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Demography plays a large role in cultural evolution through its effects on the effective rate of innovation. If we assume that useful inventions are rare, then small isolated societies will have low rates of invention. In small populations, complex technology will tend to be lost as a result of random loss or incomplete transmission (the Tasmanian effect). Large populations have more inventors and are more resistant to loss by chance. If human populations can grow freely, then a population-technology-population positive feedback should occur such that human societies reach a stable growth path on which the rate of growth of technology is limited by the rate of invention. This scenario fits the Holocene to a first approximation, but the late Pleistocene is great puzzle. Large-brained hominins existed in Africa and west Eurasia of perhaps 150,000 years with, at best, slow rates of technical innovation. The most sophisticated societies of the last glacial period appear after 50,000 years ago and were apparently restricted to west and north-central Eurasia and North Africa. These patterns have no simple, commonly accepted explanation. We argue that increased high-frequency climate change around 70,000–50,000 years ago may have tipped the balance between humans and their competitor-predators, such as lions and wolves, in favor of humans. At the same time, technically sophisticated hunters would tend to overharvest their prey. Perhaps the ephemeral appearance of complex tools and symbolic artifacts in Africa after 100,000 years ago resulted from hunting inventions that allowed human populations to expand temporarily before prey over exploitation led to human population and technology collapse. Sustained human populations of moderate size using distinctively advanced Upper Paleolithic artifacts may have existed in west Eurasia because cold, continental northeastern Eurasia–Beringia acted as a protected reserve for prey populations.

Keywords
cultural evolution, origins of agriculture, tool kits, cultural innovation, paleodemography, paleoecology, Tasmanian effect, carrying capacity, population growth, Neanderthals, anatomically modern humans.

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Cultural Innovations and Demographic Change

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Abstract Demography plays a large role in cultural evolution through its effects on the effective rate of innovation. If we assume that useful inventions are rare, then small isolated societies will have low rates of invention. In small populations, complex technology will tend to be lost as a result of random loss or incomplete transmission (the Tasmanian effect). Large populations have more inventors and are more resistant to loss by chance. If human populations can grow freely, then a population-technology-population positive feedback should occur such that human societies reach a stable growth path on which the rate of growth of technology is limited by the rate of invention. This scenario fits the Holocene to a first approximation, but the late Pleistocene is a great puzzle. Large-brained hominins existed in Africa and west Eurasia for perhaps 150,000 years with, at best, slow rates of technical innovation. The most sophisticated societies of the last glacial period appear after 50,000 years ago and were apparently restricted to west and north-central Eurasia and North Africa. These patterns have no simple, commonly accepted explanation. We argue that increased high-frequency climate change around 70,000–50,000 years ago may have tipped the balance between humans and their competitor-predators, such as lions and wolves, in favor of humans. At the same time, technically sophisticated hunters would tend to overharvest their prey. Perhaps the ephemeral appearance of complex tools and symbolic artifacts in Africa after 100,000 years ago resulted from hunting inventions that allowed human populations to expand temporarily before prey overexploitation led to human population and technology collapse. Sustained human populations of moderate size using distinctively advanced Upper Paleolithic artifacts may have existed in west Eurasia because cold, continental northeastern Eurasia–Beringia acted as a protected reserve for prey populations.

In October 1838, that is, fifteen months after I had begun my systematic inquiry, I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence

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KEY WORDS: CULTURAL EVOLUTION, ORIGINS OF AGRICULTURE, TOOL KITS, CULTURAL INNOVATION, PALEODEMOGRAPHY, PALEOECOLOGY, TASMANIAN EFFECT, CARRYING CAPACITY, POPULATION GROWTH, NEANDERTHALS, ANATOMICALLY MODERN HUMANS.

> which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The results of this would be the formation of a new species. Here, then I had at last got a theory by which to work.
> —Charles Darwin, from his autobiography (1968 [1902])

Demography famously played a foundational role in Darwin's formulation of the theory of natural selection. It is also central to the discipline of ecology. The big lesson that Darwin took from Malthus was that the potential for exponential population increase ensured that the struggle for existence would be a general feature of nature. True, the first individuals to reach a remote island might not experience appreciable competition for a few generations. But exponential growth would soon lead to a large population, generating competition. Natural selection would then begin to favor any heritable variation for competitive ability that existed in the population. A glance at modern textbooks on ecology and evolution reveals a continuing concern in these disciplines with the interaction of demographic and evolutionary processes (e.g., N. Barton et al. 2007; Begon et al. 2006). Topics of contemporary interest are far broader than Darwin might have imagined. Ecologists are interested in the evolution of the basic demographic properties of species (life history theory). Evolutionists are interested in how population size and density affect evolution by drift and density-dependent selection. These are just a small sample.

Cultural evolution exhibits many of the same properties as genetic evolution, although the details are different (Boyd and Richerson 2005; Campbell 1965; Cavalli-Sforza and Feldman 1981; Durham 1991). One of the main differences between cultural and genetic evolution is that cultural evolution is more rapid than genetic evolution, potentially much more rapid. Cultural evolution includes the possibility of individuals actively seeking out new cultural variants. Desirable innovations are often passed from person to person on a much shorter time scale than the human generation time. Another major difference is that the cultural system is expensive. If we assume that our long juvenile period and large brain are necessary to maintain an advanced system of cultural inheritance, then humans pay a high overhead cost for having culture. Aiello and Wheeler (1995) and Kaplan et al. (2000) discuss how human life history has adapted to exploit the advantages of culture while paying its costs.

Darwin's basic idea implies a time scale separation between demographic and evolutionary processes. In this paper we explore whether the separation of time scales also applies to the human case with the faster pace of cultural evolution. We explore three time periods, the Middle and Upper Paleolithic, the Holocene up to the emergence of modern societies, and the modern period. We conclude that separation of time scales works for all but the modern period. The idea of time scales is used in the physical environmental sciences to simplify problems with

complex interactions between processes. If one process happens on a short time scale and the other one on a long time scale, then one can often assume that the short time scale process is at an equilibrium (or in some more complex state that can be described statistically) with respect to factors governed by the long time scale process. If the short time scale and long time scale processes interact, we can often imagine that at each time step in the evolution of the long time scale process, the short time scale process is at "equilibrium." A separation of time scales, if justified, makes thinking about many problems of coupled dynamics much easier.

The capacity for exponential growth at growth rates we actually observe implies that the demographic time scale is quite short. The evolutionary time scale is much longer. Darwin had some appreciation that the evolutionary time scale was of the same order as the geological time scale, which he estimated (correctly) to be some hundreds of millions of years for the then-known fossil record beginning with the Cambrian. A separation of time scales is normally justified in organic evolution. Populations reach some quasi-equilibrium [there is much ecological complexity implied by this term; see, e.g., Strong (1986)] that depends on the existing adaptation of the population. Selection will favor slow improvements in the adaptation of the population, with each increment of adaptive improvement rapidly resulting in the re-equilibration of the population given the new adaptation. In the words often used by archaeologists, population pressure is to a first approximation a constant. The struggle for existence can be counted on to apply approximately steady and constant selective pressure on populations. The direction of the pressure may vary as environments change, but the struggle for existence itself will only occasionally relax for brief periods. In such a world, the relationship between demography and evolution is simple and straightforward. Think in terms of the logistic model of population regulation. Populations will typically be at a fair fraction of carrying capacity most of the time. Population pressure generated by the struggle for existence will act to raise the carrying capacity. The second process, responses to selection on the part of the heritable variation of the population, will be the rate-limiting step in the evolution of new adaptations.

Because of the more rapid pace of cultural evolution, we need to worry about whether there is a time scale separation between the demographic and cultural evolutionary time scales. Malthus had the intuition that the cultural evolutionary time scale was rapid but still essentially linear relative to the potential for exponential population growth. The linear versus exponential claim is not necessary to Malthus's argument. The rate of change in subsistence supply could also be exponential but at a slower exponential factor than the rate of increase of a population far from carrying capacity. Malthus did not rely just on mathematics to school his intuition. Lindert (1985) examined the data that Malthus had available to him in his lifetime. Within the limits of his day, Malthus's knowledge of demographic patterns in different countries was extensive. Lindert argues that not until after Malthus's death did the English economy begin to produce sustained per capita growth. On the other hand, the time in which Malthus lived was the beginning of the Industrial Revolution. Most likely, the rate of technological improvement that

Malthus inferred from the data available to him was indeed rapid compared with most periods in human history. The Acheulean lasted a million years, and the Aurignacian and Gravettian industries of the west Eurasian Upper Paleolithic lasted many thousands of years. In the Holocene the first states follow the origins of agriculture by about 5,000 years. Thus a separation of the time scales of demographic and evolutionary processes is probably normally justified for cultural evolution. However, some caution is necessary. In some situations culture may evolve on the same time scale as population growth or even faster. In the modern Industrial Revolution and demographic transition, major changes in culture and population growth rates have occurred on the same time scale. Something similar could have happened when the Americas were first colonized by humans (Hamilton and Buchanan 2007). The Clovis hunters might have been a colonizing adaptation that evolved into other Paleo-Indian cultures as population pressure took hold a few centuries after their advent in North America.

To interpret the historical, archaeological, and paleoanthropological record of hominin evolution, we can appeal to three basic causal elements in constructing our models: environment, genes, and culture. Environments generate selective pressures to which genes and culture respond. The processes of genetic and cultural evolution (and gene-culture-environment coevolution) can greatly complicate the translation of selection pressures into responses that are visible in the empirical record. For a progressive record such as that of the hominins, in which trends toward larger brain size and greater cultural sophistication are the dominant large-scale pattern in the data, an interesting question is, What limited "progress" at different periods of our evolution? Was environmental change leading the trajectory by means of a more or less monotonic increase in selection for larger brains and increased cultural sophistication? Or were genes or culture slow to respond to selection pressures that were exerted from the beginning of the Pleistocene or even far earlier? In general, we can expect the evolution of any given lineage to be historical in the sense of "one damned thing after another," as Toynbee's famous objection to mainstream history has it (Boyd and Richerson 1992). Even a fairly straightforward progressive evolutionary trajectory such as that of the hominins may well contain several different regimes in which environment, genes, and culture played somewhat different roles.

In this paper we review a model that captures some of the ideas just reviewed. We use the model to interpret three important "evo-demo" problems in human history. The first is the puzzling features of late Pleistocene culture. Hominins with large brains apparently arose around 200,000 years ago, including anatomically modern people in Africa and Neanderthals in western Eurasia. However, with some interesting but controversial exceptions, these species did not produce artifacts of a complexity that we observe in living hunter-gatherers until 50,000 years ago. Then both big-brained forms—certainly anatomical modern humans and most likely Neanderthals—began to produce modern-looking stone tool kits, perhaps in parallel. Second, we review events surrounding the origins of agriculture and its Holocene aftermath. Agricultural innovations led to population

increases, but the Holocene agricultural transition occurred in different places at different times and reached some places only with the Columbian European conquest. Finally, we look at the case of the population explosion and later declines in fertility of the last few centuries. The data here are far better than in the more ancient cases, but the processes are also unique to this situation. However, this uniqueness is important because it demonstrates how the consequences of the cultural evolutionary time scale shrinking to the point that it was faster than the demographic time scale produces dramatic results. If similar processes had occurred in the past for any length of time, we could be confident that they would have produced a dramatic archaeological signal.

Our objectives here are limited. We cannot provide a thorough review of the literature on paleodemography, paleoecology, and paleoanthropology. We realize that many elements of our scenarios rest on controversial evidence if not rank speculation. We do hope to clarify the relationship between demographic and cultural evolutionary processes so that we can formulate better hypotheses about several of the puzzling aspects of the paleoanthropological record as we currently understand it.

A Malthusio-Darwinian Model

The Malthusio-Darwinian model was developed to explicate the separation of time scales implied by Darwin's reading of Malthus (Richerson et al. 2001). The application was to the origin of agriculture, but the model was meant to be general.

Start with the Logistic Model. The logistic equation is one simple, widely used model of population growth. The rate of change of population density N is given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1}$$

where r is the intrinsic rate of natural increase (i.e., the rate of growth of population density when there is no scarcity) and K is the carrying capacity (i.e., the equilibrium population density when population growth is halted by density-dependent checks). In the logistic equation, the level of population pressure is given by the ratio N/K. When this ratio is equal to 0, the population grows at its maximum rate; there is no population pressure. When the ratio is 1, density dependence prevents any population growth at all. It is easy to solve this equation and calculate the length of time necessary to achieve any level of population pressure $\pi = N/K$:

$$T(\pi) = -\frac{1}{r}\ln\left[\left(\frac{\pi}{1-\pi}\right)\left(\frac{1-\pi_0}{\pi_0}\right)\right], \tag{2}$$

where π_0 is the initial level of population pressure. Let us conservatively assume that the initial population density is only 1% of what could be sustained with the

use of any given subsistence system and that the maximum rate of increase of human populations unconstrained by resource limitation (r) is 1% per year. Under these assumptions, the population will reach 99% of the maximum population pressure (i.e., $\pi = 0.99$) in only about 920 years. Serendipitous inventions (e.g., the bow and arrow) that increase carrying capacity do not fundamentally alter this result. For example, only the rare single invention is likely to so much as double carrying capacity. If such an invention spreads within a population that is near its previous carrying capacity, it will still face half the maximum population pressure. At an r of 1% such an innovating population will again reach 99% of the maximum population pressure in 459 years. Recent work using ratios of young people to older people in ancient cemeteries suggests just such a picture when agriculture first made sedentism possible. Birth rates shot up and a new local population equilibrium several times as dense as the previous mobile hunter-gatherers (some of whom may have done some farming) was reached in a few centuries (Bocquet-Appel and Bar-Yosef 2008; Kohler et al. 2008).

One might think that this result is an artifact of the simple model of population growth. However, it is easy to add much realism to the model without any change of the basic result. Richerson et al. (2001) considered the effects of dispersal and more realistic population dynamics. Malthus's basic conclusion is robust; the potential for exponential population increase when rare means that even a relatively low-fecundity population, such as that of humans, can fill continent-size areas with people experiencing considerable population pressure in less than a millennium, even if initial population sizes are small.

The Dynamics of Innovation. So far we have assumed that the carrying capacity of the environment is fixed (save where it is increased by fortuitous inventions). However, we know that people respond to scarcity caused by population pressure by intensifying production, for example, by shifting from less labor intensive to more labor intensive foraging or by creating innovations that increase the efficiency of subsistence (Boserup 1981). Because innovation increases carrying capacity, intuition suggests that it might therefore delay the onset of population pressure. However, this intuition, too, is faulty.

Consider a population of size N in which the per capita income of the population is given by

$$y = \frac{y_m I}{I + N}, \tag{3}$$

where y_m is the maximum per capita income and I is a variable that represents the productivity of subsistence technology. Thus per capita income declines as population size increases, but for a given population size, greater productivity raises per capita income. As in the previous models, we assume that as population pressure, now measured as falling per capita income, increases, population growth decreases. In particular, assume that

$$\frac{dN}{dt} = \rho N(y - y_s), \tag{4}$$

where y_s is the per capita income necessary for subsistence. If per capita incomes are above this value, population increases; if per capita income falls below y_s, population shrinks. If I is fixed, this equation is another generalization of the logistic equation. In an initially empty environment, population initially grows at a rate $\rho(y_m - y_s)$, but then slows and reaches an equilibrium population size $I(y_m - y_s)/y_s$. To allow for intensification, we assume that people innovate whenever their per capita income falls below a threshold value y_i. Any new technique or skill that contributes positively to the human population growth rate, as described by Eqs. (3) and (4), would count as an innovation. Thus

$$\frac{dI}{dt} = aI(y_i - y). \tag{5}$$

When per capita income is less than the threshold value y_i, people innovate, increasing the carrying capacity and therefore decreasing population pressure. The maximum rate at which innovation can occur is governed by the parameter a. When per capita income is greater than the threshold, people will "deinnnovate." This may seem odd at first, but such abandonment of more efficient technology has been observed occasionally. In the prehistoric Great Basin, for example, early Holocene lithic technology is noticeably simpler than the Paleo-Indian technology that immediately preceded it, likely reflecting increased resource abundance that accompanied Holocene climatic amelioration (Bettinger 1991, Figure 5.4). Later, we discuss the Tasmanian effect, in which population size has a direct effect on the rate of innovation and in which complex technology tends to be lost in small populations. The basic idea is that the larger the population, the more innovators there are independent of the motivation to innovate described by Eq. (5). Diamond (1997) made this idea famous in his book *Guns, Germs, and Steel*. Boone (2002) argues that frequent density-independent mortality events may have had the effect of keeping Pleistocene hunter-gather populations well below the environmental carrying capacity. If this were true (and we have been unable to make it work in a simple model), it would lower the rate of innovation in our model. Thus an important limitation of the formal model here is that the rate of innovation does not depend on N.

Aside from population size, it is interesting to consider other factors that might regulate the size of a and hence the rate of technological progress. Karl Marx suggested that the rate of social innovation is slow compared with the rate of technical innovation and that social conservatism retards the rate of technical progress. This idea recurs in many guises (Bettinger and Baumhoff 1982; North and Thomas 1973). The gene-culture coevolution process may also be a rate-limiting factor. Recent sequence data from the Hap-Map project (Hawks et al. 2007) suggest that agricultural innovations induced rapid evolution of human genes. The dietary changes associated with a shift to starch-rich diets and exposure to epidemic diseases as agriculture

made large dense populations possible apparently can account for many of these changes. The adult secretion of lactase to digest milk sugar in dairying populations is an example of dietary change, and the several alleles that confer resistance to malaria are examples of exposure to epidemic diseases. The need for major genetic evolution may well retard the rate of cultural evolution. The model also assumes that the innovation rate is smooth. If change occurs in rare large technical revolutions, then this is not the right model. It does serve as a useful, relatively simple point of departure to link demography and cultural evolution in a sensible model.

If a small pioneer population enters an empty habitat, it experiences two distinct phases of expansion. Initially, per capita income is near the maximum, and the population grows at the maximum rate. As population density increases, per capita income drops below y_i, and the population begins to innovate, eventually reaching a steady-state value

$$\hat{y} = \frac{\rho y_s + a y_i}{\rho + a}. \tag{6}$$

The steady-state per capita income is above the minimum for subsistence but below the threshold at which people experience population pressure and begin to innovate. At this steady state, population growth continues at a constant rate

$$\hat{\rho} = \frac{a\left(y_i - y_s\right)}{\rho + a} \tag{7}$$

that is proportional to the rate of growth of subsistence efficiency, measured in terms of either human labor or land area, whichever is limiting.

Figure 1 shows the results of the model. A small population initially grows rapidly. As population pressure builds, population growth rate slows to a steady state in which population pressure is constant, and just enough innovation occurs to compensate for population growth. For plausible parameter values the second phase of the population growth steady state is reached in less than a thousand years. Interestingly, increasing the intrinsic rate of innovation or the innovation threshold reduces the waiting time until population pressure is important. Innovation allows greater population increases over the long run, but it does not change the time scales on which population pressure occurs. The most important factor on time scales of a millennium or greater (if not a century or greater, given realistic starting populations) is the rate of intensification by innovation, not population growth. Thus in the conventional Darwinian picture population pressure plays an exceedingly important role but on a short time scale. The struggle for existence can be taken for granted. Evolution plays out as adaptive innovations on the long time scale increase the carrying capacity for the environment for the population in question.

This picture of the interaction of demography and innovation leads to predictions that are quite different from those of such scholars as M. N. Cohen (1977). For example, we do not expect to see any systematic evidence of increased population pressure immediately before major innovations. Population growth is likely to result from innovations, not the other way around, on the time scales

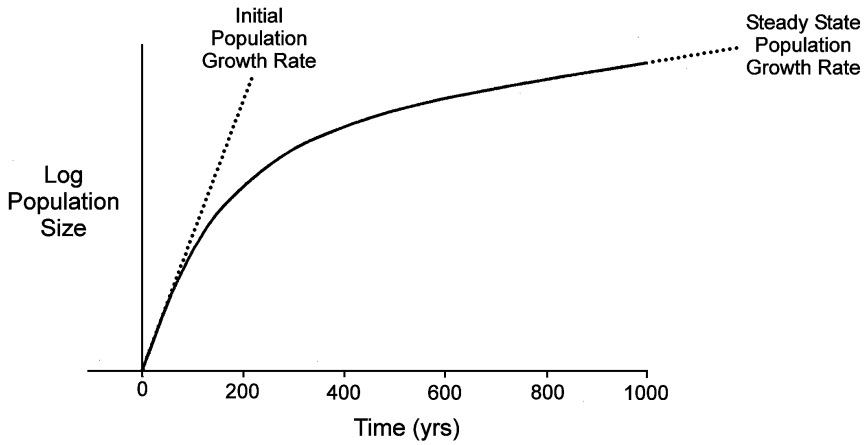

Figure 1. In the first century in a new habitat, a small population of humans will initially grow exponentially. By 200 years the population is already experiencing some population pressure and begins investing in innovations that raise the environment's carrying capacity. By 600 years, the population has settled into a steady-state growth rate determined by the rate of innovation. The precise shape of the curve will depend on the parameter values chosen. For large parts of human history, population growth rates on the millennial time scale were close to 0 (i.e., a steady-state growth rate near 0 even though populations no doubt fluctuated on the century time scale as a result of environmental stochasticity). Note that in a population that on average was at 50% of K as a result of environmental stochasticity, population pressure would still on average be substantial, presumably tending to lead to innovation unless y_i is small relative to y_m.

that we normally observe in the archaeological record. Some examples of actual human population growth and cultural innovation do remind one of Figure 1. For example, the period between the origins of agriculture and the Industrial Revolution are roughly along the lines of Figure 1.

Figure 2 shows the relationship between wages and population in England and Wales from the centuries before, during, and after the Industrial Revolution. The high real wage in the 16th century reflects the aftermath of plague reductions of population. As high population growth overtook the economy of the time, real wages fell, which was then followed by a long period of population stagnation. Real wages peaked again in the mid-18th century and then declined considerably by Malthus's time in the late 18th and early 19th centuries. Until Malthus's time, his argument held. Population could easily grow faster than the economy, and the result was not a commensurate or more than commensurate increase in the supply of food and other necessities but rather a fall in wages and a fall in the birth rate because of the immiseration of working people. An upward trend in population appears to have existed, but wages varied cyclically with no marked upward trend.

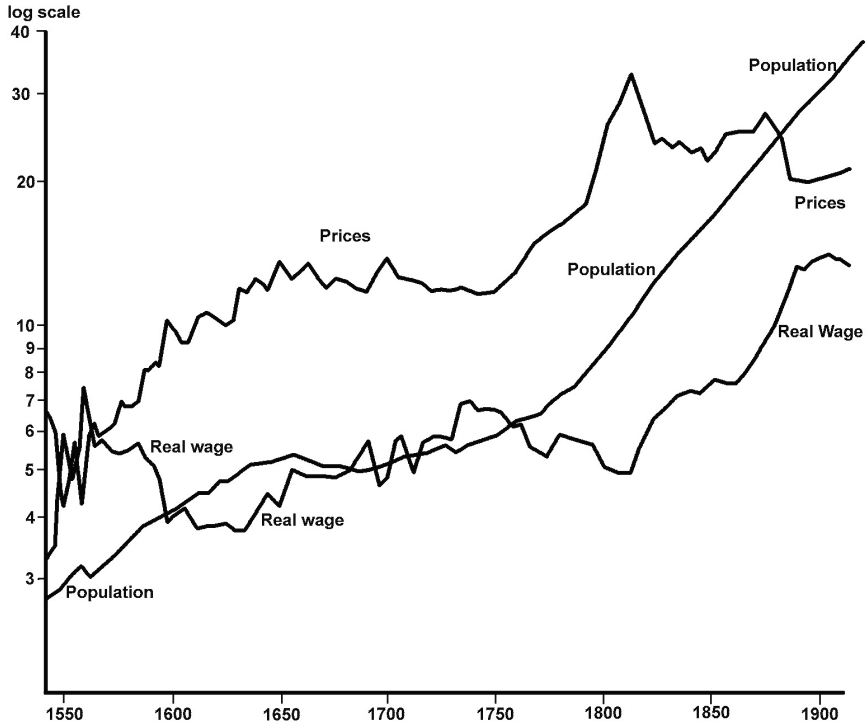

Figure 2. Real wages, prices, and population in England and Wales, 1541–1913. Based on Lindert (1985). The real wage rate and prices derive from data on the wages for southern English craftsmen, 1451–1475 (= 10 in this figure). The price index basis in this figure is for the same years and equals 20. Both sets of data are from Phelps Brown and Hopkins (1956). The population data are for England less Monmouth (Wrigley and Schofield 1981). Only after about 1820 does the Malthusian pattern of sharply rising population leading to depressed wages and rising prices end.

Malthus was probably wrong in thinking that the growth rate of population during the Holocene was linear. Actually it was probably something like exponential, as was the rate of growth of the technology-generated carrying capacity (J. E. Cohen 1995). However, the potential rate of exponential population increase was almost certainly well in excess of the rate limits set by technologically induced increases in human carrying capacity until the last two centuries. Malthus's argument broke down after about 1830 in England. Technological improvements began to lead to markedly lower prices and to raise real wages even though population growth rates were high. A little reflection will convince us that the rates of technological innovation supporting the increase in carrying capacity of the last two centuries must be unique in human history. Population growth rates of the order of 1–3% per year lead to a large population quickly on the archaeologist's

time scale. A rate of technological progress sufficient to raise carrying capacities fast enough to sustain or outrun such growth rates necessitates dramatic changes. Does anything looking like the last two centuries exist anywhere else in the historical or archaeological record? Perhaps the rapid growth of some Neolithic populations and archaic states during their preclassical and classical phases bears a careful look in this regard. For the rest of our history, we apparently lived in a world very much like Darwin and Malthus imagined. As an aside, archaeologists do not seem to try to estimate rates of cultural change, so we do not really know whether rates of cultural evolution have, in general, accelerated toward the present, although most of us have the impression that this is so, perhaps for the whole of hominin history. An interesting and puzzling fact, if true.

What Happened in the Late Pleistocene?

The stylized facts of the late Pleistocene resemble Figure 1 hardly at all. Two large-brained hominins lived in Africa and western Eurasia from around 250,000 years ago to the present: Neanderthals and anatomically modern humans. If Trinkhaus (2005) is correct, early anatomically modern humans show many archaic features, and well-attested fully modern forms appear only after 30,000 years ago. Anatomically modern humans (of an archaic cast) date back to about 200,000 years ago in Africa (McDougall et al. 2005), just before the second to last glacial period. During that glacial period and the previous interglacial period, both big-brained hominins went on making mode 3 (middle Stone Age/Mousterian) stone tools. By around 50,000 years ago, anatomically modern humans in Africa were making mode 4 (late Stone Age/Upper Paleolithic) tools and ornaments at least in some places in Africa, and they had begun to spread to Eurasia and Australia. Neanderthals and other hominins became extinct shortly afterward. Most of the details regarding these events are controversial. Some authorities believe that several different groups in Africa made mode 4 tools and ornaments as early as 75,000 years ago in South Africa (e.g., Mellars 2006b). Some see a gradual record of increasing cultural sophistication from 200,000 to 50,000 years ago (McBrearty and Brooks 2000), whereas others think an abrupt increase around 50,000 years ago better explains the data (Klein 2000). Some controversial evidence suggests that Neanderthals independently began making mode 4 tools before they had any contact with anatomically modern humans (d'Errico 2003), and anatomically modern humans certainly made mode 3 tools for most of their history, including those that reached Australia (Foley and Lahr 1997). Anatomically modern human populations in Africa and southwest Asia also made mode 3 tools for tens of thousands of years leading up to the Upper Paleolithic (west Eurasia) and late Stone Age (Africa). The same seems true of South Asia (James and Petraglia 2005).

Even more interesting, several investigators suggest that the last glacial period was a palimpsest of mode 3 and mode 4 tool-making cultures in Africa and Europe and that both big-brained forms made both tool kits (d'Errico 2003; Jacobs et al. 2008; McBrearty and Brooks 2000; Milliken 2007; Trinkhaus 2005).

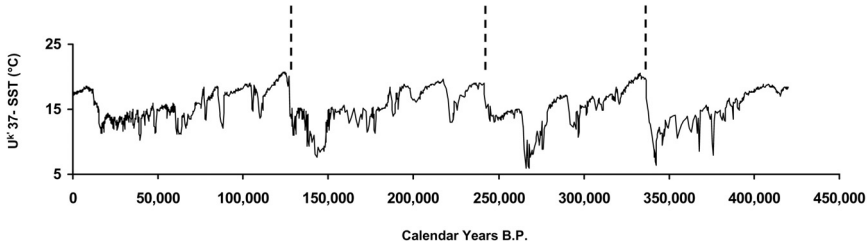

Figure 3. Estimated sea-surface temperature in the Eastern Temperate North Atlantic. Modified from Martrat et al. (2007). See Martrat's paper for methods for computing sea-surface temperature from ratios of different alkenones preserved in the sediment cores.

The industries with a mode 4 aspect do become more common and add more features in Africa, especially in the period 100,000–50,000 years ago. Mode 4 tools plus a full suite of symbolic artifacts, such as paintings and carved art objects, dominate the record after about 40,000 years ago in western Eurasia. Elements resembling those of the west Eurasian Upper Paleolithic occur in Africa, for example, at Blombos Cave (Henshilwood et al. 2002) and in "pre-Aurignacian" situations in Eurasia (Mellars 2006a). However, the duration and sophistication of the west Eurasian Aurignacian and Gravettian appear so far to be unique. In northwest China, for example, tools characterized as early Upper Paleolithic (mode 4 but lacking many of the fancier elements of the classic Upper Paleolithic) enter the area fairly late and are replaced by a much simpler tool kit during the last glacial maximum (L. Barton et al. 2007), when human population densities seem to be quite small in the area.

Late Pleistocene environments were characterized by high-frequency high-amplitude climate variation (often called Dansgaard-Oeschger, or D/O, cycles). This variation was first resolved in ice cores from Greenland (Ditlevsen et al. 1996). Subsequent ice and ocean cores have documented this variation in additional ice cores and in lake and marine sediments (Richerson et al. 2005). A marine core recently raised from the Atlantic margin near Spain provides high-resolution data for the last four glacial-interglacial cycles (Martrat et al. 2007). This core suggests that the high-frequency fluctuations in the last glacial period were especially pronounced compared with the two previous glacial periods and especially compared with the fourth glacial period (Figure 3). A core from the South Atlantic (40° S) shows a similar pattern (Cortese et al. 2007). The apparent intensification of the Dansgaard-Oeschger cycles over time may have driven much of the evolution in human cultures in the last 250,000 years. The very intense Dansgaard-Oeschger cycles after 60,000 years ago are a potential explanation for the spread of modern humans out of Africa and the evolution of mode 4 toolmakers in western Eurasia. But why would cold, dry, variable environments have favored increases in the cultural sophistication of humans?

Highly variable paleoclimates no doubt led to highly variable ecosystems that potentially had large effects on human evolution and demography. Recent advances in understanding the distribution of Pleistocene cultures in terms of their ecology promise to one day let us understand human paleoecology in some detail (Banks et al. 2006). However, methodological problems are rather severe. For example, carbon-14 dates are far too error prone to permit us to link archaeological sites to specific Dansgaard-Oeschger stadial and interstadial periods. Glacial environments were not necessarily unfavorable for humans. Glacial environments tended to be sunnier and more arid, as well as colder, than interglacial ones. Forests were correspondingly reduced, and open steppe and savanna biomes covered larger areas than in the interglacial periods (Huntley and Allen 2003). Open grassy biomes have relatively high secondary productivity simply because the vegetation is exposed to efficient large-bodied herbivores that are attractive to human hunters (Guthrie 1990). Forests, by contrast, produce much less game because most of the biomass is in leaves high in the canopy or in trunks and limbs, and this biomass is inaccessible to efficient large herbivores. The paleoecology suggests that during the coldest phases of the Dansgaard-Oeschger events, large areas of the world were either very dry or very cold. Human populations in these areas were absent or reduced to small numbers. In western Eurasia, Upper Paleolithic people lived at reasonable densities but probably only in the southwest and Mediterranean regions during cold stadial periods (Banks et al. 2006), whereas in warmer, wetter periods they seem to have expanded as far as central Siberia (Klein 2009). Forest expansion during short Dansgaard-Oeschger interstadial periods was probably limited because trees could not expand their ranges fast enough to recolonize them before the next stadial period (Coope 1977). Interstadial warmth and precipitation probably created large areas of moist steppe-forest mosaic Mammoth Steppe biome that would sustain fair densities of human big game hunters.

Variable environments might seem likely to limit rather than favor human populations. However, the factor of culture suggests that our species might be able to take special advantage of environmental fluctuations. Because cultural evolution is more rapid than organic evolution, culture is a plausible adaptation to Dansgaard-Oeschger cycles (Richerson et al. 2005). Culture may thus have given Upper Paleolithic mode 4 toolmakers an adaptive advantage over their competing top carnivores. Human rarity before about 50,000 years ago (Atkinson et al. 2008) might well have been a result of stiff competition with other carnivores.

Caro and Stoner (2003) reviewed the extensive competition within the predatory guild of Africa. Today, cheetah and wild dogs are driven from prime areas for large and medium-size herbivores by lions and are restricted to habitats with relatively low herbivore density. Both species have low genetic diversity as a consequence of their rarity, as do humans. Pliocene-Pleistocene hominin hunter-scavengers probably had already found a narrow niche in competition with the diverse hunting and scavenging guild of the savanna long before the time we focus on here (Brantingham 1998). Both mode 3 and mode 4 toolmakers were focused

on taking big game, although at least Upper Paleolithic mode 4 people also hunted fleet small game (Stiner 2002).

Upper Paleolithic people were also capable of exploiting plant seeds (Weiss et al. 2004), although most excavations do not contain evidence of heavy exploitation of low-ranked plant resources. Because low-ranked plant resources typically require laborious milling to make digestion of starch grains efficient, the presence or absence of heavy milling stones should be diagnostic of heavy plant use, even in the absence of plant remains. Humans could probably have tracked the ever-changing kaleidoscope of large animal prey more easily than their competitors (lions, dogs, wolves, and hyenas). Humans could find the dynamic, ephemeral situations where an herbivore population was temporarily out of equilibrium with their prey and exploit the windfall before our competitors could figure out the rapidly changing ecosystems.

Mode 4 hunters may also have had the weapons and social organization to effectively reduce competition from other predators by actively hunting or trapping them. Hominins may have been driving predators away from kills for a long time. The idea that other predators were our competitors and that lowering their populations favored humans was probably well within the capacities of big-brained late Pleistocene humans to understand.

The highly dynamic, more productive glacial environments would present three adaptive challenges for big herbivore hunters. The first challenge would be the ability to take large herbivores on a routine basis, in competition with a suite of efficient competitors for this resource. This problem was solved in Middle Paleolithic times by mode 3 toolmakers (Lee-Thorp and Sponheimer 2006; Stiner et al. 2000), if only marginally.

The second challenge would be to cope with the uncertainty of a noisy environment. Food security problems on time scales ranging from weeks to years would presumably have been more severe than for most ethnographically known hunter-gatherers. West Eurasian populations of the Upper Paleolithic/late Stone Age were evidently much larger than west Eurasian populations in the preceding Mousterian/Middle Paleolithic, although both peoples hunted the same suites of big game. Upper Paleolithic/late Stone Age people may have found solutions to the food security problem that escaped Middle Paleolithic people. Social systems for risk reduction are one candidate for such adaptations, in accord with evidence for social complexity at least among some Upper Paleolithic people.

The third challenge would be the problem of maintaining a cultural evolutionary system capable of responding to intense millennial and submillennial scale variation. Even completely modern people appear to lose the more complex elements of their culture when populations become too small. The most expert makers of artifacts are few, and in small populations they may be lost by chance. The famous case is the Tasmanians, whose tool kit simplified after they were cut off from Australia by rising sea level (Henrich 2004; see also Shennan 2001). The population on Tasmania at contact times numbered a few thousand. The much more complex mainland tool kit was maintained by a population at contact times

of a few hundred thousand. Kline and Boyd (n.d.) have shown that technological complexity is correlated with population size in Oceania. O'Connell and Allen (2007) reviewed evidence that modern humans in Australia during the Pleistocene lived at low population densities and maintained Middle Paleolithic style stone tools (see also Brumm and Moore 2005). Powell et al. (2009) simulated a metapopulation composed of many subpopulations. The effective population size can remain high in such populations if migration between subpopulations is high. Social organization innovations that knit formerly isolated small subpopulations together might allow complex tools to be acquired and maintained in the cultural repertoire even when populations of equivalent overall density but less connected maintain only simpler tool kits.

Perhaps the palimpsest of mode 3 and mode 4 industries in time and space reflects the demographic fortunes of populations subject to highly variable conditions. Populations so small that they lose complex tools would also have a less responsive cultural evolutionary system more generally. Perhaps over a wide range of herbivore productivities, human population densities were bistable (or multistable). A high population density equilibrium would generate a fancy technology and a rapid evolutionary response to millennial and submillennial scale variation. Hence a complex culture could maintain a reasonably high population density even in the face of considerable environmental deterioration. A small population in the same conditions would have a simple tool kit and a slow response to variation and hence would remain small. Outside this middle range, an especially rich environment might allow a simple system to jump to the complex equilibrium, whereas an especially poor one would reduce a complex population to simplicity. Perhaps in good times in good places anatomically modern humans and Neanderthals could achieve population sizes adequate to sustain more complex tool kits, whereas in poorer times and places they could sustain only simpler technologies. If environments remained poor enough for long enough, a population that had achieved Upper Paleolithic complexity might suffer a Tasmanian-style loss of complexity and drop back to the Middle Paleolithic equilibrium. This sort of dynamic is sometimes called a hysteresis loop. Rather than reacting directly to an environmental change, a population will have a strong tendency to remain either large or small. Given a sufficiently large and persistent increase in K, it will jump to a higher equilibrium, where it will persist under deteriorating environmental conditions under which the high equilibrium can be sustained but cannot be attained by a population at the low equilibrium. Time lags will be built into the cultural system. Complex elements of technology will not be gained or lost instantly.

We do not seem to have a good sense of potential rates of cultural innovation in the late Pleistocene, but the innovations that make up the Still Bay and Howison's Poort industries appear more rapidly than the best dating can resolve (Jacobs et al. 2008). Such cultural responses to climate variation might explain the coexistence of technologies with a late Stone Age cast with those of a Middle Paleolithic appearance in Africa during much of the last glacial period. The ability

of anatomically modern humans to displace "archaic" species, such as the Neanderthals, may have depended less on differences in innate abilities and more on having attained the complex cultural equilibrium and sustaining it long enough to reach such places as Australia, where the environment was so poor that humans tumbled back to the simpler Middle Paleolithic equilibrium. Human populations could well have imposed their own bit of chaotic dynamics on Ice Age systems.

At least one other process might contribute to the palimpsest mixture of mode 3 and mode 4 tool traditions in Africa. When human populations become large and sophisticated, they may act as superpredators who cause their prey populations to collapse. If human populations collapsed in the wake of the prey collapse, the small resulting population might revert to mode 3 tools, and the small, unsophisticated human populations might then allow prey populations to recover. The west Eurasian Upper Paleolithic is apparently unique in maintaining mode 4 tool kits for tens of millennia. This population or populations lived on the maritime end of the huge Mammoth Steppe biome. Both Neanderthals and anatomically modern humans lived in central Siberia, at least during the favorable interstadial periods, but apparently never penetrated the Beringian region.

Beringia consisted of eastern Siberia, the expanse of the Bering Straits region exposed by low sea level and much of Alaska and far northwestern Canada. Hoffecker and Elias (2007) suggest that fuelwood shortages in the Verkhoyansk mountains on the western boundary of Beringia formed an impenetrable barrier to human settlement until substantial climate warming allowed dwarf shrubs and trees to invade the barrier region 15,000–14,000 years ago. Big game animals depended on heavy fur, not fires, as protection from cold and probably spread readily across the Verkhoyansk barrier. Thus Mammoth Steppe hunters would have had what amounted to a large natural protected reserve in Beringia. Perhaps even larger areas emptied of people during stadial periods, enlarging the reserve.

A large literature has recently developed on using protected reserves to manage fisheries [see Botsford et al. (2003) and other papers in the same special issue of *Ecological Applications* for an introduction]. Africa is entirely tropical or temperate and has no areas where large game biomass would have had a natural refuge. South and East Asia and Australia also lack the potential for natural reserves. West and north Eurasia may have formed the only region where such a refuge existed, thus explaining why a permanent population of superpredatory humans could exist there without driving the populations of game animals too low to sustain a population capable of making mode 4 tools.

Note that sheer head count is not the most important demographic factor contributing to the Tasmanian effect. Caspari and Lee (2006) used dental wear to roughly estimate the ratio of old to young adult individuals in hominin fossil death assemblages from the Australopithecines to the Upper Paleolithic. Slight increases are evident at each major change of taxa with one major exception: Upper Paleolithic people had an old to young adult ratio of about 2.1, whereas the European Neanderthals had a ratio of only 0.35. In Southwest Asia, where Neander-

thals and anatomically modern humans coexisted using Mousterian technology, the small dental sample suggests that both populations had an old to young ratio of about 1. Caspari and Lee suggest that a cultural rather than a genetic change was responsible for this difference. The changes are reciprocal in that older adults can accumulate and transmit more culture than young adults and can accumulate more individually acquired knowledge. Caspari and Lee's analysis lends weight to the idea that large-brained hominins of the late Pleistocene had bi- or multistable population dynamics.

Demographic Transitions of the Holocene

Richerson et al. (2001) argue that the relatively tranquil environments of the Holocene favored subsistence innovations focused on intensive exploitation of low-ranked but highly productive plant resources. On the evidence of the Ohalo II site (Weiss et al. 2004), the ability to exploit such resources went some way back into the Pleistocene, even though archaeological and stable isotope analysis suggests that late Pleistocene human diets were primarily carnivorous. The new plant-rich protoagricultural and agricultural subsistence systems led to a diet with poor nutritional balance. These systems were also vulnerable to weather extremes. When there was a heavy dependence on domesticated plants, subsistence depended on a few species, magnifying vulnerability to weather extremes. In the Pleistocene the out-of-equilibrium ecosystems generated by the Dansgaard-Oeschger cycles would have made a suitable plant-rich subsistence system a too rapidly moving target for cultural evolution to track. Even in the Levantine region, where the evolution of agriculture was early and rapid, a few thousand years were required to move from a marginal use of crops to a near complete dependence on them. In the late Pleistocene such a span of time would include multiple Dansgaard-Oeschger cycles, not to mention much more variation at the millennium to century time scales than in the Holocene (Ditlevsen et al. 1996). Thus in the Holocene but not in the Pleistocene, a relatively simple trajectory of one cultural innovation after another leading to continuing population increase was possible.

Richerson and Boyd (2001) reviewed several hypotheses regarding the rate of Holocene cultural evolution. Diamond's (1997) proposal that the size and orientation of continents played a large role is best known of these. His idea is basically the Tasmanian effect writ large. Indeed, Diamond (1978) commented on the simplification of the material culture of Tasmania many years ago. Our own suspicion is that the rate of increase of social sophistication is typically the rate-limiting factor in the Holocene progressive increase in cultural sophistication. This idea goes back at least to Marx; a revolution was necessary because the potential of industrial technology had outrun the capabilities of capitalist social organization, just as the earlier bourgeois revolution ended the rigidities of the feudal social system and sowed the seeds of the technological advances that led

to the Industrial Revolution. We do not discount the importance of technology, only that improvements in technology are not typically the rate-limiting step except temporarily at small time scales. As with population pressure, we see here the importance of getting the time scale of the processes right. If we were to add a positive effect of population size on the cultural innovation rate to the model behind Figure 1, we conjecture that we could produce an exponential curve of increasing cultural sophistication that would fit the data from Holocene Eurasia and (at a slower rate) the rest of the world.

The actual Holocene trajectory in any one location was much less smooth than that portrayed in Figure 1. Natural climate fluctuations (Curtis et al. 1996), human-induced environmental deterioration (Diamond 2005), and internal or external political events resulted in increases in cultural sophistication and population size that were often punctuated by more or less dramatic crashes. Turchin (2003) explored an interesting model of internally driven collapse. Borrowing from the medieval geographer Ibn Khaldun, Turchin modeled the interaction between the growth of an elite ruling class and a producer peasant class. At low densities, elites have a positive impact on the productive class by providing government services. The society grows, but the elite class, drawing a relatively larger income from taxes than the producers can enjoy, grows faster than the producers. Eventually, the too large elite extracts a heavy tax burden from the producers while providing public services inefficiently, and the system collapses. Depending on details, the collapse can affect mainly the elite class (civil war and dynastic replacement) or both classes, as in the fall of the Western Roman Empire or the collapse of most of the Mayan city-states. Turchin's model is entirely sociological and contains no cultural evolution or environmental deterioration. Thus it creates no rising trend in population and cultural sophistication.

As an aside, the ecological models that Turchin used have general application to humans (Efferson 2008). They could be easily mated to evolutionary models (Richerson and Boyd 1998). In addition, we could incorporate the niche construction modeling framework of Odling-Smee et al. (2003). These investigators consider both cultural evolution and the effects of persistent modifications of the environment by human activity. The long-term degradation of soils by erosion or their buildup by terracing and the import of organic matter are two examples of niche construction with opposite effects on human populations. Humans are master niche constructors and destructors, and accounting for these processes is an important addition to our modeling tool kit.

The Modern Demographic Transition

A Figure 1 style model with the rate of cultural evolution a positive function of population size will create a dramatic singularity when the rate of technological process approaches the human intrinsic rate of natural increase. The population will explode, as indeed it did in the last couple of centuries. In "modernizing" countries—first England and then the culturally European countries and

now China, India, Brazil, and more—the rate of technical and social innovation exceeded the intrinsic rate of natural increase of humans, and per capita incomes began to rise. This added a new impetus to technological progress as the savings and investment rates of societies increased, not least investments in human capital that fed innovation. Investments in health science and health care raised the intrinsic rate of increase and lowered death rates across the life span. Absolutely enormous rates of population increase became possible. They are currently realized in a few countries and in isolated subcultures in countries that have otherwise undergone dramatic reductions in fertility, such as conservative Anabaptist congregations (Hurd 2006).

In most populations demographic events have moved dramatically against the population explosion trends of the initial generations of modernity. Nothing in the models so far considered predicts the modern demographic transition. But evolutionary social scientists have taken considerable interest in explaining the demographic transition (Borgerhoff Mulder 1998). Some models are premised on the idea that great wealth per capita would exaggerate the lack effect because wealthy people could leave large endowments to a few children, who might in turn maximize the number of their grandchildren so that increasing wealth will cause an adaptive reduction in the number of children (Rogers 1992). If parents had as many children as they could afford, those children might not be competitive in their turn. The parents who overproduce children might not produce as many grandchildren as parents who produced fewer children but endowed them with better food, a better education, and an inheritance to spend raising the grandkids. A large sample of men's reproductive success in Albuquerque showed no signs of such an effect (Kaplan et al. 1995). On average, the best way to have lots of grandchildren was to have lots of children. No quantity-quality tradeoff appeared. Kaplan (1996) went on to suggest that large material endowments trigger a maladaptive psychology of overinvestment in children. The current situation in wealthy countries is evolutionarily unprecedented. Thus the hypothesis that some aspect of human psychology misfires in such an environment is plausible.

The nature of cultural transmission in modern societies is also unusual compared with that in traditional societies. Important parts of child socialization are given over to professional teachers. Many of the important people in our lives are people who occupy other achieved roles, such as bosses at work and military officers. Richerson and Boyd (1984) developed a model in which selection for success in achieved roles, such as being a teacher, favors education. Educational success is in turn favored by growing up in a small family and by delaying marriage to finish school and establish a career. People in prestigious achieved roles, perhaps inadvertently, transmit small-family norms to people they influence. Small-family norms can spread in the model even if the absolute importance of kin in socialization is greater than the importance of people in achieved roles. This happens if the people in achieved roles are more highly selected for small families than people in kin roles are for having larger families. In any case, the relative importance of kin also declined as residential mobility moved people

from traditional villages to cities. Because kin tend to have an interest in each other's reproductive success, a social network dense in kin will support pronatalist norms, whereas networks rich in co-workers and unrelated friends will allow pronatalist norms to be lost by successive generations of modern humans. This is another mechanism by which modernization favors small-family norms (Newson et al. 2007). Mass media provide alluring opportunities to spend wealth on consumption goods rather than on large families. In Latin America, telenovelas (extremely popular soap opera style programs featuring the romantic lives of middle-class people) have been implicated in the demographic transitions in these countries (Bongaarts and Watkins 1996).

Some of the evidence in favor of a cultural-evolutionary explanation for the modern demographic transition comes from various special cases in which nonmodern populations underwent modernlike demographic transitions or in which modern populations failed to undergo transitions. Knauft (1986) cites historical evidence that ancient and early modern cities had a combination of low birth rates and high death rates compared with rates in the countryside. If these data are correct, then urban society was essentially a cultural parasite that persisted by tempting countryfolk with the bright lights because they were otherwise demographically unsustainable. In recent history the urban upper and professional classes often reduced their birth rates in the early modern period long before such practices became general (Livi-Bacci 1977). On the other side, religious groups, such as the Amish, maintain high population growth even as they participate in the modern economy as commercial farmers. They do so by culturally isolating themselves from modern achievement-oriented occupations, avoiding mass media, and living in kin-based communities (Kraybill and Bowman 2001). If the modern demographic transition is a sort of culturally transmitted disease, then Anabaptists have a culturally transmitted immunity! In many modernized countries fertility has fallen well below replacement with little sign of a flattening or return to even replacement levels. Efferson's (2008) ecological model has a scenario in which human population goes to 0 as wealth per capita goes to infinity.

Conclusion

Culturally transmitted innovations have probably been a major determinant of human demographic behavior for as long as we have been a seriously cultural species. Our argument in this paper is that nothing about humans in the last 250,000 years makes sense without considering cultural innovations (and their loss from small populations). The role that cultural innovation has played seems to be divisible into at least four regimes during that period. The first was the regime from about 250,000 to 75,000 years ago. Innovation rates were slow (but not necessarily zero) during this period, and human populations remained small. From our vantage point, this regime is puzzling. For more than a whole glacial-interglacial cycle, large-brained hominins making moderately complex stone tools made little progress toward modernity. The climates that these people lived

in were highly variable in space and time but were only subtly different from the last glacial-interglacial cycle when so much happened.

After about 75,000 years ago and certainly by about 50,000 years ago, a significant modernization of cultures took place, resulting, most spectacularly, in the Upper Paleolithic of western Eurasia. Once developed, however, the Upper Paleolithic seems to have been conservative. Elsewhere, as far as the evidence goes, human populations perhaps varied under the influence of fluctuating environments, and cultural advances were often followed by retreats. Or perhaps the advances are illusory. Because the pace of change in both of these regimes is far below the rates of cultural change we know to be possible, something must have been severely limiting the rates of cultural innovation relative to more recent times. One possible answer is that genetic factors limited cultural innovation and evolution as late as about 50,000 years ago. Our big-brained ancestors may have lacked some crucial cognitive innovation that made language or some similar essential cultural innovation impossible, as Klein (2009) argues. Another possible answer is that environmental factors limited cultural innovation rates. If human populations remained small, perhaps hemmed in by competing predators, cultural advance would be limited by the Tasmanian effect. On the other hand, when the drumbeat of the Dansgaard-Oeschger cycles increased in frequency about 50,000 years ago, culture may have become a decisive advantage in competition with slower adapting members of the top carnivore niche. Perhaps that advantage was particularly strong on the western end of the Mammoth Steppe, leading to the Upper Paleolithic phenomenon. The maritime fringe of western Eurasia may have sustained Upper Paleolithic hunters in numbers that permitted them to maintain a complex culture during the most unfavorable parts of the Dansgaard-Oeschger cycles. Of course, a mixture of these two explanations (and others) is also plausible. Perhaps the increase in frequency of the Dansgaard-Oeschger cycles just before anatomically modern humans left Africa selected for genes that made higher rates of cultural innovation possible, rather than the innate cognitive change having been a rare mutation that would have been favored in earlier environments.

The transition to the Holocene ushered in a regime of sustained increases in human population densities and cultural sophistication. This period looks most like the simple Malthusio-Darwinian model we have reviewed in this paper. The rate-limiting factor over this 11,500-year-long regime was probably the rate of cultural innovation, possibly especially the rate of innovation of social institutions. But the rate of coevolutionary response on the part of genes could have been a major factor, especially in the first half of the Holocene. Probably the rate of innovation on average increased during this regime because the rate of innovation is tied to population size, as Jared Diamond argues, or because of some other autocatalytic process.

When the rate of cultural innovation rose to the point at which rates of technological progress permitted subsistence to advance at near the intrinsic rate of increase of human populations or above it, the modern regime began. Populations first exploded, but then the modern demographic transition occurred. Consumption per capita continues to rise, surely temporarily, while populations begin to

stabilize or contract. We hope to transition to a sustainable regime, but the form that will take is for futurologists to guess about.

The tools we have for understanding the past grow at modern rates. The archaeological, historical, and statistical data improve. Some areas are neglected. For example, archaeologists could expend more effort trying to estimate population sizes and rates of technological progress so that we could better understand the relationship between them. Mathematical models appropriate to study long-run technological change, especially the link between demography and innovation rates, are still limited. Experimentalists are in their golden age, especially in biology. We already know a bit about when various important genes came under selection. We are rapidly learning more about how genetic and developmental regulatory systems work. Surely almost everything we write today will look childish in the not so distant future. A small slice may look prophetic. J. B. S. Haldane caught the strange nature of our quest, we think, in his remark that "the world is not only queerer than we suppose, it is queerer than we can suppose!"

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