

A bioeconomic view of the Neolithic transition to agriculture

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Abstract. The adoption of agriculture at the expense of hunting and gathering was the dramatic precondition for all of modern civilization. Recent data suggest, however, that, as a result of this transition, humans at first became more prone to disease, lived shorter lives, were less well-fed and were smaller in stature. Why then would individuals who had the choice of the two economic systems have chosen agriculture? As an explanation, the present paper develops a simple model of the evolution of preferences over the quality and quantity of children, as would have been generated by our long run history as a species. These preferences would have induced the choice of agriculture, but also would have led to these otherwise puzzling health effects.

1. Introduction

The aim of the present paper is to illuminate a remarkable episode in human history. This was the displacement of hunting and gathering (foraging) by agriculture. Agriculture began perhaps ten thousand years ago in the fertile crescent in the Middle East, and not long after that in China and in the Western Hemisphere. Although this obviously was the precondition for modern civilization, there was not an unambiguous improvement in the human condition right after this shift. Apparently, instead, infectious diseases became more prevalent, malnutrition became more common, life expectancy decreased, and humans became smaller in stature. How can these effects be reconciled with the relentless spread of agriculture across Europe? Why does this spread not violate any reasonable account of rational individual choice?

The present paper shows that these phenomena are generated by a simple biological model. There are two overlapping age classes—young and adult. Young individuals are subject to mortality, so not all of them survive to be adult. Adults determine both the quantity of their offspring and their quality. The quality of offspring is interpreted as the energy invested in each individual, largely as somatic or bodily capital.

A key assumption is that the preferences regarding the quantity and quality of offspring are evolutionarily optimal, deriving from maximizing the long-run number of descendants over all of our history as hunter-gatherers. These preferences are taken to be fixed in the short-run. However, short-run behavior during the transition remains completely consistent with the maximization of biological fitness. It is also important that there are feedback

effects from the size of the population that eventually restrict growth. One such feedback effect reduces individual output, reflecting limited natural resources such as land. The probability of individual survival incorporates another negative feedback effect from increased population, that arising from increased infectious disease.

The instigating factor for the Neolithic transition is a technology shift to agriculture that raises output. This implies that individuals would prefer agriculture over foraging if both economic systems were available. The model then predicts that the transition will raise mortality, because it raises population, in the long run. Fertility rises but somatic capital falls, also in this long run. That is, individuals put greater emphasis on the quantity of children at the expense of their quality. Finally, detailed dynamic properties of the transition are derived, with short-run effects that exaggerate those arising in the long run.

The apparently anomalous health effects during the transition to agriculture are then derived from economically reasonable and unchanging preferences over the quantity and quality of offspring. Furthermore, these preferences might well have been generated by natural selection over our history as hunter-gatherers.

The present paper focuses on why the transition to agriculture had the effects on human health that it did. Previous literature that is directly relevant to this issue is considered in the following section. The present paper is less directly concerned with the fascinating questions of why the transition occurred when and where it did, but this background obviously remains important. The literature dealing with these more obvious questions is discussed and related to the present paper in Section 4.

2. Facts and issues surrounding the Neolithic transition to agriculture

2.1 The spread of agriculture in Europe, population growth

The large scale adoption of agriculture and a settled way of life at the expense of hunting and gathering occurred a remarkably short time ago. Agriculture seems to have arisen in the fertile crescent in the Middle East roughly 10,000 years ago. It started spreading about 9,000 years ago, taking about 4,000 years to spread to the northern and western fringes of Europe—Scandinavia, England and Spain—thus moving at about 1 kilometer a year. This transition was associated with a sharp rise in population. Cavalli-Sforza and Cavalli-Sforza (1995, Chapter 6) discuss the traces that this left in the modern European gene pool.¹

Indeed, the genetic make up of modern individuals across locations in Europe correlates well with the estimated date at which agriculture was adopted there. That is, the map derived from the first principal component of the distribution of modern human genes closely matches the map of the spread of agriculture as estimated from radiocarbon dating of the associated remains. Cavalli-Sforza and Cavalli-Sforza (1995) therefore hypothesize that the genotype of the hunter-gatherers originally in the fertile crescent differed noticeably from those in Europe. As the population of farmers rose, there was a wave of emigration into neighboring lands. The genotype of these agricultural emigrants was then diluted by that of the original hunter-gatherer inhabitants. Hence, as this wave progressed further away from the Middle East, the resulting dilution increased. Cavalli-Sforza and Cavalli-Sforza emphasize that the spread of agriculture was not purely the spread of an idea, but involved the movement of people themselves.²

More direct evidence concerning the sharp rise in population following the transition to agriculture is provided by Bocquet-Appel (2002), who studies the age distribution of skeletons found in Neolithic graveyards. Other things equal, that is, the higher the proportion of skeletons of the young, the more rapidly growing the population is deduced to have been. He finds such evidence of a wave of population growth spreading across Europe that is consistent with the genetic and radiocarbon evidence for the transition. The population growth rate apparently rose from about zero before the transition to about 1% after. At first blush, this might not seem like much, but only about 460 years of such growth would suffice to generate a 100-fold increase in population.

2.2 Evidence on disease, life expectancy, nutrition, and stature.

Inevitably enough, this transition to agriculture was once considered a first step towards modern industrial society—perceived as part of the triumphant march of human progress. Recently, however, a much more complex and interesting picture has been emerging.³

In the first place, the greater incidence of skeletal lesions suggests that the adoption of agriculture was associated with a rise in infectious disease. (These lesions are essentially an extra layer of bone, and are often evident on larger bones in particular. The formation of this extra layer is a reaction to the presence of the disease in the membrane surrounding the bone.) Such diseases may have been less prevalent among hunter-gatherers because of their low population densities, but became more prevalent with the greater densities implied by agriculture.

In the second place, and now verging on the paradoxical, the advent of agriculture was

apparently associated with a higher incidence of chronic malnutrition. Evidence for this can be found in the porosity of the skull associated with anemia, since the likely cause of this latter disorder is inadequate nutrition.⁴ Indeed, agriculture seems not even to have reduced the variability in the food supply from that under foraging, since the occasional famine caused by crop failure may have been more severe than the shortfalls in food obtained from foraging. This is suggested by evidence of physiological stress. That is, if a growing individual suffers significant but temporary food deprivation, this interrupts the growth of bones and teeth, generating lines in bones and ridges in dental enamel.⁵

Thirdly, a decrease in height and physical stature, more generally, seems to have accompanied the transition to agriculture. This decrease in stature can be seen not only in malnourished individuals, but also in individuals with no other signs of malnutrition, suggesting, in latter case, that the decrease in stature was adaptive to the new circumstances. Of relevance here is that hunting and gathering seems to have been more physically demanding than agriculture, at least in terms of the peak effort required rather than total work load. The data indicate a reduction in arthritis, for example, after the advent of agriculture, and the incidence of arthritis in some particular joint is believed to be linked to the peak stress on the joint.

Finally, estimates of the age at death for the skeletons that are available, combined with estimates of the steady state growth rate of the population, imply a dramatic decrease in life expectancy resulted from agriculture. For example, Galor and Moav (2007) estimate that life expectancy fell by 30% from the Mesolithic to the Neolithic.

2.3. Issues

The conclusions drawn here have not escaped criticism. For example, Wood *et al* (1992) suggest that the data are equally consistent with an improvement in health in the transition from foraging to agriculture. That is, the presence of bone lesions in a particular skeleton might mean that this individual was actually more resistant to the associated diseases than was another individual who succumbed before forming any such lesions. If there were a decrease in disease with the transition, the adoption of agriculture would be less puzzling from a rational choice perspective.

The best way to address such issues is to consider additional evidence. For example, recent populations in which infectious diseases were largely untreated could illuminate whether there is a positive or negative correlation between bone lesions in skeletons and the incidence of disease among the living. Such populations might exhibit a positive correlation between population density and the incidence of disease. Further, the perhaps surprising affluence and health of present day hunter-gatherers helps to reinforce the original conclusions. Sahlins (1988) coined the phrase “the original affluent society” to reflect the apparent high output of the !Kung, for example, in acquiring plant and animal food.⁶ Robson and Kaplan (2003) also summarize data from a number of sources showing that hunter-gatherers have surprisingly low mortality rates and high life expectancy.

Indeed, the increase in population density makes an increase in infectious disease *per se* an inherently unsurprising implication of agriculture. In any case, the stance adopted here is: Suppose all the original “naive” interpretations concerning various aspects of health outlined

in the previous subsection withstand further scrutiny. Is it then impossible that rational individuals would have chosen agriculture at the expense of foraging so that agriculture would spread? The contribution of the present paper is to show that these naive interpretations do not conflict with a simple biological model.

3. The Model

The model here straightforwardly predicts that population will rise because agriculture shifts up the per capita production function. This increased population density results in greater incidence of disease and a reduction in life expectancy. Less straightforwardly, the increase in mortality also tends to reduce somatic capital, or stature, as is also consistent with the evidence. At the same time, fertility rises, so individuals are induced, by a change in the feasible set, to make a different trade-off between the quality and quantity of offspring.

In detail then, consider a population in which there are just two overlapping age classes— young and adult. For simplicity, individuals reproduce asexually. Subject to her output, each adult chooses the quantity of her offspring and the amount of capital, K , say, invested in each of these. Capital is interpreted as largely somatic or embodied capital, reflecting stature and strength. Undoubtedly, this is subject to genetic influence, which might entail only slow modification. However, somatic capital is also subject to rapid discretionary change, since it is greatly affected by nutrition, especially during growth.

Adult output available for transfers to offspring is then a function of somatic capital, $K > 0$. Additional arguments of output are the total number of adults, $N > 0$, and a parameter, $\alpha = 0$, or 1 , to reflect the production functions for foraging and agriculture,

respectively. The following restrictions are then imposed on these production functions:

Assumption 1. i) As a function of K , the production function for adult output for transfers is similar to that used in the theory of perfect competition.⁷

More precisely, for each $N > 0$ and $\alpha = 0$ or 1 , there exists $\bar{K} > 0$ such that $F(K, N, \alpha) = 0$, for $K \in [0, \bar{K}]$; $F_K(K, N, \alpha) > 0$ and $F_{KK}(K, N, \alpha) < 0$, for all $K > \bar{K}$; and $F_K(K, N, \alpha) \rightarrow 0$, as $K \rightarrow \infty$.⁸

ii) The shift to agriculture is advantageous, in that $F(K, N, 1) > F(K, N, 0)$, for all $K > \bar{K}$ and $N > 0$. On the other hand, an increase in the number of adults, N , decreases output, since there are fixed factors such as land. That is, $F_N(K, N, \alpha) < 0$, for all $K > \bar{K}$ and $N > 0$.⁹

The implications of Assumption 1 i) concerning the dependence of output on capital are represented in Figure 1. There is then a unique capital stock, $K(N)$, that maximizes the average product of capital.

INSERT FIGURE 1 HERE

The transition from young to adult is governed as follows:

Assumption 2. The probability of survival from young to adult is $p(N) \in (0, 1)$, where $p'(N) < 0$, for all $N > 0$.

That is, perhaps the key feedback effect of population N is on survival, reflecting the increased prevalence of infectious diseases in a denser population. Such increased prevalence would arise not only from closer proximity to other humans but also from closer proximity to domesticated animals.¹⁰

An important generalization of the model here would be to allow mortality to be influenced by individual characteristics. For example, if an individual dedicated more energy to immune function, by increasing the range and depth of antibodies, this could increase survival. Perhaps the simplest way to make individual characteristics matter like this would be for somatic capital to be an additional argument of survival probability, so that this became $p(K, N)$, where $p_K(K, N) > 0$. Thus greater investment in somatic capital would increase survival as well as adult output. The same results obtain if the function $p(K, N)F(K, N, \alpha)$ satisfies the restrictions imposed here on $p(N)F(K, N, \alpha)$.

3.1 The equilibrium steady state

In any steady state such that $N > 0$ is constant, the ratio of adults to the young is p . For each unit mass of young individuals, who each require an energy input of K , there is then a mass of p adults, each of whom has $F(K, N, \alpha)$ output available to transfer. Economic feasibility then yields the following characterization of a steady state: $p(N)F(K, N, \alpha) = K$. This model then gives a prominent role to intergenerational transfers from adults to the young.¹¹ Consider further an “equilibrium steady state” where, in addition to this steady state condition, K solves $\max_{K>0} \frac{F(K, N, \alpha)}{K}$:

Proposition 1. From Assumption 1, it follows that, for each $N > 0$, there exists a unique optimal $K(N) > \bar{K} > 0$, say, maximizing $\frac{F(K,N,\alpha)}{K}$. If $\frac{p(N)F(K(N),N,\alpha)}{K(N)} > 1$, when $N > 0$ is small enough, but $\frac{p(N)F(K(N),N,\alpha)}{K(N)} < 1$, when N is large enough, there exists a unique equilibrium steady state, $(N, K(N)) \gg 0$, satisfying¹²

$$p(N)F_K(K, N, \alpha) = 1 \text{ and } p(N)F(K, N, \alpha) = K. \quad (1)$$

Proof. See Appendix.

This equilibrium steady state has the property that any alternative type that enters in small numbers will do worse in terms of ultimate descendants. That is, this state is the long run prediction of the model.¹³ To see this, note that, if a given adult has productivity $F(K_0, N, \alpha)$, the number of her adult descendants at date $t + 1$ is

$$\begin{aligned} \frac{F(K_0, N, \alpha)}{K_1} p(N) \frac{F(K_1, N, \alpha)}{K_2} p(N) \dots \frac{F(K_t, N, \alpha)}{K_{t+1}} p(N) = \\ \frac{F(K_0, N, \alpha)}{K_{t+1}} p(N)^{t+1} \prod_{\tau=1}^t \frac{F(K_\tau, N, \alpha)}{K_\tau}. \end{aligned} \quad (2)$$

This follows since the fertility of the adult descendant at any date τ is $\frac{F(K_\tau, N, \alpha)}{K_{\tau+1}} \equiv f_\tau$, say. It is intuitive then that any type that does not maximize $\frac{F(K_t, N, \alpha)}{K_t}$ at every date t is *eventually* dominated by the type that does this. A formal statement and proof of this result is given as Lemma 1 in the Appendix.

Maximization of $\frac{F(K_t, N, \alpha)}{K_t}$ at every date t is equivalent to the maximization of $\frac{F(K_{t-1}, N, \alpha)}{K_t} F(K_t, N, \alpha)$ at every t , since $F(K_{t-1}, N, \alpha)$ is given. This criterion is proportional

to the total output of all the immediate surviving descendants of a given adult at date $t - 1$. Alternatively, it can be interpreted as the product of the number of offspring, $f_t = \frac{F(K_{t-1}, N, \alpha)}{K_t}$, and the “quality,” $F(K_t, N, \alpha)$, of each of them. These preferences over quantity and the particular functional form of quality would be favored by natural selection.

Further, these individual decisions concerning the quantity and quality of offspring are the optimal decisions for the group. That is, although hunter-gatherer groups solved various problems that individuals encountered alone, a group of individuals could do no better than maximize $\frac{F(K_{t-1}, N, \alpha)}{K_t} F(K_t, N, \alpha)$, per capita, under the assumptions of the model here.¹⁴

The hypothesis underlying this model is then that humans were selected to have these flexible preferences by 2 million years of hunting and gathering. It is not that humans were selected to make particular numerical choices of quantity and quality. Rather they are assumed to recognize the impact that investment in offspring has on the adult output of these offspring, and hence on the potential offspring of these offspring, regardless of the functional form involved. Such flexibility would be needed for humans in foraging societies to make the right decisions in the wide spectrum of circumstances that presumably arose during this period. It is important that it is not required that natural selection occur during the relatively brief transition to agriculture itself; rather the characteristics of this transition just express these preferences. Indeed, the behavior induced by these preferences during the transition is fully biologically optimal even in the short run. Once these preferences are in place, that is, no further reliance need be placed on the slow process of biological evolution.¹⁵

3.2 Population maximized

Given the inclusion of population, N , in the production and survival functions, it is of interest that there is no “biological externality” here. That is, the equilibrium steady state yields the maximum population that could be obtained, even in principle, in any steady state. Individuals make the optimal steady state choices from the viewpoint of the group. Technically, maximizing descendants as if N were fixed is appropriate because N is itself maximized.

Proposition 2. Suppose that, in addition to Assumption 1, $p(N)F(K, N, \alpha) > K$, if N is small enough, but $p(N)F(K, N, \alpha) < K$, if N is large enough, where $K > 0$ is arbitrary. Then the unique equilibrium steady state is also the unique solution to $\max_{K>0} N$ s.t. $p(N)F(K, N, \alpha) = K$.

Proof. See Appendix.

The above argument shows that maximization of N entails maximization of “profit,” $p(N)F(K, N, \alpha) - K$, for that value of N . The individual interest in maximizing “average product,” $\frac{p(N)F(K, N, \alpha)}{K}$, is then consistent with the social efficiency condition on the “marginal product,” $p(N)F_K(K, N, \alpha) = 1$, given that “profit” is zero. This is reminiscent of the theory of perfect competition, although the incentives of the individual and society here are not precisely analogous to those that apply there.

It follows that this equilibrium steady state also maximizes the total population of young and adults, $\frac{N(1+p(N))}{p(N)}$, since this is an increasing function of N . On the other hand, this steady

state does not maximize GNP, G , say, where $G = NF(K, N, \alpha)$, since $\frac{dG}{dK} = NF_K > 0$, if $\frac{dN}{dK} = 0$. By the same token, neither does it maximize per capita productivity, $F(K, N, \alpha)$.

3.3. An example—comparative statics of the steady state

In order to illustrate the present approach, consider the particular production function $F(K, N) = A[K^\beta N^{-\gamma} - B]$ and survival function $p(N) = CN^{-\delta}$, where the parameters $A, B, C, \gamma, \delta > 0$ and $\beta \in (0, 1)$. We will obtain an agricultural production function from a foraging production function of this form by applying multiplicative shifts to A and B . We concentrate here on the long run comparison of the steady state with foraging to the steady state with agriculture. Partly this is because the model produces unambiguous long run comparative statics under weaker conditions than are required for the short run. Mainly, however, it is because there are inadequate short run data to compare with the theoretical predictions.

This example can readily generate plausible effects on population N , stature K , and life expectancy, which is just p in this two period model. The multiplicative shifts in these variables— R_N , R_K , and R_p , respectively—are estimated as follows. First, Polgar (1972) estimates that the advent of agriculture in France generated a 100-fold increase in population. Second, Angel (1975) presents a small data set in which average male height declined from 177.2 cms in the Upper Paleolithic at 30,000 B.C. to 166.5 cms to in the Later Neolithic at 5000 B.C.¹⁶ Average female height decreased over the same period from 165 cms to 154.4 cms. With an equal number of males and females, this is an overall average decline in height by a factor of 0.94. Assuming a constant Body Mass Index, BMI, this implies a decline in weight

by a factor of 0.88.¹⁷ Third, Galor and Moav (2007) summarize data on life expectancy. This falls from about 30 years in the Mesolithic to about 21 years in the Neolithic, or by a factor of 0.70. To summarize, we wish to generate

$$R_N = 100, R_K = 0.88 \text{ and } R_p = 0.70. \quad (3)$$

Consider now the steady states before and after agriculture. We have $KF_K = F$, giving the following expression for K in terms of N

$$K = \left(\frac{BN^\gamma}{1-\beta} \right)^{1/\beta}. \quad (4)$$

In addition, a steady state requires that $pF_K = 1$. It follows that the solution for N is

$$N = (\beta AC)^{\beta/(\gamma+\beta\delta)} \left(\frac{B}{1-\beta} \right)^{-(1-\beta)/(\gamma+\beta\delta)}$$

so the solution for K follows from (4) and that for p from $p(N) = CN^{-\delta}$.

These solutions generate constant multiplicative shifts in N , K , and p from given multiplicative shifts in A and B . Suppose then these multiplicative shifts in A and B are a and b , respectively. The multiplicative shifts R_N , R_K , and R_p are then

$$\ln R_N = \frac{\beta}{\gamma + \beta\delta} \ln a - \frac{(1-\beta)}{\gamma + \beta\delta} \ln b \quad (5)$$

$$\ln R_K = \frac{\gamma}{\gamma + \beta\delta} \ln a + \frac{\gamma + \delta}{\gamma + \beta\delta} \ln b \quad (6)$$

$$\ln R_p = -\frac{\beta\delta}{\gamma + \beta\delta} \ln a + \frac{(1-\beta)\delta}{\gamma + \beta\delta} \ln b \quad (7)$$

It follows immediately from (5) and (7) that $\delta = -\frac{\ln R_p}{\ln R_N}$.

Given that the shifts in the production parameters are unobservable, there are excess degrees of freedom here, with five unknown parameters and three equations. To eliminate

these, suppose, for example, that $\beta = 0.5$ and that $\gamma = \delta = -\frac{\ln 0.70}{\ln 100} = 0.077$. It follows that (5), (6) and (7) are satisfied with $\ln a = 0.65$ and $\ln b = -0.42$, or $a = 1.92$ and $b = 0.66$. Thus, a shift from a foraging production function given by

$$F(K, N, 0) = A[K^{0.5}N^{-0.077} - B],$$

to an agricultural production function of

$$F(K, N, 1) = 1.92A[K^{0.5}N^{-0.077} - 0.66B],$$

where $p(N) = CN^{-0.077}$ throughout, generates the desired long run multiplicative shifts in N , K and p , as in (3), from this transition to agriculture.

3.4 General comparative statics of the steady state

To obtain a general result, we now impose additional simplifying assumptions on the production functions $F(K, N, \alpha)$. First, it is plausible that primitive hunting was more physically demanding than agriculture, at least in terms of the peak demands.¹⁸ We assume then that $F_K(K, N, 1) \leq F_K(K, N, 0)$.¹⁹ In addition, we assume that the marginal product of stature is not increased by a greater population, or that $F_{KN}(K, N, \alpha) \leq 0$.²⁰ This is not as compelling an assumption, but the results below follow if $F_{KN}(K, N, \alpha)$ is positive but sufficiently small. These two particular assumptions are made in the interests of expositional simplicity.

Consider now the effect of a sudden increase in α from 0 to 1, representing the shift to agriculture. Note first that an individual right at the boundary between agriculture

and foraging would have a private incentive to adopt agriculture, or to continue with it, simply because agriculture improves each child's production function, given $F(K, N, 1) > F(K, N, 0)$. Agriculture would then spread at the expense of hunting and gathering.

Indeed, any individual engaged in agriculture after the transition would also see foraging as an unambiguously worse alternative. This argument does not rely on the network externalities that imply it would be difficult to be the only forager in an agricultural population, despite the likely importance of these.

We have then the following general comparative static results:

Theorem 1. Impose Assumptions 1 and 2 and the additional hypotheses of Proposition 1. In addition, suppose the transition to agriculture does not increase the marginal product of somatic capital, so that $F_K(K, N, 1) \leq F_K(K, N, 0)$. Similarly, neither does a larger population increase the marginal product of capital, so that $F_{KN}(K, N, \alpha) \leq 0$. It then follows that population and fertility both rise with the advent of agriculture. It also follows that physical stature decreases. Finally, given that $\frac{F_K}{KF_{KK}} < -1$, productivity F falls.

Proof. See Appendix.

From the point of view of the entire population, it is inevitable that fertility rises if mortality rises, as a consequence of the characterization of a steady state in Proposition 1. From the point of view of an individual, however, the rise in fertility is part of a free

decision to choose a greater quantity of offspring at the expense of their quality, or per capita endowment, K .

An intuition for the individual motivation for this key shift is as follows. An increase in mortality decreases the marginal benefit of the quantity of offspring, simply because this quantity is deflated by the probability of survival. However, quality is related to the potential number of grandchildren, and this number is then doubly subject to the increase in mortality. Thus, an increase in mortality reduces the marginal benefit of quality by more than it reduces the marginal benefit of quantity.

Although no direct information seems to be available on the impact of the Neolithic transition on output, these predictions are otherwise consistent with the observations discussed in Section 2.

3.4. Dynamics

Consider now a population in an equilibrium steady state, which is subjected to an increase in α from 0 to 1. The short run dynamics by which the new equilibrium steady state is reached are now explored.²¹

First consider how the population evolves in general, without the steady state requirement. If there is a single type choosing an arbitrary somatic stock K_t , the adult population, N_t , is governed by the difference equation:

$$N_{t+1} = N_t p(N_t) F(K_t, N_t, \alpha) / K_{t+1}. \quad (8)$$

It simplifies matters to consider the differential equation associated with this difference

equation. Where $N(t)$ is population, this is:

$$\frac{1}{N(t)} \frac{dN(t)}{dt} = \frac{p(N(t))F(\tilde{K}(t), N(t), \alpha)}{\tilde{K}(t)} - 1, \quad (9)$$

where $\tilde{K}(t)$ is the arbitrary continuous-time counterpart of K_t . Suppose now that $\tilde{K}(t) \equiv K(N(t)) \equiv \arg \max_{K>0} \frac{F(K, N(t), \alpha)}{K}$. Any equilibrium of (9), defined now as N^* , say, is the unique solution for N of $\frac{p(N)F(K(N), N, \alpha)}{K(N)} = 1$, yielding the unique equilibrium steady state, as in (1).

Use of such an associated differential equation is appropriate in general if the length of each generation is small relative to the time for the transition. This seems reasonable here with an intergenerational time of perhaps 20 years and a time for the transition of perhaps a thousand years. In any case, the differential equation (9) focuses on the salient features of the difference equation (8).²²

The differential equation has the following properties, where α is constant:²³

Theorem 2. Suppose that Assumptions 1 and 2 hold, as do the additional hypotheses of Proposition 1 and Theorem 1. If $N(0) < N^*$, then (9) implies that population $N(t) \uparrow N^*$. Fertility $f(t) = \frac{F(K(N), N, \alpha)}{K(N)} \downarrow f^* = \frac{F(K(N^*), N^*, \alpha)}{K(N^*)}$. If, in addition, $F_{KN} > F_N/K$, somatic capital $K(t) \uparrow K^* = K(N^*)$. Productivity, F , may increase or decrease in general. If, in addition, $\frac{F_K}{KF_{KK}} < -1$ and F_{KN} is close enough to zero, then $F(t) \uparrow F(K^*, N^*, \alpha)$. If F increases, then so must somatic capital.

Proof. See Appendix.

The description of the short run dynamics is then completed by deriving the immediate implications of the initial jump in α :

Theorem 3. Suppose that Assumptions 1 and 2 hold, as do the additional hypotheses of Proposition 1 and Theorem 1. If α jumps from 0 to 1, there can be no jump in N . There is a jump up in fertility, f , but a jump down in somatic capital, K . Productivity, F , jumps down given that $\frac{F_K}{KF_{KK}} < -1$.

Proof. See Appendix.

The implications of Theorems 1, 2 and 3 for population, N , fertility, f , somatic capital, K , and productivity, F , are sketched in Figure 2. The assumptions underlying the detailed short run effects on somatic capital and productivity, as in Theorems 2 and 3, are stronger than those needed to obtain the long run effects, as in Theorem 1. Under these assumptions, however, the initial jumps in fertility, somatic capital, and productivity, as in Theorem 2, are exaggerations of the long run effects, as in Theorem 1. The exaggerated effects on fertility and somatic capital would have made these shifts easier to identify empirically.

INSERT FIGURE 2 HERE

4. Related literature

There are several papers with prehistoric settings that also share the present paper's biological basis. First, Weisdorf (2009) accounts for some of the phenomena observed during the transition to agriculture by arguing that successful early farmers had metabolic systems that were suited to the long hours of toil required. As he indicates, doubt would be cast on this theory if modern foragers were found not to have metabolic systems that are very different from modern farmers.

Second, Galor and Moav (2002) develop a theory of the industrial revolution that relies upon natural selection and indeed gives a central role to the quantity-quality trade-off for offspring. In particular, they argue there was selection in favor of a preference for greater quality of offspring during the agricultural period, which then precipitated the industrial revolution. Third, Galor and Moav (2007) reconsider the biological implications of the transition to agriculture. They allow that the immediate effect of an increase in extrinsic mortality during the transition to agriculture may have been to reduce longevity. However, in the long run, they suggest, such higher mortality provoked a genetic reaction that led to an increase in longevity. They buttress this argument by showing that a significant determinant of longevity in modern countries is the time elapsed since the advent of agriculture.

Although Seabright (2008) is less explicitly biological, there is a similar overall motivation to that here—to address the puzzle of the declining health produced by the transition to agriculture. He proposes that, although agriculture made an improved standard of living possible, this improvement was outweighed by the extra expense of the military defence now

needed to protect concentrated and valuable resources. That this could be so is reminiscent of the prisoner’s dilemma. This contrasts with the assumption here that more disease resulted directly from greater crowding and therefore indirectly from the greater output of agriculture. The emphasis here, however, is on the implication of this for decreased stature, interpreted as somatic capital, and increased fertility.

Perhaps three main candidates can be identified in the literature as interrelated precipitating factors behind the transition to agriculture—a “population push” hypothesis, a “decreased available biomass” hypothesis, and a “technological innovation” hypothesis. Of these three, the last is most readily consistent with the approach of the present paper.²⁴

Boserup (1965) was an early proponent of population push—the anti-Malthusian view that population growth provided the impetus for the shift to agriculture. Cohen (1977) develops this view further, arguing that human beings were able to respond to population pressure by adopting a technology whose main advantage was the production of more calories per acre. He also points out that the population push hypothesis would explain the nearly simultaneous appearance of agriculture in widely separated regions, given that there were mechanisms to help equalize population pressure.

Kremer (1993) sharpens considerably the hypothesis that population growth is a cause as well as an effect. He presents a model where innovation is spurred by a large population, but where population is also limited by technology, as in Malthus. This model generates the prediction that the rate of growth of population will be higher in larger populations. It is shown that this prediction is empirically valid for the historical record. In addition,

societies with higher initial populations are shown to have experienced faster growth rates of population and higher rates of technological change.

The decreased biomass hypothesis is that the transition to agriculture was precipitated by increasing scarcity of foraged animal and plant food. Smith (1975) proposed that the common property nature of large prey, in particular, led to their overexploitation by humans and eventual extinction. This is an alternative to an older theory that the end of the last ice age led to dessication of plant food and hence a reduction in these prey animals.

Locay (1989) develops a model of the transition to agriculture in which these three key hypotheses can be embedded. He emphasizes that these hypotheses agree on many empirical predictions, but might be distinguished by means of a few of these. In particular, it would help distinguish between the various hypotheses if key variables could be tracked more precisely before and after the advent of agriculture.²⁵ If the human population grew rapidly before the transition, for example, this would reinforce the population push hypothesis. If the declines in health, stature, and life expectancy arose before the transition, this favors the decreased available biomass hypothesis. If measures of health rose after the transition, Locay argues this would favor the technological shock hypothesis.

But the present model shows that this last implication is not inevitable. The technological shock here leads, that is, to an immediate shift in favor quantity of offspring over quality. Even in the longer run, when the present model predicts increased mortality due to the diseases induced by greater population density, there is still a less dramatic shift in favor of quantity over quality.

The shortage of detailed historical data is addressed by Pryor (2005), who uses a spectrum of modern societies from foragers to farmers as empirical evidence concerning the transition to agriculture. He finds that the two most promising candidates as precipitating factors are a rise in population and a decrease in available biomass. Baker (2008) also uses such a spectrum of modern societies to test his theory concerning the roles played by population growth and technological change. He does not find strong evidence that population growth led to technological change in foragers, but does find evidence of the importance of information spillovers.

A further auxiliary hypothesis for the transition to agriculture concerns the development of private property rights. Such rights apparently either contributed to the transition or were a consequence of it. North (1981) refines the decreased biomass hypothesis by arguing that the shortage of food led to the assertion of property rights over what was left and thus ultimately facilitated the shift to agriculture. On the other hand, Baker (2003) develops a model of how the ecology might influence private ownership of land. He discovers, in contrast to North, that relatively plentiful and predictable resources tend to generate stable territorial systems. Such relatively dense resources repay the expense needed to defend an ownership claim on land. Again, more detailed data would help distinguish these two accounts of property rights as a cause of the transition, or whether property rights instead arose as an effect of the transition.

Marceau and Myers (2006) essentially reverse the explanations based upon overexploitation of a common property resource, as in Smith, and the development of property rights,

as in North and Baker. They apply a theory of coalition formation in a model where the advent of agriculture is precipitated by technological change. Before this transition, there was a grand coalition that avoided overexploitation of the environment. Just after the transition, the grand coalition splintered, resulting in a loss of efficiency that resulted in lower output at first.

Finally, the present paper takes the geographic incidence of the transition to agriculture as given. It is interesting, however, to consider this spatial context. For example, Olsson and Hibbs (2005) develop further the central thesis of Diamond (1997) that geography was a key factor driving the transition. More particularly, Diamond argues that the great West to East extent of Eurasia generated most of the handful of domesticable species that existed anywhere in the world. Thus the preconditions were favorable for the transition to occur somewhere at a temperate latitude in Eurasia. Once this innovation arose, this West to East dimension also meant that agriculture spread rapidly to a large population who enjoyed a similar climate. Olsson and Hibbs present further evidence in favor of this hypothesis, showing, in particular, that modern levels of economic development are directly significantly affected by geography.

5. Conclusions

The present paper develops a model that replicates the puzzling shifts observed during the Neolithic transition to agriculture. A key feature of the model is to introduce somatic capital in a simple way. The simplicity of the model serves to illuminate the basic issues. However, it cannot be taken literally. One desirable direction for generalization would be to

include more than two age classes, where individuals at various ages allocate scarce resources among existing offspring of various vintages and to current reproduction. A second desirable extension would be to allow consumption. A form of consumption that is consistent with the present biological perspective is expenditure to maintain health and hence to reduce mortality. Such generalized models, however, should remain capable of producing the effects found here.

Appendix. Proofs.

Proof of Proposition 1. Assumption 1 implies that, for each $N > 0$, there exists a unique optimal $K(N) > \bar{K}$ maximizing $\frac{F(K, N, \alpha)}{K}$. Further, if $V(N) = \frac{p(N)F(K(N), N, \alpha)}{K(N)}$, then $V'(N) = \frac{p'F + pF_N}{K} < 0$. Given that $V(0) > 1$, and $V(N) < 1$, for large N , existence of the unique equilibrium steady state follows. Finally, $K(N)$ is the only solution for $K > 0$, of the first-order condition $F_K(K, N, \alpha)K = F(K, N, \alpha)$. It follows that the equilibrium steady state is the only solution for $N > 0$ and $K > 0$ of $p(N)F(K, N, \alpha) = K$ and $p(N)F_K(K, N, \alpha) = 1$.

■

Lemma 1. Suppose Assumption 1 and the additional conditions of Proposition 1 all hold. Consider an equilibrium steady state for a continuum population composed of one type that chooses $K_t = K(N)$, say, $t = 1, 2, \dots$, where $K_0 = K(N)$ also.²⁶ An adult of the original type at $t = 0$ has one adult descendant at each date $t > 0$. Suppose \tilde{N}_t is the similar stream of adult descendants for an adult at date $t = 0$ of any alternative type choosing K_t that do not maximize

$\frac{F(K_t, N, \alpha)}{K_t}$ at every $t = 1, 2, \dots$. It follows that there exists a time T and $\delta > 0$ such that

$$\tilde{N}_t < 1 - \delta, \text{ for all } t \geq T. \quad (10)$$

In the short run, an individual of an alternative type may do well, increasing the number of her descendants above 1. Nevertheless, in the long run, the number of descendants of the deviating individual must fall strictly below 1 (which is the number for the original type) and remain there permanently.

Proof of Lemma 1. Note first that the introduction of a single new individual has no effect on the population, N . If there is a finite number of deviations from $K(N)$, (10) is immediate from (2), for any T after the last deviation. Suppose then that there are infinite number of deviations, but (10) does not hold. Thus, for all $\delta > 0$, there exists a sequence $\{t_i\}_{i=1}^{\infty}$ such that $\tilde{N}_{t_i} \geq 1 - \delta$, for all t_i . It is without loss to suppose t_1 is strictly after the first deviation. However, assuming δ is small enough, the only way to obtain $\tilde{N}_{t_i} \geq 1 - \delta$, despite this fixed first deviation, is to choose $\tilde{K}_{t_i} \leq K(N) - \varepsilon$, for some $\varepsilon > 0$. Thus every date in the sequence $\{t_i\}_{i=1}^{\infty}$ involves such a deviation. Further, since these deviations are all at least $\varepsilon > 0$, the only way to counteract their cumulative effect is to have fertility tending to infinity in the sequence $\{t_i\}_{i=1}^{\infty}$. However, this requires eventually that $\tilde{K}_{t_i} \leq \bar{K}$ so offspring output is zero and the deviating line must become extinct in the next period. ■

Proof of Proposition 2. Under the stated conditions, the constraint $p(N)F(K, N, \alpha) = K$ yields $N > 0$ as a function of $K > 0$. It then follows that $(p'F + pF_N)\frac{dN}{dK} + pF_K = 1$, so that

$\frac{dN}{dK} = 0$ if and only if $pF_K = 1$. Further, $\frac{d^2N}{dK^2} = \frac{-pF_{KK}}{p'F + pF_N} < 0$, whenever $\frac{dN}{dK} = 0$, so that the equilibrium steady state is the unique maximizer of N . ■

Proof of Theorem 1. Consider the effect that a shift from $\alpha = 0$ to $\alpha = 1$ throughout the population has on the resulting equilibrium steady state, characterized as in (1). It is convenient to extend the definition of the production function to all $\alpha \in [0, 1]$ as

$$F(K, N, \alpha) = \alpha F(K, N, 1) + (1 - \alpha)F(K, N, 0).$$

This satisfies Assumption 1 and the additional assumptions of Proposition 1 and Theorem 1. In addition, we have $F_\alpha(K, N, \alpha) > 0$, and $F_{K\alpha}(K, N, \alpha) \leq 0$. We can now differentiate the second equation in (1) with respect to α to obtain

$$p'F \frac{dN}{d\alpha} + pF_K \frac{dK}{d\alpha} + pF_N \frac{dN}{d\alpha} + pF_\alpha = \frac{dK}{d\alpha}.$$

The first equation in (1) then implies that the terms in $\frac{dK}{d\alpha}$ cancel so that

$$\frac{dN}{d\alpha} = \frac{-pF_\alpha}{p'F + pF_N} > 0. \quad (11)$$

Hence the shift to agriculture raises the long run level of the population, as a direct consequence of the greater output of agriculture. In addition, $\frac{dp}{d\alpha} = p' \frac{dN}{d\alpha} < 0$, so that mortality rises, due to this increased crowding.

Differentiating the first equation in (1) now yields

$$\frac{dK}{d\alpha} = \frac{-pF_{K\alpha} - (p'F_K + pF_{KN}) \frac{dN}{d\alpha}}{pF_{KK}} < 0, \quad (12)$$

so stature declines as a consequence of the shift to agriculture. That this key comparative static result is implied by (1) can be seen as follows. Given the shift from $\alpha = 0$ to $\alpha = 1$,

the expected marginal product of capital, $p(N)F_K(K, N, \alpha)$, falls because the increase in population increases mortality, as reflected in the term $p'F_K < 0$ in (12), thus helping reduce the demand for capital. The assumptions that $F_{K\alpha} \leq 0$ and $F_{KN} \leq 0$ serve to reinforce this reduction. Fertility, $f = \frac{F(K, N, \alpha)}{K} = \frac{1}{p(N)}$, say, on the other hand, must rise with the shift, $\frac{df}{d\alpha} > 0$, since N rises.

The rise in the quantity of offspring is regardless of the effect of the transition on productivity, $F(K, N, \alpha) = \frac{K}{p(N)}$. This effect can be found as follows:

$$\begin{aligned} \frac{dF}{d\alpha} &= \frac{dK}{d\alpha} - \frac{dp}{dN} \frac{dN}{d\alpha} = \\ &= -\frac{F_{K\alpha}}{KF_{KK}} - \left(\frac{p'F_K}{pKF_{KK}} + \frac{F_{KN}}{KF_{KK}} + \frac{p'}{p} \right) \frac{dN}{d\alpha}. \end{aligned} \quad (13)$$

It is then sufficient for $\frac{dF}{d\alpha} < 0$ that $\frac{F_K}{KF_{KK}} < -1$. (This condition is that the factor demand for K is elastic.) This condition and Assumption 1 can be satisfied, for example, if $F(K, N, \alpha) = K^\beta \Psi(N) - b$, for all $\beta \in (0, 1)$, where $b > 0$, for all $K > 0$. It is plausible then that productivity falls with the advent of agriculture. Productivity must, however, fall by a smaller percentage than somatic capital, given that fertility rises. ■

Proof of Theorem 2. Since $\frac{p(N)F(K(N), N, \alpha)}{K(N)}$ is a strictly decreasing function of N , an increasing path for N is immediate from (9). Fertility, f , falls since $\frac{df}{dN} = \frac{F_N(K(N), N, \alpha)}{K(N)} < 0$, by the envelope theorem. Since $\frac{dK}{dN} = \frac{F_N - KF_{KN}}{KF_{KK}} > 0$, K is increasing. Productivity, F , rises since $\frac{dF}{dN} = F_K \frac{dK}{dN} + F_N = F_N \left(1 + \frac{F_K}{KF_{KK}} \right) - \frac{F_K F_{KN}}{F_{KK}} > 0$, given that $\frac{F_K}{KF_{KK}} < -1$ and $F_{KN} \leq 0$ is sufficiently close to zero. The last assertion is obvious, but also follows since $\frac{dF}{dN} > 0$ implies $F_{KN} > F_N/K$. ■

Proof of Theorem 3. Consider again the extended production function defined in the proof of Theorem 1, namely $F(K, N, \alpha) = \alpha F(K, N, 1) + (1 - \alpha)F(K, N, 0)$.²⁷ Fertility jumps up since $\frac{df}{d\alpha} |_{N=\bar{N}} = \frac{F_\alpha(K(N), N, \alpha)}{K(N)} > 0$, by the envelope theorem, holding N constant. Capital jumps down, however, since $\frac{dK}{d\alpha} |_{N=\bar{N}} = \frac{F_\alpha - KF_{K\alpha}}{KF_{KK}} < 0$. Productivity jumps down since $\frac{dF}{d\alpha} |_{N=\bar{N}} = F_K \frac{dK}{d\alpha} |_{N=\bar{N}} + F_\alpha = F_\alpha \left(1 + \frac{F_K}{KF_{KK}}\right) - \frac{F_K F_{K\alpha}}{F_{KK}} < 0$, assuming $\frac{F_K}{KF_{KK}} < -1$. ■

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Lead footnote

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Notes

¹See also Ammerman and Cavalli-Sforza (1984), and Cavalli-Sforza, Menozzi and Piazza (1994, Chapter 5.11).

²Corroborating evidence is provided by Gray and Atkinson (2003), who use statistical linguistic analysis to infer that the English language, for example, originated about 9,000 years ago in what is now Turkey.

³Diamond (1997, Chapters 4-10), and Tudge (1998), provide informal accounts of this new view. The basic reference for all the following precise evidence is Cohen and Armelagos (1984). This is a symposium of work on the effect of this transformation world-wide, as summarized in Chapter 23. Steckel and Rose (2002) is a more recent symposium, concentrating on the Western Hemisphere, but coming to generally similar conclusions.

⁴Such porosity is particularly evident in the thin bone that forms the eye socket.

⁵The “Harris” lines in bones may disappear, but the ridges in teeth are less prone to do so.

⁶Sahlins argues, however, that this affluence of the !Kung is achieved in part by lowered expectations.

⁷It is purely a notational convenience to write the two production functions as $F(K, N, \alpha)$ where $\alpha = 0$ or 1 rather than as $F(K, N)$ and $G(K, N)$, say.

⁸Strictly, \bar{K} should be described as $\bar{K}(N, \alpha)$.

⁹Lee (1987) provides cogent arguments for the relevance of such “carrying capacity” constraints to human demography. If humans have institutions that prevent the absolute biologically maximal population being

reached, but that anticipate the same limits, a density-dependent model would still be appropriate.

¹⁰Such “zoonotic” diseases remain prevalent today. Modern world-wide seasonal influenza epidemics seem to originate in domesticated animal populations.

¹¹See Robson and Kaplan (2003) for data from hunter-gatherer societies concerning the importance of these transfers.

¹² $(N, K(N))$ is also the only solution of (1) for $N > 0$ and $K > 0$.

¹³This result can be extended to a population that is not in a steady state. See Section 3.4.

¹⁴Perhaps the most obvious problems groups of foragers solve concern risk, such as that arising from hunting large animals. A related function of groups relevant here is that they smooth out transfers from parents to children.

¹⁵In other respects, evolved preferences may be inappropriate in modern contexts. Perhaps, for example, our intense cravings for sweet and fatty foods, which were adaptive when calories were limited, now lead to harmful overindulgence.

However, see Robson and Woutersen (2007), for models in which it is evolutionarily optimal for an increase in the food supply to decrease longevity.

¹⁶Angel estimates that population density increased by a factor of 70 over this period, which is roughly consistent with Polgar.

¹⁷BMI is constant for weight proportional to height squared.

¹⁸The higher rate of arthritis in forager populations than in agricultural populations is evidence in favor of this claim, as was discussed in Section 2.2.

¹⁹The previous example shows this condition is not necessary.

²⁰This condition holds in the example.

²¹For the sake of simplicity, the increase in α is instantaneous, but qualitatively similar results would hold if agriculture were phased in sufficiently rapidly.

²²As an example of how matters are simplified, note that it is possible (but non-trivial) to formulate and prove a generalization of Lemma 2 for (8). That is, it remains optimal, in the sense of Lemma 2, to choose

K_t to maximize $\frac{F(K_t, N_t, \alpha)}{K_t}$ at every $t = 1, 2, \dots$, even when population, N_t , is time-varying. However, in continuous time, as in (9), it is immediate that any type that deviates from $K = K(N(t))$ on a set of times of positive measure will fall permanently behind. That is, individuals who choose the optimal K in terms of the the given preferences over the quality and quantity of children cannot be biologically outperformed by any alternative choice, even in this general dynamic setting.

²³Theorem 2 is applied in the case that $\alpha = 1$ but it is formally valid also for $\alpha = 0$.

²⁴Weisdorf (2005) is a recent survey of anthropological and economic theories of the neolithic transition. Most of these emphasize the key issue of the timing of this transition.

²⁵More detailed data like that collected by Cohen and Armelagos [1984], would help here.

²⁶Each individual here is “infinitesimally small” and also divisible.

²⁷Suppose, indeed, the additional assumptions of Lemma 1 apply to $F(K, N, \alpha)$, for all $\alpha \in [0, 1]$.

FIGURE LEGENDS (IN THE ORDER THEY APPEAR ON THE NEXT TWO PAGES)

Figure 1: Adult Energy Output

Figure 2: Dynamics



