Long-Run Trends in Human Body Mass

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Abstract:

Over the past two million years human body mass first increased, and later declined, peaking about 50,000 years ago. This paper sets up a model with natural selection among body types to explain this pattern. Population, technology, and average body mass evolve endogenously and interdependently in such a way that a take-off in technological progress generates rising population density and resource depletion. This in turn makes large bodies less useful in food procurement, while keeping their metabolism requirements fixed. The result is a shift in the reproductive advantage from big to small bodies and an endogenous reversal of the time trend in body mass.

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1 Introduction

This paper describes some trends in human body mass over the very long run, and proposes a theory which can explain these trends. The first humans arose about two million years ago. Up until about 50,000 years ago humans grew bigger, whereafter human body mass began to decline. Indeed, the decline over the last 50,000 years has been comparable in size to the preceding incline but much faster. We suggest that these physiological trends can be understood by linking them to trends in human population density and technology.

By "humans" we here mean members of the whole genus *Homo*, not only the species *Homo sapiens* (anatomically modern humans). The task is thus to model a process through which humanity as we know it came to be. Many changes occurred in this process, not least in the size and organization of the brain. However, changes in body mass are particularly interesting because they were not monotonic, and because they seem to relate to changes in the ecological environment.

The facts described here should not be confused with humans becoming both taller and fatter over the last three centuries, or so, which is probably due to improved nutrition and health as humans have left a stage of Malthusian stagnation and incomes have started to grow (see e.g. Fogel and Costa 1997). The focus here is on a completely different epoch, and much longer time spans: not three hundred years but several tens of millennia, and more. Physiological changes over such long time spans are more likely to be driven by natural selection than changes in e.g. food supply. Notably, humans are *smaller* today than 50,000 years ago but it is hard to argue that we were less undernourished then.[1]

This paper sets up a growth model which can explain these facts and give them a useful interpretation. This contributes to a growing literature using economic theory to analyze issues in anthropology and biology (e.g. Smith

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[1] Section 4 offers some thoughts on the role played by natural selection in shaping human body size in more recent times.

1975, 1992; Brander and Taylor 1998; Galor and Moav 2001, 2002, 2005; Robson and Kaplan 2003), none of which has yet explicitly analyzed trends in body mass.

The starting point of the theory proposed here is that large body types can procure more food than small, but also carry higher costs in terms of metabolism. An agent's fertility depends on food procurement net of his metabolic needs. A denser population makes a big body less useful in food procurement, while keeping metabolism requirements fixed. Thus, population growth shifts the reproductive advantage from large to small bodies. Moreover, the model generates a population growth path which produces this reproductive shift endogenously.

The initial population is assumed to be sparse and dominated by small types (which is consistent with fossil data and the first humans having just evolved bipedalism). This generates an initial slow parallel rise over time in average body mass and population density. Rising population levels at some stage spur faster technological progress, and thus even denser population, and eventually a reversal in body trends.

The critical assumption is that body mass and technology have low complementarity so technological advancements affect small and big types' reproduction symmetrically. However, the rise in population density that follows from technological progress adversely affects big types.

Physical anthropologists do not have many theories of what caused these trends. Rather, their work is mostly descriptive and whatever explanations can be found are often little more than lists of other facts, and quite "partial equilibrium" in character. For example, Ruff (2002) explains the rising trend in body mass by human habitats expanding into colder regions (like Europe) where many of the bigger fossils have been found. It is well known that a big body protects against cold. However, that does not explain why body mass declined over the last 50,000 years. Robson and Kaplan (2003) focus on rising brain-to-body ratios in human history, which in part was driven by decreasing body mass in the most recent phase, but do not address why body and brain mass increased in tandem before that. The model proposed here explains both the rise and the decline in body mass. It is also consistent with selection for smaller body documented among other animals in response to resource limitation, in particular so-called island dwarfism.

The rest of this paper is organized as follows. This section proceeds by describing the facts (Subsection 1.1), and linking the paper to some recent work (Subsection 1.2). Next, Section 2 sets up the base-line model, including a quantitative illustration (Subsection 2.5). The base-line model is among the simplest in which the results go through, but most results can be replicated in alternative and richer models, as shown in Section 3: for example, body mass (and technology) can be used in competition for food against other humans (Subsection 3.1); body mass and technology need not be perfect substitutes (Subsection 3.2); and the resource base may evolve endogenously over time (Subsection 3.3). Section 4 ends with a concluding discussion.

1.1 Empirical motivation

1.1.1 Body mass

The facts described here refer to body mass (or weight) but humans have changed also in other ways over the last two million years. Examples of changes include the development of bipedalism, increased brain-to-body mass (or encephalization) ratio, increased longevity, reduced hair cover, and changes in height and body shape. Neanderthals, for example, who died out about 40,000 years ago, had shorter limbs and larger trunks compared to humans alive today. Part of their greater weight was thus due to different body proportions, rather than height. When it comes to setting up a model we shall think of changes in one single variable, body mass.

Knowledge about body mass (or other characteristics) of individuals who lived so long ago is based on inferences made from the population of living humans and other primates. From that population physical anthropologists know quite well the correlation between the size and shape of many small bones, and the age, sex, and body weight of the individual it belongs to. With the right statistical techniques, even small and scattered fossil bones can thus generate useful inferences about e.g. body mass. There is a debate in the profession about how to interpret several individual fossils but the general long-term trends in body mass described here do not seem very controversial.[2]

Table 1 lists the estimated body weights for different samples of humans and their respective time ranges.[3] Figure 1 shows a time plot based on the data in Table 1. Body mass increased up until about 50,000 years ago and then declined. Since the decline is so rapid compared to the preceding incline the changes are easier to see by using a logarithmic time scale.

We are not the first to note this inversely U-shaped pattern, even in the economics literature. For example, the same body mass trends can bee seen in Robson and Kaplan (2003, Figure 1), although in a different context (and also somewhat harder to distinguish because the time scale is not logarithmic). There is also complementary evidence supporting these trends. Ruff (2002, p. 216) points out that many large-sized material artifacts have been found from the periods during which human body mass estimates are relatively big. This suggests that the people who used them were big too.

These changes in body mass also reflect the rise and fall of various human species and changes in geographical habitats. For example, the decline is partly reflected in the extinction of the Neanderthals (late archaic *Homo sapiens* in Table 1), who were a separate species from modern humans and physically adapted to a colder climate. However, also within our own species, and after the Neanderthals were extinct (i.e., from 35,000 years ago and onwards), body mass has declined over time.

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[2] See Ruff (1994, 2002) and Ruff et al. (1997) for a more detailed description and discussion of the facts. McHenry (1992) discusses the regression techniques.

[3] The data over living humans to which the fossil body weights are compared refer to a large set of ethnic groups from all over the world; from Irish, to Australian aborigines, to Inuites, to Yemenite Jews (Ruff 1994).

Initial conditions In the model set up later, in order to replicate the incline in human body mass over the earlier phase of human development the population must start off dominated by small body types; this is consistent with the data in Figure 1 and Table 1. One explanation for this initial state of "disequilibrium" is that pre-human species lived in trees. Like for many of our primate relatives today, the bodies of tree dwellers are constrained in size by what tree branches can carry. About two million years ago, as the environment where our ancestors lived became more open and less forested, humanity started to evolve in the form of several new bipedal and terrestrial species. Having just "climbed down from the trees," these first humans were thus relatively small. In fact, there was a small initial leap in body mass: the first human species were bigger than their pre-human predecessors. However, the upward trend in body mass continued also among subsequent human species (Ruff 2002, p. 214 and Figure 1).

1.1.2 Population and technology

Whereas body mass has not evolved monotonically, population and technology have. Figure 1 shows the time trend for total world population from one million B.C. The numbers are of course not precise but the general trend is not too controversial.

Technology, and its growth rate, have been increasing over time, at least as measured by the number of innovations per millennium; see Tables 2 and 3.[4] Notably, technological progress increased also before the agricultural revolution, which dates to some time after 10,000 B.C. Also, Table 2 suggests an initial rise in technological progress around 40,000 B.C., about the time body mass began to decline. This coincides with the arrival of anatomically modern humans in Europe, able to produce culture, music and art, displacing the technologically and culturally backward Neanderthals. This is sometimes referred to as the "Great Leap Forward" (Diamond 1992, Ch. 2).

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[4] One could consider weighing these innovations in various ways; Abhijit Sengupta suggested that beer should count as five inventions.

In the model presented later technology and population interact in such a way that population growth generates technological progress, or new ideas, and thus further population growth. This relates to a broad literature on scale effects in growth models, going back at least to Kremer (1993); see Jones (2005) for an overview. Such mechanisms may be particularly relevant in the very long-run historical context considered here. For example, many archeologists argue that the invention of agriculture and many pre-agricultural innovations were driven by rising population pressures and the extinction of large prey (e.g. Smith 1975, Cohen 1977; see Weisdorf 2005 for an overview).

1.1.3 Resource depletion and declining body mass

Resource depletion may also have driven the decline in human body mass. The benefits of having a big body in food procurement are presumably greater in hunting, in particular of large prey (e.g. mammoths), compared to gathering food, hunting small prey (e.g. rabbits), or using slash-and-burn farming. For example, spears would be easier to use for big individuals; later technologies like fish gorgets or bow and arrow (see Table 3) would not require the same physical strength or body mass (Frayer 1981).

At the same time, there are costs of having a big body in terms of greater energy requirements. According to data from FAO/WHO, the maintenance energy required by an adult weighing 65 Kg. is about 2600 kcal per day; the corresponding requirement of a 10 year-old of 31 Kg. is 1750 kcal per day (Payne 1992, Table 3.1). Although there is some debate about the formulas used, these requirements are supposed to give a rough idea of what an individual needs to survive.[5] Moreover, these numbers exclude energy requirements for growth and physical activities (both of which are greater for 10-year olds) and may thus indicate how energy requirements would dif-

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[5] In this example, energy requirements are calculated as 1.5 times the so-called basal metabolism rate (BMR), which in turn is a linear function of age, sex, and body mass. Payne (1992) suggests energy requirements should rather be calculated as 1.27 times BMR.

fer between full-grown individuals of the same weights. These numbers then imply that a reduction in body size by about 50% (from 65 to 31 Kg.) would reduce the amount of food needed for survival by about 33%, arguably not a negligible amount.

This seems to suggest that resource depletion may have shifted the advantage from big to small bodies. Moreover, that such depletion took place is well documented by, among others, Smith (1975) and Diamond (1992, Chs. 17-18). Examples include mammoths, bear-sized beavers, saber-toothed cats, and various species of lion, cheetah, camel, rhino, and horse. The timing seems roughly right too: these extinctions preceded (and perhaps caused) the introduction of agriculture 10,000 B.C.; presumably some prey began to be scarce and harder to find long before that.

Island dwarfism It is well known among biologists that large mammals – in particular carnivores, like humans – tend to be smaller in ecologically isolated environments, most notably on remote islands, known in biology as the "island rule" (Foster 1964).

Similar to the mechanisms at work in the model presented here, biologists believe that such dwarfism is driven by the limited amount of resources available on islands. When resources are locally depleted on the mainland animals can simply migrate to new areas but on islands they either become extinct, or only smaller specimen survive (Lomolino 1985).

Many examples of such island dwarfism have been documented among other animals, e.g. elephants (Roth 1992) and three-toed sloths (Anderson and Handley 2002). The evolution of reduced size can also be relatively rapid. Anderson and Handley (2002) document a divergence in skull length of sloths, from around 8 cm on the mainland to 7 cm on the island Isla Escudo off the coast of Panama, which was separated from the mainland about 9,000 years ago. The age of first reproduction for sloths is about 3 years; this makes about 3,000 generations. Equally many generations for humans would amount to 60,000 years if each generation corresponds to 20 years. This is in the same order of magnitude as the 50,000-year phase of body mass reduction among humans from 80 Kg. to 60 Kg. (cf Table 1).

In fact, it was only recently that a fossil of a previously unknown *human* species, about one meter tall when fully grown, was found on the island Flores in the Indonesian archipelago, thus named *Homo floresiensis* (Brown et al. 2004, Diamond 2004, Mirazón Lahr and Foley 2004). In a sense, the model presented here can be thought of as an "island dwarfism" story; it explains the decline in body mass of modern humans over the past 50,000 years, or so, as the result of resource depletion on the larger "island" of planet Earth.

1.2 Previous literature

This paper contributes to a number of recent economic theories on human evolution. Galor and Moav (2002) seek to explain the "origin of growth" in a model where agents have different preferences over quality and quantity of children, which are inherited (see also Galor and Moav 2001). High-quality agents invest more in their offspring, raising incomes and thus reproductive success of the next generation of the dynasty. Over time, natural selection thus works to expand the high-quality agents' representation in the population. Through a skill-technology complementarity this eventually sparks a take-off in technological progress.

Others study the role played by natural selection in the shaping of the human mind, e.g. risk preferences and rationality (Robson 2001, 2002, 2003, Galor and Michalopoulos 2006).

This paper abstracts from the evolution of preferences, but may indirectly contribute something to the mentioned theories, since changes in body mass and other physical characteristics could be genetically linked to behavior and preferences.[6]

Galor and Moav (2005) model changes in human longevity, suggesting

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[6] For example, dogs are smaller and behaviorally different from wolves from which they were bred (see further the discussion in Section 4). Also, different from preferences, changes in body structure can be documented and estimated from fossil remains.

that rising population density, and the associated rise in extrinsic mortality (e.g. diseases), increased the reproductive advantage of agents predisposed to high somatic investment (e.g. improved immune systems). The model can replicate an empirically observed non-monotonic pattern in life expectancy: an initial decline and a subsequent rise in longevity.[7]

Robson and Kaplan (2003) focus on the interaction between longevity and brain size, suggesting that modern humans started to evolve due to a drier climate, an expanding savannah-like environment, and an increase in high-energy foods, like nuts. These foods required skills to harvest, thus raising the value of large brains. Brains are costly to build and maintain early in life and bring benefits late in life, so a large brain implies a greater value of longevity. Longer lives further increase the returns to large brains, in a mutually reinforcing process of human evolution.

Again, this paper does not focus on evolutionary changes in longevity or brains, but rather on changes in body mass, or "brawns."

Horan et al. (2005) analyze the extinction of the relatively large-sized Neanderthals about 35,000 years ago (see also Faria 2000). The model set up here seeks to explain both the initial rise in body mass and the subsequent decline (notably, humans have become smaller also after the Neanderthals died out). Also, technological progress plays a more central role here, compared to Horan et al. (2005) who focus on the rise of trade and cooperation. Arguably, many factors played a role and no single model contains all relevant components; rather these models should be seen as complementary.

The role played by resource depletion in this model relates to an environmental literature analyzing the effects and causes of such depletion in

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[7] Another paper focussing on diseases is Borghans et al. (2005), who document that characteristics of the so-called Major Histocompatibility Complex (MHC), which determines defence against infections, are correlated with certain economic and health outcomes, and levels of trust, in cross-country data. Since infectious disease spread through contamination one agent's resistance to a disease exhibits externalities. The authors theorize that societies with more cooperation better internalize such externalities, generating the observed co-variation in the data.

pre-industrial and pre-agricultural societies (Brander and Taylor 1998, Smith 1975, 1992). In the Brander-Taylor model humans consume out of a finite renewable natural resource. This can explain the expansion and subsequent downfall of human populations, as illustrated by the geographically isolated Easter Island. In the Brander-Taylor model agents are identical so resource depletion impacts only the size of the population, and not its composition. Here resource depletion exerts different effects on different body types, thus affecting the distribution of body types through natural selection. This story arguably makes sense over very long time spans and in a global context, where the "island" is planet Earth rather than Easter Island. It also resembles the so-called island dwarfism phenomenon, as discussed in Subsection 1.1 above.

There are other papers which do not model natural selection but study growth over relatively long time spans of several thousand years (e.g. Galor and Weil 2000, Lagerlöf 2003, 2006). The aim is typically to explain, or account for, growth rates in living standards being stagnant for very long and then taking off just some hundred years ago with the industrial revolution, simultaneously with first a rise, and later a decline, in population growth rates (a demographic transition). The task here is to explain changes in body mass, population and technology, occurring in the much more distant past.[8] Therefore we abstract from many components which drive those models, such as a quality-quantity trade-off in children. However, Section 4 briefly discusses these issues in the context of more recent time trends.

2 The base-line model

Consider an overlapping-generations model where people live for two periods. They are active as adults, and rear passive children. There is only one sex.

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[8] Some related papers study the transition from hunting and gathering to agriculture (e.g. Marceau and Myers 2006). Others study institutions during the pre-agricultural phase of development without analyzing transitions to later stages (e.g. Baker 2003). See also Weisdorf (2005) for a recent overview. However, these papers do not model changes in body size and the role played by natural selection in that process.

Agents are heterogenous with respect to body mass. There are G dynasties, and dynasty i has body mass B_i, where

$$B_i \in \mathbb{B} = \{B_1, B_2, ..., B_G\}. \tag{1}$$

Note that the set of types, $\mathbb{B}$, is exogenous. In other words, there are no mutations involved, and changes in average variables arise only through changes in the composition of the population. Let $z_{i,t}$ denote the fraction of the population with body mass B_i in period t. Average body mass in period t is then given by

$$B_t = \sum_{i=1}^{G} z_{i,t} B_i. \tag{2}$$

A dynasty-i agent active in period t earns an income (or procures an amount of food) given by

$$Y_{i,t} = F(A_t, L_t, B_i), \tag{3}$$

where A_t denotes the level of technology, and L_t is land, or resources, per agent. For simplicity, this section treats the resource base as exogenous and normalized to unity, so we can write

$$L_t = \frac{1}{P_t}, \tag{4}$$

where P_t denotes the total (adult) population size in period t. In that sense, rising population and resource depletion here mean the same thing. (Section 3.3 considers a setting where the amount of available resources evolves endogenously.)

It makes sense that income should be increasing in each of its three arguments, holding fixed the other two inputs. More resources (for example land) per agent means more food procured per agent; having a larger body amounts to more physical strength, which should have a positive effect on success in hunting;[9] finally, an agent procures more food with more advanced technologies.

We also assume that the cross derivative $\partial F(A, L, B)/\partial A \partial B$ is small, meaning that new technologies are *substitutes* for body mass. The world described here is one where new technologies enable both big and small humans to kill more prey. However, technology does not itself raise the marginal value of body mass in food procurement (at least not by too much).

To generate simple analytical results the following parametric specification is useful:

$$Y_{i,t} = L_t^{\eta} \left[A_t + \beta B_i \right] = \frac{A_t + \beta B_i}{P_t^{\eta}}, \tag{5}$$

where $\eta > 0$ and $\beta > 0$. That is, technology and body mass are assumed to be perfect substitutes. Section 3.2 examines how the results change with a functional form exhibiting constant elasticity of substitution.

2.1 Reproductive success

The reproductive success of an agent of type i is given by his number of (surviving) children, $n_{i,t}$. This is assumed to depend on resources invested in child rearing, which is given by the difference between the agent's food procurement and his own nutritional needs (his metabolism), which depend on his body mass.

We are going to use this simple functional form:

$$n_{i,t} = Y_{i,t} - \alpha B_i, \tag{6}$$

where $\alpha > 0$ denotes the metabolic needs per unit of body mass, B_i, and the product αB_i is referred to as subsistence consumption.[10] Using (5) and (6)

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[9] A large body may also be useful when competing for food with other humans; see Section 3.1.

[10] A more precise way to write (6) would be as $n_{i,t} = \max\{0, Y_{i,t} - \alpha B_i\}$. This would serve to explicitly take into account that types whose incomes fall below their subsistence

fertility becomes

$$n_{i,t} = \frac{A_t}{P_t^\eta} + B_i \left(\frac{\beta - \alpha P_t^\eta}{P_t^\eta} \right). \tag{7}$$

Since both income and subsistence consumption are linear in body mass, so is fertility. Thus, if $\partial n_{i,t}/\partial B_i > 0$ big types have more offspring than small types and increase their relative fraction of the population, making average body mass increase from period t to $t+1$; vice versa, if $\partial n_{i,t}/\partial B_i < 0$ small types have more offspring than big types and average body mass decreases. Using (7) it is seen that $\partial n_{i,t}/\partial B_i > (<)0$ whenever $P_t < (>)(\beta/\alpha)^{1/\eta}$. That is, there exists a threshold population level, $(\beta/\alpha)^{1/\eta}$, such that average body mass decreases (increases) over time if population exceeds (falls below) that threshold.

Thus, letting population expand exogenously would shift the reproductive advantage from big to small types and generate the inversely U-shaped trend seen in the data. However, since population evolves endogenously it remains to see whether this actually happens.

2.2 Population

Since fertility is linear in body mass the average fertility rate takes the same form as in (7), that is:

$$n_t = \sum_{i=1}^{G} z_{i,t} n_{i,t} = \frac{A_t}{P_t^\eta} + B_t \left(\frac{\beta - \alpha P_t^\eta}{P_t^\eta} \right), \tag{8}$$

where we have used (2). Population evolves according to

$$P_{t+1} = P_t n_t = P_t \left[\frac{A_t}{P_t^\eta} + B_t \left(\frac{\beta - \alpha P_t^\eta}{P_t^\eta} \right) \right]. \tag{9}$$

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consumption levels become extinct. However, in any period t, fertility will still be given by (6) for all types which are not becoming extinct in that period. In the quantitative two-type example considered in Subsection 2.5 below, no type ever becomes extinct.

2.3 Technological progress

The final component of this model is a scale effect in the creation of new technologies. In order to make the model consistent with technology being fixed in levels at early stages of development technological progress is modelled as a stochastic event. The larger is the number of people who can think about new ideas, the more likely is technological progress to occur. More precisely, technology can be either stagnant or progress at some exogenously given rate $g > 0$, and the probability of progress depends on population size, according to:

$$A_{t+1} = \begin{cases} A_t & \text{with probability } 1 - q_t \\ (1+g)A_t & \text{with probability } q_t \end{cases}, \tag{10}$$

where q_t is given by:

$$q_t = \max\left\{0, 1 - \frac{\theta}{P_t}\right\}. \tag{11}$$

This particular functional form for q_t is chosen arbitrarily but has a reasonable interpretation. The parameter θ is a critical mass of agents needed for technological progress to be feasible; technological progress occurs with positive probability only if $P_t > \theta$. For $P_t > \theta$ the probability of technological progress increases with population, and sustained population growth means sustained technological progress at rate g (since $\lim_{P_t \to \infty} q_t = 1$).

2.4 Dynamics

To analyze the dynamics in a phase diagram it helps focussing on the case where there are only two body types. In terms of (1), the set of body types can be written as $\mathbb{B} = \left\{\overline{B}, \underline{B}\right\}$, where $\underline{B} < \overline{B}$.

First, consider the phase of development when technology is stagnant, $A_t = A_0$. Recall from (10) and (11) that this holds with certainty when $P_t \leq \theta$, and with positive probability otherwise.

We also assume that $A_0 < \beta/\alpha$. This ensures that, in the technologically stagnant phase, population is greater in the steady state where big types dominate.

The dynamic behavior of this economy is illustrated in Figure 2, and formalized by the following proposition.

Proposition 1 *Let income be given by (5) and fertility by (6). If there are two body types, $\underline{B} < \overline{B}$, and technology is constant at its initial level $A_0 < \beta/\alpha$, the following holds.*

(a) Population evolves according to:

$$\Delta P_t = P_{t+1} - P_t \gtreqless 0 \Longleftrightarrow B_t \gtreqless \frac{P_t^\eta - A_0}{\beta - \alpha P_t^\eta}. \tag{12}$$

(b) Body mass evolves according to:
if $B_t = \underline{B}$ or $B_t = \overline{B}$, then $\Delta B_t = B_{t+1} - B_t = 0$;
if $B_t \in (\underline{B}, \overline{B})$, then

$$\Delta B_t = B_{t+1} - B_t \gtreqless 0 \Longleftrightarrow P_t \lesseqgtr \left(\frac{\alpha}{\beta}\right)^{\frac{1}{\eta}}. \tag{13}$$

(c) There are two steady states: one where small types ($\underline{B}$) dominate, and one where big types ($\overline{B}$) dominate; the population is larger in the steady state where type $\overline{B}$ dominates.

The proof is found in Section A.1.1 of the appendix.

The dynamics are illustrated in the phase diagram in Figure 2. If the economy starts off with a collapsed distribution where the big body type is extinct it converges to the steady state **SS**, following a path given by the horizontal line $B_t = \underline{B}$; there are no body mass dynamics. If the initial fraction large agents is very small but strictly positive, the economy rapidly gravitates toward the neighborhood of point **SS**. It is thus natural to consider **SS** as the starting point of human history two million years ago, just after humans had become bipedal.

An economy starting off close to **SS** stays there for a long time, and eventually follows a trajectory close to the $(\Delta P_t = 0)$-locus, with expanding population and growing average body mass, approaching **SS'**. The steady state **SS'** has larger population than **SS** given that $A_0 < \beta/\alpha$. The trajectory is illustrated by the dotted path in Figure 2. Note that the population grows *as a result of* increasing average body mass: aggregate population expands because the composition of the population shifts toward big types who in a low-technology environment have higher reproductive rates.

Absent the possibility of technological progress the economy stays forever at **SS'** in Figure 2, where big types dominate and population is non-growing. Something akin to this may have happened to many non-human species, who never began to develop new technologies (at least not to the same extent as humans). Gorillas could be one primate example.

Now allow for technological progress. Recall from (10) and (11) that as population reaches the threshold θ, technological progress occurs with positive probability. Once a rise in technology has occurred the feedback loop between population and technological progress sets in. This is illustrated in Figure 3, where population is expanding throughout the whole range of P_t considered. [The dynamics of body mass do not depend on technology so the $(\Delta B_t = 0)$-locus is the same as in Figure 2.] As population comes to exceed $(\alpha/\beta)^{1/\eta}$ the reproductive advantage shifts to small types and average body mass starts to decline.

Moreover, the decline in body mass is faster than the preceding incline, since the trajectory it follows is situated farther from the $(\Delta B_t = 0)$-locus.

Letting P_t go to infinity and B_t go to $\underline{B}$ in (8) or (9) one can deduce the following.

Proposition 2 *An economy where technology grows at rate* g *converges to a balanced growth path where* $A_t/P_t^{\eta} = (1+g)^{1/\eta} + \alpha\underline{B}$, *and population grows at rate* $(1+g)^{1/\eta} - 1$.

The proof is in Section A.1.2 of the appendix.

This balanced growth path should not be thought of as describing the modern economy in which we live today, but rather the state of slow but positive technological progress prevailing in the pre-agricultural phase of development before 10,000 B.C. (see Tables 2 and 3).

2.5 A quantitative illustration

The phase diagrams in Figures 2 and 3 illustrated an economy where technology was either constant or growing. To examine how the economy behaves if technology evolves endogenously and stochastically, following (10) and (11), this section presents a simulation.

Due to lack of data, and the stylized setting, we cannot really calibrate the model, but there is at least some logic to how the parameter values are chosen. These values are summed up in Table 4.

Sticking to the two-type setting described above, the body types $\underline{B}$ and $\overline{B}$ can be thought of as fractions of 100 Kg., so that the bigger type ($\overline{B} = 0.8$) weighs 80 Kg., and the smaller ($\underline{B} = 0.6$) 60 Kg. (cf Figure 1).

Initial technology, A_0, is set to unity.

As described already, the economy starts off with almost only small types, capturing a state in which humans had just climbed down from the trees and begun developing bipedalism. That is, the initial fraction big agents is set close to zero, so that initial average body mass, B_0, is close to (but slightly greater than) $\underline{B}$.

Given that there are very few of the large type initially their fraction changes very slowly at first. To avoid initial rapid adjustments in population we initialize population to $[(A_0 + \beta\underline{B})/(1 + \alpha\underline{B})]^{1/\eta}$, corresponding to population at point **SS** in Figure 2.

Setting η sufficiently small ensures that P_t^{η} is close to unity in the technologically stagnant phase, when P_t is not too large. That way, $\beta - \alpha$ roughly measures the marginal effect on fertility from an extra unit of body mass during the stagnant phase, and $-\alpha$ measures the same marginal effect when population levels become very large. Setting β and α close to one another, and sufficiently small, also ensures that both types have positive fertility in all periods, so that no type becomes extinct. The values chosen here also generate roughly the right speed in the decline in body mass.

We set θ, the critical mass of people necessary for technological progress, just below population in the steady state corresponding to point **SS'** in Figure 3. Recall that this is the steady state the economy would converge to if technology remained stagnant. This ensures that at some point in time the chain reaction of population expansion and technological progress sets in.

The rate of technological progress, g, is set to generate reasonable values for the expansion in population and technology. Since we are concerned primarily with the era before the agricultural revolution we choose to set g to 3/10,000 per period (about 20 years). This gives a growth rate of technology around 1.5% per millennium on the balanced growth path, which seems reasonable for the pre-agricultural era up to 10,000 years B.C., given the numbers in Tables 2 and 3.

The economy is run for 80,000 periods, but to limit the size of the figure files the time paths are generated using data from every 200th period. Due to the way technological progress is modelled the timing of the take-off in technological progress is random but varies very little across runs, usually arriving after 55,000 to 60,000 periods. In the simulation reported in Figures 6 to 8 average body mass reaches a maximum in period 57,853 (about 1.2 million years after the first period if each period is 20 years long). Around the same time population reaches the critical mass for technological progress, and technology starts to grow.

The time path for body mass is shown in Figure 6. As seen, it is consistent with the pattern in Figure 1.

Figure 7 shows that average fertility [as given by (8)] stays close to unity in the stagnant phase, and then rises and stabilizes at $(1 + g)^{1/\eta}$ on the balanced growth path (cf Proposition 2). Since fertility is strictly greater than one during the stagnant phase, over thousands of periods population levels rise, as shown in Figure 8. (Note that Figure 8 shows only the first

60,000 periods.) The take-off in technological progress arrives as population reaches the threshold θ, leading to a rapid acceleration in population growth. It is possible to see how population in the absence of a take-off in technological progress would converge to a constant level, associated with the steady state **SS'** in Figure 2.

3 Extensions

The base-line setting presented so far is one of the most intuitive and transparent models which can replicate the trends described earlier. However, as we shall see next, many assumptions can be relaxed without changing the underlying mechanics and results.

3.1 A competition model

Having a large body may be an advantage when competing with other humans for food. If so, not only absolute body mass, B_i, may affect food procurement, but also *relative* body mass, B_i/B_t.

Consider the extreme case where only relative body mass matters, and absolute body mass plays no role at all. Analogous to the specification in (5), let

$$Y_{i,t} = P_t^{-\eta}\left[A_t + \frac{\beta B_i}{B_t}\right]. \tag{14}$$

With this formulation there is no net food gain as the average agent grows bigger; the average agent procures $P_t^{-\eta}(A_t + \beta)$ independently of B_t. Using the expression for fertility in (6), $n_{i,t} = Y_{i,t} - \alpha B_i$, it can then be seen that

$$n_{i,t} = \frac{A_t}{P_t^{\eta}} + B_i\left(\frac{\beta - \alpha B_t P_t^{\eta}}{B_t P_t^{\eta}}\right). \tag{15}$$

As in the base-line model, the sign of $\partial n_{i,t}/\partial B_i$ determines which type (big or small) has the reproductive advantage and increases its share of the population. From (15) it thus follows that body mass decreases (increases) over time if $B_t P_t^{\eta} > (<)\beta/\alpha$.

Holding constant the level of technology at some level A, the dynamics of B_t and P_t can be analyzed in a two-dimensional phase diagram. First consider a formal characterization of the dynamics.

Proposition 3 *Let fertility be given by (6) and income by (14). If there are two body types, $\underline{B} < \overline{B}$, and technology is constant at some level A, the following holds.*

(a) Population evolves according to:

$$\Delta P_t = P_{t+1} - P_t \gtreqless 0 \Longleftrightarrow B_t \lesseqgtr \frac{A+\beta}{\alpha P_t^{\eta}} - \frac{1}{\alpha}. \tag{16}$$

(b) Body mass evolves according to:
if $B_t = \underline{B}$ or $B_t = \overline{B}$, then $\Delta B_t = B_{t+1} - B_t = 0$;
if $B_t \in (\underline{B}, \overline{B})$, then

$$\Delta B_t = B_{t+1} - B_t \gtreqless 0 \Longleftrightarrow B_t \lesseqgtr \frac{\beta}{\alpha P_t^{\eta}}. \tag{17}$$

(c) For all levels of technology two steady states exist, where either small types ($\underline{B}$) or big types ($\overline{B}$) dominate; the population is smaller in the steady state where $\overline{B}$ dominates.

(d) For intermediate levels of technology, $A \in (\beta/(\alpha\overline{B}), \beta/(\alpha\underline{B}))$, there also exists a steady state where body mass equals $B = \beta/(\alpha A) \in (\underline{B}, \overline{B})$, and population equals $P = A^{1/\eta}$.

The proof is found in Section A.2.1 of the appendix. Figure 4 illustrates the dynamics for the case with a low level of technology, $A < \beta/(\alpha\overline{B})$; and Figure 5 the case with intermediate technology, $A \in (\beta/(\alpha\overline{B}), \beta/(\alpha\underline{B}))$.

The point **SS** in Figure 4 is a stable steady-state equilibrium with small population and large average body mass. It can be seen from (15) that an (exogenous) rise in technology has no direct effect on the sign of $\partial n_{i,t}/\partial B_i$, thus leaving the ($\Delta B_t = 0$)-locus unchanged. However, an increase in technology raises fertility of all agents and thus makes the ($\Delta P_t = 0$)-locus shift out, pushing the steady state towards smaller bodies and larger populations; see point **SS** in Figure 5.

Like in the base-line setting one can allow for a scale effect in technology production, as in (10) and (11). This would make an initial rise in technology generate an expansion in population, thus spurring more technological progress, and so on. The result is a chain process by which the ($\Delta P_t = 0$)-locus shifts out at an increasingly rapid rate, pushing the steady state down along the ($\Delta B_t = 0$)-locus (cf Figure 5). In that sense, a competition model can indeed replicate a pattern of declining body mass parallel with explosive growth in population and technology, just as in the base-line setting and in the data (see Figure 1).

However, the competition model does not fully replicate the type of gradual and simultaneous rise in population and body mass that characterized the earlier phase of human evolution in Figure 1. In the base-line model the economy followed a path of slow and gradual increases in population since the path stayed close to the ($\Delta P_t = 0$)-locus (cf Figure 2). Here, however, a path close to the ($\Delta P_t = 0$)-locus displays rising body mass and *falling* population. Intuitively, there is no net food gain as the average agent grows bigger, only higher metabolic costs. Therefore greater average body mass leads to lower average fertility and thus to smaller steady state population. (If the economy instead starts off close to $B_t = \underline{B}$ and $P_t = 0$ it would display an initially too rapid rate of population growth.)

However, a (perhaps more realistic) model where body mass affects food procurement *both* in absolute and relative terms can in principle generate the same gradual and simultaneous rise in population and body mass as seen in the base-line model.

Non-human species and Cope's Rule Interestingly, the simultaneous incline in body mass and decline in population in this type of competition model may be relevant for other species and eras. Valkenburgh et al. (2004) document how over the past 50 million years many carnivorous animal species native to North America displayed increasing body mass prior to becoming extinct. Similar to the mechanics of the competition model presented in this section, their explanation is that selection for large bodies was driven by the competitive advantage of larger size, known as Cope's Rule. Given that energy requirements are greater for bigger agents this can lead to declining population of the whole species, and even its extinction. In other words, natural selection can promote bigger bodies because it is associated with higher reproductive success of the individual agent, but it may nevertheless result in a population decline (and eventual extinction) of the whole species.

3.1.1 Technology as input in competition

An alternative competition model is one where both technology and body mass are used in competition. As an extension of (14), let

$$Y_{i,t} = P_t^{-\eta}\left[A_t + \beta\left(\frac{\gamma A_t + B_i}{\gamma A_t + B_t}\right)\right], \tag{18}$$

for some $\gamma \geq 0$; setting $\gamma = 0$ brings us back to (14). Note that technology is not only an input in competition; there is also (as before) a direct food gain from technological progress, since the average agent procures $P_t^{-\eta}(A_t + \beta)$ (but there is no food gain for the average agent as average body mass increases).

With this formulation technological progress functions as an equalizing force in competition, since it reduces the excess amount of food procured by big types. Compared to the production function in (14), the implication in terms of the phase diagrams in Figures 4 and 5 is that increases in technology here lead to an inward shift of the ($\Delta B_t = 0$)-locus. [To see this, use (18) and (6) and note that $\partial n_{i,t}/\partial B_i$ is decreasing in A_t.] The qualitative predictions are thus the same as in the previous competition model: rising technology leads to expanding population and declining body mass. The difference is that technological progress here directly drives the decline in body mass by lowering the competitive value of a big body.

3.2 Technology and body mass as imperfect substitutes

The production function used in (5) had technology and body mass as perfect substitutes. Another formulation is to let these inputs be imperfect substitutes, using a function exhibiting constant elasticity of substitution:

$$Y_{i,t} = \frac{[A_t^\rho + \beta B_i^\rho]^{\frac{1}{\rho}}}{P_t^\eta}, \tag{19}$$

where $\rho \in (0, 1]$, and $\rho = 1$ brings us back to (5).[11]

As before, fertility is given by (6), i.e., $n_{i,t} = Y_{i,t} - \alpha B_i$. In this setting it is convenient to assume a continuum of types, so that the economy in the limit is dominated by the body type for which $\partial n_{i,t}/\partial B_i = 0$. Holding technology constant (denoting it A, without the time subscript) it can be seen that body mass and population converge to a (locally) stable steady-state equilibrium, where steady-state body mass (denoted with a superscript $*$) is given by:

$$B^* = \left[\frac{\beta}{\alpha A^\rho}\right]^{\frac{1}{1-\rho}}. \tag{20}$$

As seen, if $\rho \in (0, 1)$ steady-state body mass falls with technology, A. Two effects are involved here. First, given that $\rho < 1$ a rise in technology leads to an increase in body mass, since there is some complementarity between technology and body mass. As a second effect, the rise in A tends to decrease body mass through an increase in population levels and decline in the per-capita resource base. As long as $\rho > 0$ the population effect dominates. Letting $\rho \to 0$ [so that (19) becomes $Y_{i,t} = A_t B_i^\beta / P_t^\eta$] the population and technology effects cancel, and steady state mean body mass is not affected by changes in technology.

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[11] An even more general formulation would be:

$$Y_{i,t} = \left[(A_t^\rho + \beta B_i^\rho)^{\frac{\sigma}{\rho}} + \eta L_t^\sigma\right]^{\frac{1}{\sigma}},$$

where (recall) $L_t = 1/P_t$. The formulation in (19) corresponds to $\sigma = 0$.

The mechanics of a model with $\rho \in (0, 1)$ would thus be roughly the same as in the setting where $\rho = 1$. An economy starting off with a low level of technology, and with average body mass below B^* in (20), would see average body mass grow, approaching B^*. As the composition of the population shifts toward bigger agents with higher fertility, population levels rise.

If technology were to evolve endogenously, as in (10) and (11), A would start to grow at the point in time when population comes to exceed the threshold for technological progress [θ in (11)]. This would lower steady-state body mass, B^*, and reverse the time trend so that body mass starts to decline.

3.3 Endogenous resource base

In (4) it was assumed that the resource base is constant and normalized to one. Now instead let per-capita resources be given by X_t/P_t, where X_t denotes the resource base in period t. Instead of the formulation in (5), income is now given by

$$Y_{i,t} = \left(\frac{X_t}{P_t}\right)^{\eta} \left[A_t + \beta B_i\right]. \tag{21}$$

A standard way of formulating the dynamics of a resource base takes the following form:[12]

$$X_{t+1} = X_t + rX_t \left[1 - \frac{X_t}{\overline{X}}\right] - H_t, \tag{22}$$

where r is the maximum re-generation rate, $\overline{X}$ is the carrying capacity, and H_t is the period-t harvest. For example, if X_t is the total number of living mammoths, then H_t is the number of mammoths killed; $\overline{X}$ is the steady state that X_t would converge to absent any hunting; and r is the maximum growth

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[12] Brander and Taylor (1998) use a continuous-time version of this functional form. The discrete-time formulation used here, and several variations of it, can be found in many biology textbooks, such as e.g. Allman and Rhodes (2004).

rate of the mammoth population (the growth rate absent hunting and given an initial stock close to zero).

The harvest, H_t, here equals total population, P_t, times average income, $(X_t/P_t)^\eta [A_t + \beta B_t]$, where (recall) B_t is average body mass [see (2)]. Using (22) we then get a dynamic equation for X_t:

$$X_{t+1} = X_t + rX_t \left[1 - \frac{X_t}{\overline{X}}\right] - X_t^\eta P_t^{1-\eta} [A_t + \beta B_t]. \qquad (23)$$

Fertility, as before, is given by (6), i.e., $n_{i,t} = Y_{i,t} - \alpha B_i$. Averaging across agents and using (21) this gives a dynamic equation for population [corresponding to (9) in the base-line setting]:

$$P_{t+1} = X_t^\eta P_t^{1-\eta} [A_t + \beta B_t] - \alpha P_t B_t. \qquad (24)$$

There are now four state variables: P_t, B_t, A_t, and X_t. The dynamics for X_t and P_t are given by (23) and (24), respectively; and the dynamics for A_t by (10) and (11), like before.

To find the dynamics for B_t recall (6) again and use (21) to see that:

$$n_{i,t} = \left(\frac{X_t}{P_t}\right)^\eta A_t + B_i \left[\beta \left(\frac{X_t}{P_t}\right)^\eta - \alpha\right]. \qquad (25)$$

As in the base-line setting, fertility is linear in body mass. If $\partial n_{i,t}/\partial B_i > 0$ big types have the reproductive advantage and expand their fraction of the population over time, and vice versa if $\partial n_{i,t}/\partial B_i < 0$. As seen from (25), the sign of $\partial n_{i,t}/\partial B_i$ depends on the population-to-resource ratio, P_t/X_t. If this ratio exceeds (falls below) $(\beta/\alpha)^{1/\eta}$ average body mass decreases (increases) over time. In other words, body mass declines in densely populated and resource scarce environments; comparing (25) to (7) it is seen that the base-line model amounts to the special case where $X_t = 1$ in all periods.

A useful approach to understand the dynamics is to first treat technology as exogenous (similarly to Sections 3.1 and 3.2, now denoted just A, without the time subscript). One can then examine how steady state levels (again denoted with a superscript $*$) of population and body mass change in response to exogenous changes in technology.

Proposition 4 *Consider an economy where income is given by (21), resource dynamics by (23), and fertility by (6). Assume that there are two body types, $\underline{B} < \overline{B}$, and that technology is constant at some level A. If no type becomes extinct in any (finite) period, the economy converges to a steady state where average body mass, B^*, is given by*

$$B^* = \begin{cases} \overline{B} & \text{if } A < \beta/\alpha \\ \underline{B} & \text{if } A > \beta/\alpha \end{cases} . \tag{26}$$

The proof is given in Section A.3.1 of the appendix. In the knife-edge case when $A = \beta/\alpha$ it can be seen that B^* would equal something between $\underline{B}$ and $\overline{B}$. (The condition that no type becomes extinct serves to rule out "collapsed" paths, where body mass is stuck at $\underline{B}$ or $\overline{B}$.)

Proposition 4 implies that letting technology expand exogenously generates a shift in steady-state body mass, from $\overline{B}$ to $\underline{B}$, as A comes to exceed β/α. Now think about the dynamics. If the initial levels of population and body mass are low, and resources abundant, the reproductive advantage lies with the big types (as long as $[X_t/P_t]^\eta > \alpha/\beta$). Moreover, it can be deduced that population is expanding (as long as $[X_t/P_t]^\eta > [1 + \alpha B_t]/[A + \beta B_t]$). Initially, body mass and population thus grow in tandem.

Moreover, if technology were to evolve endogenously following (10) and (11) it can be understood how technology would start to grow with positive probability as population comes to endogenously reach the threshold, θ in (11). This spurs population growth and as the population-to-resource ratio exceeds $(\beta/\alpha)^{1/\eta}$, the reproductive advantage shifts to small types. The mechanics are thus not too different from the case with a fixed resource base.[13]

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[13] One difference in this setting, compared to the base-line setting, is that perpetual growth in technology and population here cannot be sustained. It can be seen that steady-state population becomes zero when $A = r^\eta(1 + \alpha B^*)^{1-\eta} - \beta B^*$. However, the economy will not converge to a steady state with zero population, since technology stops growing when population becomes too small [recall (11) again].

4 Conclusions

We have presented a model of endogenous growth in population and technology, together with natural selection among body types. The model can explain why humans were becoming bigger up until 50,000 years ago, and since then have been declining in size. The central mechanism driving these results is that technological progress does not in itself affect the relative reproductive advantage of big and small types, but it does bring with it denser population and depletion of resources and thereby shifts the reproductive advantage to smaller body types.

This story is not meant to be an exhaustive explanation of human physiological history but may serve as a starting point for thinking about related mechanisms at work between the same variables. For example, it seems that changes in body mass over time reflect changes in human habitats. The fossils of the largest humans over the past two million years have been found predominantly (but not only) in colder regions (Ruff 2002). The reason is that heat saving becomes more important in colder climates, which works better with bigger bodies and more "cubic" forms, i.e., larger trunks and shorter limb segments, known as Allen's and Bergmann's rules, respectively.[14] However, this does not really explain the decline in body mass over the last 50,000 years.

Body mass may also have declined as a way to rapidly increase the brain-to-body (encephalization) ratio and thus intelligence (Kappelman 1996, 1997; Robson and Kaplan 2003). Up until about 50,000 years ago encephalization had increased as brains and bodies expanded in tandem. One may conjec-

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[14] Think of the human body as a cube with side x, so that its volume equals x^3 and its surface $6x$; the volume-to-surface ratio is thus given by $x^2/6$. The higher is this ratio the lower is the heat loss, so larger bodies (with higher x) are more beneficial in cold climates. This is Allen's rule. Likewise, if the body is a rectangle of fixed volume, V, and variable sides x, y, and z, then it can be seen that the volume-to-surface ratio is maximized when $x = y = z = V^{1/3}$, that is, when the rectangle is a cube. This is Bergmann's rule. See Jurmain et al. (2000, pp. 423-426) for a textbook overview.

ture that selective pressures for intelligence then increased, due to denser populations making cooperation more important, more advanced technologies being developed, and/or language evolving around this time (Diamond 1992). This could have increased the reproductive value of high encephalization, but it is not clear why rising encephalization would come with declining body mass only over the last phase of development. Also, the examples of island dwarfism among other species (cf Section 1.1) suggest that declining body mass can occur also without the development of human-like levels of intelligence.

Other hypotheses are more speculative. One can be labelled *human self-taming.*[15] The idea is that humans evolved reduced body mass as they became hard-wired for more peaceful, cooperative behavior, just like e.g. wolves evolved into more peaceful dogs. Notably dogs resemble puppy wolves, having e.g. floppier ears, shorter snouts, and smaller size, and these physical characteristics and the associated non-aggressive behavior are closely genetically linked. For example, attempts to breed tamer foxes have resulted in foxes with similar physical characteristics as dogs (Ridley 2003).[16] Selecting for one developmentally immature trait, such as less aggressive behavior, may bring other juvenile features along, a smaller body being one of them. Just as dogs have evolved from wolves through natural selection to live peacefully with humans, humans themselves may have evolved to become more "domesticated" as we have begun to live closer to other humans, i.e., as population has grown denser. Again, however, this does not really explain the inversely U-shaped time trend in body mass.

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[15] This idea has some common elements with unpublished work by Richard Wrangham and co-authors, as cited by Ridley (2003, pp. 31-37). The discussion here is based on Ridley.

[16] The biochemical triggers involved are called gene promoters. They determine when to switch what genes on and off. For example, one genetic cause of less aggressive/more social behavior lies in how long a certain section of the brain disinhibiting aggression (called "area13") is allowed by the gene promoters to develop. See Ridley (2003) for a more detailed discussion.

Aside from the body trends discussed here, there are a number of interesting related issues which could be worth studying. For example, it seems that human body mass reached a global minimum a couple of centuries ago. Since then humans have grown bigger and taller mostly in response to improved nutrition, as technological progress has come to outpace population growth. However, also over this shorter time period natural selection may have played a role in shaping human bodies. For example, Diamond (2003) suggests that food history can explain geographical variation in obesity and diabetes today. Europeans experienced improved nutritional supply earlier than the native populations in other parts of the world. This lowered the reproductive benefits of genes which enables the body to store fat, so-called "thrifty genes." Such genes improve the chance of surviving starvation but also make the carrier more susceptible to obesity and diabetes. When food supply improved in Europe this reduced the reproductive advantage of thrifty genes; other populations went through this transition much later, if at all.

The model presented here assumes that in any given period the existing technology is available to all agents. This makes sense in a world where tools and weapons are very crude and simple, like most of the early ones listed in Table 3. However, as technological progress gradually picked up pace some time after the agricultural revolution skills may have started to become more important to master new technologies. This may have tilted the reproductive advantage to agents who were either genetically predisposed to higher intelligence; or whose preferences were such that they chose to have fewer children but educate each child better, thus raising the income and fertility of the next generation. Such quality-quantity substitution may have happened over the most recent millennia, and would fit with the theory of Galor and Moav (2002).

A Appendix

A.1 The base-line model

A.1.1 Proof of Proposition 1

Part (a): the ($\Delta P_t = 0$)-locus Consider first the segment of the phase diagram where $P_t < A_0^{1/\eta}$; this in turn implies that $P_t < (\beta/\alpha)^{1/\eta}$ (since $A_0 < \beta/\alpha$). The first of these two inequalities implies that $A_0/P_t^\eta > 1$; the latter implies that $B_t(\beta - \alpha P_t^\eta) > 0$ (since $B_t > 0$). From (9) this is seen to imply that $P_{t+1} > P_t$; thus population is always growing when $P_t < A_0^{1/\eta}$.

Consider next the segment of the phase diagram where $A_0^{1/\eta} < P_t < (\beta/\alpha)^{1/\eta}$. Using (9) we see that $P_{t+1} \gtreqless P_t$ holds when $B_t \gtreqless (P_t^\eta - A_0)/(\beta - \alpha P_t^\eta)$, which is (12). The ($\Delta P_t = 0$)-locus in Figure 2 is given by (12) holding with equality.

Consider next the segment of the phase diagram where $(\beta/\alpha)^{1/\eta} < P_t < ([\beta + A_0/B_t]/\alpha)^{1/\eta}$. These inequalities imply that $A_0/P_t^\eta < 1$, and $B_t(\beta - \alpha P_t^\eta) < 0$, so using (9) it is seen that $P_{t+1} < P_t$; thus population is decreasing in this region of the phase diagram.

Note, for completeness, that $P_t > ([\beta + A_0/B_t]/\alpha)^{1/\eta}$ would imply negative fertility (or fertility being constrained to zero) and thus the population becoming extinct.

Part (b): the ($\Delta B_t = 0$)-locus When all agents belong to the same body type the composition cannot change. When there are only two body types, $\underline{B}$ and $\overline{B}$, B_t must thus be constant whenever either body type dominates the population, that is, when $B_t = \underline{B}$ or $B_t = \overline{B}$. Mean body mass is also constant when $\partial n_{i,t}/\partial B_i = 0$. Using (7), this is seen to hold whenever $\beta - \alpha P_t^\eta = 0$, which gives (13).

Part (c) From (12) and (13) it is seen that the denominator of (13) is zero if $\Delta B_t = 0$ for $B_t \in (\underline{B}, \overline{B})$. Thus, the only steady states that can exist must be such that $B_t = \underline{B}$ or $B_t = \overline{B}$. These steady states do exist since

$\Delta P_t = \Delta B_t = 0$ at: $(B_t, P_t) = (\underline{B}, \underline{P})$, where $\underline{P} = [(A_0 + \beta\underline{B})/(1 + \alpha\underline{B})]^{1/\eta}$; and $(B_t, P_t) = (\overline{B}, \overline{P})$, where $\overline{P} = \left[(A_0 + \beta\overline{B})/(1 + \alpha\overline{B})\right]^{1/\eta}$. Since $\underline{B} < \overline{B}$, and $[(A_0 + \beta B)/(1 + \alpha B)]^{1/\eta}$ is increasing in B for $A_0 < \beta/\alpha$, it must hold that $\underline{P} < \overline{P}$. *Q.E.D.*

A.1.2 Proof of Proposition 2

Use (9) to see that if P_t grows at a sustained constant rate, and thus B_t approaches $\underline{B}$, then fertility (and thus population growth) approaches $A_t/P_t^\eta - \alpha\underline{B}$. For this growth rate to be constant, A_t/P_t^η must be constant. Since $A_{t+1} = (1+g)A_t$ it follows that $P_{t+1}^\eta = (1+g)P_t^\eta$, or $P_{t+1} = (1+g)^{1/\eta}P_t$; this gives $A_t/P_t^\eta = (1+g)^{1/\eta} + \alpha\underline{B}$. *Q.E.D.*

A.2 A competition model

A.2.1 Proof of Proposition 3

Part (a): the ($\Delta P_t = 0$)-locus Treating technology, A, as fixed, and using $P_{t+1} = P_t n_t$, (2) and (15), it is seen that

$$P_{t+1} = P_t n_t = P_t \left(\frac{A}{P_t^\eta} + \frac{\beta - \alpha B_t P_t^\eta}{P_t^\eta} \right). \tag{27}$$

Setting $P_{t+1} = P_t$ in (27) we get $B_t = (A + \beta)/(\alpha P_t^\eta) - (1/\alpha)$, which is (16). Likewise, when $B_t > (<)(A+\beta)/(\alpha P_t^\eta) - (1/\alpha)$ it is seen from (27) that $P_{t+1} < (>)P_t$.

Part (b): the ($\Delta B_t = 0$)-locus As in Section A.1.1 of this appendix, we note that $B_{t+1} = B_t$ either when one single type dominates the whole population (so that, in the two-type case, $B_t = \underline{B}$ or $B_t = \overline{B}$); or when $\partial n_{i,t}/\partial B_i = 0$, which when using (15) gives (17).

Part (c) From (16) and (17), it is seen that $\Delta P_t = \Delta B_t = 0$ when $(B_t, P_t) = (\underline{B}, \underline{P})$, where $\underline{P} = [(A + \beta)/(1 + \alpha\underline{B})]^{1/\eta}$; and $(B_t, P_t) = (\overline{B}, \overline{P})$, where $\overline{P} = \left[(A+\beta)/(1+\alpha\overline{B})\right]^{1/\eta}$. Since $\underline{B} < \overline{B}$, and $[(A+\beta)/(1+\alpha B)]^{1/\eta}$ is decreasing B, it must hold that $\underline{P} > \overline{P}$.

Part (d) If a steady state where $B_t \in (\underline{B}, \overline{B})$ exists, then (16) and (17) say that both $B_t = \beta/(\alpha P_t^\eta)$ and $B_t = (A+\beta)/(\alpha P_t^\eta) - (1/\alpha)$ must hold. Solving for B_t and P_t gives $P_t = A^{1/\eta}$ and $B_t = \beta/(\alpha A)$; and $\beta/(\alpha A) \in (\underline{B}, \overline{B})$ is equivalent to $A \in (\beta/(\alpha\overline{B}), \beta/(\alpha\underline{B}))$. *Q.E.D.*

A.3 Endogenous resource base

A.3.1 Proof of Proposition 4

At any given B^*, steady-state resource and population levels are given by setting $X_{t+1} = X_t = X^*$ and $P_{t+1} = P_t = P^*$ in (23) and (24), and solving for X^* and P^*. From (23) we get

$$P^* = \left[\frac{A + \beta B^*}{1 + \alpha B^*}\right]^{\frac{1}{\eta}} X^*, \tag{28}$$

Next use (25) and (28) to note that large types have the reproductive advantage ($\partial n_{i,t}/\partial B_i > 0$) if $(X^*/P^*)^\eta = (1+\alpha B^*)/(A+\beta B^*) > \alpha/\beta$, which is seen to amount to $A < \beta/\alpha$; vice versa, small types have the reproductive advantage if $A > \beta/\alpha$. This gives the expression for steady-state average body mass, B^*, in (26). *Q.E.D.*

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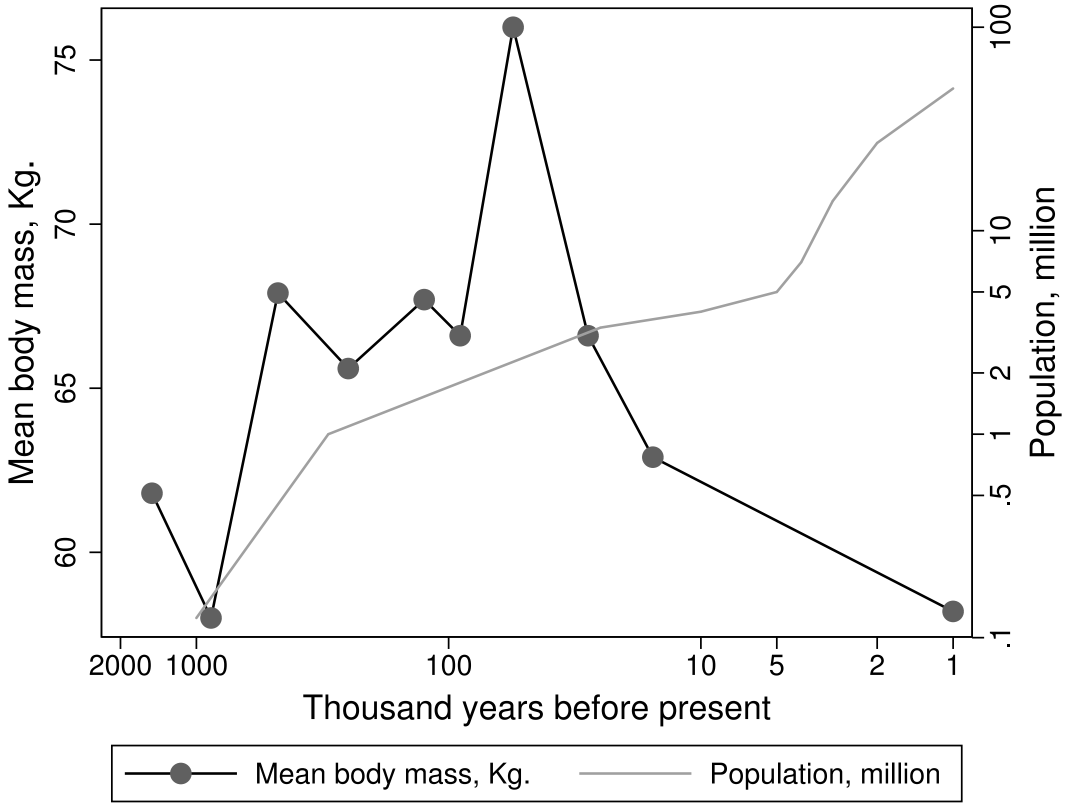

Figure 1: Trends in human body mass and total world population. Sources: for population Kremer (1993); for body mass, see Table 1 (the times are chosen as the mid points of the periods reported).

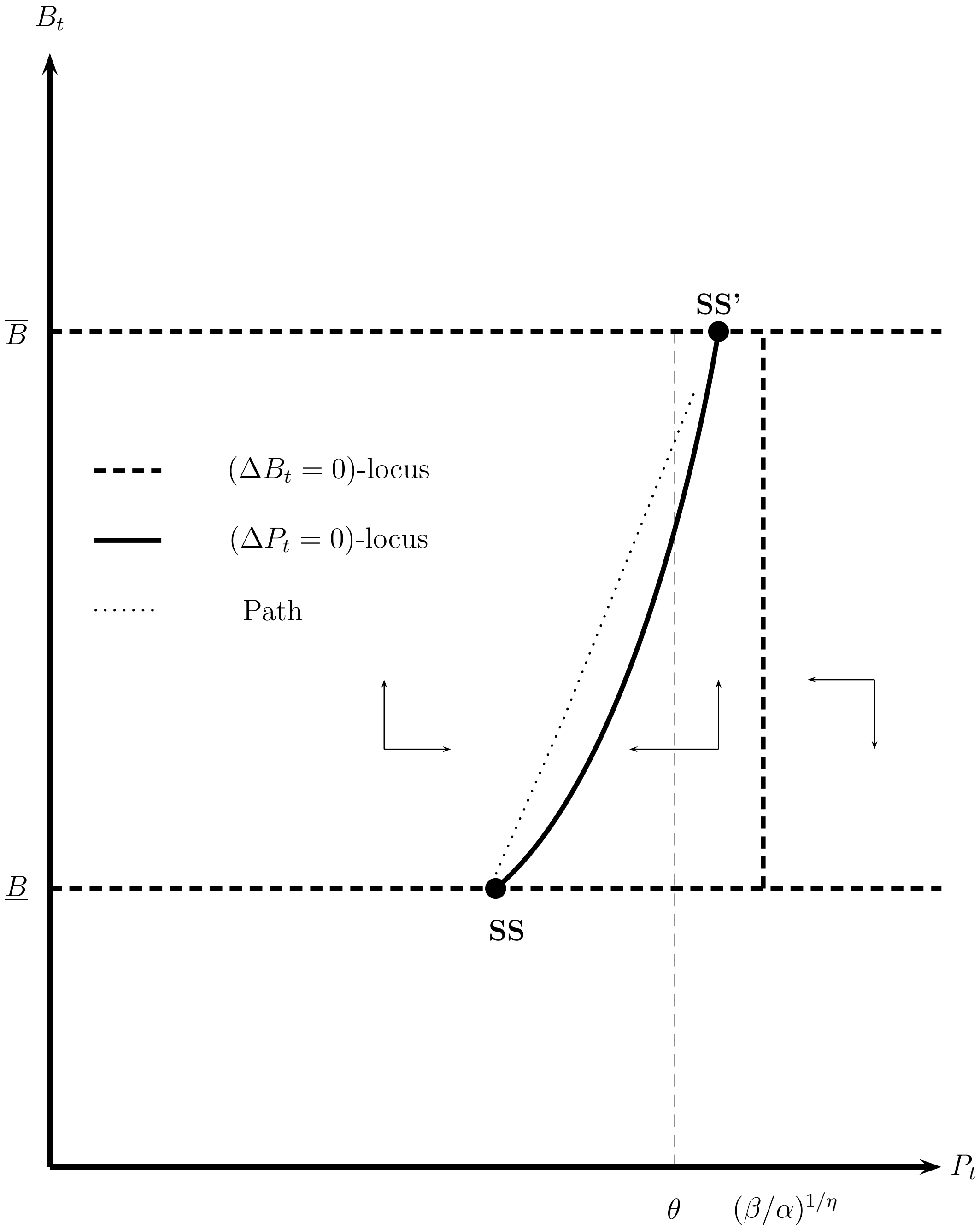

Figure 2. Base-line model dynamics with non-growing technology.

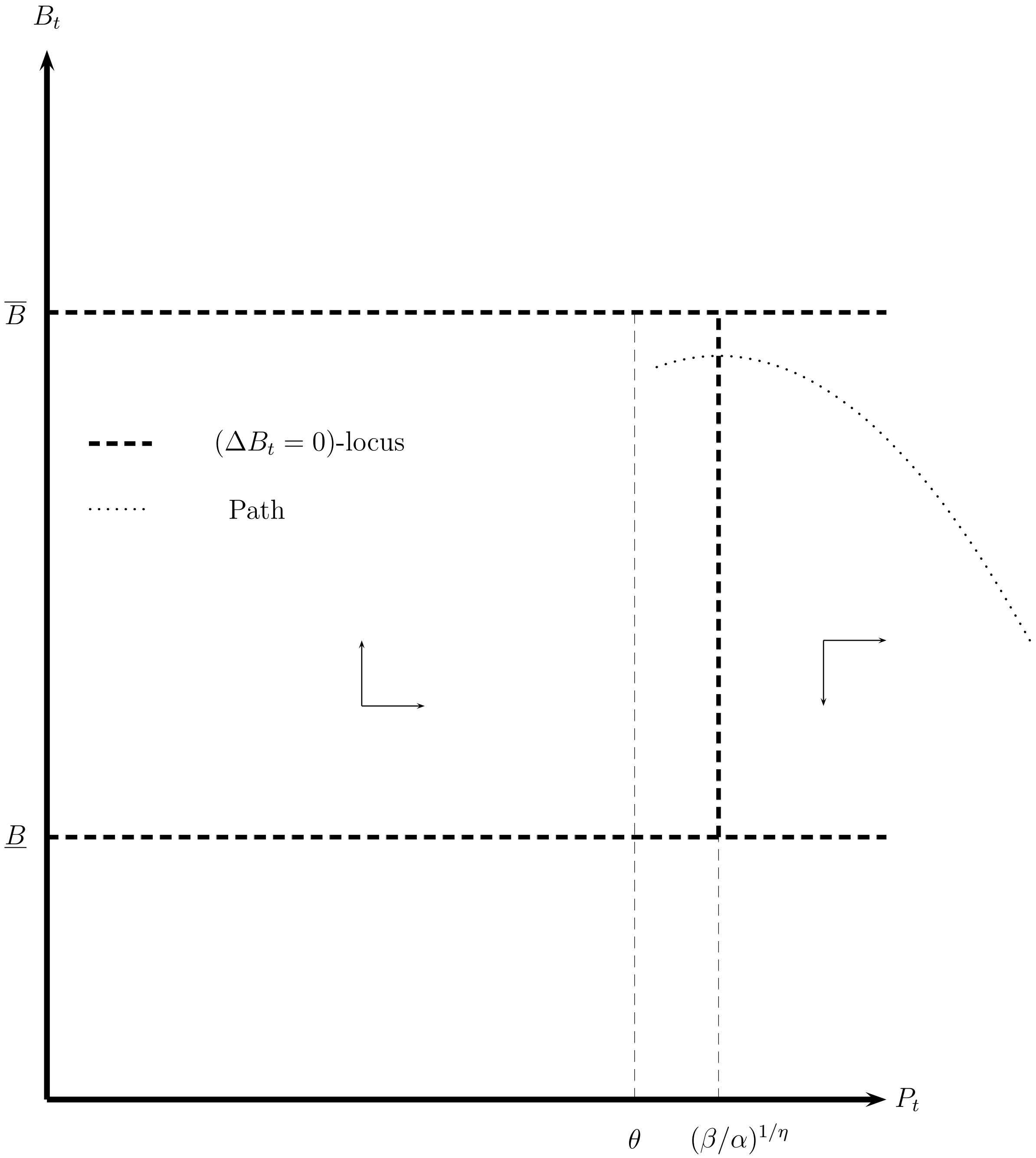

Figure 3. Base-line model dynamics with growing technology.

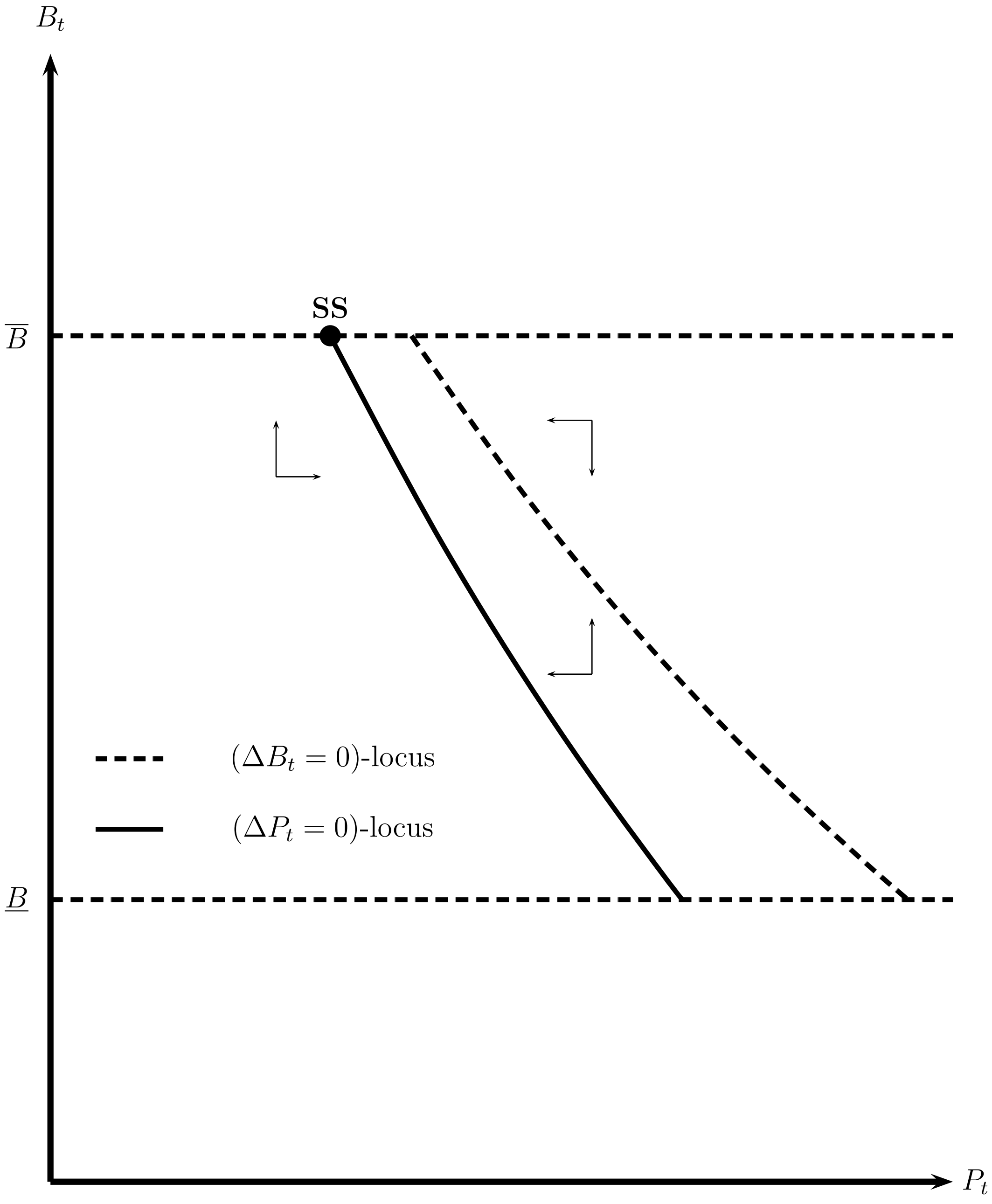

Figure 4. Competition model dynamics with low technology

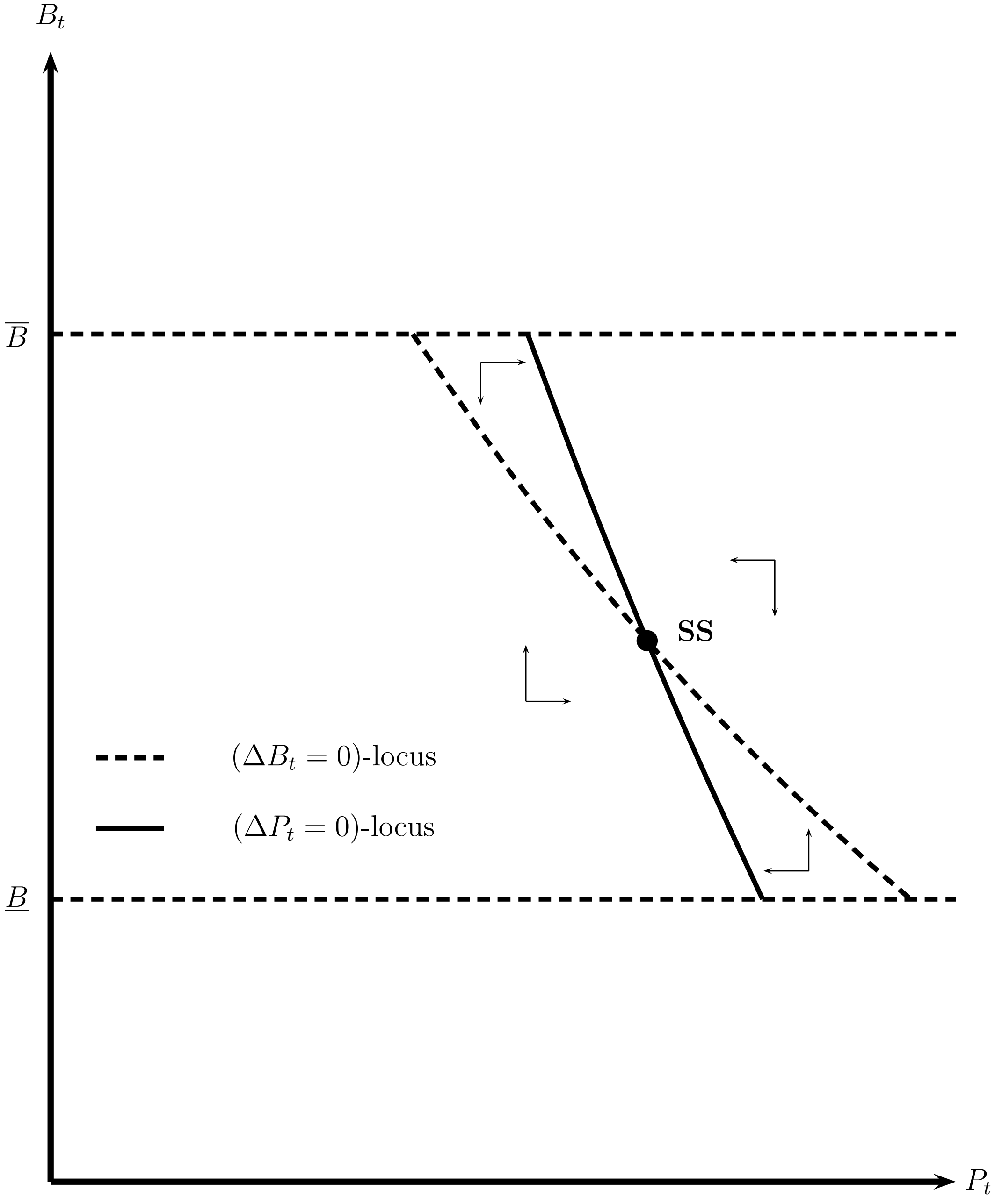

Figure 5. Competition model dynamics with intermediate-level technology

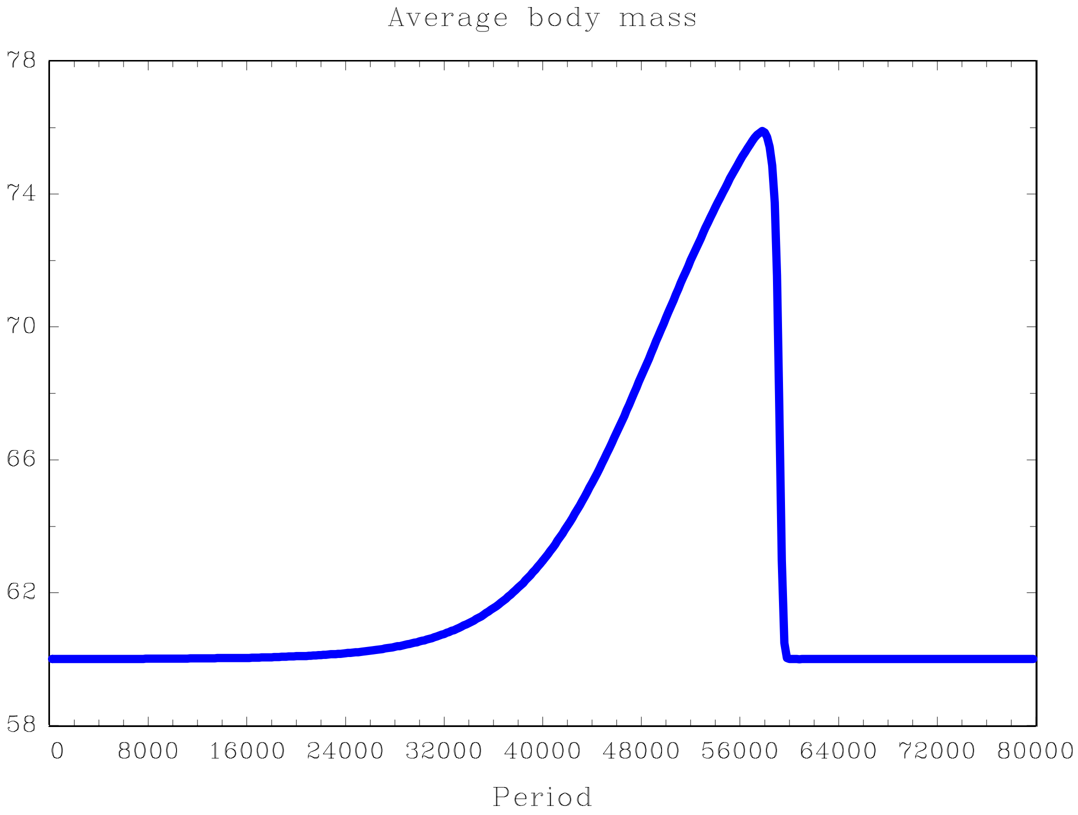

Figure 6: Simulated time path for average body mass across types, B_t.

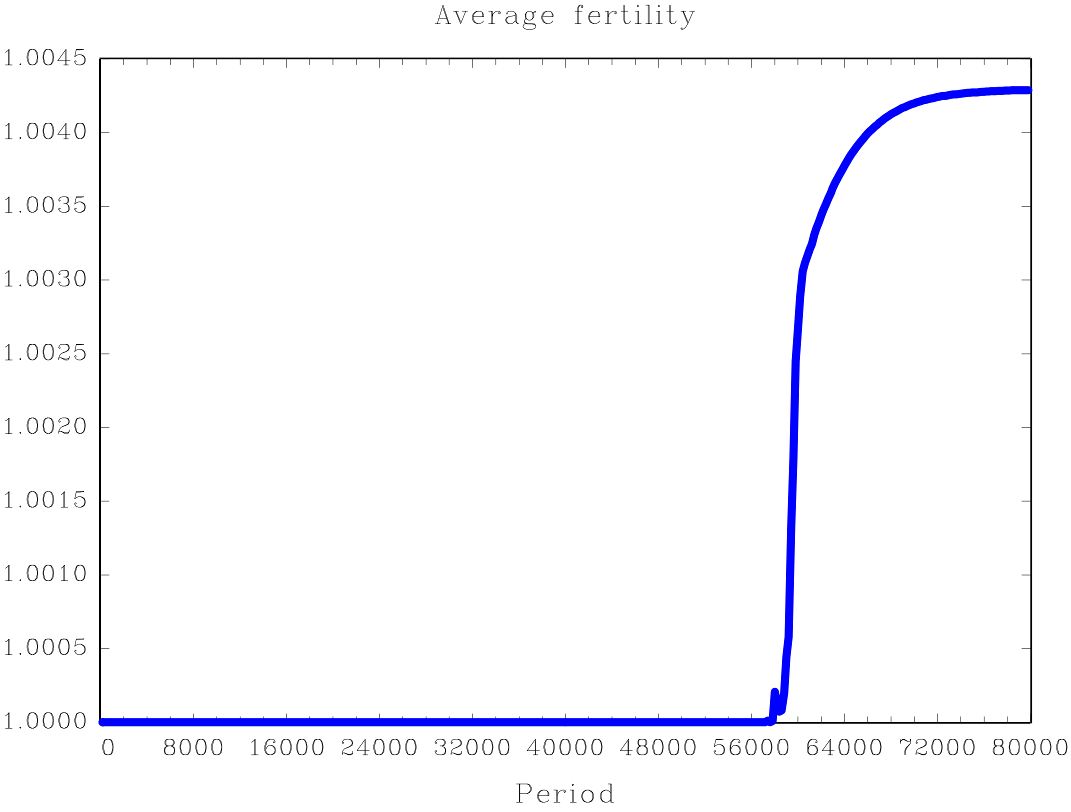

Figure 7: Simulated time path for average fertility, n_t.

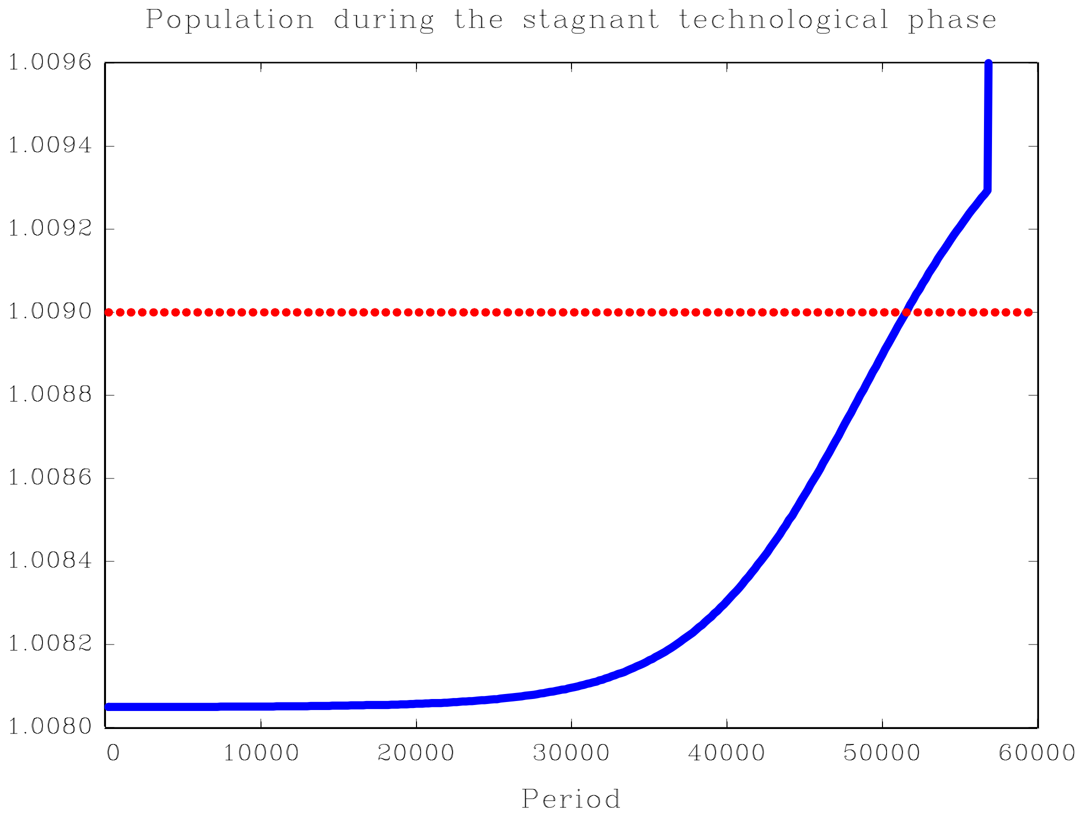

Figure 8: The solid line shows the simulated time path for population before the take-off in technological progress. The dotted line indicates θ, the critical level of population above which technological progress becomes possible.

Sample	Temporal range (thousand years ago)	Mean body mass (Kg.)
Living worldwide	-	58.2
Late Upper Paleaolithic	10-21	62.9
Early Upper Paleolitic	21-35	66.6
Late archaic H. Sapiens	36-75	76.0
Skhul-Qafzeh	90	66.6
early Late Pleistocene	100-150	67.7
late Middle Pleistocene	200-300	65.6
middle Middle Pleistocene	400-550	67.9
late Early to early Middle Pleistocene	600-1,150	58.0
Early Pleistocene	1,200-1,800	61.8

Table 1: Body-mass data. The numbers refer to the mean of the estimated body weights of fossil samples from the periods indicated. Source: Ruff et al. (1997, Table 1).

Time period	**No. of innovations** as listed in Table 3	**Rate of progress** (% change per 1000 years)
4,000,000 to 100,000 B.C.	6	-
100,000 to 40,000 B.C.	4	0.86%
40,000 to 10,000 B.C.	20	2.34%
10,000 to 8,000 B.C.	16	73%

Table 2: Early rates of technological progress. We assume an initial stock of zero innovations by 4 million years B.C. Source: Nolan and Lenski (1999, Table 5.1)

Time period	**List of innovations**	
4,000,000 to 100,000 B.C.	Hand ax	Wooden spear
	Use of fire	Colored pigments
	Shelters	Fire-hardened spear point
100,000 to 40,000 B.C.	Bone for tools	Skin clothing
	Handles on tools	Harpoon heads
40,000 to 10,000 B.C.	Spear thrower	Bow and arrow
	Lamps	Pins and awls
	Fish gorgets	Cord
	Needles with eyes	Antler hammers
	Shovels and scoops	Mattocks
	Stone saws	Graving tools
	Spoons	Stone ax with handle
	Jewelry	Pestles and grinding slabs
	Separate handles	Musical instruments
	Boats	Domestication of dogs
10,000 to 8,000 B.C.	Beer	Fishhooks
	Fish traps	Fishnets
	Adzes	Sickles
	Plant cultivation	Domestication of sheep
	Basketry	Cloth
	Grinding equipment	Leather-working tools
	Paving	Sledge
	Ice picks	Combs

Table 3: Early technologies. Source: Nolan and Lenski (1999, Table 5.1).

Parameter	β	α	η	θ	g
Value	0.9	0.8986	0.07	1.009	0.0003
Parameter	P_0	A_0	z_0	$\overline{B}$	$\underline{B}$
Value	1.00805	1	0.0001	0.8	0.6

Table 4: Parameter values.