrand, P.O. and Rodahl, K., 1970. Body dimensions and muscular work, in: P.O. Astrand and K. Rodahl (eds.) *Textbook of Work Physiology*, McGraw-Hill, New York, 321-39.

- Auerbach BM and C.B. Ruff CB, 2004. Human body mass estimation: a comparison of “morphometric” and “mechanical” methods. *American Journal of Physical Anthropology* 125, 331–342.
- Barro, Robert and Jong-Wha Lee, 2013, ”A New Data Set of Educational Attainment in the World, 1950-2010. *Journal of Development Economics*, vol 104, pp.184-198.
- Becker G., 1960. An economic analysis of fertility. In: *Demographic and economic change in developed countries*. Conference of the Universities-National Bureau Committee for Economic Research, a Report of the National Bureau of Economic Research. Princeton University Press, Princeton, NJ, pp 209-240
- Bergmann, C., 1847. Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. *Göttinger Studien* 3, 595-708.
- Betti, L. and N.V. Cramon-Taubadel, and S. Lycett, 2012. Human pelvis and long bones reveal differential preservation of ancient population history and migration out of Africa. *Human Biology*, 84, 139–152.
- Caldwell, J. and P. Caldwell, 2001. Regional paths to fertility transition. *Journal of Population Research* 18, 91–117.
- Cervellati M. and U. Sunde, 2005. Human capital formation, life expectancy, and the process of development. *American Economic Review* 95, 1653-1672.
- Cervellati, M. and U. Sunde, 2015. The economic and demographic transition, mortality, and comparative Development. *American Economic Journal: Macroeconomics* 7, 198–225.
- Charnov, E.L., 1991. Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences of the United States of America* 88, 1134-1137.
- Charnov, E.L., 1993, *Life History Invariants*, Oxford University Press, Oxford.
- Charnov, E.L. and S.K.M. Ernest, 2006. The offspring - size / clutch - size trade-off in mammals. *The American Naturalist* 167, 578-82.
- Dalgaard, C-J. and H. Strulik, 2013. The history augmented Solow model. *European Economic Review* 63, 134–49
- Dalgaard, C-J. and H. Strulik, 2015. The physiological foundation of the wealth of nations. *Journal of Economic Growth* 20, 37-73.
- Dalgaard, C-J. and H. Strulik, 2016. Physiology and development: Why the West is taller than the rest. *Economic Journal* 126, 2292–2323.
- Dalgaard, C-J., A.S. Knudsen and Pablo Selaya, 2016. The Bounty of the Sea and Long-Run Development. Mimeo (University of Copenhagen)
- De la Croix, D., O. Licandro, 2013. The child is father of the man: Implications for the demographic transition. *Economic Journal* 123, 236-261.

- Galor, O., 2010. The 2008 Lawrence R. Klein Lecture - Comparative development: Insights from unified growth theory. *International Economic Review* 51, 1-44.
- Galor, O. and D. Weil, 2000. Population, technology and growth: From Malthusian stagnation to the demographic transition and beyond. *American Economic Review* 90, 806-828.
- Galor, O., and O. Moav, 2002. Natural selection and the origin of economic growth. *Quarterly Journal of Economics* 117, 1133-1191
- Genoves, S., 1967. Proportionality of the long bones and their relation to stature among Mesoamericans. *American Journal of Physical Anthropology* 26, 67-77.
- Goldewijk, K. K. , A. Beusen, M. de Vos and G. van Drecht (2011). The HYDE 3.1 spatially explicit database of human induced land use change over the past 12,000 years, *Global Ecology and Biogeography* 20(1): 73-86
- Goldewijk, K. K. , A. Beusen, and P. Janssen (2010). Long term dynamic modeling of global population and built-up area in a spatially explicit way, HYDE 3 .1, *The Holocene* 20(4): 565-573.
- Gustafsson, A. and Lindenfors, P., 2009. Latitudinal patterns in human stature and sexual stature dimorphism. *Annals of Human Biology* 36, 74-87.
- Hancock, A.M., V.J Clark, Y. Qian and A. Di Rienzo, 2010. Population genetic analysis of the uncoupling proteins supports a role for UCP3 in human cold resistance. *Molecular Biology and Evolution* 28, 601-14.
- Hagen, E.H., H.C. Barrett, and M.E. Price, 2006, Do human parents face a quality-quantity tradeoff? Evidence from a Shuar Community, *American Journal of Physical Anthropology* 130, 405-418.
- James, G.D., 2010. Climate-related morphological variation and physiological adaptations in homo sapiens. In: Larsen, C.S. (eds.): *A Companion to Biological Anthropology*. Blackwell Publishing.
- Kaplan, H., 1996. A theory of fertility and parental investment in traditional and modern human societies. *American Journal of Physical Anthropology* 101, 91-135.
- Katzmarzyk, P.T. and Leonard, W.R., 1998, Climatic influences on human body size and proportions: ecological adaptations and secular trends, *American Journal of Physical Anthropology* 106, 483-503.
- Kelly, M., Mokyr, J., and O'Grada, C., 2015. Roots of the Industrial Revolution. Mimeo (University College Dublin)
- Kleiber, M., 1932, Body size and metabolism, *Hilgardia* 6, 315-353.
- Kremer, M., 1993. Population growth and technological change: One million B.C. to 1900. *Quarterly Journal of Economics* 108, 681-716.

- Lagerlöf, N., 2006. The Galor–Weil model revisited: A quantitative exercise. *Review of Economic Dynamics* 9, 116–142.
- Litina, A., 2016. Natural Land productivity, Cooperation and Comparative Development. *Journal of Economic Growth*, 21, 351–408
- Lucas, R.E. Jr., 2002, The industrial revolution: Past and future, in: Lucas, R.E. Jr., *Lectures on Economic Growth*, Cambridge, Massachusetts: Harvard University Press.
- NCD Risk Factor Collaboration (NCD-RisC), Bjerregaard, P., Bugge, A., Christensen, K., Eriksen, L., Grntved, A.; Moeller, Niels Christian; Tarp, Jakob; Tolstrup, J. S. (2016). A century of trends in adult human height. *eLife*, 5, [e13410]. DOI:10.7554/eLife.13410
- Markovic, G., and S. Jaric, 2004. Movement performance and body size: the relationship for different group of tests. *European Journal of Applied Physiology* 92, 139-49.
- Michalopoulos, S., and Papaioannou, E. (2013). Pre-Colonial Ethnic Institutions and Contemporary African Development. *Econometrica*, 81(1), 113-152.
- Olsson, O. and C. Paik, 2016a. A Western Reversal Since the Neolithic? The Long-Run impact of Early Agriculture. Mimeo (University of Gothenburg)
- Olsson, O. and C. Paik, 2016b. Long-Run cultural divergence: Evidence from the Neolithic. *Journal of Development Economics* 122, 197–213.
- Putterman, L. and D.N. Weil, 2010. Post-1500 Population Flows and the Long Run Determinants of Economic Growth and Inequality. *Quarterly Journal of Economics* 125, pp. 1627–82.
- Reher, D.S., 2004. The demographic transition revisited as a global process. *Population Space and Place* 10, 19–42.
- Roberts, D.F., 1978. *Climate and human variability*, Cummings Publishing Company.
- Ruff, C.B., W. W. Scott, and A. Liu, Allie, 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *American Journal of Physical Anthropology* 86, 397–413.
- Ruff, C.B., 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbook of Physical Anthropology* 37, 65–107
- Silventoinen, K., 2003, Determinants of variation in adult body height, *Journal of Biosocial Science* 35, 263-285.
- Strulik, H. and J. Weisdorf, 2008. Population, food, and knowledge: a simple unified growth theory, *Journal of Economic Growth* 13, 195–216.
- Tabellini, G. (2010). Culture and institutions: economic development in the regions of Europe. *Journal of the European Economic Association*, 8(4), 677-716.
- Walker R., M. Gurven, O. Burger and M.J. Hamilton, 2008, The trade-off between number and size of offspring in humans and other primates, *Proceedings of the Royal Society* 275, 827-33.

West G.B., J. H. Brown and B.J. Enquist, 2001. A general model of ontogenetic growth. *Nature* 413, 628-31.

Table 1. Historical latitude gradient

VARIABLES	(1)	(2)	(3)	(4)
	Population 1500 CE (log)			
Absolute latitude	-0.089*** (0.001)	-0.094*** (0.003)	-0.282*** (0.009)	-0.199*** (0.012)
Area (log)	0.482*** (0.021)	0.730*** (0.018)	0.467*** (0.044)	0.912*** (0.040)
Sample	World	World	Europe	Europe
Country FE's	No	Yes	No	Yes
Observations	20,049	20,049	4,738	4,738
R-squared	0.262	0.602	0.449	0.594

Table 2. Contemporaneous Latitude Gradient

Panel A: World Sample

VARIABLES	(1)	(2)	(3)	(4)	(5)
	Gross cell product per capita, 2000 (log)				
Absolute Latitude	0.030*** (0.000)	0.017*** (0.001)	0.016*** (0.000)	0.014*** (0.000)	0.011*** (0.001)
UV-R		-0.003*** (0.000)			-0.001*** (0.000)
Country FE's	No	No	Yes	No	Yes
Language FE's	No	No	No	Yes	Yes
Observations	17,379	17,373	17,379	17,379	17,373
R-squared	0.372	0.379	0.921	0.925	0.934

Panel B: European Sample

VARIABLES	(1)	(2)	(3)	(4)	(5)
	Gross cell product per capita, 2000 (log)				
Absolute latitude	0.025*** (0.000)	0.022*** (0.003)	0.034*** (0.001)	0.028*** (0.001)	0.028*** (0.001)
UV-R		-0.001 (0.001)			
Country FE's	No	No	Yes	No	Yes
Language FE's	No	No	No	Yes	Yes
Observations	4,521	4,516	4,521	4,521	4,521
R-squared	0.153	0.153	0.685	0.716	0.719

Robust standard errors in parentheses; *** p<0.01, ** p<0.05, * p<0.1

Table 3. Bergman's rule: Historically and contemporaneously

VARIABLES	(1) Weight (pre 1500)	(2) Height (pre 1500)	(3) World	(4) World	(5) Pnative>.9	(6) Europe	(7) World	(8) World	(9) Pnative>.9	(10) Europe
Absolute latitude	0.176*** (0.051)	0.074* (0.038)	0.151*** (0.014)	0.160*** (0.021)	0.138*** (0.025)	0.259*** (0.045)	0.248*** (0.013)	0.178*** (0.018)	0.175*** (0.026)	0.140*** (0.042)
Sample	.	.	World	World	Pnative>.9	Europe	World	World	Pnative>.9	Europe
Continent FE's	No	No	No	Yes	Yes	.	No	Yes	Yes	.
Observations	24	24	154	154	79	36	154	154	79	36
R-squared	0.371	0.129	0.416	0.684	0.707	0.552	0.635	0.744	0.814	0.252

Robust standard errors in parentheses; *** p<0.01, ** p<0.05, * p<0.1

Figure 4. Body size and the timing of the fertility transition

Panel A: Rehrer's data

VARIABLES	(1)	(2)	(3)	(4)	(5)
	Year of transition				
Height (1900)			-4.107*** (0.652)	-2.574*** (0.473)	-3.406** (1.569)
Weight (pre 1500)	-4.555*** (0.623)				
Height (pre-1500)		-3.933** (1.489)			
Continental FE's	.	.	No	Yes	.
Sample	.	.	World	World	Europe
Observations	21	21	128	128	17
R-squared	0.517	0.234	0.277	0.741	0.306

Robust standard errors in parentheses; *** p<0.01, ** p<0.05, * p<0.1

Panel B: Caldwell and Caldwell's data

VARIABLES	(6)	(7)	(8)	(9)	(10)
	Year of transition				
Height (1900)			-4.764*** (0.742)	-1.958*** (0.745)	-2.897* (1.386)
Weight (pre 1500)	-6.007*** (0.975)				
Height (pre-1500)		-5.765** (2.485)			
Continental FE's	.	.	No	Yes	.
Sample	.	.	World	World	Europe
Observations	20	20	104	104	21
R-squared	0.395	0.211	0.332	0.658	0.090

Robust standard errors in parentheses; *** p<0.01, ** p<0.05, * p<0.1

Table 5. Historical body size and economic development in 2000 CE

VARIABLES	(1)	(2)	(3)	(4)	(5)
	GDP per capita (log)				
Height (1900)			0.096*** (0.019)	0.074*** (0.021)	0.038 (0.035)
Weight (pre 1500)	0.139*** (0.033)				
Height (pre 1500)		0.086 (0.082)			
Sample	.	.	World	World	Europe
Continent FE's	No	No	No	Yes	.
Observations	24	24	181	181	37
R-squared	0.302	0.059	0.105	0.432	0.023
	Urbanization (log)				
	(6)	(7)	(8)	(9)	(10)
Height (1900)			0.027*** (0.009)	0.025** (0.011)	0.022* (0.012)
Weight (pre 1500)	0.052*** (0.014)				
Height (pre 1500)		0.011 (0.023)			
Sample	.	.	World	World	Europe
Continent FE's	No	No	No	Yes	.
Observations	24	24	189	186	40
R-squared	0.320	0.007	0.041	0.247	0.086
	Years of schooling				
	(11)	(12)	(13)	(14)	(15)
Height (1900)			0.310*** (0.040)	0.273*** (0.057)	0.168*** (0.047)
Weight (pre 1500)	0.198*** (0.069)				
Height (pre 1500)		0.077 (0.155)			
Sample	.	.	World	World	Europe
Continent FE's	No	No	No	Yes	.
Observations	22	22	135	135	34
R-squared	0.171	0.015	0.250	0.577	0.243

Robust standard errors in parentheses; *** p<0.01, ** p<0.05, * p<0.1