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# The Physiological Foundations of the Wealth of Nations\*

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**Abstract.** Evidence from economics, anthropology and biology testifies to a fundamental trade-off between the number of offspring (quantity) and amount of nutrition per child (quality). This leads to a theory of pre-industrial growth where body size as well as population size is endogenous. But when productive quality investments are undertaken the historical constancy of income per capita seems puzzling. Why didn't episodes of rising income instigate a virtuous circle of rising body size and productivity? To address this question we propose that societies are subject to a "physiological check": if human body size rises, metabolic needs - our conceptualization of "subsistence requirements" - rise. This mechanism turns out to be instrumental in explaining why income growth does not take hold and societies remain near an endogenously determined subsistence boundary. When we use the theory to shed light on pre-industrial cross-country income differences we find that 60-70% of the income differences in 1500 can plausibly be accounted for by variations in subsistence requirements.

*Keywords:* Malthusian stagnation, Subsistence, Nutrition, Body size, Population growth.

*JEL:* O11, I12, J13.

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## 1. INTRODUCTION

It is increasingly recognized that the dynamic forces which shaped the “Malthusian epoch” are key factors in explaining the transition to sustained growth and thus in explaining contemporary income differences. Still, important aspects of the pre-industrial growth record remain ill understood. In particular, existing theories ignore the dynamics of human body size and its links to population dynamics and average living standards. This state of affairs is problematic in two related respects.

First, ignoring body size prevents a full understanding of the forces that engendered stagnating income per capita levels during most of human history. Evidence surveyed below strongly suggest that societies throughout history faced a fundamental body size-number trade-off; a trade-off involving how many children to bear, and how well to feed each of them. This evidence indicates that episodes of rising income should have instigated intensified investments in offspring body size (in addition to child quantity). But in this case the standard Malthusian positive check may not suffice to bring the growth process to a halt as the tendency for diminishing returns to labor input would be counterbalanced by body size induced productivity gains.<sup>1</sup> If so, what (other) mechanisms contributed to the observed long-run constancy of income per capita prior to the take-off? Why did episodes of technological change fail to ignite a virtuous circle of rising body size and income? By ignoring the dynamics of human body size during the Malthusian epoch the existing literature is incapable of addressing these central issues.

Second, by ignoring body size the existing literature is largely silent about the determination of the level of income per capita during Malthusian times: “the level of subsistence”. Biologically subsistence requirements are inescapably linked to the size of the human body; bigger bodies are more energy requiring. Without an adequate theory of the long-run determination of human body size, the determinants of subsistence remain obscure, and predictions about comparative income differences across pre-industrial societies becomes untenable. As a consequence the existing literature is incapable of fully describing the economic circumstances prevailing prior to industrialization.

The present paper proposes a theory of long-run growth where body size as well as “subsistence requirements” are endogenously determined. Families face a trade-off between how many

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<sup>1</sup>See e.g., Fogel (1994, 1997), Behrmann and Rosenzweig (2004) and Weil (2007) for evidence on the positive link between body size and labor productivity.

children to have and how well to feed each of them. At the same time they are constrained by income and metabolic consumption requirements. A positive shock to income will induce households to expand fertility and nutritional investments in their children. However, in the following period a “physiological check” sets in: adults of the next generation are larger and as such more energy requiring. This limits fertility and nutritional investments per child, and serves to equilibrate the economy. As a result, the economy remains in a state of stagnation even though households invest in child quality.<sup>2</sup>

Subsistence requirements of adults are endogenously determined in the model and turn out to be affected by genetic factors, preferences, as well as the cost structure of child rearing. To get a sense of magnitudes we use data on body size from contemporary hunter-gatherer societies and less developed economies, which we use to calibrate subsistence requirements. Since income per capita, according to the proposed theory, is linked to the level of subsistence this exercise allows us to gauge the sources of pre-industrial cross-country income variation. According to Maddison’s (2003) data income per capita varied by a factor of 2 in 1500. We find that variation in adult subsistence requirements may plausibly have accounted for 60-70% of those differences. This finding goes a long way towards reconciling the notion that pre-industrial societies were “stuck” at the level of subsistence with the fact that per capita income levels exhibited non-trivial cross-country variation in 1500.

The differential timing of the take-off to sustained growth has helped shape the current global distribution of per capita income (Galor, 2006, 2009; Lucas, 2000). Yet in order to understand the timing and speed of the transition, it is necessary to fully understand the country specific economic circumstances that prevailed at the time of the take-off. The present paper proposes a theory of how key preconditions were formed and how they varied at the eve of the industrial revolution.

The model features overlapping generations. Individuals live for two periods; childhood and adulthood. Children are passive recipients of nutrition, determined by the parent, who is the economically active agent; we ignore matching in the marriage market and allow agents to reproduce asexually. The economic components of the model are fairly standard. A unique output good is produced using body size augmented labor, land, and technology; since we are

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<sup>2</sup>Much like Malthus’ positive check, we view the physiological check as fundamental in the sense that its relevance extends beyond the human species. Malthus’ also proposed a “preventive check”, which he argued was uniquely human.

focusing on pre-industrial times, technology is assumed to be parametrically fixed, and land is also a fixed factor of production. Accordingly, diminishing returns to labor input prevail. Aside from this the theory builds on three novel elements.

First, parents derive utility from quantity and quality (nutrition) of children. Both quality and quantity are normal goods; preferences are homothetic. Second, the metabolic rate of the parent, our conceptualization of “subsistence”, is increasing in both body size and fertility. The parent is required in each period to cover these needs. Whereas body size is predetermined at the time of optimization, fertility is a control variable. Theory and empirical evidence from biology provide this important “bio-economic” constraint, right down to the functional form and its parameters. The substantive implication of the constraint is that if the number of children is expanded, the parent will need to consume more for herself, leaving less resources for quality investments in the offspring. Taken together these two elements generate a natural size-number trade-off which is strongly supported by empirical evidence reviewed below. The third element is the law of motion for body size, which we derive from first principles, starting at the cellular level. The substantive implication of it is that more nutrition during childhood leads to larger adults.

These elements interact in the following way. A positive productivity shock will induce parents to have more children and invest in more nutrition per child. The better nourished children will grow up to be larger adults than their parents. However, their elevated body size implies that they will be more energy requiring adults. This prevents them from providing the same amount of nutrition per child that their parents provided, even if their productivity and income is the same as that of their parents. Thus the increase in body size is “checked” by rising metabolic needs, which puts downward pressure on nutritional investments as well as expenditure on family size. Consequently growth does not take hold, and the economy remains in a state of stagnation. The new steady-state is characterized by unaltered body size, constant income per capita, and a higher population density.

The model is able to shed light on a series of historical events that hitherto has been left unexplained. Recent research has documented that population size responded to changes in the technological environment in preindustrial times; technological progress prompted higher population density (e.g., Baker, 2008). Similarly, in the centuries following a major innovation of the diet - the introduction of the potato - population density rose as a consequence (Mokyr,

1981; Nunn and Qian, 2008). At the same time, however, historians have documented that average height of Europeans exhibited no significant trend over the two millennia preceding the take-off into sustained growth (Kunitz, 1987; Koepke and Baten, 2005a). But why would improvements in the living conditions of the European population not instigate greater body size in addition to population density? The theory provides an answer; the physiological check on households served, across generations, to bring down nutritional investments in children thus limiting average body size. Temporary increases in body size gradually eroded, while temporary increases in fertility served to elevate population density on a persistent basis. While productivity gains do not raise body size in the long run, human body size nevertheless remains a good marker of income per capita.

In the aftermath of the Neolithic revolution puzzling demo-economic events took place. By all accounts, the shift to sedentary agriculture was associated with rising working hours and population density. Meanwhile, however, average stature declined. We argue that a central difference between hunter-gathering and the agrarian lifestyle lies in the non-metabolic costs of children. As a matter of comparative statics, the model predicts that body size should fall and population density rise, contingent on declining time costs of children. This result is robust to the simultaneous emergence of higher productivity in the wake of the Neolithic revolution. That is, even if agriculture brought permanently higher levels of productivity (e.g, Diamond, 1997) the central comparative static with regards to stature remains intact.

The model also sheds light on seemingly puzzling differences between historical and contemporary patterns of comparative development. It is a well known regularity that prosperity today tends to be higher in areas further away from the equator (e.g., Ram, 1997). Yet, in pre-industrial times this configuration would seem to have been reversed. Examining the Malthusian model empirically Ashraf and Galor (2008) document that population density in 1500 seems to *decline* in the distance from the equator, conditional on other relevant controls. This would suggest that productivity during Malthusian times was higher near the equator. However, an alternative interpretation can be advanced on the basis of the model we develop below: distance from the equator may be capturing the influence from average body size. While the model does not articulate evolutionary processes it is capable of capturing the consequences of selective pressures that may have been at play in a more distant past. We show that in societies where citizens are selected to limit heat loss, as would be relevant in cooler climates further away from the equator,

average body size would be larger and population density lower. Hence, the historical latitude gradient vis-a-vis population density may reflect these climate related evolutionary pressures.

The present paper is related to the literature on growth in the very long run, which models Malthusian stagnation and the transition to modern growth (e.g., Galor and Weil, 2000; Galor and Moav, 2002; Lucas, 2002; Hansen and Prescott, 2002; see Galor, 2006 for a survey). These theories focus on the intricate and changing relationship between income and population during long-run development, and provide a theoretical explanation for the emergence of sustained growth. In contrast to the present paper, however, these studies ignore the evolution of body size, and assume the level of subsistence consumption is exogenous (if introduced at all).

The paper is also related to the anthropometric history literature, where height and fertility has been discussed in a unifying way. Weir (1993), in particular, provides a perspective on the quality-quantity trade-off that is similar to ours, and uses it to conceptually motivate an empirical analysis of the impact from the French fertility transition on height developments.

More broadly, the anthropometric literature has long observed a link between changes in body size and movements in fertility, since nutrition during childhood influences not only adult stature but may also have a direct effect on fertility. For example, the age of menarche is reached earlier within well fed populations. A careful discussion is found in Komlos (1989), analyzing the period of take-off in the Habsburg Monarchy.

The paper proceeds as follows. In Section 2 we survey evidence on the quantity-quality trade-off between fertility and body size. Section 3 develops the model. Section 4 proves existence and stability of the steady-state equilibrium and provides a series of comparative static results. Section 5 discusses comparative dynamics. Section 6 accounts for the wealth of nations in 1500, and Section 7 concludes.

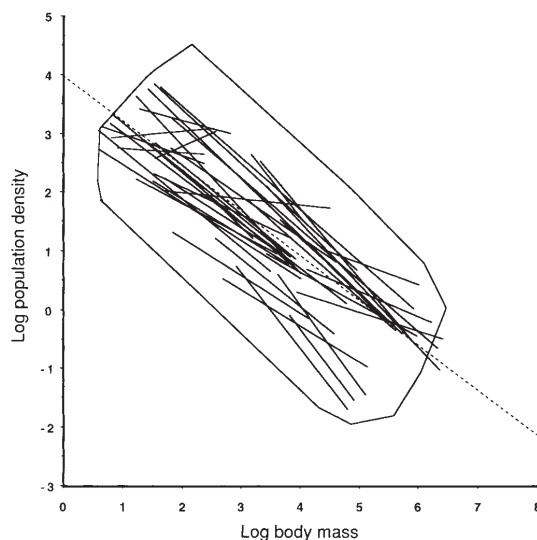
## 2. SIZE VERSUS NUMBER OF OFF-SPRING: A QUANTITY-QUALITY TRADE-OFF

In this section we review evidence from biology, anthropology and economics which strongly suggest an operative quantity-quality trade-off between body size and family size. The important implication is that families throughout history have made quality investments, in the sense of nutrition. Periods of plenty would therefore imply an expanding number and size of people, which challenges the sufficiency of Malthus' positive check in equilibrating the economy.

Convincing evidence in favor of a quantity-quality trade-off is found in biology. At the level of the individual mammalian species, the inverse association between body size and rate of reproduction is by now well documented (Charnov and Ernest, 2006; Walker et al., 2008). Indeed, experimental studies manipulating offspring number or environment exist, which document the trade-off (Roff, 2002).

A manifestation of this quantity-quality trade-off, at the more aggregate level, is found in “Damuth’s law”, which involves a negative correlation between body size and population density (Damuth, 1981; 1993). Figure 1, taken from Damuth (1993), provides an impression of the strength and pervasiveness of the correlation.

Figure 1: Population density (log) vs. Mass (log): 557 Mammalian Species



Notes. Dotted line: Full sample. Other lines: Species divided by feeding guilds, habitat and geo-zones. Estimates by OLS.

As seen from the figure, within essentially all of the 557 mammalian species the negative correlation is found. While the position and slope of the line is somewhat species dependent, and varies across geo-zones as well, the overall negative association is visually obvious. Moreover, the coefficient on (log) body size, as reflected in the dotted “trend” line in the figure, is  $-3/4$ . Hence, Damuth’s law, for a varied sample of species, can be stated  $L/X = \text{constant} \cdot m^{-3/4}$ , where  $L/X$  is population density, and  $m$  is body size (measured in kilograms).<sup>3</sup>

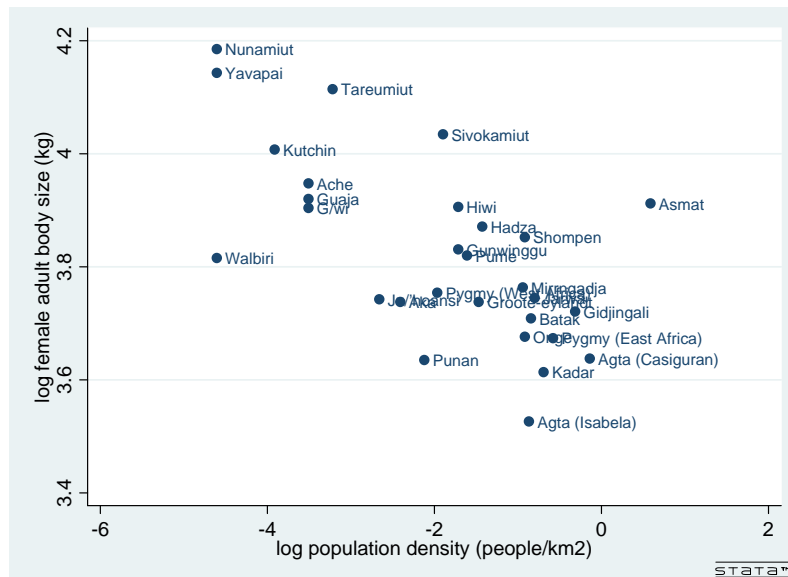
<sup>3</sup>See Brown et al. (2004) for a survey of the empirical literature.



In the context of human populations micro evidence of the size-number trade-off is also available. In subsistence societies the inverse association between family size and size of the offspring has received support by the work of Hagen et al. (2006), who examine the trade-off in the “Shuar” society, which resides in the tropical rainforests of Ecuador. Similarly, Walker et al. (2008) demonstrate a negative link between body size and family size across a sample of 16 subsistence-based societies.<sup>4</sup>

At a higher level of aggregation Figure 2 depicts the correlation between population density and average female body weight for 29 hunter-gatherer societies. Consistent with Damuth’s law the correlation is visibly negative; in more densely populated societies individuals are smaller.

Figure 2: Population Density (log) vs. Mass (log): 29 Hunter-Gatherer Societies



Notes. Data source: Walker and Hamilton (2008).

The most natural interpretation of Damuth’s law is as a manifestation of a very basic form of a quality-quantity trade-off: the division of resources between nutrition per child and number of offspring.<sup>5</sup> In micro data the trade-off should manifest itself as an inverse association between body size of siblings, and the size of the family. Moreover, since nutrition during childhood inevitably affects adult body size, and investments in the quantity of children will work so as to raise population size, one would expect to see an inverse association between body size and population density (at least, conditional on resource availability).

<sup>4</sup>See Cole (2000) and Silventoinen (2003) as well.

<sup>5</sup>This is indeed the interpretation in biology. See e.g., Smith and Fretwell (1974), Charnov and Ernest (2006).

From the perspective of the present study the evidence amassed by biologists and anthropologists is of substantive importance, since it makes plausible that the size-number trade-off is a fundamental one. The systematic link between reproduction and body size in economically primitive societies suggests that the trade-off must have been active for a very long time; certainly before the take-off to sustained growth occurred in Western Europe. As a consequence, temporary income gains should be expected to translate into greater nutritional expenditure on children, implying “quality” investments. The fact that the trade-off transcends the human species implies that the mechanism responsible for it must be generic; the “physiological check”, much like Malthus’ positive check, fulfills this criteria.

In post-industrial societies evidence of the trade-off is found as well. In an early contribution Douglas and Simpson (1964) examined the results from a national survey of health and development in the UK. Specifically, the survey focused on 1,557 boys and 1,456 girls born in 1946. The physical development of these children was tracked and central health indicators were collected, including height, date of entry into puberty and age of menarche. In addition socio-economic indicators for the households were obtained, including occupation and educational background of the parents. This enabled Douglas and Simpson to categorize the families into social classes, ranging from “lower manual” to “upper middle”.<sup>6</sup> Figure 3 shows the association between the mean body size of girls at age of 7 and the number of siblings in the family, as reported by Douglas and Simpson.<sup>7</sup>

The general pattern that emerges is one where a large family size is associated with smaller mean body size of the offspring. In addition, for the size of the family given, the average body size of the offspring, measured by height, generally increases as the socio-economic circumstances improve. Douglas and Simpson document that similar patterns persist to the ages of 11 and 15 for both boys and girls.

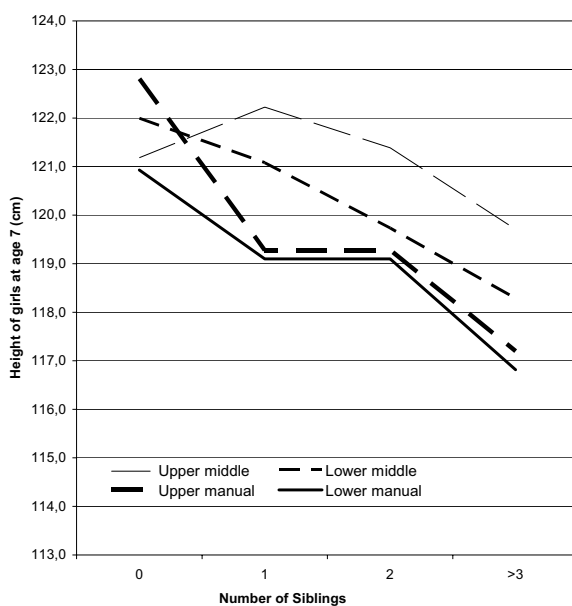
The 1946 cohort has more recently been analyzed by Kuh and Wadsworth (1989). Their regression based analysis confirms the general impression conveyed by Figure 3; conditional on

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<sup>6</sup>In the “upper middle class” we find parents with a secondary education, families where the father has a non-manual occupation, and where at least one of the parents was brought up in a middle class family with similar characteristics. In contrast, the “lower manual” group is characterized by the father being a manual laborer, by both parents only having primary education, and by upbringing; both parents were raised in a working-class family. Between these two extremes we find the “lower middle class” and “upper manual class”; these groups are differentiated from “upper middle class” and “lower manual class” mainly by their educational attainment.

<sup>7</sup>The picture for boys is very similar.

Figure 3. Body Size of UK Girls at Age 7 and the Number of Siblings



Notes. The individual lines refer to individual social classes, as defined in the text. Data source: Douglas and Simpson (1964), Table 7.

a host of environmental factors, each additional sibling implies a reduction in mean height of about 6 mm.

At a higher level of aggregation Weir (1993) demonstrates a strong negative association between height and fertility rates across regions in France during the period 1840-1911. Following up on Weir’s findings, Schneider (1996) documents similar patterns across nine European countries, covering the period 1750-1920. Controls for health and income do not overturn these findings.

In light of this evidence it is of interest to inquire whether these associations have left a “Damuth’s law” pattern when a cross-section of countries is considered. To examine this issue we obtained data for population density from World Development Indicators. In the present context we consider the year 2000, due to the availability of data on body size. Data on body size were obtained from Demographic and Health Surveys 2006. This database has recently been used by Akachi and Canning (2007) to explore health determinants in Sub-Saharan Africa. In the present context we utilize the information collected on body size of women, measured by their weight.<sup>8</sup> The data pertains to the 1990s, and if multiple surveys were made in a single

<sup>8</sup>Using data on height yields similar results, see footnote 12.

country we use the data point closest to 2000. This leaves us with 50 country observations on population density and body size.<sup>9</sup> The countries in our sample are all poor or middle income ones (see Appendix A for a listing).

The simple correlation between log body size and log population density is -0.31, significant at the 5% level. Naturally, one may wonder whether this correlation represents the macro counterpart to the trade-off found at the micro level, or whether it is a spurious correlation due to lack of control for intervening variables; income, mortality etc.

Table 1, columns 1-4, shows the results from estimating the association between body size and population density, while conditioning on log income per capita in 2000, infant mortality in 2000 and log calorie consumption per person per day in 2000. The correlation between density and body size is robust to the inclusion of these controls.<sup>10</sup>

While the inclusion of calorie consumption in the specification does provide some control for diet's influence on population size, it probably only does so imperfectly. Aside from macronutrients like calorie intake, micro nutrients (such as various vitamins) also matter for fertility, as well as for body size. In addition, it is known that the composition of the diet tends to change during development. As a result, we also attempt to control for the diet in a more detailed manner. Specifically, we obtained data from the FAO Statistical Yearbook on the share of various dietary components of food consumption. The categories are: cereals (CER); vegetable oils (VEG); sugar and sweeteners (SUG); meat and offals (MEAT); roots and tubers (ROOT); milk, eggs and fish (MILK); fruits and vegetables (FRU); animal fats (AFAT); pulses (PUL), and "others".<sup>11</sup> The last category is excluded in the regression, to avoid perfect collinearity.

The results from including this information in the regression are reported in column 5. The central result is that the negative correlation between body size and population density is robust to a more rigorous control for diet. In fact, when the composition of the diet is controlled for the association is strengthened, in the sense that body size is significant at the 1 % level.<sup>12</sup> Note also that the specification in column 5 does a fairly good job at motivating the variation in the

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<sup>9</sup>The survey data is available from <http://www.measuredhs.com>.

<sup>10</sup>Calorie consumption per person, per day, is obtained from the FAO statistical Yearbook, and refers to the years 2001-2003. Data is found at: [http://www.fao.org/ES/ESS/yearbook/vol\\_1\\_1/site\\_en.asp?page=consumption](http://www.fao.org/ES/ESS/yearbook/vol_1_1/site_en.asp?page=consumption). Data on (PPP) GDP per capita and infant mortality is from World Development Indicators.

<sup>11</sup>The data can be downloaded from [www.fao.org/statistics/yearbook/vol\\_1\\_1/pdf/d02.pdf](http://www.fao.org/statistics/yearbook/vol_1_1/pdf/d02.pdf)

<sup>12</sup>Data for height can also be obtained from Demographic and Health Survey 2006. The pure correlation between this measure of body size, and population density, is slightly higher than that involving weight: -0.4, and significant at the 1% level. In the multivariate setting the results are slightly weaker. In a specification identical to that of Table 1, column 5, the coefficient for (log) height is -13.8, with a p-value of 0.084.

TABLE 1. POPULATION DENSITY VS. BODY SIZE IN A CROSS-SECTION OF COUNTRIES

Independent variable <sup>a</sup>	1 <sup>b,c,d</sup>	2	3	4	5	6 <sup>e</sup>
Log (body size)	-4.26** (2.11)	-5.04** (2.51)	-6.10*** (1.93)	-6.69*** (2.44)	-5.83*** (1.53)	-6.90** (3.13)
log y		0.18 (.32)			-0.31 (.45)	-0.61 (-0.70)
Infant M			-0.014** (.001)		-0.03*** (.001)	-0.03** (0.01)
LogCal				2.67* (1.40)	0.94 (1.44)	1.45 (2.38)
CER					0.03 (.04)	0.00 (0.09)
VEG					0.10 (0.06)	0.09 (0.13)
SUG					0.04 (0.05)	0.04 (0.12)
MEAT					-0.18** (0.07)	-0.28* (0.16)
ROOT					0.01 (.04)	-0.01 (0.01)
MILK					-0.21*** (0.05)	-0.20 (0.12)
FRU					0.10 (0.07)	0.08 (.14)
AFAT					-0.19 (.21)	-.27 (0.43)
PUL					0.16* (0.08)	0.03 (.14)
Estimator	OLS	OLS	OLS	OLS	OLS	LAD
R <sup>2</sup>	0.09	0.1	0.19	0.17	0.74	..
N	50	50	50	44	43	43

Dependent variable: Log population density 2000. Notes: (a) The variables in the table are: Body size is measured by weight in kg; log y is log PPP GDP per capita; Infant M is the mortality rate at birth; LogCal is calorie consumption per person per day. The remaining variables are dietary shares (in percent) of food consumption. See text for definitions. (b) All regression include a constant term. (c) \*\*\*, \*\*, \* refer to significance at the 1, 5 and 10% level, respectively. (d) Standard deviations (in parenthesis) are robust to heteroscedasticity. (e) In the LAD regressions standard deviations are bootstrapped with 1000 repetitions.

data (albeit multicollinearity renders a number of the dietary coefficients insignificant); the R<sup>2</sup> is 0.74.

As a final check of robustness we re-estimated the model from column 5 by running outlier robust median (LAD) regressions. The results are shown in column 6; body size continues to be significantly negatively correlated with population density.

Similar results are reported in Koepke and Baten (2005a,b) using archaeological data on height. Their data is based on skeletal remains and pertain to Europe during the past two millennia. In order to examine the regional determinants of body size, Koepke and Baten provide regression results where population density (and a set of additional controls) is regressed on height; in all cases the coefficient for density is negative and appears economically significant, albeit the association is somewhat imprecisely estimated.

In sum, the evidence discussed above pertaining to human societies as well as non-human samples quite strongly suggest an operative quantity-quality trade-off between size and number of offspring. In the next section we provide a model which encompasses this fundamental trade-off.

### 3. THE MODEL

We develop the model in a series of steps. First, Section 3.1 provides a brief introduction to the field of allometry, from which we draw an essential equation in pinning down subsistence consumption. Section 3.2 then explains how subsistence consumption is determined in the model, after which we turn to the intergenerational law of motion for body size in section 3.3. Finally, Section 3.4 and 3.5 discuss the preferences and optimization problem of the household and production, respectively.

**3.1. An Introduction to Allometric Scaling and Energy Consumption.** Allometric scaling is a technique used in biology to study how selected biological variables of an organism correlate with the size of the organism. A fundamental allometry is found between energy consumption  $B$  and body mass  $m$  of a mammal, and is known as “Kleiber’s Law” (Kleiber, 1932):

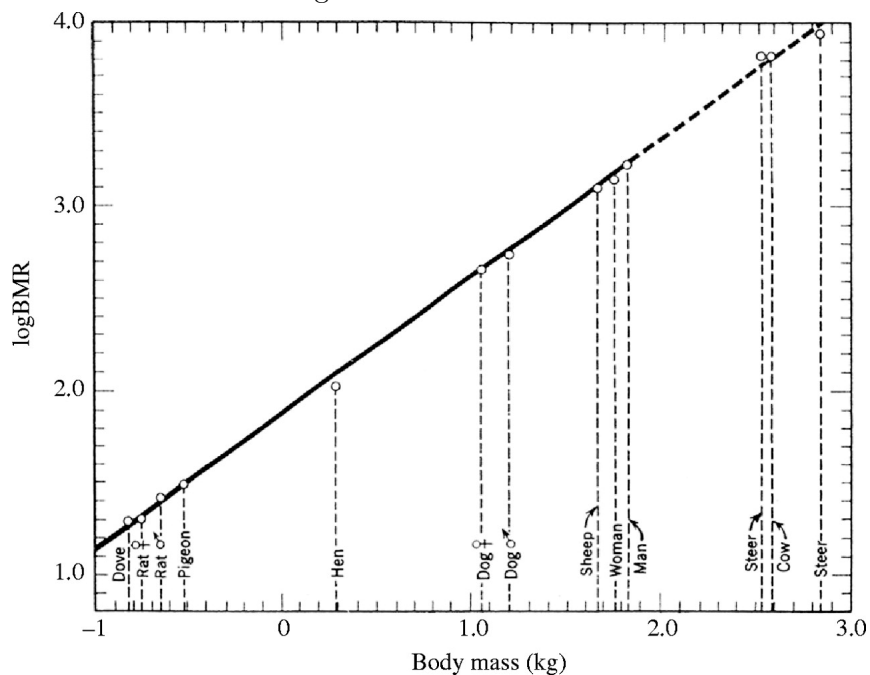
$$B = B_0 \cdot m^b, \quad \text{with } b = 3/4, \quad (1)$$

where  $B$  is the basal metabolic rate and  $B_0$  is a species-dependent constant.<sup>13</sup> Thus, drawn on log-log paper the energy-body mass relationship is linear with slope of 3/4, see Figure 4. A slope of 3/4 has been verified by Brody (1945) for almost all terrestrial animals yielding the famous “mouse-to-elephant curve”.<sup>14</sup>

<sup>13</sup>“Metabolism” refers to the biochemical processes by which nutrients are transformed into energy, which allows the organs of the body (i.e. ultimately the cells of the body) to function. The “basal metabolic rate” is defined as the amount of energy expended while at rest.

<sup>14</sup>Admittedly, there still exists some debate about the *exact* magnitude of  $b$ . Yet it seems to be fair to say that the possible variance under discussion is trivialized in comparison with the precision of parameter estimates associated

Figure 4: Kleiber's Law



Kleiber's original Figure as reproduced in West and Brown (2005).

Recently biologists and physicists managed to provide a theoretical explanation for Kleiber's law. A living organism needs to feed its cells. For that purpose energy and material is transported through hierarchically branching networks like blood vessels in mammals. The network in use, however, is not of arbitrary structure. Given that organisms have evolved through natural selection, it must be one that minimizes energy used for transport i.e. one that minimizes hydrodynamic resistance. West et al. (1997) have shown that organisms, viewed as energy transporting networks that minimize energy dissipation, fulfil Kleiber's law.

The beauty of this theory lies in its foundations on first principles. This makes it very general, and in fact it has already been applied to a multitude of biological problems from "genomes to ecosystems" (West and Brown, 2005). Some of the applications and extensions, for example those on fertility, are clearly relevant for economic analysis.

**3.2. Subsistence Requirements.** We employ Kleiber's law in order to characterize adult subsistence requirements in an overlapping generations model with endogenous fertility. According to the OLG setup life is separated into two periods. First, childhood (after weaning), defined as

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with "laws" in the social sciences. For example, Darveau et al., 2002, found exponents between 0.76 and 0.79 and around 0.82 for exercising animals.

the period of body growth and dependence on food provided by the parent. Second, adulthood, defined as the period of constant body size, work effort and reproduction.

The body size of an adult is predetermined by the individual’s nutritional intake during childhood. Accordingly, we assume that the body size of an adult remains constant.<sup>15</sup> Subsistence consumption of an adult, however, is not completely predetermined, since it also depends on fertility. From the physiological literature we use the fact that rearing up a child from conception to weaning increases the mother’s metabolic needs by a factor  $\rho$ , where  $\rho \approx 0.2$  (Prentice and Whitehead, 1987; Sadurkis et al., 1988). Denoting by  $B_t$  energy used up by the parents own body, and  $n_t$  the number of children, total metabolic needs of an adult,  $E_t$ , is thus given by:

$$E_t = (1 + \rho \cdot n_t) \cdot B_t = (1 + \rho \cdot n_t) \cdot B_0 m_t^b. \quad (2)$$

In (2)  $E_t$  measures metabolic needs in terms of energy, expressed, for example, in kcal. per period. In order to convert energy into goods we introduce the *energy exchange rate*  $\epsilon$ , which is measured in kcal. per unit of a unique consumption good. While consumption expenditure is a control variable for parents, the energy extracted from a unit of consumption depends on the food staple available, which we treat (similar to technological progress) as exogenous. Later we will vary  $\epsilon$  to investigate exogenous shifts in human diet, as would be caused, for example, by the introduction of the potato.

Employing the energy exchange rate we get *subsistence requirements*, i.e. the metabolic needs of an adult in terms of consumption goods,  $\bar{c}_t = E_t/\epsilon$ . Note that, in contrast to the existing literature in economics, the subsistence requirement is *not* a constant but depends on the individual body size and fertility in adulthood. The variable  $\bar{c}_t$  is therefore generation-dependent and thus indexed by  $t$ .

**3.3. The Intergenerational Law of Motion for Body Size.** In order to establish the intergenerational link between body sizes we draw on West, Brown, and Enquist’s (2001) model of ontogenetic growth.<sup>16</sup>

The starting point is an energy conservation equation which reads as follows:

$$E_t^c = b_c N_t + e_c (N_{t+1} - N_t), \quad (3)$$

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<sup>15</sup>From now on we refer to  $m_t$  as body size rather than body mass. This is done for semantic reasons. The term “body size” is closer to the literature in anthropology and economic history, which focusses on human height. It also avoids confusion with the body mass index.

<sup>16</sup>“Ontogeny” describes the origin and the development of an organism from the fertilized egg to its mature form.



where  $E_t^c$  is energy consumption during childhood after weaning (prior consumption is covered by adult metabolic needs),  $N_t$  denote the number of human cells in period  $t$ ,  $b_c$  the metabolic energy a cell requires during childhood for maintenance and replacement, and  $e_c$  the energy required to create a new cell. Hence the left hand side is energy “input”, and the right hand side captures energy use.

To proceed we insert the fact that body mass of a child  $m_t^c$  consists of the mass of a single cell  $\bar{m}$  times the number of cells, i.e.  $m_t^c = \bar{m}N_t$ , and solve for the change in body mass. This gives a relationship between the size of a child after weaning  $m_t^c$  and as a grown up. That is, the size of next generation’s adult  $m_{t+1}$  is:

$$m_{t+1} = \frac{\bar{m}}{e_c} E_t^c + \left(1 - \frac{b_c}{e_c}\right) m_t^c. \quad (4)$$

Next, we use from the science of life history the fact that a child after weaning equals  $\mu$  times the size of the mother (Charnov,1991, 1993), so  $m_t^c = \mu m_t$ . This provides a simple mapping of body size across generations.<sup>17</sup> Finally, denote by  $c_t$  the consumption of a child, to be determined below from optimization. Then total energy intake during childhood is  $c_t \cdot \epsilon = E_t^c$ . Inserting this into (4) leaves us with a law of motion for body size across generations:

$$m_{t+1} = a \cdot \epsilon \cdot c_t + (1 - d) \cdot \mu \cdot m_t \quad (5)$$

where  $a \equiv \bar{m}/e_c$  and  $d \equiv b_c/e_c$ .

For future reference, note that  $d$  and  $a$  can be viewed as deep physiological parameters, which may exhibit some variation across humans due to natural selection. That is, due to processes whereby large or small body sizes were selected depending on e.g. climate related circumstances.

**3.4. Individual’s Optimization.** A parent maximizes utility derived from child quality and quantity where quality is in the Beckerian (1960) sense measured by expenditure for consumption (i.e. nutrition) per child,  $c_t$ . For simplicity we impose a logarithmic form for the utility function:

$$U(c_t, n_t) = \log(c_t) + \gamma \log(n_t), \gamma > 1, \quad (6)$$

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<sup>17</sup>A physiological justification for this assumption is that child development until weaning depends on energy consumption *in utero* and during the breast feeding phase. Since larger mothers consume absolutely more energy in the model (by construction) 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.

with  $\gamma$  denoting the weight of child quantity in utility, and  $n_t$  the number of offspring. These preferences, and the restriction  $\gamma > 1$ , can be given an evolutionary motivation.

Suppose nature maximizes genetic fitness, given by the total number of descendants produced. Denote by  $\pi_t$  the fraction of surviving children. Then genetic fitness of the current generation is given by  $\prod_{t=0}^{\infty} \pi_t n_t$ . As the solution of the maximization problem is invariant to a monotonous transformation of the objective function, we let nature maximize the logarithm of genetic fitness so that the objective becomes  $\max \sum_{t=0}^{\infty} \log \pi_t + \sum_{t=0}^{\infty} \log n_t$ . From the allometric literature we know that longevity (survival probability) of free living animals scales with body mass at factor 1/4 (e.g., Brown et al., 2004), i.e.  $\pi_t \propto m_t^\psi, \psi = 1/4$ . Evaluating (5) at the steady-state, we find that  $m_t \propto c_t$  and thus  $\log \pi_t \propto \psi \cdot \log c_t$ . Inserting this information into “nature’s objective function” and dividing through by  $\psi$ , we find that maximizing genetic fitness is tantamount to maximizing  $\sum_{t=0}^{\infty} [\log(c_t) + (1/\psi) \cdot \log(n_t)]$ . This is fulfilled when parents’s of each generation maximize (6) and  $\gamma$  equals  $1/\psi$ . Note that evolutionary considerations thus predict  $\gamma \approx 4$ , providing a foundation for the assumption about the utility weight on child quantity:  $\gamma > 1$ .

Total child expenditure is constrained by parental income and subsistence consumption of the parent. Furthermore we assume that each parent is endowed with one unit of time and rearing a child requires a certain fraction  $\tau$  of parental time. Let  $y_t$  denote potential income such that available income of a family is  $y_t(1 - \tau \cdot n_t)$ . Combining the budget constraint with energy requirements (2) and applying the energy exchange rate leads to a single constraint:

$$y_t(1 - \tau \cdot n_t) - c_t n_t - (1 + \rho n_t) B_o m_t^b / \epsilon = 0. \quad (7)$$

Observe that the model captures the full cost profile of children: the metabolic costs which are relevant until weaning ( $(1 + \rho n_t) B_o m_t^b$ ) as well as the economic costs (time,  $\tau$ , nutrition,  $c$ ) that pertain to the period after weaning. It is worth stressing that our main results go through without a temporal trade-off for parental time (i.e. for  $\tau = 0$ ) due to the presence of the *biological* trade-off originating from the fact that larger parents need more energy to sustain their own body. In spite of this we allow the time costs to appear in the interest of realism and to better relate the model to the literature on the standard quantity-quality trade-off. Moreover, the presence of time costs allow for some interesting comparative statics, as will be seen below.

Parents maximize (6) s.t. (7), by choosing fertility  $n_t$  and nutritional expenditure per child  $c_t$ . From the first order conditions we obtain optimal child quality and quantity:

$$c_t = \frac{\rho(B_0/\epsilon)m_t^b + \tau y_t}{\gamma - 1}, \quad (8a)$$

$$n_t = \frac{(\gamma - 1) [y_t - (B_0/\epsilon)m_t^b]}{\gamma\rho(B_0/\epsilon)m_t^b + \gamma\tau y_t}. \quad (8b)$$

Observe that  $\partial n_t / \partial m_t < 0$  and  $\partial c_t / \partial m_t > 0$ . Higher metabolic needs of fertility induce larger parents to prefer to have less children and to nourish them better. Note furthermore that  $\partial n_t / \partial y_t > 0$  and  $\partial c_t / \partial y_t > 0$ . With higher income parents prefer to have more children *and* to nourish them better implying that the quantity-quality trade off is driven by metabolic needs and not by income.

**3.5. Production and Demographics.** The components of the model that we have introduced so far are relevant (subject to variation in parameter values perhaps) for any mammalian species. However, humans naturally differ in their ability to modify their environment. The most basic manifestation of this ability lies in the assumption that humans can operate a production technology. Specifically, we assume that total income,  $Y$ , is determined at the macro-level by a body size adjusted technology:

$$Y_t = Am_t^\phi L_t^\alpha X^{1-\alpha} = y_t \cdot L_t, \quad \phi > 0, \alpha \in (0, 1). \quad (9)$$

The parameter  $\phi$  quantifies the return to body size. As usual  $A$  captures technological knowledge,  $L_t$  denotes the size of the adult population in period  $t$  and  $X$  is land. According to standard Malthusian theory, i.e. ignoring body size, the technology implies stagnation in the long-run unless general productivity  $A$  is growing without bound since land is constant. Taking into account the physiological fact that larger bodies exert more muscles force and are thus more productive ( $\phi > 0$ ), Malthusian stagnation follows less immediately since, in principle, living standards could improve continuously in line with increasing body size. As will be shown below, long-run stagnation in this case, requires a further condition – the physiological check – to hold.

For other species, beyond humans, a more appropriate benchmark could be to think of total “income” as simply given by quality adjusted land:  $Y = A \cdot X$ . Accordingly, resource availability per individual ( $Y_t/L_t$ ) would decline as the species in question becomes more abundant. We can capture this case by putting  $\alpha = \phi = 0$  in the production function above. Of course, some

primates (beyond humans) are able to work in groups and employ tools in the context of food procurement. This could be seen as a manifestation of a (primitive) sort of production function. More generally, then, one could think of the production function as being species dependent, with  $\alpha$ ,  $\phi$  and  $A$  varying. However, it should be uncontroversial to assert that only human populations are able to produce technological progress, as would be captured in a rising level of  $A$ .

Finally, the adult population evolves according to

$$L_{t+1} = n_t L_t, \quad (10)$$

where  $n_t$  is given by equation (8b).

With equations (1) to (10) the model is complete.

#### 4. STEADY STATE EQUILIBRIUM AND COMPARATIVE STATICS

**4.1. Steady-state.** At a steady-state equilibrium we observe  $n^* = 1$  and thus from (8b) we find that  $Y_t/L_t \equiv y_t$  is

$$y^* = \frac{(\gamma\rho + \gamma - 1) B_0}{(\gamma - 1 - \gamma\tau)\epsilon} \cdot (m^*)^b. \quad (11)$$

We next substitute energy consumption per child (8a) into the law of motion for body size (5) and fertility (8b) into the law of motion for population size (10). This renders the two-dimensional dynamic system (12), with  $y_t$  determined by (9).

$$m_{t+1} = \frac{a\epsilon}{\gamma - 1} \left[ \rho(B_0/\epsilon)m_t^b + \tau y_t \right] + (1 - d)\mu m_t \quad (12a)$$

$$L_{t+1} = \frac{(\gamma - 1) [y_t - (B_0/\epsilon)m_t^b]}{\gamma[\rho(B_0/\epsilon)m_t^b + \tau y_t]} \cdot L_t. \quad (12b)$$

**PROPOSITION 1. Existence of a steady-state equilibrium.** *There exists a unique steady-state equilibrium  $(m^*, L^*)$  at*

$$m^* = \left\{ \frac{aB_0}{(\gamma - 1)[1 - (1 - d)\mu]} \left[ \rho + \frac{\tau(\gamma\rho + \gamma - 1)}{\gamma - 1 - \gamma\tau} \right] \right\}^{1/(1-b)} \quad (13a)$$

$$\frac{L^*}{X} = \left[ \frac{A\epsilon(\gamma - 1 - \gamma\tau)}{(\gamma\rho + \gamma - 1)B_0} \right]^{1/(1-\alpha)} \cdot (m^*)^{\frac{\phi-b}{1-\alpha}}. \quad (13b)$$

Proof: Inserting (11) into (12a) (evaluated at  $m_{t+1} = m_t$ ) provides equilibrium body size. Using (11) and (9) in (12b) we obtain population density as a function of body stature.

$$\frac{L_t}{X} = \left[ \frac{A\epsilon(\gamma - 1 - \gamma\tau)}{(\gamma\rho + \gamma - 1)B_0} \right]^{1/(1-\alpha)} \cdot m_t^{\frac{\phi-b}{1-\alpha}}. \quad (14)$$

Evaluated at  $m^*$ , equation (14) provides (13b).

In order to assess stability and other important features of the steady-state we introduce the physiological check.

**ASSUMPTION 1. The Physiological Check.** *The body size elasticity of metabolic needs exceeds the body-size elasticity of productivity:  $b > \phi$ .*

Applying Kleiber's law, the physiological check requires that  $\phi < 3/4$ . In the calibration below we argue in favor of a value for  $\phi$  of 0.25, implying that the physiological check is fulfilled. As will become evident below, the case where the physiological check is *not* fulfilled generates dynamics that are inconsistent with the pre-industrial growth record suggesting the check must have been in place throughout history. Intuitively, the physiological check requires that the elevated subsistence needs exceed the productivity gains associated with rising body size. In this regard it is interesting to observe the correspondence to Malthus' positive check, which also involves a restriction on elasticities: the population size elasticity of food demand exceeds the population size elasticity of food supply,  $1 > \alpha$ .

In order to investigate stability we insert (9) into (12a), which provides the isocline along which body size remains constant,  $\Delta m = m_{t+1} - m_t = 0$ , implicitly given by

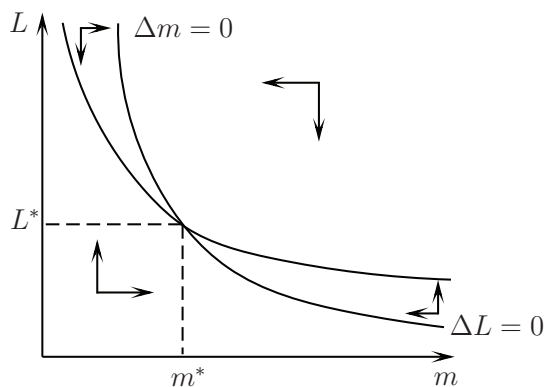
$$G(m_t, L_t) = [1 - (1 - d)\mu] \frac{\gamma - 1}{a\epsilon} - \rho \frac{B_0}{\epsilon} m_t^{b-1} - \tau A m_t^{\phi-1} L_t^{\alpha-1} = 0. \quad (15)$$

Implicitly differentiating we obtain  $dL_t/dm_t < 0$ ; the  $\Delta m = 0$ -isocline is negatively sloped. Observe that  $\Delta m < 0$  when  $m_t$  to the right of the isocline and  $\Delta m > 0$  when  $m_t$  lies to the left of the isocline. Moreover, observe that  $L_t \rightarrow 0$  for  $m_t \rightarrow \infty$  and  $L_t \rightarrow \infty$  for  $m_t \rightarrow \bar{m} > 0$ . The resulting curve and arrows of motion are shown in the phase diagram of Figure 6.

The  $\Delta L = 0$ -isocline in  $(m_t, L_t)$ -space has already been obtained by solving for equation (14). Given the physiological check,  $b > \phi$ , the isocline is a hyperbola with  $L_t \rightarrow 0$  for  $m_t \rightarrow \infty$  and  $L_t \rightarrow \infty$  for  $m_t \rightarrow 0$ . Recall that for the  $\Delta m = 0$ -isocline  $L_t \rightarrow \infty$  for  $m_t \rightarrow \bar{m} > 0$ . Hence, there is a unique intersection between the  $\Delta L = 0$  and  $\Delta m = 0$ -isoclines. Finally, observe that,

when the physiological check is operative,  $\Delta L_t < 0$  above the isocline and  $\Delta L_t > 0$  below the isocline.

Figure 5: Phase Diagram



The arrows of motion in Figure 5 suggest that the steady-state is a globally stable spiral or node. Since time is discrete, however, a second possibility arises, since there maybe overshooting and explosive behavior (Galor, 2007). In Appendix B we evaluate stability numerically and show that the equilibrium is indeed stable when both the positive check ( $1 > \alpha$ ) and the physiological check ( $b > \phi$ ) are operative.

We also demonstrate in Appendix B that the positive check is not sufficient to generate stability. For a wide range of parameters, the economy becomes unstable if the physiological check is not operative, i.e. if  $\phi > b$  *although* the positive check is operative, i.e.  $\alpha < 1$ . Intuitively, the  $\Delta L = 0$  isocline becomes positively sloped for  $\phi > b$  and the arrows of motion point toward larger  $L$  above the isocline. If  $\phi$  becomes sufficiently large the arrows of motion for  $m$  also point towards larger body sizes above the  $\Delta m = 0$  isocline. Taken together, this leads to a perpetual expansion path in northeastern direction. Without an operative physiological check it is thus theoretically possible that both population size and body size expands perpetually. The absence of such a trajectory in the historical record suggest that the positive check *and* the physiological check must have been in place. Henceforth we thus assume that the physiological check holds (as well as the positive check) and proceed to examine the steady state predictions of the model.

Inspection of the equilibrium provides the following general conclusion:

PROPOSITION 2. **Damuth’s law.** *In steady-state equilibrium there is a negative association between population size and body size. Humans of larger stature live in less densely populated areas.*

As explained in Section 2, the overall allometric equation estimated by Damuth is that  $L/X = \text{constant} \cdot m^{-3/4}$ . However, there is considerable variation in the slope and position of the allometry between size and density across different species. The present theory provides an interpretation of this variation.

First, the constant term encompasses  $A$  and  $\epsilon$ , which quite naturally would vary across species and geo-zones. The general prediction is that species living in “richer” environments (high  $A$  or  $\epsilon$ ) should be able to sustain a larger density, for given (average) body size.

Second, the slope of the allometry is also predicted to be species dependent, since production function parameters show up in the scaling law. As argued above it seems reasonable to assume that the ability to invoke a production function in food procurement varies from one species to the next. In general the model would predict an allometry of the form  $L/X \propto m^{(\phi-b)/(1-\alpha)}$ .

An interesting special case is where there is no production function in the sense that the species under consideration has a total “endowment” of food, which is proportional to the area it occupies:  $Y = A \cdot X$ . In this case the allometry becomes  $L/X \propto m^{-b}$ . As, by Kleiber’s law,  $b = 3/4$  this is exactly consistent with Damuth’s “average” finding across a large number of different species.

Moving on to human societies Damuth’s law seems to involve a different elasticity. Using data for the hunter-gatherer (HG) sample depicted in Figure 2, we obtain  $-5.7$  with a  $(-7.70, -3.78)$  95% confidence interval. The comparable estimate for our sample of development countries (DC) is  $-4.29$  with a  $(-8.59, -.014)$  confidence interval around it (Column 1, Table 1). Hence, in terms of the point estimates the elasticities are (in absolute value) about six times larger than what is observed across (other) mammals on average. Undoubtedly our estimates for the human populations are biased. But it is nevertheless worth examining whether the model can account for elasticities of these orders of magnitude.

In the calibration below we invoke a land share of 0.35, and an elasticity of body size with respect to productivity of 0.25 as benchmark values. Since  $b$  is  $3/4$ , we obtain an elasticity of  $-1.4$  using benchmark parameter values, which is broadly consistent with the correlation from our DC sample, but too large to match the correlation found in the HG sample. Broadly speaking,

however,  $\phi$  may reasonably be varied from 0.1 to 0.6, as explained in Section 5. Moreover, the land share could plausibly go as low as 0.2.<sup>18</sup> If  $\phi$  is allowed to go as low as 0.1 and the land share is reduced to 0.2, we obtain  $-3.25$  which is in the vicinity of the point estimate obtained the DC sample,  $-4.29$ , yet still outside the 95% confidence interval for the HG sample. The most probable explanation for our lack of an ability to match the hunter-gatherer societies is that the land share is too large for the HG case where human effort almost surely accounts for nearly all income creation. Accordingly, if the land share is reduced further to 0.15, the elasticity declines to  $-4.33$ , which is consistent with the HG sample, and essentially matches the point estimate for the DC sample exactly. Hence, the model is able to account reasonably well for Damuth's law; qualitatively as well as quantitatively, inside and outside the human species.

Next, inspect (11) to conclude

**PROPOSITION 3. Income per capita and body size.** *In the steady-state equilibrium there exists a positive association between body size and income per capita. Societies with larger citizens are richer.*

This is consistent with the empirically observed positive correlation between body size and income per capita (e.g., Steckel, 1983; Brinkman et al., 1988). The proposition thus implies that body size (e.g., measured by height) is a sensible indicator of long-run income per capita, as is commonly assumed by anthropologists and economic historians.

**4.2. Comparative statics.** Observe that technology  $A$  enters the equation for  $L^*$  but does not matter for  $m^*$ . In combination with (11) this leads to the following conclusion:

**PROPOSITION 4. Technological innovations.** *A discrete increase in productivity ( $A$ ) leads to a more densely populated area but leaves equilibrium body size and income per capita unaffected.*

In the model, a temporary increase in productivity will lead to temporary increases in nutrition and fertility. However, due to the biological feed-back loop from subsistence, nutritional expenditures per child will be lower (and so will be fertility) in the following generation. This process will continue until  $n = 1$  once again. At this point the temporary gain in body size has fully eroded, and the only result from the innovation is a larger population size. In the long run

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<sup>18</sup>Caselli and Coleman (2001) calculate a land share in US agriculture in the 20th century of 0.19.



income per capita does not change since the larger population fully offsets the increase in  $A$ . Note also that similar results can be derived for alternative parameter changes associated with technology improvement. Lower dependence on limited land (larger  $\alpha$ ) and higher efficiency in using brawn (increasing  $\phi$ ) both lead to a higher population density without an equilibrium effect on body size and – according to (11) – on income.

As noted in the Introduction, there is convincing evidence testifying to the fact that technological change did increase population density in the aggregate, in pre-industrial times (e.g., Ashraf and Galor, 2008; Baker, 2008). However, the *lack* of a long-run time trend during the last two millennia as a whole, in terms of body size, has also been established (Kunitz, 1987; Koepke and Baten, 2005a). The present theory thereby suggests that these potentially conflicting observations are in fact reconcilable.

At the same time we reiterate that these steady-state results do not preclude a positive *short-run* impact of productivity gains on income and body size. Comparative dynamics will be discussed in the next section.

Next we turn to dietary innovations. One might expect that human stature would depend on the type of food consumed via the energy exchange rate ( $\epsilon$ ). That is, via the nutritional content of the food staple that people are subsiding on. In the present model we can examine the consequence for population density and body size of a change in the energy content of food, by varying  $\epsilon$ . Interestingly, inspection of (13) and (11) reveals the following.

**PROPOSITION 5. Dietary innovations.** *A higher energy exchange rate ( $\epsilon$ ), leads to higher population density, but leaves body size unaltered. Steady state income falls.*

The chain of effects is as follows. When  $\epsilon$  rises, people of the next generation become larger and thus more productive. With higher income they expand their family, and population grows temporarily. With the population growing, however, productivity is decreasing. The productivity loss increasingly circumvents the initial efficiency gain through the energy exchange rate. In the long-run the demo-economy stabilizes at a constant population and lower income. A lower level of income resulting from the production side is nevertheless sufficient to support a larger population because of the improved energy exchange rate. In other words, the standard of living in terms of calories consumed – and thus body size – is the same as at the initial state before the change in diet. Yet population size is higher and income is lower than before.

In a recent study Nunn and Qian (2008) examine the impact on population size from the diffusion of the potato, which held distinct dietary benefits compared with existing food staples. We may (crudely) capture this event by an increase in  $\epsilon$ . Their estimates reveal a significant impact on population size, in keeping with Proposition 5. At the same time, the lack of any time trend in the average height of Europeans suggest this innovation had no persistent impact on body size, as the proposed theory would suggest as a matter of steady-state prediction.

Taking the derivative of (13) and (11) with respect to  $\tau$  provides the following result:

**PROPOSITION 6. Organizational innovations.** *A decrease of time costs ( $\tau$ ) for child rearing leads to higher population density, smaller stature, and lower potential income.*

This comparative static result may shed light on puzzling demographic events that occurred in the aftermath of the Neolithic revolution: population density rose, yet body size seem to have declined (Clark, 2007; Weisdorf, 2005). This could have been the result of a declining time cost of children.

There are several reasons why time costs may have dropped. First, a drop in  $\tau$  could be the consequence of a reduced need for knowledge transmission. One might imagine that life as a farmer involves more routine work than life as a hunter-gatherer. Consequently, the time investment required to teach a child what it needs to know in order to survive as a hunter-gatherer may well have been larger. This would suggest a larger  $\tau$  in hunter-gatherer societies. Second, it seems plausible that life as a hunter-gatherer involved a sharper distinction between work and child rearing than settled agriculture. Bringing children along hunting seems more problematic than bringing them along into the fields, for example. Hence, one might hypothesize that the onset of the Neolithic revolution brought with it an organizational innovation in child rearing; time cost per child went down.<sup>19</sup> This interpretation is consistent with the observation that work hours arguably went up in the aftermath of the Neolithic revolution (Weisdorf, 2005); in steady-state, a reduction in  $\tau$  is equivalent to an increase in work hours in production. Whatever the exact reason for a decline in time costs of children, the end result will be increasing relative costs of child quality. As a consequence, population density rises and body size falls.

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<sup>19</sup>More generally, of course, division of labor within the household would allow the female to rear children full time in the hunter-gatherer context. But as a matter of *average* time spend on children (man and women, taken together) agriculture would allow for a higher time allotment for child rearing, compared to the hunter-gatherer existence. This is the appropriate perspective here, since we assume individuals proliferate asexually.

Importantly, this result is robust to a more detailed modeling of a Neolithic revolution including technological innovations  $(\phi, \alpha, A)$ . As shown above, productivity improvements will only serve to increase population density, but will not affect body size. Accordingly, even if farming also involves higher productivity body size will decline, and population density will rise, as a result of changing time costs of child rearing.

Finally, observe from (11) that a reduction in  $\tau$  has an ambiguous effect on *actual* income per capita. On the one hand people work more “in the fields”, on the other hand there is a negative impact on productivity from rising population density and declining body size.

**PROPOSITION 7. Biological innovations.** *In areas where humans are selected to be larger (smaller  $d$  or larger  $a$ ) income per capita is larger, and population density lower.*

Physical anthropologists and biologists argue that some of the observed differences in human body size, across regions and countries, may be attributed to selection (see e.g., Walker and Hamilton, 2008). In particular, one may argue that larger individuals have had a selective advantage in colder climate zones: This idea has its roots in *Bergman’s rule*, which states that the body size of mammals tend to rise, as one moves away from the equator (e.g., Ruff, 2002).

There are two parts to the argument. First, there is the geographic observation that as one moves away from the equator the temperature drops, which makes it more challenging to keep warm. Second, there is the geometric observation that as body size goes up the surface to volume ratio declines, which limits the extent of heat loss per unit of body mass. Since limited heat loss is an advantage in cooler climates, selection may have favored larger bodies in cooler areas.

If indeed such genetic differences have emerged in human societies they may be captured by  $a$  and  $d$  in our model. To see this observe that equation (3) does not allow for heat loss. Accordingly, the consequences of heat loss is implicit in the parameters of the energy conservation equation. Specifically, larger energy costs of running and maintaining a body cell would capture greater heat loss. In the model this is equivalent to a larger value for  $b_c$  and thus  $d$ . The evolutionary argument above could thus be interpreted as saying that individuals with larger values for  $d$  would have a selective advantage in areas close to the equator since it implies more heat loss, which is useful in keeping body temperature down in warm and humid environments. Observe that increasing cell costs in this way, according to the model, would *produce* smaller

asymptotic body size. As a result, in areas where  $d$  is larger (close to the equator) individuals will be smaller and population density will be greater, *ceteris paribus*.

Empirically, there is a clear latitude gradient to body size in human populations. For instance, Walker and Hamilton (2008) document it for the hunter-gather society depicted in Figure 2. This finding is consistent with historically operating selective pressures on body size; in colder climates larger individuals have a selective advantage.

In light of the quantity-quality trade-off, documented in Section 2, these considerations may explain the negative correlation between latitude and pre-industrial population density, recovered in Ashraf and Galor (2008). Since the authors do not control for body size, the latitude gradient should pick it up. As larger bodies are selected in colder climates, away from the equator, we would expect a negative correlation between latitude and density.

Finally, in light of Kleiber’s law and equation (15a) we have

**PROPOSITION 8. Determinants of subsistence.** *“The level of subsistence” is declining in the preferences for child quality ( $\gamma$ ) and increasing in the physiological parameters ( $B_0, a, d, \rho$ , and  $\mu$ ) and in the time cost of children ( $\tau$ ).*

Ultimately, of course, the determinants of subsistence consumption in steady state tracks the determinants of long-run body size; in regions inhabited by larger individuals energy requirements are greater. Thus, the comparative statics follow from the parameters’ impact on  $m^*$ .

Notice that we may write steady state subsistence requirements as  $(1 + \rho) \cdot B_0 \cdot (m^*)^b$ . If we compare this expression with the expression for income from equation (11), a few things follow. First, the level of income per capita exceeds subsistence requirements in the long run. The logic is that subsistence requirements speak to the basal metabolic rate of adults. Naturally, resources are also needed to feed the offspring. Second, *living standards* defined as the *ratio* between income and energy requirements are independent of body size; societies inhabited by larger individuals would therefore not experience higher standards of living (in this sense of the word). Nevertheless, the level of income per capita would vary across pre-industrial societies. In Section 6 we attempt to gauge whether variations in subsistence requirements can account for the observed differences in income per capita prior to industrialization.

## 5. COMPARATIVE DYNAMICS

**5.1. Parameter values.** In order to simulate the model and study the implied dynamics we proceed with a calibration. We start with the biological components. We put  $B_0 = 70$  and  $b = 0.75$  according to Kleiber's (1932) law. Following Prentice and Whitehead (1987) we set  $\rho = 0.2$  implying that a woman pregnant with one child must consume 1.2 times the energy of a non-pregnant woman. According to WHO (2006) a grown up American female weighs on average  $m = 59$  kg. Child weight after weaning is 9 kg implying  $\mu = 0.15$ . For calibration of  $d$ , the amount of energy used for cell maintenance relative to cell creation, we turn to West et al.'s (2001) model on ontogenetic growth in continuous time, and investigate the human growth process. For that purpose we use standardized weight-for-age curves for US females as provided by the WHO. We take data points in kg for body mass at the age of fourteen ( $m_v = 50$  for  $v = 14$ ) and for grown up females ( $m_s = 59$ ). This yields the estimate  $d = 0.63$ .<sup>20</sup>

We set the fraction of parental time spend on child rearing  $\tau$  to 0.1, thereby implicitly assuming that it takes two years to rear a child. This parameter value is a compromise. On the one hand, it overestimates the value of child care in the home caused by pre-schoolers for modern societies (estimated to be between 1.5 and 2.8 percent of GDP for Sweden; Gustafsson and Kjulin, 1994). On the other hand, together with our other parameter estimates it implies that a traditional couple (one breadwinner) with 2 children uses 17 percent of their income for child expenditure and spend 36 percent of potential income (including opportunity costs) on their children. These figures underestimates child expenditure of such a couple in today's Australia (where the figures are between 23 and 34 and between 49 and 54 percent, respectively; see Apps and Rees, 2002).

Because 56 kg is the mean female weight in our sample of less developed countries (Table 1) we set the remaining bioeconomic parameter  $a$  such that  $m^* = 56$ . Since we are investigating subsistence economies we have deliberately set  $m^* < m_s$  to allow for the possibility of a permanent ontogenetic growth spurt along with industrialization and perpetual economic growth. This provides the estimate  $a = 0.32$

For the economic part of the model we set  $\alpha = 0.65$  according to Clark's (2007) estimates. We set  $\gamma = 4$  in keeping with the evolutionary argument behind the utility function. To calibrate the impact on body size on productivity we proceed in two steps. As a first step, we observe

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<sup>20</sup>The continuous time ontogenetic growth equation is given by  $\dot{m} = \delta m^b + dm$ , where  $d$  is the energy used for cell maintenance relative to cell creation (West et al. , 2001). From that we obtain  $d = -\log\left([1 - (m_v/m_s)^{1/4}]/[1 - (m_0/m_s)^{1/4}]\right) \cdot 4/v$

that productivity can be related to nutritional needs. Using the production function (9) and Kleiber’s law (1), we obtain:

$$\log (y_t) = \log (Z) + \frac{\phi}{b} \log (B_t) + (1 - \alpha) \log (X/L)$$

with  $\log (Z) \equiv \log (A) + (\phi/b) \log (B_0)$ . Assuming energy *needs* is a reasonable proxy for energy *consumption* we can employ Strauss (1986) estimates for the impact of nutrition on farm productivity to calibrate  $\phi$ . Strauss finds that the elasticity of farm output with respect to nutrition is about 1/3 (with a standard error of 0.11), which in theory reflects  $\phi/b$ . Since  $b$  is 3/4, it follows that a reasonable value for  $\phi$  is 1/4, which we will use below.<sup>21</sup>

To get at  $\epsilon$  we do the following. Suppose equilibrium income is 400 (international Dollars) per year. In that case, during the period of adulthood measured by the length of the fecundity period (assumed to be 20 years), equilibrium income is \$ 8000. These values pin down  $\epsilon$  to 0.26. We have one further parameter,  $A$ , which could be used to calibrate a particular equilibrium population size (or density). Yet, we found it more informative to report population density as relative deviation from stationary population (and thus normalized  $A = 1000$ ). Parameters and steady-state values are summarized in Table 2.

TABLE 2: PARAMETERS OF THE BIO-ECONOMY

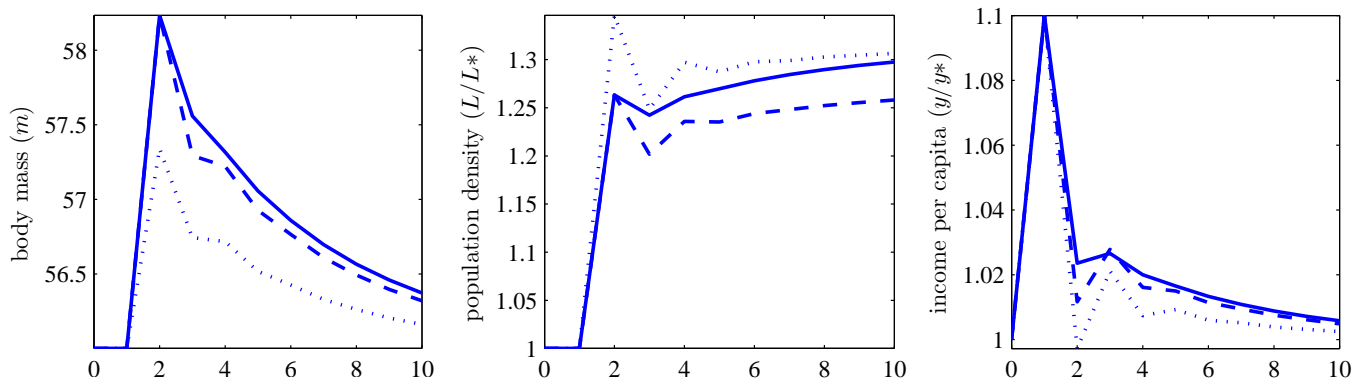
$a$	$b$	$d$	$\mu$	$\rho$	$\epsilon$
0.32	0.75	0.63	0.15	0.2	0.26
$\tau$	$\alpha$	$\phi$	$m^*$	$y^*$	$A$
0.1	0.65	0.25	56	400	1000

**5.2. Experiments: Dynamic Properties of the Model.** Our first numerical experiment is a permanent rise of productivity  $A$  by 10 percent. This could have been the result of introducing a new agricultural technique (e.g. fertilizer), or a shock to climate. Adjustment dynamics are qualitatively identical for a permanent rise of the energy exchange rate  $\epsilon$ , which could arise due to the cultivation or import of a new crop. In the phase diagram the parameter change leads to an upward shift of both the  $\Delta m = 0$ -locus and the  $\Delta L = 0$ -locus leaving the intersection at  $m^*$  unchanged. As a consequence the economy leaves the initial equilibrium in north eastern

<sup>21</sup>The variation in  $\phi$  alluded to in Section 4.1. in the context of the discussion of Damuth’s law emerges if one allows Strauss point estimate (1/3) to move two standard deviations to either side.

direction. People react on the improved conditions by having more kids and nourishing them better. Adjustment dynamics shown in Figure 6 set in.

Figure 6: Adjustment Dynamics after Permanent Technology Shock



Parameters from Table 2 (solid lines); and  $\alpha = 0.6$  (dashed lines) and  $\tau = 0.05$  (dotted lines). Population density and income are measured relative to initial steady-state. The  $x$  axis measures time in generations after the shock.

Solid lines in Figure 6 show the resulting adjustment dynamics for benchmark parameters. Robustness checks have shown that the economic system is primarily sensitive to changes in the parameter values for  $b$ ,  $\alpha$ , and  $\tau$ . Since  $b$  is fixed by nature, we provide sensitivity analysis with respect to  $\alpha$  (dashed lines) and  $\tau$  (dotted lines).

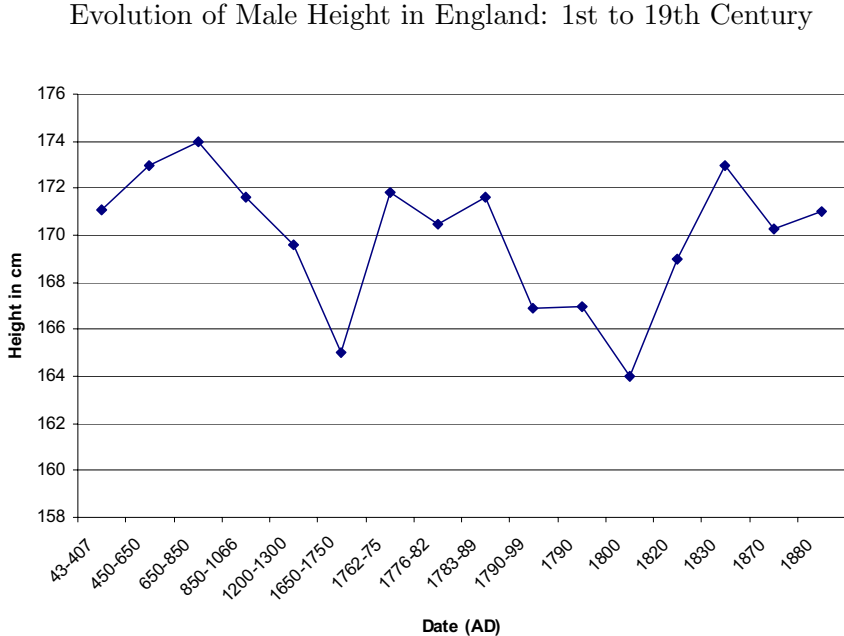
Higher productivity (or an increase in the energy exchange rate) leads to a *temporary* rise in body size and a *permanent* rise of population size (and density) where the importance of land in production and child rearing time determine the oscillatory behavior along the adjustment path. Generally, however, the second generation born after the shock is too large with respect to both population size and body size. Productivity is relatively low and – compared to period 1 after the shock – parents reduce fertility and investment in child quality, both of which remain nevertheless above pre-shock level. As a consequence of lower population density, income of the third generation is a little higher than income of the second generation and the system adjusts in damped oscillations towards its initial equilibrium of income and body mass. Since fertility, however, along the transition stayed above steady-state level, population density at the new equilibrium is *permanently* higher.

These patterns of population and body size dynamics, are rather similar to what is found in the data. The long-run evolution of population trends are fairly familiar to historians and

economists working on growth in the long run. Briefly, up until somewhere in the 19th century population growth was slow in Western European countries. Accordingly, for most of the preceding millennia, prior to the onset of the industrial revolution, the growth trajectory is slightly upward sloping, with occasional disruptions, for example, those caused by the Black Death (e.g., Galor, 2006).

At a finer level, however, existing evidence reveals that population growth followed an oscillatory trajectory, much like what we see in Figure 6. The population oscillations are found empirically at the level of parishes in rural England (Duncan et al., 2001), as well as on the macro level (Galloway, 1986; Lee and Loschky, 1987); the cyclicity appears to be a pervasive phenomenon.

Figure 7, drawing on data compiled by Kunitz (1987), show the evolution of height in England over roughly 2 millennia. The data should be interpreted with care, as they draw on a variety of archaeological excavations, which may not be equally representative. Moreover, in later periods the data is historical and refers to average size of army recruits. In addition, the time intervals are somewhat irregular. Nevertheless, the general impression is one of oscillations around a roughly constant trend level of height (circa 170 cm), which have to serve as a proxy for body size (technically speaking measured in kg).



Data source: Kunitz (1987), Table 1.



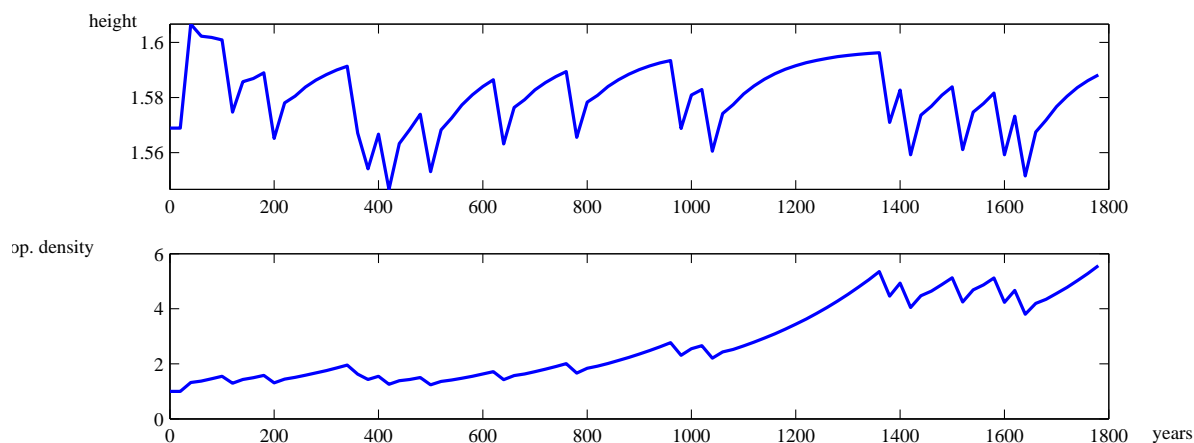
The study by Koepke and Baten (2005a), which also draws on height data derived from skeletal remains, finds strong evidence in favor of oscillations in body size around a constant trend, during the last two millennia in Europe as a whole. The sample size is much larger in Koepke and Baten’s study than that implicit in Figure 7, and statistical tests reveal that the deviations from trend are significant.

Komlos and Baten (2004) discuss evidence on body size deriving from historical sources; their analysis draws on data stemming from army recruits from various regions. This evidence broadly follows similar regularities compared with the data stemming from skeletons, albeit the period in question is much shorter (18th and 19th century). Woitek (2003) provides rigorous time series tests, documenting fluctuations in body size for Americans and Europeans (army recruits) during the 18th and 19th centuries; Woitek detects cycles of 7-10 year duration, as well as cycles of higher frequency.

Taken together this evidence suggests that prior to the industrial revolution human societies witnessed step-wise increases in population (punctuated by occasional declines), while at the same time height exhibited very little trend in either direction (see also Clark, 2007). Instead, cyclical movements in height, around a constant trend, seem to have been the norm, in the very long-run. Cyclical adjustment to trend has also been the norm for population. These patterns are qualitatively consistent with the simulations shown in Figure 6.

However, at a more detailed level the data series for height, as depicted in Figure 7, exhibits considerable persistence while population was growing at a low but positive rate during the middle ages. To capture these phenomena with a simulation of our model we conduct a business-cycle-cum-growth experiment by introducing discretionary productivity shocks. Specifically we assume that  $A_{t+1} = A_t$  with probability 0.85,  $A_{t+1} = 1.02 \cdot A_t$ , i.e. a positive productivity shock with probability 0.15, and  $A_{t+1} = 0.92 \cdot A_t$ , i.e. crop failure or technological regress (Aiyar et al., 2008), with probability 0.15. After simulating we have transformed the scale of variables for better comparison with the empirical time series. In particular, we converted body mass (i.e. weight) to height using a constant body mass index such that average height is 1.57 m, i.e. the average height of females in our sample of less developed economies (cf Section 2); and we converted time from generations to years using the length of the fecundity period (20 years). The initial population density is normalized to one.

Figure 8: Female Body Size and Population Size from Year 0 to Year 1800



Parameters as for Figure 8. Productivity shocks as explained in the text. Conversion of time from generation to years using the fecundity period and of body size from weight to height using the body mass index

Figure 8 shows an example of a trajectory for our benchmark economy from Table 2. We simulated the economy for 90 generations, which yields the demo-metabolic history of a society from year 0 to year 1800. The result corresponds quite well with the actually observed history. That is, the trajectories display long periods of smooth development, interrupted by abrupt changes and cyclical recovery. During the period under investigation population size has approximately increased sixfold (in accordance with the empirical facts, Kremer, 1993). At the same time there are cyclical fluctuations but no visible positive trend of body size.

## 6. ACCOUNTING FOR PRE-INDUSTRIAL INCOME DIFFERENCES

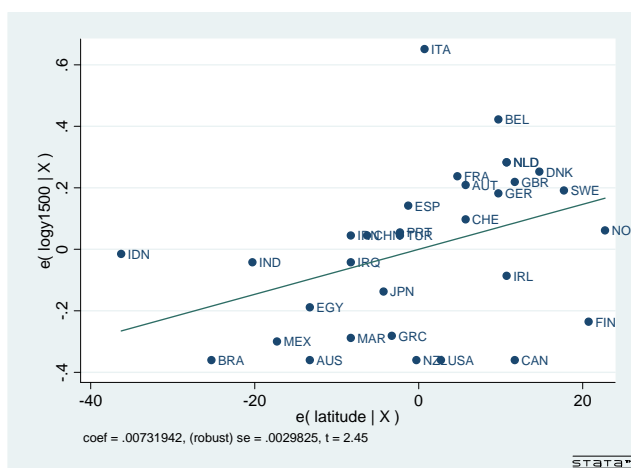
As documented below per capita income levels varied substantially in 1500, though obviously far less than they do today. Still, the observed variation begs an explanation, and existing theories of pre-industrial development provides none.

A unique feature of the proposed theory is that steady state income per capita is linked to endogenously determined minimum metabolic needs. This gives rise to the prediction that per capita income varied systematically across countries prior to industrialization, as a consequence of the underlying cross-country variation in subsistence needs. Hence, it is of interest to examine how much of the GDP per capita variation in 1500 we can attribute to variations in subsistence

requirement.<sup>22</sup> To gauge the contribution from subsistence we inevitably have to take indirect approaches as data on body size (measured in kg) is not available for the pre-industrial era.

As a point of departure we revisit the link between absolute latitude and pre-industrial development; the puzzling negative correlation between latitude and population density detected by Ashraf and Galor (2008). In Section 4 we argued that a plausible explanation for this correlation is that latitude is picking up the influence from body size. But for this explanation to be consistent with the model, absolute latitude must be *positively* correlated with GDP per capita in the year 1500 since body size is linked to metabolic requirements. Figure 9 provides a visual impression of the link between absolute latitude and GDP per capita in 1500.

Figure 9: GDP per capita 1500 vs Absolute latitude: 32 countries



The figure shows the correlation between GDP per capita and latitude conditional on a constant. The line in the figure is estimated by OLS: Data source: GDP per capita data from Maddison (2003).

Reassuringly there is a significant positive correlation between the two variables, consistent with the hypothesis that latitude is conveying information about body size, thus capturing variation in pre-industrial per capita income, which relates to subsistence requirements. Admittedly, the correlation is not robust to the inclusion of continent dummies. But this may not be puzzling

<sup>22</sup>We focus on 1500 for the measurement of income per capita mainly motivated by the fact that Galor and Weil (1999) classifies it as a plausible end date for the pure “Malthusian regime”. They label the period 1500 until somewhere in the 18th century as a period of “take-off”, citing rising population levels. The Malthusian perspective is still relevant here of course, as shown in Section 5. See also Clark (2007) who puts the end of the “Malthusian era” at around 1800.

if latitude is capturing evolutionary pressures; given the small sample the variation in latitude within continents is simply too limited.<sup>23</sup>

The latitude/income per capita regression involves a  $R^2$  of 0.15, implying that metabolic needs are of some importance to pre-industrial income variation, yet leaves most of the variation unexplained. A key difficulty, however, in using the  $R^2$  as indicative of the influence from subsistence is that body size is affected by other factors beyond evolutionary ones as apparent from the model; preferences and the time cost of children (being key determinants of nutritional investments) influence long-run stature as well. As a result, the  $R^2$  from the simple regression above would be unlikely to capture fully the influence from subsistence requirements on cross-country income differences in 1500. At best it would constitute a lower bound.<sup>24</sup>

Hence, as a second exercise we try a more direct approach to the issue at hand. While we do not have data on pre-industrial body size, we do have such data for contemporary hunter-gatherer societies carefully assembled by anthropologists (HG sample), and similar data for currently less developed countries from Demographic Health Surveys (DC sample). Both refer to the body size of females. Using these data we can work out the variation in subsistence that these data can support, and subsequently relate this calibrated variation to the income per capita variation in 1500.<sup>25</sup>

We proceed as follows. From equation (11) we calculate, contingent on data for  $m$ , predicted income differences as given by minimum metabolic needs:  $\widehat{(y_i^*/y_j^*)} = (m_i^*/m_j^*)^b$  where  $i, j$  are country indices. We can then ask how much subsistence requirements can account for in terms of observed income differences by calculating  $\hat{\theta} = \widehat{(y_i^*/y_j^*)} / (y_i^*/y_j^*)$ . Table 3 provides summary statistics for the distribution of income per capita in 1500, as well as the distribution of body size in our two samples.<sup>26</sup>

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<sup>23</sup>Indeed, by Fisher's fundamental theorem of natural selection, if a trait is subject to selection its variation declines. This underscores the need for large samples to identify the influence from selective pressures. Population density in 1500 is available for more than 100 countries.

<sup>24</sup>Another problem is that we cannot exclude the possibility that latitude is capturing other information beyond body size. Note, however, that any such alternative would need to account for both a negative correlation with population density and a positive correlation with income per capita, which is not straight forward.

<sup>25</sup>The issue of comparability of the three samples is important, and we address it momentarily.

<sup>26</sup>A couple of remarks on the approach. First, actual income (in the steady state) is as stated in (11) though with correction for child rearing; thus strictly speaking  $(1 - \tau)y^*$ . Second, when "calibrating" subsistence by comparing  $m^b$  we are implicitly ignoring other parameters that influences income per capita and determines  $m^*$ ;  $\tau$  in particular. This, of course, is a familiar problem in development accounting. If we assume (in standard notation)  $y = Ak^\alpha$  and calculate the "contribution of capital" by  $\widehat{(y_i^*/y_j^*)} = (k_i^*/k_j^*)^\alpha$  we are ignoring  $A$  which in theory affects the level of capital per unit of labor,  $k$ .

TABLE 3: DISTRIBUTION OF INCOME AND WEIGHT

	%1%	5%	25%	50%	75%	95%	99%	95/5 ratio	lat.var.	obs.	$\hat{\theta}$
GDP	400	400	443	600	700	875	1100	2.19	(5,64)	32	
body size HG	34	37	41	45	50	63	66	1.70	(2, 71)	29	68%
body size DC	44	46	54	56	59	65	70	1.41	(0.2, 47)	50	59%

Note: GDP is GDP per worker (Geary-Khamis PPP \$) in year 1500, data from Maddison (2003). Body size HG is female body size in kg for hunter-gatherer societies, data from Walker and Hamilton (2008). Body size DC is female body size in kg for contemporary societies in developing countries, data from Demographic Health Surveys (see section 2 for details). lat.var. is absolute latitude variation in degrees.  $\hat{\theta}$  is the ratio of the 95/5 ratio of body size, raised to the power of 3/4, divided by 95/5 ratio for income. See text for details.

The first seven columns trace out the percentiles for the distribution of income and weight. As for income we may note that going from the bottom 5% of the distribution to the top 5% roughly doubles income. This is the variation we will attempt to account for by way of subsistence requirements.

Thus, we next turn to the distribution of body weight in the two samples. For the HG sample we find substantial variation in female body weight, from 34 to 66 kg; nearly a doubling, going from one extreme of the distribution to the other. The distribution of body size for females in the DC sample is comparable, but median body size is larger, and the amount of variation is smaller. An explanation for this latter difference might be that the HG societies basically span the globe, whereas the DC sample does not. As seen from the table the HG sample spans about 70 degrees latitude (from Australia to Alaska), whereas the DC sample only spans roughly 50 degrees latitude. *Ceteris paribus*, if selection plays a role, the variation should be larger in the HG sample than in the DC sample.

These considerations raises the important issue of comparability: is our income sample at all comparable to our weight samples? Starting with variations in location we see from the table that the latitude variation in the income sample is smaller than that of the HG sample, yet *larger* than that which we span with the DC sample. Hence, whereas the HG sample might exaggerate the variation in subsistence, due to its extreme variation in the location of the individual societies and thus resulting body size variation, the opposite may be the case for our DC sample.<sup>27</sup> A second line of influence on body size variations could be food security. If the food supply is very volatile, it could serve to increase recorded body size variation. It might be reasonable to

<sup>27</sup>This is also true in terms of the “95/5” variation. In the income sample latitude varies by 46 degrees, whereas the DC sample varies by 42 degree’s latitude. For the HG sample the number is 66 degree’s latitude.

expect the food supply to be less secure in the context of a HG society, than what was true for the countries in our income sample. By 1500 trade likely had already expanded sufficiently to elevate food security beyond what was true for the HG society. Of course, by the same reasoning we would expect even greater food security in our year 2000 DC sample. If so, then the HG sample will exaggerate weight variation vis-a-vis the income sample, and the DC sample will underestimate it. The over-all stage of development may also play a role in limiting variation in body size. Again one might argue that our HG sample therefore overestimates body size variation in 1500, while our sample of development countries underestimate it. In sum, one may hope that the actual variation in body size and subsistence requirements for our income sample is somewhere in between that which is suggested by our two weight samples. In lack of better options we venture this leap of faith.

If we thus use these numbers as ball-park figures for plausible variation in body size in our pre-industrial income sample, we can gauge the contribution from subsistence on income differences as done in the last column of Table 3. Subsistence substantially contributes to income differences in the order of magnitude of between 60% and 70%. If we take the model seriously, the remaining variation is attributable to unmeasured factors, like the energy exchange rate  $\epsilon$ . This variable should rightly be attributed to the metabolic component, as it converts energy needs into needs measured in units of goods. One may therefore worry about its exclusion. However, in theory  $\epsilon$  should not affect long-run body size (cf. Proposition 5). As a result, we would expect a low (zero) covariance between variations in  $\epsilon$  and  $m$ .<sup>28</sup> From this perspective its omission may be less problematic, and will simply account for part of the left-over residual, possibly elevating the importance of subsistence variations further.

## 7. CONCLUSION

The theory developed in the present paper proposes that child quality investments have been made throughout history. These quality investments in child nutrition were productive and served to elevate individual productivity. Nevertheless, a take-off did not occur. We hypothesize that a take-off was prevented by a “physiological check”: when body size increases subsistence requirements grow, which limit further nutritional advances and stabilizes the economic system

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<sup>28</sup>Naturally, one may imagine other dimensions of the diet that should correlate with body size; protein intake for instance. But this aspect of the diet is not part of minimum metabolic requirements, which solely depends on calorie intake. Of course, one might envision a generalized theory of subsistence needs, which also involves the composition of the diet at the level of micro nutrients. Such a theory is the burden of future research.

around an endogenously determined subsistence boundary. We argue this is a key mechanism in explaining the absence of per capita income growth, which characterized most of human history, and represents a fundamental reason why episodes of technological change did not instigate a virtuous circle of rising body size and productivity. In fact, with quality investments taking place the Malthusian positive check is not sufficient to equilibrate the economy.

The theory elucidates the determinants of subsistence requirements and thereby comparative development during the pre-industrial era. We present evidence that suggests variations in subsistence requirements can account for the bulk of observed income differences in 1500. The theory is thereby able to provide important insights into the determination of key structural characteristics – per capita income and body size as well as population size – which characterized the pre-industrial society prior to the take-off, and most likely influenced the timing and speed of the transition to sustained growth. Moreover, our accounting results broadly reconciles the long standing view that societies, prior to industrialization, stagnated near “subsistence” with the observation that income per capita levels varied considerably across countries in 1500.

The model is able to shed light on a range of interesting questions related to the historical record. Why did dietary innovations, like the introduction of the potato, increase population density but leave average body size unaffected? Why did the Neolithic revolution lead to higher population density, but smaller individuals? Why was population density seemingly higher close to the equator in pre-industrial times? What unifying forces can account for a negative association between population density and average body size in human populations as well as in other species?

In the analysis above we have focused on the era which preceded the industrial revolution. An important next step is to provide a unified account of the trajectory of human body size until present day. This will enable an understanding of the origins of contemporary cross-country differences in average body size, and thereby provide new insights into the sources of global income disparities.

## **Appendix A**

The 50 countries for which we have data on body weight are: Armenia (ARM); Benin (BEN); Burkina Faso ( BFA ); Bangladesh (BGD); Bolivia (BOL); Brazil (BRA); Central African Republic (CAF); Cote d’Ivoire (CIV) ; Cameroon (CMR) ;Colombia (COL); Comoros (COM) ;

Dominican Republic (DOM); Egypt, Arab Rep.( EGY); Eritrea (ERI); Ethiopia(ETH); Gabon (GAB); Ghana (GHA); Guinea (GIN); Guatemala (GTM); Haiti (HTI); India (IND); Jordan (JOR); Kazakhstan (KAZ); Kenya (KEN); Kyrgyz Republic (KGZ); Cambodia (KHM); Morocco(MAR); Madagascar (MDG); Mali (MLI); Mozambique (MOZ); Mauritania (MRT); Malawi (MWI ); Namibia (NAM); Niger (NER ); Nigeria (NGA); Nicaragua (NIC); Nepal (NPL); Peru (PER); Rwanda (RWA); Senegal (SEN); Chad (TCD); Togo (TGO); Turkmenistan (TKM) ; Turkey (TUR); Tanzania (TZA); Uganda (UGA); Uzbekistan (UZB); Yemen, Rep. (YEM); Zambia (ZMB); Zimbabwe (ZWE).

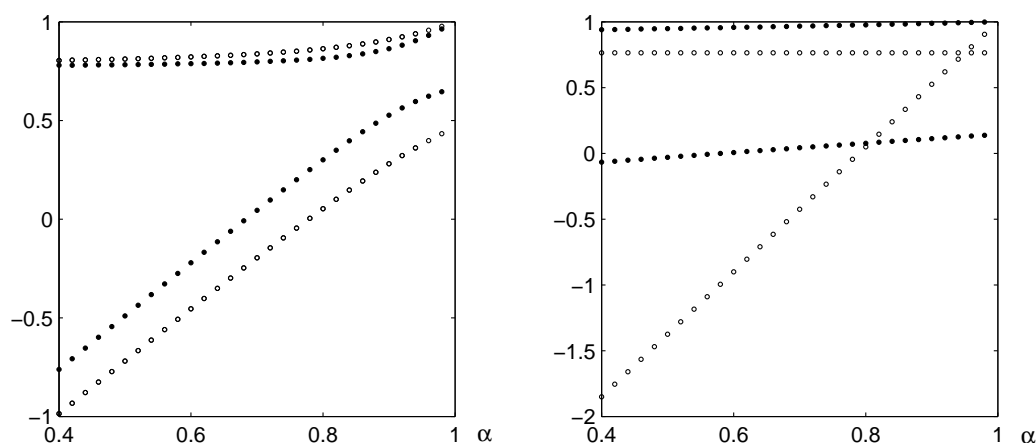
## Appendix B

For stability analysis we evaluate the Jacobian determinant of system (12) numerically. Given the value of  $b$  fixed by nature, we have identified the elasticities  $\alpha$  and  $\phi$  and weight on child quantity in utility  $\gamma$  as the parameters whose change induces the strongest reaction of dynamic behavior. Figure A shows the eigenvalues of the Jacobian and alternative  $\alpha$ . White dots on the left hand side demonstrate robustness of our benchmark calibration with parameters from Table 2. Black dots reflect results for the case of  $\phi = 2$ , indicating a strong violation of the physiological check. The system becomes now unstable for  $\alpha > 0.8$ .

While the region of instability under violation of the physiological check is relatively small for our benchmark scenario, it can be easily become salient in alternative settings. This is in particular the case if  $\gamma$  is low, implying that parents' utility depends relatively strongly on child quality. A low value of  $\gamma$  introduces a tendency for instability since parents react on improving economic conditions mainly by nourishing their offsprings better. The panel on the right hand side shows the eigenvalues for  $\gamma = 1.2$ . White dots represent a scenario for which all other parameters are taken from Table 2. In particular,  $\phi = 0.25$ , implying an operative physiological check. Both eigenvalues are smaller than unity over the whole range of  $\alpha$ 's, indicating stability. If, on the other hand,  $\phi = 1.5$ , indicating a violation of the physiological check, the system is unstable for all  $\alpha > 0.5$ . In conclusion the positive check (i.e.  $\alpha < 1$ ) is, generally, not sufficient to stabilize a Malthusian economy. It needs to interact with the physiological check.



Figure A: Eigenvalues



Parameters from Table 2 and alternative values of  $\alpha$ . Left hand side: white dots: benchmark case from Table 2. black dots:  $\phi = 2$ . Right hand side: Lower weight on child quantity ( $\gamma = 1.2$ ) and  $\phi = .25$  (white dots) and  $\phi = 1.5$  (black dots). All other parameters from Table 2

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