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Natural Selection, Technological Progress, and the Origin of Human Longevity

Lothar Grall*

July 20, 2016

Abstract

This paper suggests that feedback effects between technological progress and human longevity lie at the heart of their common emergence in human history. It connects two major research questions. First, the long life span after menopause is a unique but puzzling feature of humans among primates. Second, the shift in human behavior at least 50,000 years ago, which led to an unprecedented pace of technological progress, is still not well understood. The paper develops an evolutionary growth theory that builds on the trade-off between the quantity and the quality of offspring. It suggests that early technological advances gradually increased the importance of intergenerational transfers of knowledge. Eventually, the fertility advantage shifted towards individuals that were characterized by higher parental investment in offspring and a significant post-reproductive life span. Subsequently, the rise in human longevity reinforced the process of development and laid the foundations for sustained technological progress. As a key feature, the theory resolves the debate about a “revolution” in human behavior in an entirely new way. It shows that a gradual emergence of modern behavior is sufficient to trigger a demographic shift that appears as a “behavioral revolution” in the archeological record.

Keywords: Behavioral Revolution, Economic Growth, Human Longevity, Natural Selection, Somatic Investment, Technological Progress.

JEL Classification Numbers: J13, N30, O10, O30.

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1. Introduction

The long life span of humans—women outlive their reproductive period by decades—is a unique feature of humans among primates. The intriguing fact, however, is not menopause itself, but the long life span afterwards. Recent research suggests that extensive longevity is not restricted to modern times, but very characteristic for our species. Gurven and Kaplan (2007) estimate a modal life span of about seven decades for a sample of extant hunter-gatherers. They show that at least one-fourth of the population is likely to live as grandparents for 15–20 years. Konigsberg and Herrmann (2006) confirm this life history pattern for several samples of prehistoric hunter-gatherers. The specific pattern of a significant post-reproductive life span seems to have evolved within our species. Caspari and Lee (2004) calculate the ratio of old to young adults for different hominid groups. As depicted in Figure 1, they show that the number of adults who live to be old is significant at least since the Upper Paleolithic.¹ Hence, it seems that a take-off in human longevity has occurred at some point in time between the emergence of *Homo sapiens* and the Out-of-Africa expansion of modern humans around 50 kya.²

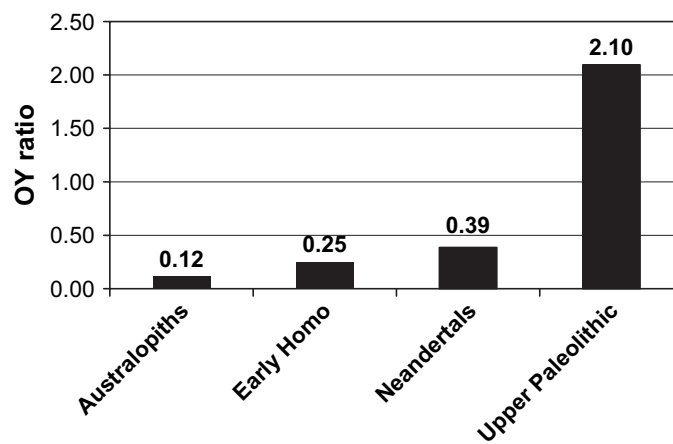


Figure 1: Old-Young Ratios for Different Hominid Groups (Caspari and Lee 2004).

Any evolutionary explanation of the long post-reproductive life span builds on the idea that old individuals maintain “reproductive value” by increasing their fitness through non-reproductive means. The influential “grandmother hypothesis” focuses on intergenerational transfers among women and proposes that older women increase their inclusive fitness by supporting their grandchildren (Hawkes et al. 1998; Hill and Hurtado 1991). The “embodied

¹ Hawkes and O’Connell (2005) question the use of OY ratios as a measure for human longevity, arguing that the ratio of the adult life span and the age at maturity should be a life history invariant across species in terms of Charnov (1993). In a reply, Caspari and Lee (2005a) argue that there is no theoretical basis for the expectation that OY ratios should be invariant and show that—in fact—they aren’t.

²Minichillo (2005) argues that the study of Caspari and Lee (2004) supports an emergence of extended longevity as early as 500 kya and is therefore not restricted to our species (see also Caspari and Lee 2005b).

capital hypothesis” focuses on resource flows from parents to offspring and proposes that the human life span is the result of parental investment into the “embodied capital” of offspring (Kaplan et al. 2000; Robson and Kaplan 2003). The life span co-evolved with the length of the juvenile period, increased brain capacities, and intergenerational resource flows, since productivity increases with age in a skill-intensive feeding niche and adults who cease reproducing in their 40s will not finish parenting until they are 60 or older (Gurven and Kaplan 2007).

However, the inclusive fitness benefits associated with grandmothering don’t seem to be large enough to explain the evolution of increased longevity by natural selection under reasonable assumptions (Kachel et al. 2011). Furthermore, both hypotheses link the benefit of a longer life span to the emergence of the hunter-gatherer life style of early *Homo*, i.e. to a genus level explanation of the evolutionary advantage of a long post-reproductive life span.³ This contradicts the findings of Caspari and Lee (2004) shown in Figure 1.

In this paper, I focus on intergenerational transfers of knowledge and explore the implications of the process of development on the human life span. I follow a suggestion by Caspari and Lee (2004, p. 10899) who argue that—if there is a single fundamental factor related to biology that underlies modern human behavior—the increase in adult survivorship might be it. While modern anatomy evolved at least 160–195 kya (White et al. 2003), the emergence of modern behavior is currently actively debated. Some researchers propose a sudden appearance, a “human revolution”, either due to a genetic mutation around 50 kya (Klein 2008, p. 271), or due to a period of significant technological and/or cultural developments in southern Africa between 60 and 80 kya (Mellars 2007, p. 4). At this time, human populations seem to have gained a significant fitness advantage that finally led to the Out-of-Africa expansion. In contrast, McBrearty and Brooks (2000) stress a gradual emergence of modern behavior, a “human evolution”, and argue that innovations indicative of modern cognition appear and disappear in the archeological record between 200 and 40 kya before becoming fully consolidated. In the context of this debate, the results provided by Caspari and Lee suggest that the decisive marker of modern behavior might not be cognitive ability, but increased longevity.

I want to pick up this idea and develop an evolutionary theory to answer four distinctive questions: (i) What is the origin of the vast increase in the human life span? (ii) Why did natural selection favor the distinctive pattern of a long post-reproductive life span in humans? (iii) What triggered the unprecedented increase in the pace of technological progress in the period centered on 60–80 kya? (iv) Is it possible to resolve the “revolution vs. evolution” debate in a meaningful way? The theory builds on three key assumptions. First, I follow McBrearty (2007, p. 137) and assume that the mental capacity for sophisticated behavior was

³Hawkes (2003) allows for a different timing in her most recent formulation of the grandmother hypothesis.

present in Africa in the earliest *Homo sapiens*. Hence, technological innovations have been possible and visible in the archeological record at least since the emergence of our species. Second, I assume that technology and education are complements. That is, early technological advances increased the importance of intergenerational transfers of knowledge. Third, I follow Rosenberg (2004) and assume that older individuals are crucial for the transfer of knowledge since they function as living repositories of information.

This paper suggests, while the mental capacity for sophisticated behavior and the ability to reach old age were present in Africa in the earliest anatomically modern humans, both traits were initially rare. However, gradual feedback effects between technological progress and human longevity over thousands of years eventually led to a demographic shift that rendered both traits common among human societies.⁴ The result was an unprecedented pace of technological and cultural innovations, known as the “behavioral revolution”, which ultimately led to the Out-of-Africa expansion of behavioral modern humans about 50 kya.

The theory builds on the fundamental trade-off between the quantity and quality of offspring. Individuals differ genetically with respect to the resources parents invest into the body of each child. Higher somatic investment in offspring is reflected by factors that increase survivability to old age, e.g., enhanced immune system or improved gene regulation. The population is heterogenous and individuals are either of a short-living, low somatic investment type, or a long-living, high somatic investment type. Nature selects the life history profile that maximizes reproductive success in any given environment. At early levels of development the level of technology is low and individuals who are genetically predisposed for low somatic investment have an evolutionary advantage. However, technology advances over thousands of years, slowly increasing the level of development and gradually raising the importance of a longer life span since older individuals are crucial for the transfer of knowledge. Eventually, at a certain level of technology, the evolutionary advantage shifts towards individuals who are genetically predisposed for high somatic investment and the fraction of long-living individuals in the population increases. The rise in human longevity reinforces the process of development and lays the foundation for an unprecedented pace of technological and cultural innovations.

A key feature of the theory is a novel resolution of the “revolution vs. evolution” debate with respect to the origins of modern human behavior. The theory proposes that the “human revolution” was the result of a shift in the evolutionary advantage towards individuals who were characterized by a long post-reproductive life span. It suggests that the demographic shift occurred in response to the process of economic development, i.e., in response to early technological advances that accumulated in Africa over thousands of years since the emergence

⁴Note that this paper uses the term *technological progress* in a wider sense that includes, e.g., increasing knowledge of natural history, i.e., increasing knowledge about the efficient exploitation of plants and animals.

of *Homo sapiens*. The theory demonstrates that a gradual emergence of modern behavior can be sufficient to trigger a demographic shift characterized by accelerated technological change that might appear as a “revolution” in the archeological record.

Interestingly, there is some secondary evidence for the hypothesis that intergenerational transfers of knowledge played an important role for phenotypic and ontogenetic differences between archaic and modern humans. First, the temporal lobe of modern humans is about 20 percent larger (Lieberman 2013; Lieberman et al. 2002). The temporal lobe is located beneath the lateral fissure on both cerebral hemispheres of the brain. It is especially associated with language recognition and long-term memory. Second, dental evidenced suggests that modern humans show a longer juvenile and adolescent period of growth than archaic humans (Smith et al. 2010). A prolonged phase of youth and adolescence provides time for learning and skill formation and might be the natural counterpart to increased longevity.

The paper is related to previous contributions that have aimed to explain the emergence of human longevity. A first strand of literature from evolutionary biology tries to explain the evolution of aging and thus of life expectancy. With focus on late-acting deleterious mutations, Medawar (1952) suggests that aging is an inevitable outcome of the declining force of natural selection in older age (*mutation accumulation theory*), whereas Williams (1957) acknowledges active accumulation of such genes if they have a beneficial reproductive effect in early stages of life (*antagonistic pleiotropy theory*). Kirkwood and Holliday (1979) propose that the selection pressure to invest metabolic resources in somatic maintenance and repair is limited; all that is required is to keep the organism in sound condition for as long as it might survive in the wild (*disposable soma theory*). All of the current evolutionary theories of aging have a common underlying theme: as a result of *extrinsic mortality*, there is a progressive weakening in the force of natural selection with increasing age (Kirkwood and Austad 2000). In line with this underlying theme, Robson and Kaplan (2003) explore the evolution of human brain size and life expectancy in hunter-gatherer societies from an economic point of view. They argue that a decrease in extrinsic mortality over the course of human history led to an increase in somatic investment, resulting in a larger brain size and a longer life span.

The paper is also related to a growing literature that explores the interaction between the process of economic development and human evolution (see, e.g., Clark 2007; Galor and Klemp 2014; Galor and Michalopoulos 2012; Lagerlöf 2007; Ofek 2001; Saint-Paul 2007). In particular, this paper shares a common theme with Galor and Moav (2002), who show that individuals with traits complementary to the process of development generated an evolutionary advantage during the epoch of Malthusian stagnation. Over thousands of years, the process of natural selection thus gradually stimulated technological progress and ultimately triggered a reinforcing interaction between investment in human capital and technological progress that

brought about the demographic transition and the onset of modern economic growth regime. More recent theories from evolutionary biology acknowledge that the adverse effect of a rise in extrinsic mortality can be counteracted by an increase in somatic investment (Williams and Day 2003). This theme is picked up by Galor and Moav (2005, 2007) who argue that the extrinsic mortality risk in fact increased over the course of human history due to a rise in population density. Consequently, they propose a theory of life expectancy evolution where the effect of extrinsic mortality on survival probability can be offset by increased somatic investment. The model developed below borrows this element with respect to the production of human capital: improvements in the level of technology reduce the value of human capital for a given level of education. This negative effect can be mitigated by increased somatic investment.

This paper is organized as follows. Section 2 formalizes the key assumptions and develops the basic structure of the model. Section 3 describes the time path of population size, population composition, and technological progress, which are the key variables of the economy. Section 4 characterizes the entire dynamical system and analyzes the evolution of human longevity along the process of development. Section 5 concludes.

2. The Basic Structure of the Model

Consider an overlapping generations economy in which economic activity extends over infinite discrete time.⁵ Individuals live for either two periods (childhood and adulthood) or three periods (childhood, adulthood, and old age). That is, adults face a mortality risk that may prevent them from reaching old age. Individuals differ genetically with respect to the resources they invest in the body of each child. Higher somatic investment in offspring increases the probability to reach old age but limits the number of offspring that can be raised. Hence, there is an evolutionary trade-off between the quality (i.e. life-expectancy) and the quantity of offspring. Adults that survive to old age do not reproduce, but use their time to educate their grand children. This assumption captures the idea that the long post-reproductive lifespan of humans is linked to the transfer of knowledge between generations.

The economy's character is Malthusian. This has two consequences. First, population size is constrained by the available resources and by the level of technology. An increase in the level of technology leads temporarily to growth of income per capita, but ultimately to a larger population. The larger population feeds back on income per capita, reducing it to the initial level. Second, in a Malthusian environment technological progress is driven mainly by population size. A rise in the level of technology increases the size of the population, which

⁵The following model borrows elements from Galor and Moav (2005) to capture the endogenous shift from a low to a high somatic investment regime.

in turn fosters technological progress. The result is a feedback loop between population and technology that leads to increasing growth rates over time.

The increasing level of technology triggers an evolutionary process that alters the distribution of genetic types within the population. Nature selects the life history profile—i.e. the level of somatic investment in offspring—that maximizes reproductive success in a given environment. Since education complements technology, improvements in the technological environment increase the benefit of education and trigger a process of natural selection that favors individuals characterized by higher somatic investment in offspring, a long post-reproductive life span, and intergenerational transfers of knowledge from old to young.

2.1. The Production of Final Output

Consider a population of L_t adult individuals that support their progeny on a fixed amount X of land or resources. In every period t , the economy produces output Y_t with aggregate efficiency units of labor H_t and land X as inputs. The production function exhibits constant returns to scale in land and efficiency units of labor and is subject to endogenous technological progress. Let A_t be the level of technology, which is endogenously determined. Furthermore, define the product $A_t X$ as “effective resources”, since the level of technology allows to use the existing land more effectively. The output produced at time t is given by the neoclassical production function

$$Y_t = H_t^{1-\alpha} (A_t X)^\alpha, \quad (1)$$

where $\alpha \in (0, 1)$. For simplicity, the amount of land is normalized to one, $X \equiv 1$. It is reasonable to abstract from property rights over land. Therefore, the return to effective resources is zero and the wage per efficiency unit of labor at time t , w_t , is given by

$$w_t = \frac{Y_t}{H_t} = \left(\frac{A_t}{H_t} \right)^\alpha. \quad (2)$$

2.2. Individuals

In each period of time a new generation of individuals is born. Reproduction is asexual. Therefore, each individual has a single parent and—in case of survival to old age—also a single grandparent. In the first period of life (childhood), individuals consume a part of their parental income and a fraction of their grandparental unit time endowment for education. In the second period of life (adulthood), they work and allocate their income between consumption and reproduction. If adults survive to the third period of life (old age), they are endowed with one unit of time that they divide evenly between the children within their dynasty to educate

them. For simplicity, I abstract from old age consumption.

Every generation consists of a variety of individuals who differ genetically with respect to the allocation of resources between the number and the quality of offspring. The quality of offspring is measured in terms of units of somatic capital. Somatic capital is, in a physical sense, embodied energy or organized somatic tissue. In a functional sense, somatic capital includes body size, physical stature, and strength, but also factors like immune function, cell maintenance, and cell repair, which directly affect life expectancy. Therefore, I assume that individuals with a higher level of somatic capital have on average a longer life. It follows that variations in the genetically predetermined level of somatic investment during childhood manifest themselves in differential survival to old age.

Let an individual of type i be genetically predetermined to invest $k^i > 0$ units of somatic capital in each child. Somatic investment during childhood is hereditary and transmitted genetically from parent to offspring with probability $\rho \rightarrow 1$. That is, individuals within a dynasty are of the same type and the relative size of each dynasty evolves over time by natural selection. However, with an infinitesimal probability $(1 - \rho) \rightarrow 0$ individuals give birth to progeny of a different type. Therefore, the population remains heterogenous at any point in time even if natural selection favors individuals of a certain type. Hence, this mechanism simply prevents that either of the types becomes extinct during the process of development due to an evolutionary disadvantage.

Let the probability that an adult individual of type i survives to old age, ϕ^i , be positively affected by the genetically predetermined somatic investment in childhood, k^i . Individuals whose genetically pre-determined somatic investment is below a certain threshold, \bar{k} , don't survive to old age. It follows that

$$\phi^i = \phi(k^i) \begin{cases} > 0 & \text{if } k^i > \bar{k} \\ = 0 & \text{if } k^i \leq \bar{k}, \end{cases} \quad (3)$$

where $\phi(k^i) < 1$, $\phi'(k^i) > 0$, $\phi''(k^i) < 0$, and $\lim_{k \rightarrow \infty} \phi'(k^i) = 0$ for all $k^i > \bar{k}$. Apparently, individuals with a higher level of somatic investment during childhood, $k^i > \bar{k}$, enjoy on average a longer post-reproductive life span, $\phi^i > 0$.

2.3. Preferences and Budget Constraints

Preferences over consumption and reproduction are represented by a simple log-linear utility function. Consider an adult of type i in period t , born and raised as a child in period $t - 1$. The utility function of the individual is defined over consumption, c_t^i , and the number of children,

n_t^i , as

$$u_t^i = (1 - \beta) \ln c_t^i + \beta \ln n_t^i, \quad (4)$$

where $\beta \in (0, 1)$ is the fraction of income that is allocated to child rearing. The utility function is strictly monotonically increasing in consumption, c_t^i , and the number of children, n_t^i , and strictly quasi-concave.

Let an adult individual of type i in period t be endowed with h_t^i efficiency units of labor. The adult earns the competitive market wage w_t per efficiency unit. Hence, the income of the adult of type i in period t is given by

$$y_t^i = w_t h_t^i. \quad (5)$$

This income is allocated optimally between consumption and reproduction. Since somatic investment per child, k^i , only depends on the type i , an adult individual of type i at time t faces the budget constraint

$$k^i n_t^i + c_t^i \leq y_t^i. \quad (6)$$

Optimizing (4) with respect to (6) yields

$$c_t^i = (1 - \beta) y_t^i \quad (7)$$

$$n_t^i = \frac{\beta y_t^i}{k^i}. \quad (8)$$

It is apparent from (8) that there is a trade-off between the number of children, n_t^i , and the amount of somatic investment in each child, k^i . For a given income, individuals who are genetically pre-determined to invest more resources in each child give birth to less children. Furthermore, the number of children is an increasing function of parental income. This feature is fundamental to the Malthusian environment, which is at the heart of the proposed theory.

2.4. The Production of Human Capital

An individual's level of human capital is determined by the transfer of knowledge from old to young (i.e. education) and by the level of technology. I assume that improvements in technology reduce the value of human capital for a given level of education. However, education lessens the adverse effect of technology on human capital. Hence, the transfer of knowledge from old to young becomes more important with the level of technology.

Within a dynasty i , the level of education of a child in period t , e^i , is determined by the average length of the post-reproductive life span of old adults in the same period, ϕ^i :

$$e^i = \phi(k^i). \quad (9)$$

This assumption is a strong simplification. First, it implies that old adults use their time endowment to educate all children within their dynasty equally, but don't educate children from other dynasties at all. Second, it abstracts from any dilution effects by population growth within the dynasty. However, this assumption captures the essence of education: the average time overlap between generations lies at the heart of knowledge transfers from old to young. In the setup of this model, the average post-reproductive life span is a function of somatic capital. Hence, the level of education increases with somatic investment per child, k^i .

The level of human capital of children of an adult of type i in period t , h_{t+1}^i , is an increasing strictly concave function of their grandparental time investment in education, e^i , and a decreasing strictly convex function of the level of technology, A_{t+1} ,

$$h_{t+1}^i = \tilde{h}(e^i, A_{t+1}). \quad (10)$$

Each child has a positive level of human capital even in without education, $\tilde{h}(0, A_{t+1}) > 0$, and the basic level of human capital is normalized to 1 for the initial level of technology, $\tilde{h}(0, A_0) = 1$. If the level of technology increases, human capital decreases to zero in the absence of education, $\lim_{A \rightarrow \infty} \tilde{h}(0, A_{t+1}) = 0$.

The adverse effect of technology on human capital accumulation is assumed to be lower for individuals that educate their children. Hence, education complements technology,

$$\tilde{h}_{eA}(e^i, A_{t+1}) > 0. \quad (A1)$$

Moreover, I assume that the elasticity of the effect of education on human capital production, $\tilde{h}_e(e^i, A_{t+1})$, with respect to education, e^i , is negative and smaller than one in absolute value,

$$-\eta_{\tilde{h}_e e^i} \equiv \left| \frac{\tilde{h}_{ee}(e^i, A_{t+1})e^i}{\tilde{h}_e(e^i, A_{t+1})} \right| < 1 \quad \text{for } e^i > 0, \quad (A2)$$

which assures that the factor demand for education in human capital production is elastic.

The level of education of a child, e^i , only depends on somatic investment per child, k^i . This leads to a human capital production function $h(k^i, A_{t+1})$, which only depends on somatic capital k^i and the level of technology A_{t+1} :

Lemma 1. *The level of human capital of children of an adult of type i in period t , h_{t+1}^i , is a decreasing strictly convex function of the level of technology, a constant function of somatic investment in offspring for $k^i < \bar{k}$, and an increasing strictly concave function of somatic*

investment in offspring for $k^i \geq \bar{k}$:

$$h_{t+1}^i = \tilde{h}(\phi(k^i), A_t) \equiv h(k^i, A_{t+1}).$$

Furthermore, for $k^i \geq \bar{k}$, somatic investment complements technology, $h_{kA}(k^i, A_{t+1}) > 0$.

Proof. Follows directly from (A1) and the properties of (3) and (10). \square

With this human capital production function, technology has two opposing effects on output per individual. On the one hand, technological progress increases the wage per efficiency unit of labor w_t —the “productivity effect”. On the other hand, it reduces the number of efficiency units of labor h_t^i —the “erosion effect”. To guarantee that a new technology is used, the productivity effect has to dominate the erosion effect. This is the case if elasticity of $h(k^i, A_t)$ with respect to A_t is negative and smaller than $\alpha/(1 - \alpha)$ in absolute value,

$$-\eta_{hA}^i(A_t) \equiv \left| \frac{h_A(k^i, A_t)A_t}{h(k^i, A_t)} \right| < \frac{\alpha}{1 - \alpha}, \quad (\text{A3})$$

as follows immediately from (5).

2.5. Evolutionary Optimal Somatic Investment

In a stationary environment, a certain type i of individuals has the largest number of offspring. Therefore, this type will dominate the population in the long run. Let k_t be the genetically determined level of somatic investment that generates the evolutionary advantage if the level of technology is fixed to A_t . This level of somatic investment is determined by maximizing the number of offspring in (8) with respect to k^i :

$$k_t = \arg \max \left\{ \frac{\beta w_t h(k^i, A_t)}{k^i} \right\} \quad \text{s.t.} \quad k^i \geq \bar{k}. \quad (\text{11})$$

Optimizing this expression implies that the implicit functional relationship between optimal somatic investment, k_t , and the level of technology, A_t , is given by

$$G(k_t, A_t) \equiv h_k(k_t, A_t) - \frac{h(k_t, A_t)}{k_t} \begin{cases} = 0 & \text{if } k_t > \bar{k} \\ \leq 0 & \text{if } k_t = \bar{k}, \end{cases} \quad (\text{12})$$

where $G(k_t, A_t)$ is the sum of the gain in quality of children and the loss in quantity of children from a marginal increase in somatic investment. For all $A_t \geq A_0$ and $k_t \geq \bar{k}$, the derivatives of (12) are readily given as $G_k(k_t, A_t) < 0$ and $G_A(k_t, A_t) > 0$.

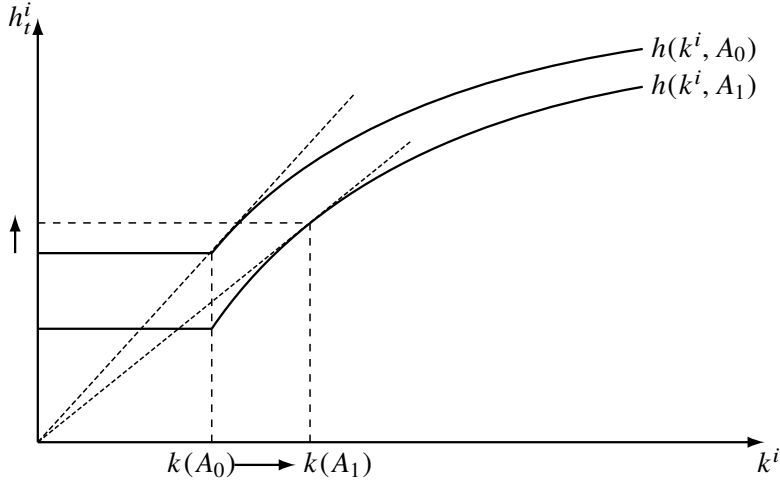


Figure 2: Evolutionary Optimal Somatic Investment for Two Levels of Technology, $A_1 > A_0$.

Individuals with a genetically determined level of somatic investment of $k^i = \bar{k}$ do not survive to old age. Therefore, they don't transfer knowledge between generations and the level of education of their children is zero. Without loss of generality, let \bar{k} be the optimal level of somatic investment at the initial level of technology, A_0 , i.e.,

$$G(\bar{k}, A_0) = 0. \quad (\text{A4})$$

Lemma 2. *Under (A1)–(A4), the genetically determined level of somatic investment, k_t , that generates the largest number of offspring, is a unique single-valued function of the level of technology,*

$$k_t = k(A_t),$$

with $k(A_0) = \bar{k}$ and $k(A_t) > \bar{k}$ for all $A_t > A_0$. Furthermore, both the evolutionary optimal level of somatic investment, $k_t = k(A_t)$, and the evolutionary optimal level of human capital, $h_t \equiv h(k(A_t), A_t)$, are increasing functions of the level of technology, i.e.,

$$\frac{\partial k(A_t)}{\partial A_t} > 0 \quad \text{and} \quad \frac{\partial h(k(A_t), A_t)}{\partial A_t} > 0.$$

Proof. Follows from (A1), (A2), (A4) and the properties of (12). \square

It is clear from (12) that the evolutionary optimal level of somatic investment, $k(A_t)$, is given by the unique tangency point between the human capital production function $h(k^i, A_t)$ and a ray from the origin, as depicted in Figure 2. It shows that the evolutionary optimal level of somatic investment is an increasing function of the level of technology since technological

progress has an adverse impact on human capital formation for all levels of k^i . As long as (A1) is satisfied, the adverse impact is lower for individuals with higher somatic investment in offspring and the ray from the origin is necessarily tangent to the function $h(k^i, A_t)$ at a higher level of k^i . Moreover, as long as (A2) is satisfied, the evolutionary optimal level of human capital is an increasing function of the level of technology. That is, the tangency between the function $h(k^i, A_t)$ and the ray from the origin would occur at a higher level of human capital if somatic investment, k^i , generates less than a proportional decrease in its positive effect on human capital formation, $h_k(k^i, A_t)$.

It is apparent from Lemma 2 that technological progress will trigger a process of natural selection that gradually increases somatic investment. A rise in somatic investment increases the survival probability to old age and gives rise to education of children, which mitigates the adverse effect of technology on efficiency units of labor. Learning becomes more important for production in a technological advanced environment and nature selects for individuals with a pattern of overlap between generations just adequate for optimal transfer of knowledge.

Thus, the theory suggests that subsequent increases in the level of technology in the run-up to the Early Upper Paleolithic altered the evolutionary optimal allocation of resources from offspring quantity to offspring quality and generated an evolutionary advantage for individuals that were characterized by higher somatic investment in offspring, a longer post-reproductive life span, and adequate transfer of knowledge from old to young.

2.6. Differential Fertility Across Types

In period 0 there is a number L_0^b of identical adult individuals of type b —the “quantity type”—that are genetically pre-determined to invest $k^b = k(A_0) = \bar{k}$ units of somatic capital in each offspring. It is clear from (A4) that this amount of somatic investment is optimal at the initial level of technology, A_0 . Individuals of this type have the largest number of offspring in every time period up to period 0. Therefore, they dominate the population in period 0. However, they never reach old age since the probability to survive to old age is zero, $\phi^b = \phi(k^b) = 0$. Per assumption, individuals of type b don’t educate their progeny. The human capital of individuals of type b is a function of the level of technology,

$$h_t^b = h(k^b, A_t) \equiv h^b(A_t). \quad (13)$$

In period 0 there is also a number L_0^a of identical adult individuals of type a with a high level of genetically pre-determined somatic investment, $k^a > \bar{k}$. This type is called the “quality type”. At the initial level of technology, A_0 , natural selection favors individuals of the quantity

type. However, since individuals of type b give birth to progeny of type a with an infinitesimal probability $(1 - \rho) \rightarrow 0$, the population consists of two homogenous groups of type a and type b in every period t ,

$$L_t = L_t^a + L_t^b. \quad (14)$$

Individuals of type a survive to old age with a positive probability of $\phi^a = \phi(k^a) > 0$. The level of education of an individual of type a is therefore $e^a = \phi(k^a) > 0$, as follows from (9). The amount of human capital of individuals of type a is given by

$$h_t^a = h(k^a, A_t) \equiv h^a(A_t). \quad (15)$$

In the process of development, the evolutionary advantage will change from the quantity type to the quality type since the optimal level of somatic capital increases with the level of technology. Hence, the fertility ratio between individuals of type a and individuals of type b is an increasing function of technology,

$$\frac{n_t^a}{n_t^b} = \frac{h^a(A_t)k^b}{h^b(A_t)k^a} \equiv \gamma(A_t), \quad (16)$$

as follows from (5) and (8).

Lemma 3. *Under (A1), (A2), and (A4), the fertility ratio $\gamma(A_t)$ is a positive, unbounded, and strictly increasing function of the level of technology, A_t ,*

$$\gamma(A_t) > 0, \quad \gamma'(A_t) > 0, \quad \lim_{A_t \rightarrow \infty} \gamma(A_t) = \infty.$$

The initial fertility ratio in period 0 is smaller than one, $\gamma(A_0) < 1$. Furthermore, the elasticity of the fertility ratio with respect to A_t is positive and smaller than $\alpha/(1 - \alpha)$:

$$\eta_{\gamma A}(A_t) \equiv \frac{\gamma'(A_t)A_t}{\gamma(A_t)} < \frac{\alpha}{1 - \alpha}.$$

Proof. Follows from (16), (A1), (A2), (A4), and Lemma 2. □

Proposition 1. *There exists a unique level of technology, $\hat{A} > A_0$, such that the fraction of individuals of each type in the population remains stationary, $\gamma(\hat{A}) = 1$. Individuals of type b have an evolutionary advantage in an environment that is characterized by a low level of technology, $A_t < \hat{A}$, whereas individuals of type a have an evolutionary advantage in an*

environment that is characterized by an advanced level of technology, $A_t > \hat{A}$. That is

$$\gamma(A_t) \geq 1 \iff A_t \geq \hat{A}.$$

Proof. The proposition is a corollary of Lemma 3. □

Once the level of technology increases above \hat{A} in the process of development, the evolutionary advantage shifts from the quantity type to the quality type. The fraction of individuals of type a increases in the population. Eventually, in the limit the population is dominated by the quality type that is characterized by higher somatic investment in offspring. A share of $\phi(k^a)$ adult individuals reach old age and experience a significant post-reproductive life span. The overlap between generations is used to transfer productively relevant knowledge from old to young.

2.7. No Food-Sharing

It is well known that hunter-gatherers practiced food-sharing outside the household (Gurven et al. 2000; Kaplan and Hill 1985; Marlowe 2005). Especially large game was shared on a regular basis. Contrary to this fact, I completely abstract from food-sharing in this model. This could be a problem, since food-sharing would allow individuals with an evolutionary disadvantage to reproduce better than accounted for by the model.

However, there are two reasons to abstract from food-sharing. First, it has been shown that the producer kept a significantly greater fraction of the food he acquired than he gave to other receivers (Marlowe 2010, p. 312). Hence, hunter-gatherers were indeed interested in feeding their families first, even if food-sharing diluted the efficiency of provisioning considerably. Second, the foods women target are also shared less extensively outside than are men's food. Because women daily acquire more reliable foods that are shared less outside the household, it is clear that their foraging strategy is aimed at provisioning their households (Marlowe 2010, p. 285). This pattern is true of virtually all tropical foragers (Marlowe 2007).

Interestingly, there is some evidence that provisioning and direct care are not inversely related. On the contrary, men who provided more direct care tended to bring back more food. So it seems some men just invest more than others in their children overall, and more in genetic children than in stepchildren (Marlowe 2010, p. 277). This is direct evidence for the presence of individuals of a high somatic investment type, as assumed by this model.

3. The Time Path of the Macroeconomic Variables

3.1. The Dynamics of Population Across Types

The relative population dynamics of both types are determined by the adult population size of each type, L_t^a and L_t^b , the fertility rates, n_t^a and n_t^b , and the probability of transmission of the same genetic type from parents to offspring, ρ . The population size of adult individuals of type i in period $t + 1$ is given by

$$L_{t+1}^i = \rho L_t^i n_t^i + (1 - \rho) L_t^j n_t^j, \quad (17)$$

where $i, j \in \{a, b\}$ and $i \neq j$. This captures the fact that individuals of type i give birth to progeny of the same type with high probability, $\rho \rightarrow 1$, but bear children of the other type with low probability, $(1 - \rho) \rightarrow 0$. Let λ_t be the share of adult individuals of type a in the total population in period t , that is

$$\lambda_t = \frac{L_t^a}{L_t}, \quad (18)$$

where $\lambda_t \in [0, 1]$. As follows from (17), this population share evolves over time according to

$$\lambda_{t+1} = \frac{\rho \lambda_t \gamma(A_t) - (1 - \rho)(1 - \lambda_t)}{\lambda_t \gamma(A_t) + 1 - \lambda_t}. \quad (19)$$

For $\rho \rightarrow 1$, this equation simplifies to

$$\lim_{\rho \rightarrow 1} \lambda_{t+1} = \frac{\lambda_t \gamma(A_t)}{\lambda_t \gamma(A_t) + 1 - \lambda_t} \equiv \theta(\lambda_t, A_t). \quad (20)$$

Lemma 4. *For all $A_t > 0$, the function $\theta(\lambda_t, A_t)$ is increasing from 0 to 1 in the share of individuals of type a in the population λ_t , i.e. $\theta_\lambda(\lambda_t, A_t) > 0$ with $\theta(0, A_t) = 0$ and $\theta(1, A_t) = 1$, strictly concave for $A_t > \hat{A}$, and strictly convex for $A_t < \hat{A}$, i.e.*

$$\theta_{\lambda\lambda}(\lambda_t, A_t) \gtrless 0 \iff A_t \lesseqgtr \hat{A}.$$

Furthermore, the function $\theta(\lambda_t, A_t)$ is increasing in the level of technology A_t , i.e. $\theta_A(\lambda_t, A_t) > 0$.

Proof. Follows immediately from (20) and Proposition 1. □

The evolution of the share of individuals of type a in the population, as follows from (20) and Lemma 4, is depicted in Figure 3. The share decreases to zero as long as the level of technology is below the threshold level \hat{A} . Thus, the population is dominated by quantity type

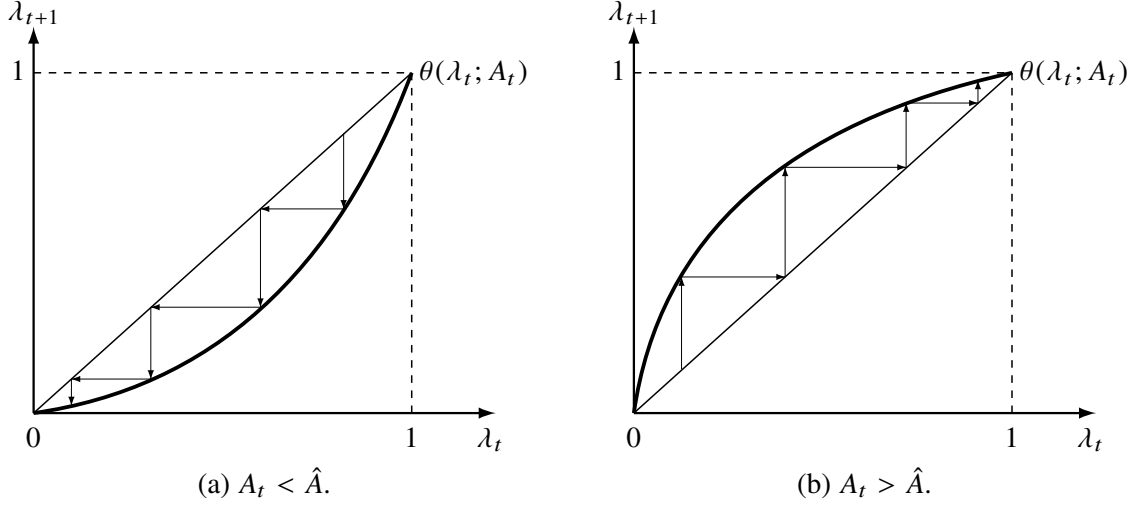


Figure 3: The Evolution of the Share of Individuals of Type a in the Population (a) for a Low Level of Technology and (b) for a High Level of Technology.

in early levels of development. When the level of technology increases above the threshold level \hat{A} , the share starts to rise and, eventually, the population is dominated by the quality type.

3.2. The Dynamics of Population Size

The size of the adult population evolves over time according to

$$L_{t+1} = L_t^a n_t^a + L_t^b n_t^b = \frac{h^b(A_t)}{k^b} \beta w_t (\lambda_t \gamma(A_t) + 1 - \lambda_t) L_t, \quad (21)$$

as follows from (14) and (17). The wage per efficiency unit of labor in period t , w_t , depends on the level of technology, A_t , and the amount of efficiency units of labor, H_t , which is given by

$$H_t = L_t^a h^a(A_t) + L_t^b h^b(A_t) = h^b(A_t) L_t (\lambda_t \gamma(A_t) \kappa + 1 - \lambda_t). \quad (22)$$

Thus, noting (2), the evolution of the population size in (21) can be written as

$$L_{t+1} = \frac{h^b(A_t)^{1-\alpha}}{k^b} \frac{\lambda_t \gamma(A_t) + 1 - \lambda_t}{(\lambda_t \gamma(A_t) \kappa + 1 - \lambda_t)^\alpha} \beta A_t^\alpha L_t^{1-\alpha} \equiv \sigma(\lambda_t, A_t) L_t^{1-\alpha} \equiv \psi(\lambda_t, L_t, A_t). \quad (23)$$

To assure that the effect of technology on population size is unambiguously positive, I assume that the ratio of the genetically pre-determined level of somatic investment of type a and type b is smaller than the inverse of α ,

$$\frac{k^a}{k^b} = \kappa < \frac{1}{\alpha}. \quad (A5)$$

Hence, the level of somatic investment of the quality type, k^a , is assumed to be larger than k^b but smaller than k^b/α .

Lemma 5. *Under (A3) and (A5), the function $\psi(\lambda_t, L_t, A_t)$ is increasing and strictly concave in the population size, i.e. $\psi_L > 0$, $\psi_{LL} < 0$, $\lim_{L \rightarrow 0} \psi_L = \infty$, and $\lim_{L \rightarrow \infty} \psi_L = 0$. It is increasing in the level of technology, i.e. $\psi_A > 0$, $\lim_{A \rightarrow 0} \psi_A = \infty$, and $\lim_{A \rightarrow \infty} \psi_A = 0$. Finally, there exists a level of technology $\bar{A} > \hat{A}$, such that*

$$\psi_\lambda(\lambda_t, L_t, A_t) \geq 0 \iff A_t \geq \bar{A}.$$

Proof. See Appendix A. □

3.3. The Dynamics of Technology

In a Malthusian framework technological progress is typically viewed as driven by population size. Recent studies, however, point to a lag between the emergence of modern human anatomy and the emergence of human behavior, which includes cultural and technological change at a significant pace. White et al. (2003) suggest that modern anatomy evolved at least 160–195 kya. By contrast, the total package of modern human behaviors that indicates a capacity for abstract thought was not in place until about 50–45 kya (Nowell 2010). It was at this time when human populations in Africa gained a significant fitness advantage that led to the Out-of-Africa expansion.

Apparently, population size doesn't seem to be a sufficient condition for technological advances. To capture this fact, I suppose that a certain level of somatic investment is necessary for individuals being able to innovate. In the present framework I simply assume that the rate of technological progress in period t depends upon the population size of the quality type, L_t^a . That is

$$\frac{A_{t+1} - A_t}{A_t} = g(L_t^a), \quad (24)$$

where $g(L_t^a) > 0$ and $g'(L_t^a) > 0$ for all $L_t^a > 0$. Hence, technological progress only occurs if the population contains individuals with a higher level of somatic investment, $k^a > \bar{k}$. Since the population size of the quality type can be expressed as $L_t^a = \lambda_t L_t$, the evolution of technology from period t to period $t + 1$ is given by

$$A_{t+1} = (1 + g(\lambda_t L_t)) A_t. \quad (25)$$

The initial level of technology in period 0 is historically given as $A_0 > 0$.

4. The Dynamical System

The development of the economy is characterized by the evolution of technology, population size, and the distribution of types within the population. It is determined by a sequence $\{\lambda_t, L_t, A_t\}_{t=0}^{\infty}$ that satisfies a three-dimensional nonlinear first-order autonomous system in every period t :

$$\begin{cases} \lambda_{t+1} = \theta(\lambda_t, A_t) \\ L_{t+1} = \psi(\lambda_t, L_t, A_t) \\ A_{t+1} = (1 + g(\lambda_t L_t))A_t. \end{cases} \quad (26)$$

To simplify the exposition, the dynamical system is analyzed in two steps. First, I assume a fixed level of technology and characterize the evolution of population and the distribution of types within the population towards a conditional steady state. Second, I relax the assumption of fixed technology and study the evolution of human longevity along the process of development.

4.1. The Evolution of Population Size and the Distribution of Types

Initially, suppose a fixed level of technology, A_t . The conditional evolution of population and the distribution of types is characterized by a sequence $\{\lambda_t, L_t\}_{t=0}^{\infty}$ that satisfies the following two-dimensional system in every period t :

$$\begin{cases} \lambda_{t+1} = \theta(\lambda_t; A_t) \\ L_{t+1} = \psi(\lambda_t, L_t; A_t). \end{cases} \quad (27)$$

This dynamical subsystem is characterized by a single globally stable steady state equilibrium $(\bar{\lambda}, \bar{L})$ for all levels of development $A_t \neq \hat{A}$. However, the position of the steady state depends on the level of technology. To see this consider the phase diagram depicted in Figure 4. The phase diagram contains a $\lambda\lambda$ locus, which denotes the set of all pairs (λ_t, L_t) for which, conditional on a given level of technology A_t , the fraction of individuals of type a in the population is constant,

$$\lambda\lambda \equiv \left\{ (\lambda_t, L_t) : \lim_{\rho \rightarrow 1} \lambda_{t+1} - \lambda_t = \frac{\lambda_t \gamma(A_t)}{\lambda_t \gamma(A_t) + 1 - \lambda_t} - \lambda_t = 0 \right\}, \quad (28)$$

and a LL locus, which denotes the set of all pairs (λ_t, L_t) for which, conditional on a given level of technology A_t , the population size is constant,

$$LL \equiv \left\{ (\lambda_t, L_t) : L_{t+1} - L_t = \sigma(\lambda_t; A_t) L_t^{1-\alpha} - L_t = 0 \right\}. \quad (29)$$

Lemma 6. For all $L_t > 0$, the $\lambda\lambda$ locus is given by

$$\lim_{\rho \rightarrow 1} \lambda_{t+1} - \lambda_t = 0 \iff \begin{cases} \lambda_t = 0 \\ \lambda_t = 1, \end{cases}$$

where $\lim_{\rho \rightarrow 1} \lambda_{t+1} - \lambda_t \geq 0$ if and only if $A_t \geq \hat{A}_t$ for all $\lambda_t \in (0, 1)$.

Proof. Follows immediately from the properties of (28) and Proposition 1. \square

Hence, the $\lambda\lambda$ locus consists of two vertical lines in the (λ_t, L_t) space, one at $\lambda_t = 0$ and one at $\lambda_t = 1$. As long as individuals of type b have an evolutionary advantage, i.e. for $A_t < \hat{A}$, the fraction of individuals of type a in the population is decreasing. When individuals of type a gain the evolutionary advantage, i.e. for $A_t > \hat{A}$, their fraction in the population is increasing. If $A_t = \hat{A}_t$, none of the types has an evolutionary advantage and there are no changes in the composition of the population over time.

Lemma 7. Under (A3) and (A5), the LL locus is given by the function $L_t = \sigma(\lambda_t; A_t)^{\frac{1}{\alpha}}$, where

$$\frac{\partial L_t}{\partial \lambda_t} \geq 0 \iff A_t \geq \bar{A}, \quad \frac{\partial L_t}{\partial A_t} > 0.$$

Furthermore, for all λ_t and A_t , $L_{t+1} - L_t \geq 0$ if and only if $L_t \geq \sigma(\lambda_t; A_t)^{\frac{1}{\alpha}}$.

Proof. Follows immediately from the properties of (29) and Lemma 5. \square

Hence, in the (λ_t, L_t) space the LL locus is downward sloping for $A_t < \bar{A}$, horizontal for $A_t = \bar{A}$, and upward sloping for $A_t > \bar{A}$. Moreover, it shifts upward when the level of technology increases. As depicted in Figure 4, the $\lambda\lambda$ locus and the LL locus intersect at two points in every period t . The dynamical subsystem is therefore characterized by two conditional steady states. As long as individuals of type b have an evolutionary advantage, i.e. for $A_t < \hat{A}$, the globally stable steady state is located on the left vertical line of the $\lambda\lambda$ locus, i.e. $\bar{\lambda} = 0$. When individuals of type a gain the evolutionary advantage, i.e. for $A_t > \hat{A}_t$ the globally stable steady state is located on the right vertical line of the $\lambda\lambda$ locus, i.e. $\bar{\lambda} = 1$. If none of the types has an evolutionary advantage, i.e. for $A_t = \hat{A}$, every point on the LL locus is a steady state since the composition of types remains unchanged.

4.2. The Evolution of Longevity Along the Process of Development

In the following, I relax the assumption of a fixed level of technology and analyze the evolution of human longevity along the process of development. Suppose that the initial level of

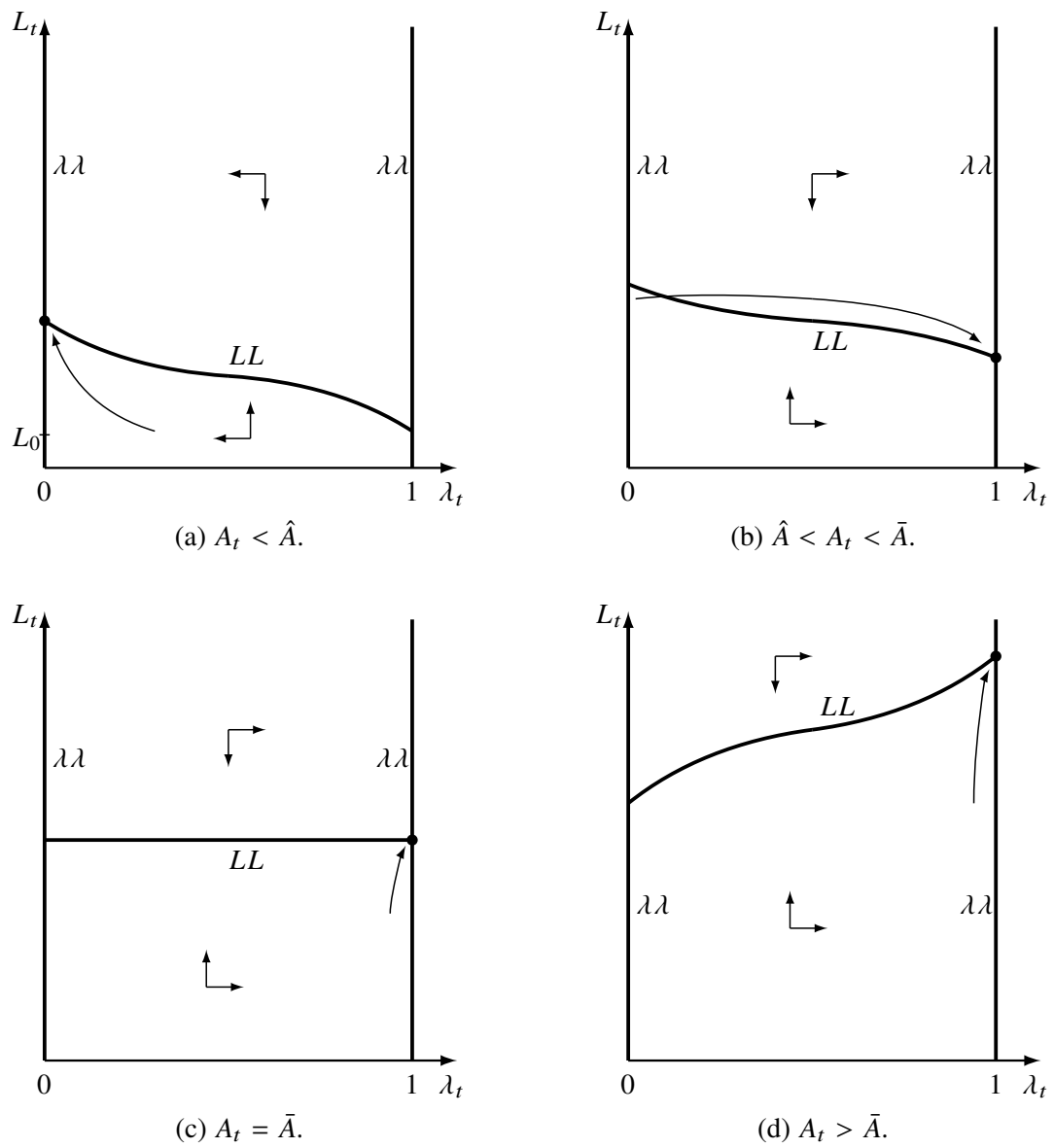


Figure 4: The Coevolution of Population Size and the Share of Individuals of Type a in the Population (a) for a Low Level of Technology, (b) for a Medium Level of Technology, (c) for a Level of Technology Equal to the Threshold Level \bar{A} , and (d) for a High Level of Technology.

technology is low, $A_0 < \hat{A}$. At this stage of development, individuals of type b have an evolutionary advantage and the population consists mainly of individuals of this type, $\lambda_t \rightarrow 0$. However, since the population is heterogenous at any point in time, there is also small population of individuals of type a , which is nearly zero, $L_0^a \rightarrow 0$. It follows that the rate of technological progress is infinitesimally small, $g(L_0^a) \rightarrow 0$.

Apparently, in early stages of development, the technological environment is stable and technological progress is nearly absent. Individuals are characterized by low somatic investment in offspring, a short life span, and the absence of intergenerational transfers of knowledge. The fraction of individuals that survive to old age is marginal.

Over long periods of time, the small number of individuals of type a in each generation is sufficient to advance the level of technology. The LL locus slowly shifts upward and the steady state level of population size increases, as depicted in Figure 4. Furthermore, the degree of the downward curvature of $\theta(\lambda_t, A_t)$ decreases. However, as long as the level of technology is below the threshold level, $A_t < \hat{A}$, the function remains convex, as depicted in Figure 3. Individuals of type b keep their evolutionary advantage, population characteristics remain unchanged, and the pace of technological progress continues to be negligible.

Ultimately, the level of technology passes the threshold level \hat{A} . At this point in time the structure of the dynamical system changes fundamentally as the curvature of $\theta(\lambda_t, A_t)$ in Figure 3 alters from convex to concave. The evolutionary advantage shifts from the quantity type to the quality type, and λ_t increases over time to the new steady state value $\bar{\lambda} = 1$. Since children of the quality type are more costly in terms of somatic investment, $k^a > k^b$, the rise in λ_t leads to a smaller population size, as depicted in Figure 4b. Once the level of technology passes the threshold \bar{A} , however, the fertility advantage of individuals of type a is large enough to sustain a larger population in absolute terms (see Figure 4d).

Over long periods of time the pace of technological change has been nearly nonexistent. This pattern changes rather suddenly when individuals of type a gain the evolutionary advantage and gradually dominate the population. After a relatively short period, the population consist mainly of individuals of the quality type, $L_t^a \rightarrow L_t$. It follows that the rate of technological progress significantly accelerates, $g(L_t) > 0$.

Apparently, in later stages of development, the economy experiences a relatively sudden acceleration in the pace of technological progress. Population growth slows down at first until the population is dominated by individuals of type a that are characterized by high somatic investment in offspring, a long post-reproductive life span, and transfers of knowledge from old to young. Human longevity increases since the fraction of individuals that survive to old age is significant. In the long run, these traits are shared by the population as a whole.

For $\lambda_t \rightarrow 1$, the economy exhibits hyperbolic growth in population and technology. To see

this, note that the dynamical system in (26) simplifies to

$$\begin{cases} L_{t+1} = \sigma(1, A_t)L_t^{1-\alpha} \\ A_{t+1} = (1 + g(L_t))A_t. \end{cases} \quad (30)$$

Apparently, the growth rate of technology increases with the level of population and the growth rate of population increases with the level of technology. Thus, there is a simple feedback loop between population and technology that leads to increasing growth rates over time. Hyperbolic growth implies that the growth rate is proportional to the level. It is thus faster than exponential growth, where the growth rate is constant. This prediction of the model is in line with empirical data about the prehistoric growth of the world population (Kremer 1993).

5. Conclusion

This paper develops a theory about the evolution of human longevity in the process of development. The theory suggests that feedback effects between technological progress and human longevity lie at the heart of their common emergence in human history. The theory has three key features. First, it builds on the fundamental trade-off between the quantity and the quality of offspring. Individuals differ genetically with respect to somatic investment in offspring. Nature selects the life history profile that maximizes reproductive success in any given environment. Thus, the theory is deeply rooted in the evolutionary history of our species, which has been shaped by biological constraints, at least until very recent times.

Second, the theory advances the idea that technological progress can be a trigger for extended longevity if technology and education are complements. It suggests that early technological advances gradually increased the importance of intergenerational transfers of knowledge. Eventually, the fertility advantage shifted towards individuals that were characterized by higher somatic investment in offspring, a significant post-reproductive life span, and knowledge transfers from old to young.

Third, the theory proposes a novel resolution of the “revolution vs. evolution” debate with respect to the origins of modern human behavior. It suggests that the “human revolution”—a significantly accelerated episode of technological change between 60 and 80 kya—is the result of a shift in the evolutionary advantage towards individuals who are characterized by a significant post-reproductive life span. The demographic shift itself is the result of a gradual expression of behavioral modernity, which has been present in Africa since the earliest *Homo sapiens*. Hence, the theory demonstrates that a gradual process of slow technological change over thousands of years has the potential to culminate in a revolutionary extension of the human

life span and thus lays the foundation for an unprecedented pace of technological and cultural innovations.

Interestingly, the suggested feedback effects between technological progress and increased human longevity still seem to be of particular importance today. The gains in human longevity over the last two hundred years correlate with an increasing demand for human capital since the Industrial Revolution. Thus, the very essence of human longevity still seems to be the necessity of knowledge transfers between generations in a skill-intensive environment. Moreover, modern growth rates in industrialized economies are partially contingent on educational efforts in human capital formation. Hence, the very essence of technological progress still seems to be the existence of individuals who are subjected to high parental investment during childhood.

Appendix A. Proofs

Derivatives of the Function $\theta(\lambda_t, A_t)$ in (20).

$$\begin{aligned}\theta_\lambda(\lambda_t, A_t) &= \frac{\gamma(A_t)}{(\lambda_t \gamma(A_t) + 1 - \lambda_t)^2} > 0 \\ \theta_{\lambda\lambda}(\lambda_t, A_t) &= -\frac{2\gamma(A_t)(\gamma(A_t) - 1)}{(\lambda_t \gamma(A_t) + 1 - \lambda_t)^3} \geq 0 \iff A_t \leq \hat{A} \\ \theta_A(\lambda_t, A_t) &= \frac{\lambda_t(1 - \lambda_t)\gamma'(A_t)}{(\lambda_t \gamma(A_t) + 1 - \lambda_t)^2} > 0\end{aligned}$$

□

Proof of Lemma 5. The function $\psi(\lambda_t, L_t, A_t)$ is increasing and strictly concave in L_t :

$$\begin{aligned}\psi_L(\lambda_t, L_t, A_t) &= (1 - \alpha)\sigma(\lambda_t, A_t)L_t^{-\alpha} > 0, \\ \psi_{LL}(\lambda_t, L_t, A_t) &= -\alpha(1 - \alpha)\sigma(\lambda_t, A_t)L_t^{-\alpha-1} < 0,\end{aligned}$$

with $\lim_{L \rightarrow 0} \psi_L(\lambda_t, L_t, A_t) = \infty$ and $\lim_{L \rightarrow \infty} \psi_L(\lambda_t, L_t, A_t) = 0$. Furthermore, as follows from (A3) and (A5), the function $\psi(\lambda_t, L_t, A_t)$ is increasing in the level of technology,

$$\begin{aligned}\psi_A(\lambda_t, L_t, A_t) &= \frac{\psi(\lambda_t, L_t, A_t)}{A_t} \\ &\cdot \left[\alpha + (1 - \alpha)\eta_{hA}^b(A_t) + \frac{\lambda_t \gamma'(A_t) A_t}{\lambda_t \gamma(A_t) + 1 + \lambda_t} - \frac{\alpha \lambda_t \gamma'(A_t) A_t \kappa}{\lambda_t \gamma(A_t) \kappa + 1 - \lambda_t} \right] > 0.\end{aligned}$$

The elasticities $\eta_{hA}^b(A_t)$ and $\eta_{\gamma A}(A_t)$ are bounded. Therefore, $\lim_{A \rightarrow 0} \psi_A(\lambda_t, L_t, A_t) = \infty$ and

$\lim_{A \rightarrow \infty} \psi_A(\lambda_t, L_t, A_t) = 0$ follow directly. Finally, the derivative of $\psi(\lambda_t, L_t, A_t)$ with respect to the share of type a individuals in the population, λ_t , is given by

$$\psi_\lambda(\lambda_t, L_t, A_t) = \frac{h^b(A_t)^{1-\alpha}}{k^b} \beta A_t^\alpha L_t^{1-\alpha} \cdot \left[\frac{(\gamma(A_t) - 1)}{(\lambda_t \gamma(A_t) \kappa + 1 - \lambda)^\alpha} - \frac{\alpha(\lambda_t \gamma(A_t) + 1 - \lambda_t)(\gamma(A_t) \kappa - 1)}{(\lambda_t \gamma(A_t) \kappa + 1 - \lambda)^{1+\alpha}} \right] = 0.$$

Apparently, this equation is equal to 0 if the following condition is satisfied:

$$\frac{\lambda_t \gamma(A_t) \kappa + 1 - \lambda_t}{\gamma(A_t) \kappa - 1} = \alpha \frac{\lambda_t \gamma(A_t) + 1 - \lambda_t}{\gamma(A_t) - 1}.$$

The function on the left hand side of this equation asymptotically approaches λ_t for $A_t \rightarrow \infty$ and becomes infinity for a certain $A_t < \hat{A}$. In contrast, the function on the right side of the equation asymptotically approaches $\alpha \lambda_t$ for $A_t \rightarrow \infty$ and becomes infinity for $A_t = \hat{A}$. Hence, there exists a level of technology, $\bar{A} > \hat{A}$, where both sides of the equation are equal. It follows immediately that $\psi_\lambda \geq 0$ if and only if $A_t \geq \bar{A}$. \square

References

- Caspari, Rachel and Sang-Hee Lee (2004). “Older Age Becomes Common Late in Human Evolution.” In: *Proceedings of the National Academy of Sciences* 101, pp. 10895–10900.
- Caspari, Rachel and Sang-Hee Lee (2005a). “Are OY Ratios Invariant? A Reply to Hawkes and O’Connell (2005).” In: *Journal of Human Evolution* 49, pp. 654–659.
- Caspari, Rachel and Sang-Hee Lee (2005b). “Taxonomy and Longevity: A Reply to Minichillo (2005).” In: *Journal of Human Evolution* 49, pp. 646–649.
- Charnov, Eric L. (1993). *Life History Invariants : Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.
- Clark, Gregory (2007). “Genetically Capitalist? The Malthusian Era, Institutions and the Formation of Modern Preferences.” Unpublished Working Paper, UC Davis.
- Galor, Oded and Marc Klemp (2014). “The Biocultural Origins of Human Capital Formation.” NBER Working Paper 20474.
- Galor, Oded and Stelios Michalopoulos (2012). “Evolution and the growth process: Natural selection of entrepreneurial traits.” In: *Journal of Economic Theory* 147, pp. 759–780.
- Galor, Oded and Omer Moav (2002). “Natural Selection and the Origin of Economic Growth.” In: *Quarterly Journal of Economics* 67, pp. 1133–1191.

- Galor, Oded and Omer Moav (2005). "Natural Selection and the Evolution of Life Expectancy." Unpublished Working Paper.
- Galor, Oded and Omer Moav (2007). "The Neolithic Origins of Contemporary Variations in Life Expectancy." Unpublished Working Paper.
- Gurven, Michael and Hillard Kaplan (2007). "Longevity Among Hunter-Gatherers: A Cross-Cultural Examination." In: *Population and Development Review* 33, pp. 321–365.
- Gurven, Michael, Kim Hill, Hillard Kaplan, Ana Hurtado, and Richard Lyles (2000). "Food Transfers Among Hiwi Foragers of Venezuela: Tests of Reciprocity." In: *Human Ecology* 28, pp. 171–218.
- Hawkes, K. and J.F. O'Connell (2005). "How Old is Human Longevity?" In: *Journal of Human Evolution* 49, pp. 650–653.
- Hawkes, K., J. F. O'Connell, N.G. Blurton Jones, H. Alvarez, and E. L. Charnov (1998). "Grandmothering, Menopause, and the Evolution of Human Life Histories." In: *Proceedings of the National Academy of Sciences* 95, pp. 1336–1339.
- Hawkes, Kristen (2003). "Grandmothers and the Evolution of Human Longevity." In: *American Journal of Human Biology* 15, pp. 380–400.
- Hill, Kim and A. Magdalena Hurtado (1991). "The Evolution of Reproductive Senescence and Menopause in Human Females." In: *Human Nature* 2, pp. 315–350.
- Kachel, A. Friederike, L. S. Premo, and Jean-Jacques Hublin (2011). "Grandmothering and Natural Selection." In: *Proceedings of the Royal Society B* 278, pp. 384–391.
- Kaplan, Hillard and Kim Hill (1985). "Food Sharing Among Ache Foragers: Tests of Explanatory Hypotheses." In: *Current Anthropology* 26, pp. 223–246.
- Kaplan, Hillard, Kim Hill, Jane Lancaster, and A. Magdalena Hurtado (2000). "A Theory of Human Life History Evolution: Diet, Intelligence, and Longevity." In: *Evolutionary Anthropology* 9, pp. 156–185.
- Kirkwood, Thomas B. L. and Steven N. Austad (2000). "Why do we age?" In: *Nature* 408, pp. 233–238.
- Kirkwood, Thomas B. L. and Robin Holliday (1979). "The evolution of ageing and longevity." In: *Proceedings of the Royal Society of London B: Biological Sciences* 205, pp. 531–546.
- Klein, Richard G. (2008). "Out of Africa and the Evolution of Human Behavior." In: *Evolutionary Anthropology* 17, pp. 267–281.
- Konigsberg, Lyle W. and Nicholas P. Herrmann (2006). "The Osteological Evidence for Human Longevity in the Recent Past." In: *The Evolution of Human Life History*. Ed. by Kristen Hawkes and Richard R. Paine. Santa Fe: School of American Research Press. Chap. 9, pp. 267–306.

- Kremer, Michael (1993). "Population Growth and Technological Change: One Million B.C. to 1990." In: *Quarterly Journal of Economics* 108, pp. 681–716.
- Lagerlöf, Nils-Petter (2007). "Long-run trends in human body mass." In: *Macroeconomic Dynamics* 11, pp. 367–387.
- Lieberman, Daniel E. (2013). *The Story of the Human Body: Evolution, Health and Disease*. New York: Pantheon Books.
- Lieberman, Daniel E., Brandeis M. McBratney, and Gail Krovitz (2002). "The Evolution and Development of Cranial Form in *Homo sapiens*." In: *Proceedings of the National Academy of Sciences USA* 99, pp. 1134–1139.
- Marlowe, Frank W. (2005). "Hunter-Gatherers and Human Evolution." In: *Evolutionary Anthropology* 14, pp. 54–67.
- Marlowe, Frank W. (2007). "Hunting and Gathering: The Human Sexual Division of Foraging Labor." In: *Cross-Cultural Research* 41, pp. 170–195.
- Marlowe, Frank W. (2010). *The Hadza: Hunter-Gatherers of Tanzania*. Berkeley and Los Angeles: University of California Press.
- McBrearty, Sally (2007). "Down with the Revolution." In: *Rethinking the Human Revolution*. Ed. by Paul Mellars, Katie Boyle, Ofer Bar-Yosef, and Chris Stringer. Cambridge, UK: McDonald Institute for Archaeological Research. Chap. 12, pp. 133–151.
- McBrearty, Sally and Alison S. Brooks (2000). "The Revolution That Wasn't: A New Interpretation of the Origin of Modern Human Behavior." In: *Journal of Human Evolution* 39, pp. 453–563.
- Medawar, Peter Brian (1952). *An Unsolved Problem of Biology*. H. K. Lewis & Co Ltd London.
- Mellars, Paul (2007). "Rethinking the Human Revolution: Eurasian and African Perspectives." In: *Rethinking the Human Revolution*. Ed. by Paul Mellars, Katie Boyle, Ofer Bar-Yosef, and Chris Stringer. Cambridge, UK: McDonald Institute for Archaeological Research, pp. 1–11.
- Minichillo, Tom (2005). "Paleodemography, Grandmothering, and Modern Human Evolution: A Comment on Caspari and Lee (2004)." In: *Journal of Human Evolution* 49, pp. 643–645.
- Nowell, April (2010). "Defining Behavioral Modernity in the Context of Neandertal and Anatomically Modern Human Populations." In: *Annual Review of Anthropology* 39, pp. 437–452.
- Ofek, Haim (2001). *Second Nature: Economic Origins of Human Evolution*. Cambridge: Cambridge University Press.
- Robson, Arthur J. and Hillard S. Kaplan (2003). "The Evolution of Human Life Expectancy and Intelligence in Hunter-Gatherer Economies." In: *American Economic Review* 93.1, pp. 150–160.

- Rosenberg, Karen (2004). "Living Longer: Information Revolution, Population Expansion, and Modern Human Origins." In: *Proceedings of the National Academy of Sciences* 101, pp. 10847–10848.
- Saint-Paul, Gilles (2007). "On market forces and human evolution." In: *Journal of theoretical biology* 247, pp. 397–412.
- Smith, Tanya M., Paul Tafforeau, Donald J. Reid, Joane Pouech, Vincent Lazzari, John P. Zermano, Debbie Guatelli-Steinberg, Anthony J. Olejniczak, Almut Hoffman, Jakov Radovic, Masrour Makaremi, Michel Toussaint, Chris Stringer, and Jean-Jacques Hublin (2010). "Dental Evidence for Ontogenetic Differences between Modern Humans and Neanderthals." In: *Proceedings of the National Academy of Sciences USA* 107, pp. 20923–20928.
- White, Tim D., Berhane Asfaw, David DeGusta, Henry Gilbert, Gary D. Richards, Gen Suwa, and F. Clark Howell (2003). "Pleistocene *Homo sapiens* from Middle Awash, Ethiopia." In: *Nature* 423, pp. 742–747.
- Williams, George C. (1957). "Pleiotropy, Natural Selection, and the Evolution of Senescence." In: *Evolution* 11, pp. 398–411.
- Williams, Paul D. and Troy Day (2003). "Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence." In: *Evolution* 57, pp. 1478–1488.