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A Bioeconomic Foundation of the Malthusian Equilibrium: Body Size and Population Size in the Long-Run*

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Abstract. This paper develops a bioeconomic Malthusian growth model. By integrating recent research on allometric scaling, energy consumption and ontogenetic growth, we provide a model where subsistence consumption is endogenously linked to body size and fertility. The theory admits a unique Malthusian equilibrium in a two-dimensional state space characterized by population density and body size (metabolic rate) of the representative adult. As a result, the analysis allows us to examine the link between human biology, economic productivity, body size, and population size. Off the steady-state we investigate the possibility of cyclical behavior of the size of a population and the size of its representative member over the very long-run. We also demonstrate that a take-off into sustained growth should be associated with increasing income, population size and body size. The increase in the latter is, however, bounded and can be viewed as convergence to a biologically determined upper limit.

Keywords: Subsistence, Nutrition, Metabolism, Population Growth, Ontogenetic Growth, Malthus.

JEL: O11, I12, J13.

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1. INTRODUCTION

The present paper studies the relationship between body size, population size and economic activity in the long run. Specifically, the paper provides a generalization of the Malthusian model so as to include the endogenous determination of human body size. In order to study the bidirectional link between economic activity and human body size we model the biological links between nutrition during youth, ontogenetic growth, and food requirements during adulthood. The novel elements of the model are based on deep micro-foundations, as explained below. Nevertheless, the fundamental interaction between body size and economic activity is superficially very simple. High income families will be able to feed their offspring better, which translates into larger adults in the future. At the same time, however, larger adults will be more energy requiring, which provides a bioeconomic constraint on the household decision to spend resources on child quantity and quality (i.e., nutrition). Since productivity is determined (in part) by labor supply this mechanism creates a dynamic feed-back loop from body size to economic activity in a Malthusian economy. The model admits a Malthusian steady-state, where both population size and body size are endogenously determined, and the theoretical structure allows for a very transparent analysis of the transitional dynamics leading to the steady-state.

Understanding the historical evolution of human body size is important since data on stature frequently is invoked as indices for long-run development (e.g., Komlos and Baten, 2004; Clark, 2007 and many others). Yet, this approach is essentially based on casual theorizing; no rigorous theoretical foundation for this practise exist. Exploring the body size/growth nexus theoretically is useful in forwarding our understanding of how anthropometric research might assist us in obtaining a clearer picture of the long-run growth record.

A rigorous analysis of the bioeconomic constraints faced by individual agents is useful as well. Such constraints are not completely unfamiliar territory to economists; economic analysis often assumes the existence of a level of “subsistence consumption”. That is, a strictly positive lower bound on consumption choice.¹ From this assumption flows a number of strong predictions. Subsistence requirements generate the prediction that the savings rate increases with income, which importantly affects the impact of inequality on growth (e.g. Galor and Moav, 2004) and may lead to poverty traps (e.g., Azariadis, 1996). In spite of its importance to analytical results,

¹The most common way of introducing subsistence consumption into a growth model involves Stone-Geary preferences, i.e. $U(c) = \frac{(c-\bar{c})^{1-\sigma}}{1-\sigma}$, where $\bar{c} > 0$ is the level of subsistence.

subsistence consumption is always treated as exogenous in the economics literature. Biologically, however, minimum consumption requirements, in the sense of basal metabolism, is inescapably linked to fertility (i.e. pregnancy leads to elevated consumption needs) and body size.² Treating minimum consumption as an endogenous variable, rather than exogenously given, has important implications. For example, it matters for the viability of poverty traps, as demonstrated below.

The model comprises three central elements which generate the novel results of the present analysis. First, consumption during childhood determines body size as an adult. Accordingly, we emphasize the non-reversible body size component. The link between child nutrition and body size has long been recognized by economists (see e.g., Fogel, 1994). Here, however, we derive the law of motion for body size from fundamental biological and physical principles. Biological parameters reflecting e.g. the energy costs associated with cell maintenance, will therefore turn out to matter for the steady-state of the model. In other words, human biology will importantly affect economic outcomes, such as per capita income, in the Malthusian environment.

Second, body size as an adult and the fertility rate determines subsistence consumption. Again, the link between subsistence, defined as basal metabolism, and fertility and body size is firmly grounded in theory and evidence stemming from the field of biology, as explained below. The fact that child bearing affects energy requirements of an adult (in the model people reproduce asexually) introduces a natural quantity-quality trade-off. Parents derive utility from the number and consumption level of their children; both are conceived to be normal goods. However, increasing fertility requires the parent to extent her own consumption, to cover enhanced subsistence needs, which comes at the cost of less consumption and future body size for the offspring.

Finally, larger individuals are assumed to be more healthy and therefore more productive. The assumption that “health” matters for labor productivity is not original to this paper (see e.g., Strulik, 2007). However, since it is a well documented fact that larger individuals are more healthy and productive, it is important to incorporate this mechanism nevertheless so as to demonstrate the viability of a Malthusian equilibrium in the presence of “health capital accumulation”.³

²Metabolism 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.

³See Strauss (1986), Fogel (1994, 1997) or Weil (2007) for evidence of the link between health and productivity.

The model holds a number of steady-state predictions which motivates empirical evidence on the relationship between body size, population size and prosperity (this evidence is summarized in the next section). For example, the level of technological sophistication does not influence steady-state body size in a Malthusian economy; there is an inverse association between (average) body size and population density, and, the composition of the diet matters for population density in the long run. The theory also makes clear that a lack of an impact from technology on long-run body size only holds in an economically stagnant environment. A permanent *acceleration* in productivity, as would be associated with a “take-off” into a modern growth regime, will permanently affect body size. Specifically, during a process whereby countries in this way emerge from a Malthusian regime, the model predicts rising body size as well as rising population density and average income. The gain in body size is bounded, however, and can be viewed as convergence to a biologically determined upper limit. The prediction that body size (and population growth) rises during the take-off to “modern growth” is consistent with evidence for Europe during the 19th century and 20th century (e.g., Steckel, 1995). In addition, the theory holds predictions about the transitional dynamics of body size and population size over time. Specifically, the model provides a micro-founded explanation for Malthusian cycles in fertility and body size over the very long run, for which evidence can be found in various regions of Europe over the last two millenia.

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 (Galor and Weil, 2000; 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. In contrast to the present paper, however, these studies ignore the evolution of body size, and assume the level of subsistence consumption is exogenous. The present paper does not model the transition to modern growth. Instead we focus on the Malthusian regime, and the process of “take-off”.

Another related strand of literature fuses biology and economics by introducing evolutionary pressures into dynamic models. The scope of this literature is broad, ranging from providing theories of selection generated take-offs to sustained growth (Galor and Moav, 2002), to the long-run changes in life-expectancy (Galor and Moav, 2005) and size of the human brain (Kaplan and Robson, 2003). The closest precursor to our work, from the point of view of this related strand

of literature, is Lagerlöf (2007). Lagerlöf aims to explain why body size seems to have followed a hump-shaped trajectory over the last 1,000,000 years. In contrast to the present paper, Lagerlöf (2007) assumes body size is exogenous at the level of the individual, thus fully determined by the genetic make-up of individuals; changes in the composition of the population is therefore required to generate changes in average body size.

Our analysis emphasizes the nutritional influence on body size rather than the impact of selection on body size. The model below links aspects of the human physiology, like certain properties of the cells in the body, to body size and long-run labor productivity. These characteristics are taken as given in our analysis, however, since we are focusing on processes over a time span of about two millennia; arguably too short a time frame for selection to be important. Nevertheless, while the genetic make-up of the agents in our model is exogenous, it is still feasible to explore the comparative static consequences for productivity, of differences across human societies in human physiology, which could have been the consequence of differential (pre-historical) evolutionary pressures.

The paper proceeds as follows. Section 2 provides evidence on the relationship between human body size, population size and economic activity. In Section 3 we present recent research from the field of allometric scaling and ontogenetic growth, on which basis Section 4 develops a bio-economic model of Malthusian stagnation. Section 5 provides an extension of the model; we introduce a lower bound for nutrition requirements below which individuals cease to be active. This section demonstrates the robustness of the Malthusian equilibrium which is derived in the baseline model without imposing such a “participation constraint”. Section 6 analyzes the impact of a “take-off” into sustained growth on income, population size and body size. Finally, Section 7 concludes.

2. EMPIRICAL EVIDENCE ON BODY SIZE AND POPULATION SIZE ACROSS TIME AND SPACE

This section presents available evidence on body size, and what appears to be known about the association between body size, population size and income across households, countries and time. We view this evidence as stylized facts that a model which attempts to come to grips with the evolution of body size and population size, needs to be able to motivate.

Below we will be using data on both height and weight as evidence on body size. In theory, the two measures could lead to different conclusions about an individual’s “size”. In practise,

however, there is no particular reason why taller individuals should tend to be wasted and short people obese. As a result, it is not surprising that data on (average) height and BMI (weight-for-height - the Body Mass Index) exhibits a low correlation. In our cross-country data set described below the correlation is a mere -0.05.⁴ From this perspective the – interchangeable – use of height and weight as measures of body size seems defensible.

2.1. Body Size and Family Size across Households. A key regularity is that there appears to be a trade-off between the number of offspring in a family and their (mean) body size. 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 menace. 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".⁵ Figure 1 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.⁶

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 improves. Douglas and Simpson document that similar patterns persist to the ages of 11 and 15 for both boys and girls.

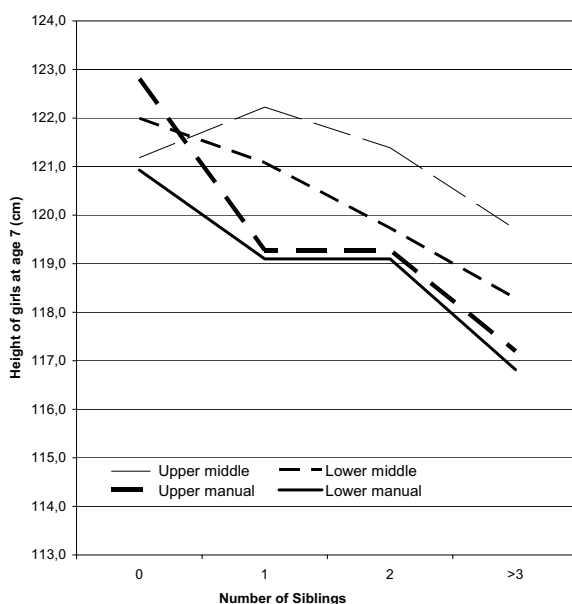
The 1946 cohort has more recently been analyzed by Kuh and Wadsworth (1989). Their regression based analysis confirms the general impression conveyed by Figure 1; conditional on a host of environmental factors, each additional sibling implies a reduction in mean height of about 6 mm.

⁴See also Floud (1998) for further documentation of this point.

⁵In 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.

⁶The picture for boys is very similar.

Figure 1: Body Size of UK Girls at Age 7 and the Number of Siblings



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

More broadly, evidence of the inverse relationship between family size and body size has been recovered on data stemming from both developed and less developed economies, as well as from hunter-gatherer societies.⁷ Finally, it is also worth observing that a trade-off between fertility and body size is not a particularly human characteristic but is known to be operative in other animals as well (e.g. Smith and Fretwell, 1974).

2.2. Body Size and Population Density: Cross-Country Correlations. In light of the household level evidence it is of interest to inquire whether a similar association can be detected at the aggregate level. In this regard it seems reasonable to view population density as the macro counterpart to “family size”. Hence, to explore the association between body size and “family size” we need data on population density, and average body size in individual countries.

Data for population density is available from World Development Indicators, and in the present context we consider the year 2000. Data on body size can be obtained from Demographic and Health Survey’s 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.⁸ The data pertains to

⁷See Cole (2000), Silventoinen (2003) and Hagen et al. (2006).

⁸Using data on height yields similar results, see footnote 13.

the 1990s, and if multiple surveys were made in a single country we use the data point closest to 2000. This leaves us with 50 country observations on population density and body size.⁹ The countries in our sample are all poor or middle income ones (see Appendix A for a listing).¹⁰ 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 covariates.¹¹

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, micronutrients (such as various vitamins) arguably matters for fertility, as well as for body size. 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".¹² 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.¹³

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

¹⁰The formal model below concerns a Malthusian economy, which does not match reality in the developed part of the world. In contemporary less developed economies, however, where the demographic transition has yet to fully transpire, Malthusian forces may still be detectable in the data.

¹¹Calorie 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. Data on (PPP) GDP per capita and infant mortality is from World Development Indicators.

¹²The data can be downloaded from www.fao.org/statistics/yearbook/vol_1_1/pdf/d02.pdf

¹³Data 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 ^a	1 ^{b,c,d}	2	3	4	5	6 ^e
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 ²	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 regressions 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.

Moreover, it is worth observing that MEAT, MILK and PUL are significant, conditional on body size, income, mortality and calorie consumption. The three significant food components are all high on protein. In the case of pulses there is also a substantial content of essential amino acid. The findings reported in column 4 and 5 suggests that the composition of the diet

matters for population size.¹⁴ Note also that the specification in column 5 does a fairly good job at motivating the variation in the data; the R^2 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, albeit imprecisely estimated in their relatively small sample.

In sum, this evidence suggests that the trade-off between size and number which can be observed at the household level is also discernable in the macro data; at least in poorer societies. Interestingly, this inverse association is found in other mammalian species as well (Damuth, 1981).

2.3. Body Size and Income in a Cross-Section of Countries. In the cross-country data set discussed above the correlation between body size (measured by weight) and log GDP per capita in 2000, is 0.54 and significant at the 1% level. This is not a surprising relationship; it is well known that as income improves, stature tends to increase as well.

Arguably, the main explanation for this association is that a rising level of income allows for improved nutritional intake, which works to increase body size (Fogel, 1994; Strauss and Thomas, 1998). Similar considerations almost surely explain the pattern discernable in Figure 1; the offspring of more well off families tends to be bigger. The effect of income and nutrition is typically viewed as the key explanation for the secular increase in body size throughout the Western world during the 20th century (e.g., Fogel, 1994).

These considerations testify to the importance of nurture in accounting for the evolution of long-run body size. Indeed, even within generally well fed populations, differences in socioeconomic circumstances explain as much as 1/5 of the variation in height outcomes; in subsistence economies this number is likely much higher (Silventoinen, 2003). Further support of this

¹⁴We also ran regressions where we control for protein and fat intake directly (also available from FAO). Neither variable was significant, however, conditional on the diet shares. The results with respect to body size are essentially unaltered.

assertion is found in the recent work by Akachi and Canning (2007). The authors document, in particular, a positive link between protein intake (grams per day) and body size on the African continent.

In sum, while genetics undoubtedly matters as well, the nexus between income-nutrition and body size seems well founded, and most likely represents the key explanation for the reduced form positive cross-country correlation between income and body size across contemporary societies.

2.4. Intertemporal Evolution of Body Size and Population Size in the Long Run. 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).

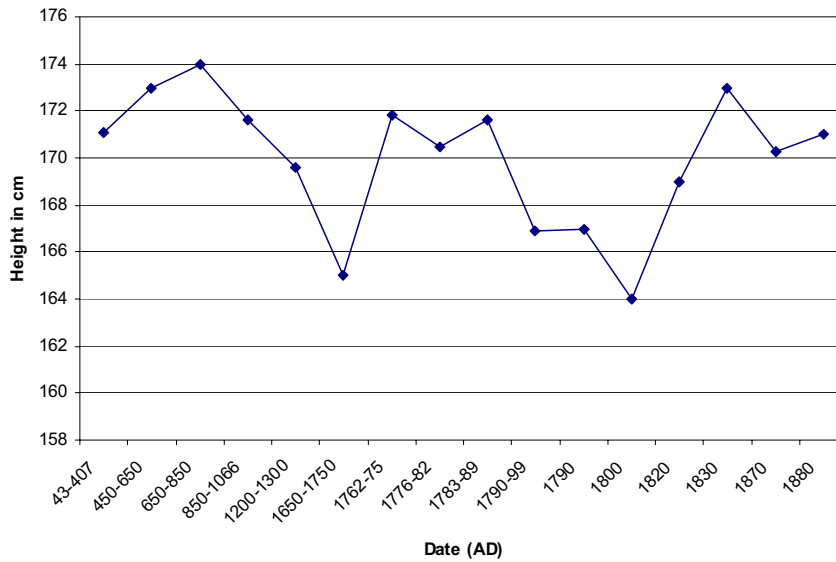
At a finer level, however, existing evidence reveals that population growth followed an oscillatory trajectory. This pattern holds at the level of parishes in rural England (Duncan et al., 2001), as well as on the macro level (Galloway, 1986; Lee and Loschky, 1987); the cyclicity appears to be a pervasive phenomenon.

If body size and population size are intimately related, as the evidence from the last section suggests, one might expect this cyclicity to be observable in the evolution of height as well. This is indeed what existing studies find.

Figure 2, drawing on data compiled by Kunitz (1987), shows 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 (i.e. are based on skeletal remains), 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).

The careful study by Koepke and Baten (2005a), which also draws on height data derived from skeletal remains, finds strong evidence in favor of cyclicity 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 2, and statistical tests reveal that the deviations from trend are significant.

Figure 2: Evolution of Height in England: 1st to 19th Century



Data source: Kunitz (1987), Table 1.

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 a (slightly) positive trend has also been the norm for population.

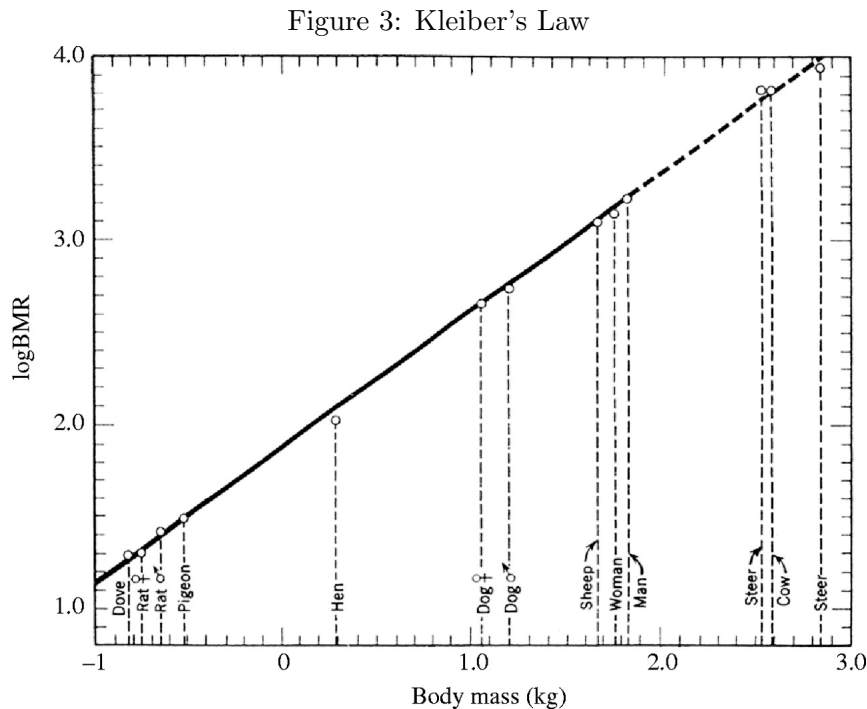
In light of the relatively short period under consideration, it seems unlikely that these patterns are driven by evolutionary mechanisms. Instead, variations in living conditions, associated with nutritional intake, would appear to be a natural candidate explanation.

3. ALLOMETRIC SCALING, ENERGY CONSUMPTION, AND ONTOGENETIC GROWTH

Allometry is a technique used in the biological sciences to describe how a variable of interest regresses against body mass. The fundamental relationship between energy consumption B and mass of a mammal m is described by Kleiber’s Law (Kleiber, 1932):

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

Here B is the basal metabolic rate and B_0 is a species-dependent constant. Thus, drawn on log-log paper the energy-body mass relationship is linear with slope of $3/4$, see Figure 3. A slope of $3/4$ has been verified by Brody (1945) for almost all terrestrial animals yielding the famous mouse-to-elephant curve.¹⁵



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

Biologists have been puzzled by the $3/4$ finding for a long time because the most obvious result from theoretical reasoning would be that b equals $2/3$. An animal x times as big as another in height is x^2 larger in terms of surface area and x^3 larger in terms of volume, or mass m . Because

¹⁵Although there exists still a debate about the *exact* magnitude of b , it seems to be fair to say that the possible variance under discussion is trivialized by the precision of parameter estimates found for so called “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.

heat exchanges through body surface, the metabolic rate should be proportional to x^2 which is itself proportional to $m^{2/3}$. Recent research has revealed that the fallacy of this reasoning lies in its application of Euclidian geometry when fractal geometry is appropriate. The beauty of the new theory, first developed by West, Brown and Enquist (1997), 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 and mortality are in particularly relevant for economic analysis.

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 that minimize energy dissipation naturally fulfil Kleiber’s law. A sketch of the proof can be found in Appendix B.

Ultimately, Kleiber’s law conveys an important piece of information: Larger animals are more energy efficient. The theory of West et al. provides a deep foundation of this fact: energy dissipation per cell decreases with body mass. Thus, as an organism gets smaller each single cell is forced to work harder. This basic insight can explain a multitude of biological phenomena like, for example, why a mouse has a faster heartbeat, sleeps more, and lives shorter than an elephant. It also provides the deep determinant of some phenomena discussed by the economics profession like, for example, why human health and productivity are positively correlated with body size (see Fogel, 1994).

One of the major applications of the theory is ontogenetic growth (West, Brown, and Enquist, 2001).¹⁶ To see how Kleiber’s law affects growth of organisms, consider the energy flow in a human body. This is generally given by

$$B(t) = B_c N(t) + E_c \dot{N}(t) \tag{2}$$

where $N(t)$ is the number of cells at time t , B_c is the metabolic rate of a single cell (inclusive maintenance and replacement) and E_c is the metabolic energy required to create a new cell. If we insert the fact that body mass consists of the mass of a single cell \bar{m} times the number of

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

cells, i.e. $m(t) = \bar{m}N(t)$, and solve for the change in body mass we get:

$$\dot{m} = \left(\frac{\bar{m}}{E_c}\right) B - \left(\frac{B_c}{E_c}\right) m.$$

Finally, insert (1) to get a differential equation for body mass:

$$\dot{m} = a \cdot m^b - d \cdot m \tag{3}$$

where $a \equiv B_0\bar{m}/E_c$ and $d \equiv B_c/E_c$.¹⁷

Equation (3) is a simple Bernoulli equation with explicit solution

$$\left(\frac{m(t)}{m_s}\right)^{1/4} = 1 - \left[1 - \left(\frac{m_0}{m_s}\right)^{1/4}\right] \cdot e^{-\frac{1}{4}dt}, \tag{4}$$

where $m = m_s \equiv (a/d)^{1/(1-b)}$ implying $m_s = (a/d)^4$ using Kleiber’s law. If we take a and d as species-specific biological constants, determined by the genetic make-up, how can we then explain the variation in body mass among adult humans? One possibility would be that reproduction and death occurs before maximum body mass is (asymptotically) reached. While this argument certainly applies to some species like, for example, cod, it is less convincing for humans. For a more sensible interpretation of (4) in the context of humans, it is important to note that it does not preclude an adult size well below the asymptotic size (Charnov, 2001). Two channels are possible.

First, imagine that maximum adult height (mass) is reached at a genetically predetermined age $t = T$. It is then determined by m_0 , the birth-weight or, more specifically, child mass after weaning. Yet m_0 is individual-specific and depends in particular on the biological and economic condition of the mother.

Alternatively, one may observe that equation (4) specifies *unconstrained growth* or, in other words, the *demand side* for energy. If energy, i.e. food, is in limited supply, new body tissue will be accumulated with less speed than the biological maximum, growth will be slower and so will be mass at time T . In other words, while the average Korean born 1980 is taller and heavier than his father (see Steckel, 1995) both have grown according to (4) and thereby fulfilled Kleiber’s

¹⁷Ontogenetic growth according to (3) should look very familiar to economists. In fact, “accumulation” of body tissue is structurally equivalent to accumulation of capital in the neoclassical growth model (which would be given by $\dot{k} = sk^\alpha - \delta k$ in standard notation; Solow, 1956). New body tissue is produced with decreasing returns whereas existing tissue depreciates at a constant rate. Recalling Solow’s model we know that there exists a unique and stable equilibrium.

law. Only, the new generation started out better initially and consumed more energy (more or better food) in childhood. It is through these channels of initial child mass, child nutrition, and its consequences for adult productivity, where economics interacts with biology.

4. A BIO-ECONOMIC MALTHUSIAN MODEL

4.1. Intergenerational Evolution of Body Size and Subsistence Consumption. Life is separated into two periods: childhood (after weaning) defined as the period of body growth and dependence on food provided by the parent, and adulthood defined as the period of constant body size and reproduction. Integrating (2) over the period of childhood one gets

$$\epsilon \cdot c_t = B_c N_t + E_c (N_{t+1} - N_t). \quad (5)$$

Here, B_c denotes the energy required to maintain a cell through childhood, and E_c is energy costs associated with cell generation.

The compound $\epsilon \cdot c_t$ is the total energy used for ontogenetic growth of a child, comprising consumption during childhood and the “energy exchange rate”, ϵ , which is measured in kcal. per consumption good (or per dollar). While consumption expenditure is a control variable for parents, the energy extracted from a unit of consumption depends on the food available, which we treat (similar to technological progress) as exogenous at the individual level. Later we will vary ϵ parameterically to investigate exogenous shifts in human diet (as would be caused, for example, by the Neolithic revolution).

To obtain the size of a grown up child we substitute the definition of body mass $m_{c,t} = \bar{m}N_t$ into (5).¹⁸

$$\epsilon c_t = \frac{B_c}{\bar{m}} m_{c,t} + \frac{E_c}{\bar{m}} m_{c,t+1} - \frac{E_c}{\bar{m}} m_{c,t} \quad \Rightarrow \quad m_{c,t+1} = \frac{\bar{m}}{E_c} \epsilon c_t + \left(1 - \frac{B_c}{E_c}\right) m_{c,t}.$$

This gives a relationship between the size of a child after weaning $m_{c,t}$ and as a grown up $m_{c,t+1}$. To establish the intergenerational link between body sizes we use the fact the a child after weaning equals μ times the size of the mother (Charnov, 1991, 1993).

$$m_{t+1} = a \cdot \epsilon \cdot c_t + (1 - d) \cdot \mu \cdot m_t, \quad (6)$$

¹⁸From now on we refer to m_t as body size rather than body mass. Recalling the explanations in the introduction on the interchangeability of height and weight it is clear that the change in terminology is made purely for semantic reasons. The term body size is closer to the the literature in anthropology and economic history, which focusses on human height. It also avoids confusion with the body mass index, a measure of obesity, which we do not address.

where m_t is the size of the child's parent, m_{t+1} is the size of the former child when it becomes itself a parent; the parameter d is defined as in the last section and the parameter a is redefined as $a \equiv \bar{m}/E_C$. Thus adult body size is a compound of energy intake during childhood and “inherited” body size.

The size of an adult is predetermined, and remains constant for the remaining part of his or her life. Hence, we are focusing on the irreversible component of body size. During adulthood, individuals are subject to subsistence requirements. Subsistence consumption depends on body size and on fertility. In particular, we use the fact that rearing up a child from conception to weaning requires a fraction ρ of the mother's metabolic energy E_t (Prentice and Whitehead, 1987; Sadurkis et al., 1988). Thus with B_t denoting energy used up by the mother's own body and n_t denoting the number of children,

$$E_t = \rho \cdot n_t \cdot E_t + B_t \quad \Rightarrow \quad \epsilon \bar{c}_t = E_t = \frac{B_t}{1 - \rho n_t} = \frac{B_0 m_t^b}{1 - \rho n_t}. \quad (7)$$

The last equality follows from employing Kleiber's law, $B_t = B_0 m_t^b$. Here, \bar{c}_t is subsistence consumption, measured in terms of goods. In contrast to the existing literature in economics, subsistence consumption is *not* a constant but depends on the individual size inherited from one's parent through birth and nourishment in childhood as well as on fertility in adulthood. Subsistence consumption is thus generation-dependent and indexed by t .

4.2. Individual's Optimization. A parent maximizes utility U derived from child quality and quantity, where quality is in the Beckerian (1960) sense measured by total expenditure for consumption (i.e. nutrition) of children, C_t . For simplicity we impose a logarithmic form for the utility function:

$$U(C_t, n_t) = \log(C_t) + \gamma \log(n_t) \quad (8)$$

with γ denoting the weight of child quantity in utility. Child expenditure is constrained by parental income y and subsistence consumption \bar{c}_t , i.e. $y_t = \bar{c}_t + C_t$. Combining the budget constraint with equation (7) leads to a single constraint:

$$y_t - C_t - \frac{B_0 m_t^b}{\epsilon(1 - \rho n_t)} = 0. \quad (9)$$

Accordingly, parents maximize (8) s.t. (9), by choosing C_t and n_t .

The first order conditions can be condensed to a single equation describing the quantity-quality trade-off:

$$\frac{\gamma}{n_t} = \frac{1}{C_t} \cdot \frac{\rho \cdot B_0 m_t^b}{\epsilon(1 - \rho m_t)^2}. \quad (10)$$

Subsequently, equations (9) and (10) can be solved for optimal child quantity and quality:

$$C_t = y_t + \frac{1}{2} [z_t + (\gamma - 1)s_t], \quad (11a)$$

$$n_t = \frac{1}{\rho} - \frac{1}{2\gamma\rho y_t} [z_t + (\gamma - 1)s_t], \quad (11b)$$

for $y_t > s_t$, with $s_t \equiv B_0 m_t^b / \epsilon$ denoting consumption needs of a childless (non-pregnant) adult and $z_t \equiv \sqrt{s_t^2(1 - \gamma)^2 + 4\gamma s_t y_t}$. If $y_t < s_t$ income is not sufficient to fuel adult's metabolism and at the corner solution where $n_t = 0$ the population becomes extinct within a generation. If $y_t > s_t$ we see immediately that $C_t > 0$. For consistency we need, in addition, $n_t > 0$. That is, whenever there is child consumption there is also a family. To that end we have to impose $\gamma \geq 1$, i.e. the utility-weight has to be not smaller for having children than for child expenditure.

4.3. Production. Total income, Y , is determined at the macro-level by a body size adjusted technology:

$$Y_t = A m_t^\phi X^\alpha L_t^{1-\alpha} = y_t \cdot L_t, \quad \phi \in (0, 1), \quad \alpha \in (\phi, 1). \quad (12)$$

Here, ϕ is thought of parameterizing the return on body size. L denotes population size and X land. Since land is assumed to be constant (and $\alpha > \phi$) the technology implies stagnation in the long-run at an equilibrium population density L/X unless general productivity A is growing without bound.

4.4. Steady-state. Generally, population evolves according to

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

where n_t is given by equation (11b). At a stationary Malthusian equilibrium we observe $n^* = 1$ and thus from (11)

$$y^* = \frac{\gamma + (1 - \gamma)\rho}{\epsilon\gamma(1 - \rho)^2} \cdot B_0 m^{*b}. \quad (14)$$

Equilibrium consumption per child is obtained as $c^* = C^*/n^* = \rho y^*/[\gamma + (1 - \gamma)\rho]$. Substituting energy consumption per child into (6) and solving for equilibrium body size we get

$$m^* = \frac{a\epsilon\rho}{[\gamma + (1 - \gamma)\rho][1 - (1 - d)\mu]} \cdot y^*. \quad (15)$$

The model therefore predicts a positive correlation between body size and income per capita, in keeping with the empirical evidence (see Section 2.3). In addition, the diet matters (as captured by ϵ), as well as (genetically determined) aspects of human biology (a and d) along with preferences (γ). These properties are broadly consistent with the findings of Akachi and Canning (2007), cited in Section 2, who finds that diet and income per capita both influences body size in Africa. They also find significant fixed effects in their panel regression, which is consistent with a genetic contribution to the cross-country variation in body size, on the African continent. The present model would support such an interpretation.

Inserting (14) into (15) provides equilibrium body size as pinned down solely by preferences and biological fundamentals:

$$m^* = \left[\frac{a\rho B_0}{\gamma[1 - (1 - d)\mu](1 - \rho)^2} \right]^{1/(1-b)}. \quad (16)$$

Observe that the solution implies that technology A does not matter for m^* . This is a useful result, since archaeological evidence suggests a lack of trend in body size over the last two millennia. Since the level of technological sophistication undoubtedly progressed over this period, long-run body size must be independent of technology in the Malthusian regime. The model delivers this result.

From equations (14) and (16) we observe that equilibrium income does not depend on general productivity (A) either. It is pinned down by metabolic constants, family preferences, and the energy exchange rate. Accordingly, steady-state GDP per capita depends on human biology and geographic circumstances (in as much as they determine the diet and thus ϵ). The root cause of the zero impact from A on y is that technology manifests itself in a different way. Using (15) and (12) we obtain equilibrium population density:

$$\left(\frac{L}{X} \right)^* = \left\{ \frac{a\epsilon\rho A}{[\gamma + (1 - \gamma)\rho][1 - (1 - d)\mu]} \cdot m^{*\phi-1} \right\}^{1/\alpha}. \quad (17)$$

In keeping with standard Malthusian models, a higher level of technological sophistication leads to higher population density. This is why A does not affect steady-state labor productivity.

Notice also that, consistent with our empirical results (Table 1), the model predicts an inverse association between population density and body size. Indeed, (17) can be viewed as a bioeconomic counterpart to Damuth’s (1981) law in biology; bigger species have lower average population density. Specifically, the allometric equation estimated by Damuth is that $L/X = \text{constant} \cdot m^{-3/4}$. For humans (17) shows a similar association founded on the access to technology. Indeed, it could be stated as $L/X = \text{constant} \cdot m^{(\phi-1)/\alpha}$, i.e. metabolic requirements are “just” showing up in the constant while technology shapes the scaling parameter. In terms of our basic calibration (Table 2 below) our model suggests that $L/X = \text{constant} \cdot m^{-3.9}$, close to the point estimate obtained in Section 2 (see Table 1, column 1).

4.5. Comparative Statics. Let’s first consider an improvement of technology. This could originate from a change towards higher productivity A , lower dependence on limited land, i.e. lower α , or higher efficiency in using brawn, i.e. increasing ϕ . In any case it “only” eventually leads to a higher population density without any effect on body size and – according to (15) – on income. Initially, a positive productivity shock increases income and parents have more children and nourish them better. The next generation of adults is therefore bigger and more numerous. Since they are more numerous, their average productivity is lower ($\alpha < 1$). Because they are bigger, their energy cost of fertility is larger. Both effects together imply that the bio-economy adjusts to the original values of income, fertility, and body size from above. The only long-run consequence is more densely populated land caused by the temporarily higher fertility rates.

Intuitively, we would expect that human stature depends on the type of food consumed, via ϵ , i.e. the calories that can be extracted from a unit of food consumption. The energy exchange rate (ϵ) changes when new forms of diet occur because, for example, new plants or animals are cultivated or imported so that more (or less) energy can be extracted from a unit of consumption. Interestingly, inspection of (16) shows that ϵ does not affect equilibrium body size.¹⁹ The model predicts that an improving energy exchange rate makes people not bigger in equilibrium but – as shown by (14) – poorer. The intuition for this seemingly puzzling effect becomes clear through inspection of (17) showing that population density rises, when energy intake (ϵ) goes up, a prediction of the model which is consistent with our cross-country findings (see Table 1, column 4).

¹⁹However, *conditional* on income diet does correlate with y (cf. equation (15)). Hence, this result is not at variance with Akachi and Canning (2007), who do document a correlation between aspects of the diet and body size, conditional on y and variables correlated with prosperity.

The chain of effects is as follows. When ϵ 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. This result demonstrates that measuring subsistence needs in terms of income can be misleading. Different levels of income can support different equilibria of subsistence \bar{c}_t . The natural unit of measurement for subsistence needs is the amount of calories, proteins, vitamins etc. consumed, which are in the model summarized in the compound $\epsilon\bar{c}_t$.

The model reveals also some interesting comparative statics with respect to γ . Suppose that the weight for child quantity increases permanently reflecting permanent change of preferences in favor of larger families. From (16) we observe immediately that body size is lower at the new long-run equilibrium, $\partial m^*/\partial\gamma < 0$. Using this result and taking the derivative of (15) we obtain that income at the new equilibrium is also lower, $\partial y^*/\partial\gamma < 0$.

The chain of effects is the following. With γ going up, family size (n_t) increases temporarily and population density increases permanently. With higher expenditure for child quantity parents spend less (calories) for child quality and the next generation of adults is more numerous but shorter. These adults have lower productivity and smaller children at birth which both affects adult size, productivity, and birth weight for the subsequent generation negatively. Again, the next generation will have lower income and for that reason prefer to adjust fertility downwards. The negative income effect operates until n_t approaches its equilibrium again and population stays constant. Thus the model predicts that an intrinsically higher preference for large families makes people shorter and poorer and land area more densely populated.

Suppose that in the wake of the Neolithic revolution, the weight on children in utility rose permanently because settled people can support a larger family.²⁰ The model then predicts a permanent decrease of body size after Neolithic revolution, a result that is confirmed empirically

²⁰Or, alternatively, that people with a large weight on n chose to be farmers, whereas individuals with a more modest preference for child quantity chose to remain hunter-gatherers.

(see e.g. Clark, 2007). The result is robust against a more detailed modelling of a Neolithic revolution including also effects of settlement on human productivity (ϕ) and technology innovations (A). As already shown, productivity improvements will only further push up population density without any long-run effect on deteriorated income and body size.

4.6. Subsistence Dynamics. In order to go as far possible with analytical results we begin by focusing on the special case of equal weights in parental utility. In a later section numerical experiments for the general case will complement our results. With $\gamma = 1$ the model simplifies tremendously. From equation (14) we get a particularly simple expression for consumption per child: $c_t = \rho y_t$. Using it in (6) we see that body size evolves according to

$$m_{t+1} = a\epsilon\rho y_t + (1-d)\mu m_t. \quad (18)$$

Inserting (11b) and (12) into (18) and (13) provides a reduced form of the model in terms of two-dimensional dynamical system for the evolution of body size and population size (land, X , has been normalized to one).

$$m_{t+1} = a\epsilon\rho A m_t^\phi L_t^{-\alpha} + (1-d)\mu m_t \quad (19a)$$

$$L_{t+1} = \frac{L_t}{\rho} - \frac{1}{\rho} \sqrt{\frac{B_0 m_t^{b-\phi}}{\epsilon A}} \cdot L_t^{1+\alpha/2}. \quad (19b)$$

For phase diagram analysis we calculate the isoclines where $\Delta m \equiv m_{t+1} - m_t = 0$, i.e.

$$L = \left(\frac{a\epsilon\rho A}{[1 - (1-d)\mu] m^{1-\phi}} \right)^{1/\alpha}, \quad (20)$$

and where $\Delta L \equiv L_{t+1} - L_t = 0$, i.e.

$$L = \left(\frac{(1-\rho)^2 \epsilon A}{B_0 m^{b-\phi}} \right)^{1/\alpha}. \quad (21)$$

The isoclines intersect once at the unique equilibrium and the $\Delta m = 0$ -locus lies above the $\Delta L = 0$ -locus *iff*

$$\frac{(1-\rho)^2 \epsilon A}{B_0 m^{b-\phi}} < \frac{a\epsilon\rho A}{[1 - (1-d)\mu] m^{1-\phi}} \quad \Rightarrow \quad m < m^*. \quad (22)$$

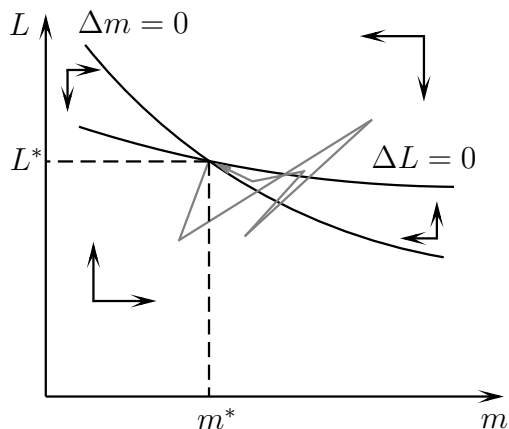
The isoclines and the implied arrows of motion are shown in Figure 4. From inspection of the figure one is tempted to immediately conclude global stability, and the equilibrium to be a

focus. Yet, because time is discrete, adjustment dynamics are less obviously assessed. Besides monotonous convergence towards the equilibrium there exist two other possibilities.

One is adjustment in damped cycles as illustrated by the gray trajectory in Figure 4.²¹ Here, the first move out equilibrium is in southeastern direction. It may have resulted, for example, after a society resting at equilibrium experienced a negative shock of A (a natural disaster, a crop failure). As a consequence of low birth rates and malnutrition the next generation of adults is smaller in stature and less numerous. With less than equilibrium population and the Malthusian mechanism at work, however, these people show productivity and thus income above equilibrium level. As a consequence of their relatively well-being the next generation is large and well fed. As drawn in the Figure, overshooting occurred so that the next generation is situated above the $\Delta L = 0$ -line. Adjustment is in damped cycles initially and then followed by monotonous convergence towards the equilibrium.

These patterns shed light on the empirical evidence discussed in Section 2. During the last 2 millennia both fertility, and body size, have undergone cyclical adjustment. In the present context these patterns emerge because of the dynamic feedback from body size to nutritional requirements.

Figure 4: Subsistence Dynamics: Phase Diagram



A second possibility, which unfortunately cannot be generally ruled out in discrete time, is that overshooting causes instability of the subsistence equilibrium so that the bio-economy leaves the

²¹Strictly speaking only the endpoints at the kinks of the trajectory are values assumed in discrete time. We have connected them with a continuous line for better visibility.

equilibrium in explosive cycles after a shock. In the Appendix C we thus show analytically that the equilibrium is indeed stable when model parameters are selected from empirically plausible ranges.

In order to draw the implied adjustment dynamics we proceed with a calibration of the model. We start with the biological part of the model. For any given $t = \tau$ we can extract d from (4).

$$d = -\log\left(\frac{1 - (m_\tau/m_s)^{1/4}}{1 - (m_0/m_s)^{1/4}}\right) \cdot \frac{4}{\tau}. \quad (23)$$

For calibration we use standardized weight-for-age curve for US males and females as provided by the WHO.²² Both sexes hit the 50 kg-line by the age of $\tau = 14$ implying $m_\tau = 50$. A female grown up weighs on average $m_s = 59$ kg. Child weight after weaning is $m_0 = 9$ kg (implying $\mu = 0.15$). Inserting the data in (23) provides $d = 0.63$ and thus $a = d \cdot m^{*1/4} = 1.69$. Following Prentice and Whitehead (1987) we set $\rho = 0.15$ implying that a woman pregnant with one child must consume 1.2 times the energy of a non-pregnant woman. We set $b = 0.75$ according to Kleiber's law.

Given these values we adjust the metabolic constant B_0 so that m^* in (16) equals 56 kg, which is the mean female weight in our sample of less developed countries (Table 1). For the economic part of the model we set $\alpha = 0.25$ according to Clark's (2007) estimates. We use Weil's (2007) data to approximate $\phi = 0.025$. To get at ϵ we do the following. Suppose equilibrium income is 400 (international Dollars) per year. In that cases, during the period of adulthood measured by the length of the fecundity period (assumed as 20 years), equilibrium income is \$ 8000. This pins down ϵ to 0.026. 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 $A = 1$). Parameters and steady-state values are summarized in Table 2.

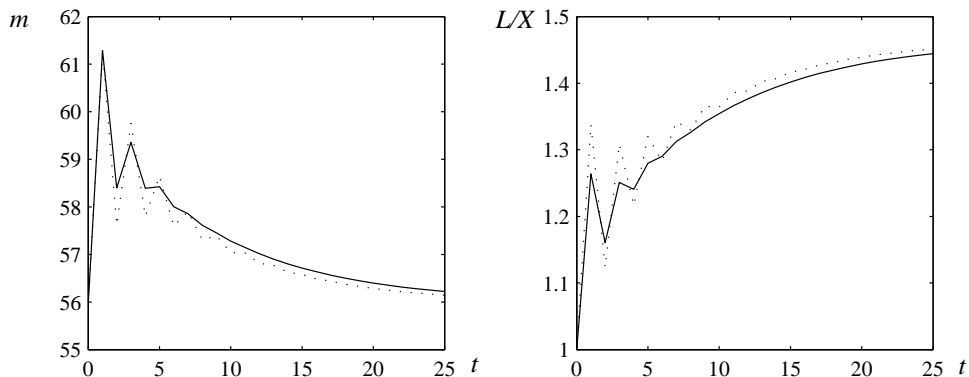
TABLE 2: PARAMETERS OF THE BIO-ECONOMY

a	b	d	μ	ρ	ϵ
1.69	0.75	0.63	0.15	0.15	0.026
α	ϕ	A	X	m^*	y^*
0.25	0.025	1	1	56	400

²²<http://www.who.int/nutgrowthdb/reference/en/>.

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 (e.g. the end of the little ice age). Adjustment dynamics are qualitatively identical for a permanent rise of the energy exchange rate ϵ , which could arise due to the cultivation or import of a new crop. In a 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^* star unchanged. The old equilibrium lies south east of the new equilibrium capturing the fact that people are too short and too few with respect to the improved conditions. As a result the next generation of children will have more nourishment at their disposal. Adjustment dynamics explained in connection with Figure 4 set in.

Figure 5: Adjustment Dynamics: Permanent Technology Shock



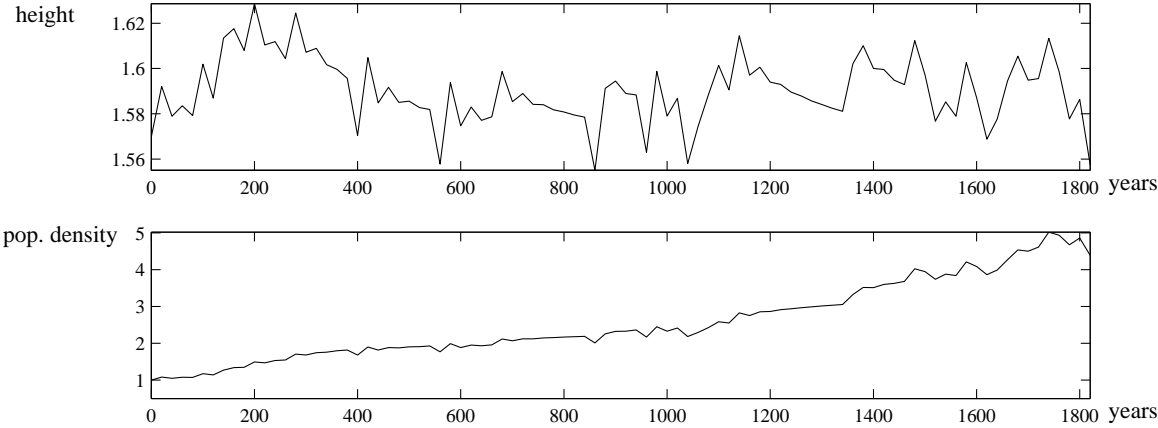
Parameters from Table 2 and $\gamma = 1$ (solid lines), $\gamma = 1.5$ (dashed lines), and $\gamma = 2$ (dotted lines). A higher value for γ makes adjustment more volatile but otherwise structurally similar.

Solid lines in Figure 5 show the resulting adjustment dynamics for benchmark parameters. Sensitivity analysis with respect to γ is represented by dotted and dashed lines. It reveals that the result is structurally stable against variation of the preference parameter. Generally, higher productivity or cultivation of more energy- providing food leads to a *temporary* rise in body size and a *permanent* rise of population size (and density). Over the first five generations (100 years) we observe cyclical adjustment behavior.

At a more detailed level the data series for height, as depicted in Figure 2, 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 0.75, $A_{t+1} = 1.03 \cdot A_t$, i.e. a positive productivity shock with probability 0.15, and $A_{t+1} = 0.93 \cdot A_t$, i.e. crop failure or technological regress (Aiyar et al., 2006), with probability 0.1. 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; 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 6: Female Body Size and Population Size from Year 0 to Year 1800



Parameters as for Figure 5. 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

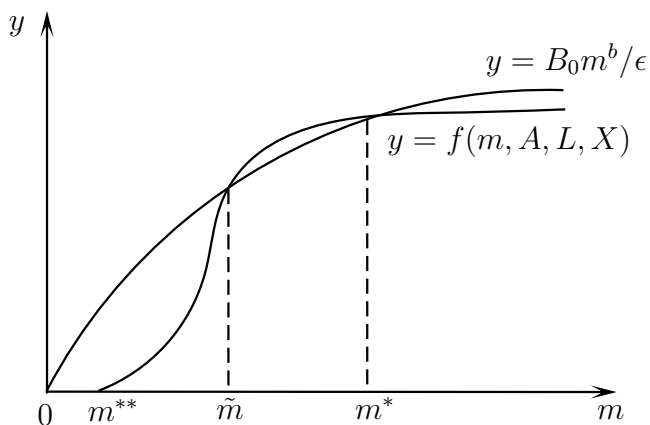
Figure 6 shows an example of a trajectory for our benchmark economy from Table 2. We simulated the economy for 90 generations, which yields the demo-metabolic history of a society from year 0 to year 1800. The result corresponds quite well with the actually observed history, as discussed in Section 2.4. That is, the trajectory displays long periods of smooth development, interrupted by abrupt changes and cyclical recovery. The fact that positive productivity shocks occur slightly more often than negative ones allows the population to grow on average. During the period under investigation it has approximately quintupled (in accordance with the empirical facts, Kremer, 1993). At the same time there are cyclical fluctuations but no positive trend of

body size discernable. Body size goes up after positive shocks and down after negative ones and returns to its long-run equilibrium afterwards. This way, our theory explains why body size is justifiably used by anthropologists and economic historians as a measure of economic well-being although – on average – positive productivity shocks in history have not manifested themselves in – on average – rising body size.

5. CONVEX-CONCAVE PRODUCTION AND THE MALNUTRITION TRAP

One seeming criticism of our modelling so far could be that the production function does not take into account a lower limit of energy intake below which productive (or any other) activity becomes impossible and labor supply goes to zero. This assumption is visualized in Figure 7 where the per-capita production function $y(m, A, L, X)$, hits the m axes at a positive value. The figure shows the most frequently discussed case in the literature (see e.g. Leibenstein, 1957, Bliss and Stern, 1978) where production is convex-concave, or s-shaped in m although this is not essential. The essential feature is that output produced lies below output (energy) needed to feed a given body size for m below a critical \tilde{m} . Production required is found from energy intake according to Kleiber’s law divided by the energy exchange rate. It is thus unambiguously concave over the whole range of m .

Figure 7: Output Produced and Production (Energy) Required



The sad fact visible in Figure 7 is that people with initial size below \tilde{m} are not capable to produce the energy required in order to maintain their own body shape. They emaciate up

to a lower bound m^{**} . If they don't starve, they survive living off the commons or begging. Although Figure 7 is a time-less graph, it suggests two stable equilibria at m^* and m^{**} . From this observation some authors have argued in favor of a malnutrition-driven poverty-trap.

Here, we are not questioning the view that such poverty-traps exist at the individual level. The indirect empirical evidence for this is overwhelming (see e.g. Fogel, 1994, who argues that one-fifth of the population was situated close to m^{**} in 18th- hundred England and France). Yet, we will challenge the possibility of a *general* equilibrium at m^{**} . In order to get this argument straight it is helpful to introduce the following definitions. An *equilibrium of subsistence* (Malthus, 1798) is defined by zero population growth. An *equilibrium of destitution* (Dasgupta, 1993) is defined by zero labor supply.

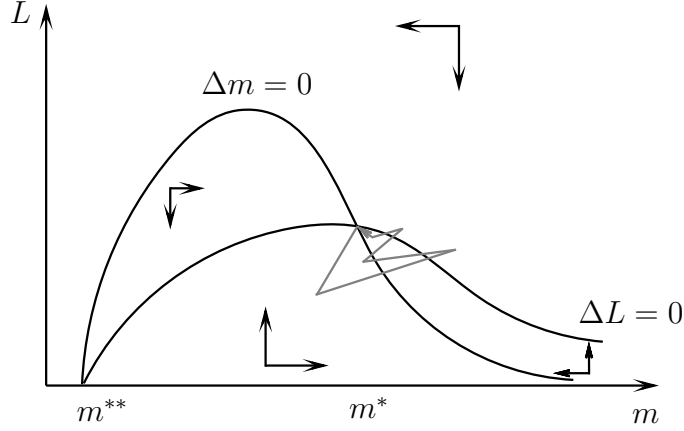
From these definitions one may already suspect that destitution cannot be a stable general equilibrium. It will now be proven. The new convex-concave production function changes the shape of the isoclines. In particular, both are now upward sloping at low m hitting the m axes at a some finite equilibrium of destitution m^{**} . The equilibrium of subsistence is observed at the intersection at some $m^* > m^{**}$. The crucial element of the proof is that it remains to be true that the $\Delta m = 0$ -locus lies above the $\Delta L = 0$ -locus *iff*

$$m^{**} < m < m^*.$$

To see this replace m^ϕ in (22) by a general $f(m)$ with $f(m^{**}) = 0$ and note that the condition is independent from any positive transformation of $f(m)$.

With (22) still being valid the phase diagram of Figure 8 results. The equilibrium of destitution is unstable. The intuition why a situation where the whole society is destituted cannot be a *dynamic* equilibrium is straightforward and follows from the Malthusian mechanism. The destitute people will only have few children. This will make the next generation (of low population density) small in body size but productive. As a result, they can afford to nourish their children comparatively well so that the following generation of adults has body size above m^{**} . An adjustment process towards m^* (possibly cyclical) is initiated. Thus, while the static-micro textbook model of the malnutrition trap suggests that there are two equilibria attainable, a dynamic-macro reformulation supports only one of these as a attainable in the long-run. Subsistence as a general equilibrium phenomenon can prevail over centuries, whereas destitution cannot.

Figure 8: Subsistence Dynamics with Convex-Concave Production: Phase Diagram



6. THE TAKE-OFF FROM SUBSISTENCE

While our two-dimensional model of the Malthusian equilibrium can be fruitfully applied to the evolution of human history it does not – like Malthus original one-dimensional theory – hold for industrial and modern societies. Modelling the full transition towards such a society is beyond the scope of this paper. We can, however, show that our model captures one particular feature of the take-off from subsistence: A permanent yet bounded increase of human body size (i.e. height, see Steckel, 1995, Clark, 2007).

The take-off is initiated by the introduction of permanent productivity growth (instead of discretionary shocks). For simplicity we assume $A_{t+1} = (1 + g)A_t$ where g is a constant rate of TFP growth. Assuming $g > 0$ renders the Malthusian equilibrium unstable. In order to discuss the new dynamics we introduce the auxiliary variable $x_t \equiv L_t^\alpha / A_t$ and thus

$$x_{t+1} = \frac{L_{t+1}^\alpha}{A_{t+1}} = \frac{n_t^\alpha}{1 + g} \cdot x_t. \quad (24)$$

with an equilibrium where $n_t = (1 + g)^{1/\alpha}$, which is larger than one for $g > 0$. Permanent technological progress triggers population growth.

In order to obtain the new two-dimensional dynamic system we insert the definition of x_t into y_t and n_t from (11b) into (24). Thus (18) and (24) are rewritten as

$$m_{t+1} = \frac{a\epsilon\rho m_t^\phi}{x_t} + (1-d)\mu m_t \quad (25a)$$

$$x_{t+1} = \frac{1}{(1+g)\rho^\alpha} \cdot \left[1 - \sqrt{\frac{B_0 m_t^{b-\phi} x_t}{\epsilon}} \right]^\alpha \cdot x_t. \quad (25b)$$

The $\Delta m = 0$ and $\Delta x = 0$ loci are given by

$$x = \frac{a\epsilon\rho}{1 - (1-d)\mu} \cdot m^{\phi-1}$$

$$x = \frac{\epsilon [1 - (1+g)^{1/\alpha} \rho]^2}{B_0} \cdot m^{\phi-b}.$$

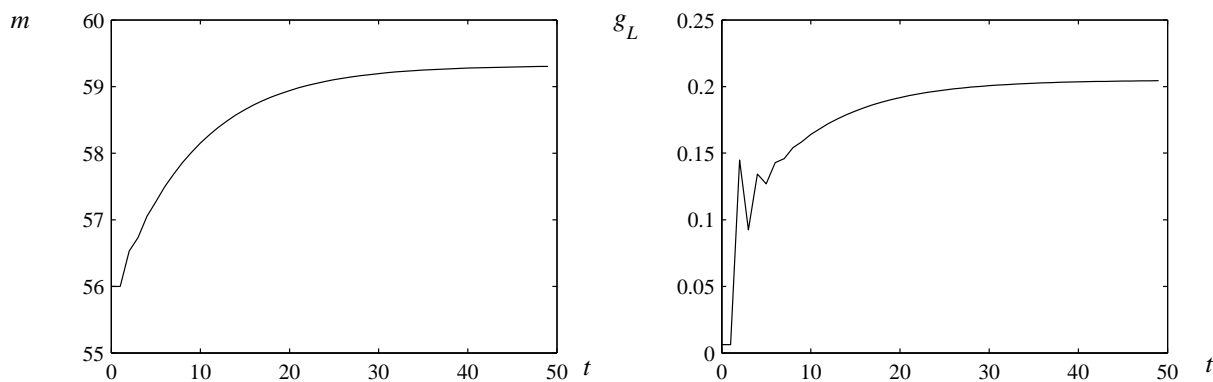
Inspection of these two equations reveal that the implied phase diagram is structurally identical to the $L - m$ diagram in Figure 3. In particular, there exists a unique non trivial positive intersection at some (x^*, m^{***}) which is stable for standard parameters. A permanent increase of g , however, shifts the equilibrium to the south-west reflecting higher labor productivity (lower $x = L^\alpha/A$) and larger body size m . Perpetual technological progress and income growth leads to a permanent yet finite increase of body size. Equilibrium size is obtained as

$$m^{***} = \left[\frac{a\rho B_0}{\gamma [1 - (1-d)\mu] (1 - (1+g)^{1/\alpha} \rho)^2} \right]^{1/(1-b)}. \quad (26)$$

Body size is increasing with the growth rate and is – as comparison with (16) shows – larger than at the Malthusian equilibrium of economic stagnation.

Figure 9 shows adjustment dynamics implied by our benchmark parameterization after a permanent rise from $g = 0$ to $g = 0.01$. Implied fertility change is recovered from (11b). The Figure shows that technological progress triggers a monotonous increase of body size and an initially cyclical and then monotonous increase of population growth. The first (generation-) periods of transition correspond well with the empirical facts for Europe in the 19th. Economic growth is accompanied by a gradual but steady increase of body size, i.e. height (see Steckel, 1995, 2001) and an initially steep and later flattening increase of population growth (Kremer, 1993). At later periods, however, results become less plausible because population growth fails to revert its trend. This result occurs because the model neglects that perpetually rising income triggers a change of fertility behavior thereby initiating a demographic transition (Galor, 2006).

Figure 9: Take-Off from Subsistence



The variable g_L denotes annual population growth per generation in percent.

7. CONCLUSION

The present paper has developed a bioeconomic model with the aim of studying the growth process during “Malthusian stagnation” and the process of “take-off” (Galor and Weil, 2000). In particular, the model contributes to the literature by describing the long-run evolution of the representative individual’s body size, and her subsistence requirements. The links between childhood nutrition, adult body size and subsistence requirements are based on deep microfoundations, drawing on recent work in the field of biology. The theory involves a two-dimensional Malthusian equilibrium concept, featuring a constant number and size of individuals.

The model demonstrates how human biology and preferences determine long-run body size. In a Malthusian state, and without evolutionary changes, the model predicts an absence of a secular trend in body size over time. Yet, if the economy is perturbed by shocks (be that technological, climatic, or diet related) oscillatory adjustment to steady-state, in body size and population, may prevail. The state of stagnation in body size comes to an end, however, if technological progress accelerates. In response to such a change in the economic environment, average body size rises gradually towards a biologically determined upper limit. These predictions are consistent with available evidence pertaining to body size (height) from 1 A.D. to the 19th century. In addition, the model predicts an inverse association between body size and population density, as well as an influence from diet on density, for body size given. Both predictions are consistent with available evidence.

The model does not allow for a full demographic transition whereby fertility ultimately declines. Such an extension could, however, be provided by incorporating another dimension of “child quality”: human capital. Following Galor and Weil (2000), this extension would involve the feature that if the underlying productivity growth rate accelerates, investments in human capital eventually rises and fertility declines. The associated rise in income per capita would support increases in body size, which elevates subsistence consumption; declining fertility works in the opposite direction however. Studying subsistence dynamics during (and after) the demographic transition, in a bio-economic setting as developed above, is left for future research.

The framework could also be fruitfully extended to include the impact of disease on subsistence requirements and body size. There is considerable evidence to suggest that illness importantly affect basal metabolism; reconvalescence is energy intensive, and thus elevates subsistence requirements. Hence, the frequency of disease shocks could prove to be an important determinant of body size, population size and productivity in a Malthusian regime. Furthermore, this extension would allow for a comparative analysis of mortality and morbidity; in the end, morbidity (associated with disease shocks) may have had a much larger impact on the trajectory for productivity in pre-industrial times than changes in mortality. This extension is not straightforward, however. While bodily temperature (fever) should work so as to speed up biochemical processes, and among them metabolism, diseases differ in terms of their impact on metabolism nonetheless. Currently there appears to be little consensus in the context of how this link is to be modeled in a unifying manner (Hoffer, 2003).

Introducing endogenous subsistence, in the manner described above, may also be important in addressing more contemporary issues. For example, it may inform the ongoing convergence debate. That is, the debate as to whether data support the club- convergence hypothesis, or rather conditional convergence. The former view involves a vision of the growth process where multiple equilibria arise while the latter is associated with a unique steady-state equilibrium. A prominent explanation for multiple equilibria involves the introduction of subsistence consumption into a neoclassical growth framework (e.g. Azariadis, 1996). Recently, this approach has been criticized on quantitative grounds in an interesting paper by Kraay and Raddatz (2007). The authors demonstrate that the “s-shaped” association between average savings and per capita income, which should arise due to a minimum consumption threshold, is not borne out in the data. However, if the threshold is better conceived as a structural characteristic, which should

be controlled for in the analysis, their tests are no longer conclusive. The present theory implies that subsistence consumption is to be conceived as a structural characteristic, and that this level may be subject to substantial variation across countries and time. Of course, it is an open question whether allowing subsistence to be endogenous still admits multiple equilibria to arise in otherwise standard neoclassical growth models. These issues also appear to be worthwhile topics for future research.

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

The basic fact exploited by West et al. (1997) is that the terminal branches of the network (the capillaries) are size-invariant units. From this and the conservation of the fluid as it flows through the system follows that the total number of capillaries is proportional to the metabolic rate. Consider a network of branching vessels with ν levels of branching and η branches per node. Let $k \in \{1, \dots, \nu\}$ indicate the level of branching. Nature optimizes through choice of the radii r_k and lengths l_k of the vessels at every level k . West et al. have solved the optimization problem given the hydrodynamic and elasticity equations for blood flow and a space-filling condition (requiring that all cells are served). They have shown that the optimal network is a self-similar fractal with two characteristics. (i) It is volume preserving so that $\nu_k l_k^3 \approx \nu_{k+1} l_{k+1}^3$ where ν_k is the number of branches at level k . (ii) It is area preserving so that $\pi r_k^2 = \eta \pi r_{k+1}^2$, i.e. the cross-sectional area of a branch at level k equals the sum of the cross-sectional area of branches at the next (lower) level. Noting that $\nu_{k+1}/\nu_k = \eta$ one gets two invariant scale factors, $\beta \equiv r_{k+1}/r_k = \eta^{-1/2}$ and $\gamma \equiv l_{k+1}/l_k \approx \eta^{-1/3}$. For example, as blood flows down through a bifurcating hierarchy ($\eta = 2$) the radii of vessels decrease with factor $1/\sqrt{2}$ whereas the length of vessels decreases at rate $1/\sqrt[3]{2}$.

Finally, West et al. showed that the total volume of blood in an energy minimizing network is proportional to body mass m . This feature combined with the fractal nature of the network implies scaling according to (1). To see this calculate the total volume of blood.

$$V_b = \sum_{k=0}^{\nu} \pi r_k^2 l_k \eta^k = \frac{1 - (\eta\gamma\beta^2)^{-(\nu+1)}}{1 - (\eta\gamma\beta^2)^{-1}} \eta^\nu V_c \approx \frac{(\gamma\beta^2)^{-\nu}}{1 - (\eta\gamma\beta^2)^{-1}} V_c$$

with V_c denoting the volume of a capillary, an invariant unit. Conclude that blood volume and thus mass is proportional to $(\gamma\beta^2)^{-\nu}$ implying that $\log(\nu)$ is proportional to $-\log(m)/\log(\gamma\beta^2)$. The metabolic rate is proportional to the number of capillaries n^ν implying that $\log(B)$ is proportional to $\nu \log(n)$ and thus to $-\log(m) \cdot \log(n)/\log(\gamma\beta^2)$. Insert β and γ to find that $\log(B)$ is proportional to $3/4 \log(m)$ which is Kleiber's law.

Appendix C

The elements of the Jacobian matrix J of dynamic system (19) evaluated at the steady-state are given by

$$\begin{aligned} J_{11} &= \phi [1 - (1 - d)\mu] + (1 - d)\mu \\ J_{12} &= -\frac{\alpha}{L^*} [1 - (1 - d)\mu] m^* \\ J_{21} &= -\frac{(1 - \rho)L^*}{2\rho m^*} (b - \phi) \\ J_{22} &= 1 - \frac{1 - \rho \alpha}{\rho} \frac{\alpha}{2}. \end{aligned}$$

Stability requires that the eigenvalues of J are less than one in absolute terms, or alternatively that $|\det(J)| < 1$ and $|tr(J)| < 1 + \det(J)$. The trace and determinant are computed as

$$\begin{aligned} tr(J) &= \phi [1 - (1 - d)\mu] + (1 - d)\mu + 1 - \frac{1 - \rho \alpha}{\rho} \frac{\alpha}{2} \\ \det(J) &= [1 - (1 - d)\mu] \left[\phi - \frac{1 - \rho \alpha}{\rho} \frac{\alpha}{2} b \right] + (1 - d)\mu \left(1 - \frac{1 - \rho \alpha}{\rho} \frac{\alpha}{2} \right) \end{aligned}$$

The condition that $|tr(J)| < 1 + \det(J)$ simplifies after some algebra to $(1 - b) [1 - (1 - d)\mu] > 0$ and is thus always fulfilled. The condition that $|\det(J)| < 1$ can be written as

$$\left| \frac{1 - \rho \alpha}{\rho} \frac{\alpha}{2} \left(b + \frac{(1 - d)\mu}{1 - (1 - d)\mu} \right) - \phi \right| < 1.$$

Given the biological parameters, it requires that α must not be too large as compared to ϕ . Intuitively, if α were too large, there would be too little Malthusian forces in the model, i.e. the positive effect of body size on productivity would overcompensate the negative effect of population size. When we plug in the biological parameters of the calibrated model, stability requires

$$\alpha < \alpha_{crit} \equiv 0.49 + 0.44\phi.$$

Our calibration of economic parameters, $\alpha = 0.25$ and $\phi = 0.025$ thus renders an equilibrium safely within the range of stable equilibria.

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