
Rethinking Paleoanthropology: A World Queerer Than We Supposed

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The universe is not only queerer than we suppose, it is queerer than we can suppose.

— J.B.S. Haldane (1927:286)

Advances in paleoclimatology and paleoecology are producing an ever more detailed picture of the environments in which our species evolved, helping us to understand the processes by which our large brain and its productions—toolmaking, complex social institutions, language, art, religion—emerged. Our large brain relative to body mass and the extreme elaboration of our cultures differentiate us from our nearest relatives. We achieved our present anatomy and behavioral repertoire *very* recently. Fossil material attributable to our species goes back perhaps 200,000 years ago (200 kya), by which time the brain of our species and of Neandertals had reached nearly modern proportions. Artifacts that strike us as representing fully modern behavior are rare early in the record of our species, and only become abundant after 50 kya, and then mainly in western Eurasia (Marean et al. 2007, Klein 2009). Our ecological dominance began with the evolution of agriculture starting about 10,000 years ago (Vitousek et al. 1997).

Explaining the late coming of human brains is a major evolutionary puzzle as most important animal adaptations are old. Eyes, internal skeletons, adaptations for terrestrial life and for flight all date back hundreds of millions of years. Many lineages of fully terrestrial animals have re-adapted

to fully aquatic life including whales and other mammals, several lineages of mesozoic reptiles, and families from most insect orders. Given that big brains and culture have been such an overwhelming success for us why did they not evolve long ago?

MACROEVOLUTIONARY EXPLANATION

Evolutionary biologists speak of microevolution and macroevolution. While microevolution describes the generation to generation changes that we can observe directly in the field or lab, macroevolution concerns longer time scale changes such as the evolution of new species or the evolution of larger and larger brains in a succession of species.

Evolutionary scholars advance two major sorts of hypotheses—internal and external—to explain big events, such as the rise of modern humans in the late Middle and Late Pleistocene (Boyd and Richerson 1992, Stearns 2002). We might imagine that evolution is a slow, halting, and biased process, limited and directed by *internal* processes. For example, the evolution of the large brains that subservise human technical and social capacities might involve many innovations, each one difficult for evolution to accomplish. Brain size increase might be slow and halting because complex new brain reorganizations cannot occur quickly even if they are strongly favored by selection. The number of mutations and recombinations required may be many. The genotype-to-phenotype mappings may be complex. Once a basic primate template for the brain of a diurnal, arboreal, visually oriented creature was laid down, the path to a larger brain may have been easier. Nevertheless, progress toward the complex human brain may have been slow and halting.

The other class of hypotheses assumes that selection is a powerful force and that genetic constraints on the rate of evolution are of modest importance. At any given time, organisms are close to an evolutionary equilibrium with current environments (Walker and Valentine 1984). According to this model, any major changes in organisms on the geological time scale will be a result of *external* processes of environmental change. Climate might favor small brains in some geological eras (e.g., the relatively small brains of Mesozoic mammals and dinosaurs), while the climates of other eras favor larger brains. Brains have been getting larger and larger in many mammalian lineages for the last 65 million years or so (Jerison 1973), suggesting an external change that parallels the evolution of brain size (Elton, Bishop,

and Wood 2001). Bird brain evolution is much less well known than that of mammals because the fragile skeletons of birds rarely fossilize. However, some birds, such as crows, have large brains for their body size and exhibit intelligent behavior comparable to that of apes. Ancient birds had small brains (Emery and Clayton 2004).

Co-evolution is another potential pacemaker of macroevolution. For example, Geerat Vermeij (1987) suggested that the evolution of shelly marine invertebrates was driven by predator-prey arms races. If crabs evolve stronger jaws, their snail prey will evolve stronger shells. If antelope become swifter to avoid predators, cheetah must become swifter still to capture them. Many predators and prey show clear evidence of many rounds of co-evolution to arrive at quite advanced adaptations for offense and defense. If these races unfold slowly, then co-evolutionary processes will have an important macroevolutionary role. Vermeij suggests that the level of energy available in ecosystems governs the equilibrium reached by an arms race when it is finally exhausted. If arms races are as rapid as the races metaphor suggests, then predator-prey arms races will be a microevolutionary phenomenon and the macroevolutionary pattern will be regulated by such external factors as the geochemical and geophysical evolution of the earth. Sometimes, ocean upwelling is active and the ocean is productive, leading to advanced arms races. Other times, the ocean may be stably stratified, keeping predator arms and prey defenses weak and simple.

Co-evolution between two organisms is just a special case of the phenomenon called niche construction (Odling-Smee, Laland, and Feldman 2003). Organisms often modify their physical as well as biological environment and then adapt to the environment they create. Humans build shelters and sew clothing in cold, cloudy environments and then need to evolve light skin to biosynthesize enough vitamin D in the small areas of skin exposed to the infrequent sun (Jablonski and Chaplin 2010). On the other hand, the need for two or more organisms to co-evolve could potentially slow the evolutionary process if both partners are evolving on complex adaptive topographies.

The alert reader will already have noticed that everyone must be an externalist, and internalist, and a co-evolutionist/niche constructionist, depending upon the scale at which the question is asked. Evolution is never instantaneous, so at short enough time scales internal processes must be important. Similarly, at long enough time scales external processes must

be important. Surely no advanced animal life was possible until the earth's atmosphere became oxidizing so that oxygen-powered respiration to drive an active life became possible. The Cambrian explosion of animal life was likely a consequence, perhaps a considerably delayed consequence, of an atmosphere with ample oxygen. Similarly, no one doubts that co-evolutionary and niche construction processes are important. The right questions to ask are what processes drive particular evolutionary events on what time scales?

What follows in this chapter is an attempt to stop people thinking in terms of what we call the "naïve internalist" hypothesis. Many students of human evolution seem to assume that the evolution of the world's most complex species must have taken a very long time, as vertebrates generally, then primates, and finally hominins gradually worked their way toward higher relative fitness using ever bigger and more complex brains. In this picture, the external environment itself did not change appreciably while our ancestors became behaviorally more and more sophisticated.

Perhaps this picture is essentially correct, but much evidence casts doubt on it. Past environments were often very different from current ones, as we shall see. At least in some cases, internal constraints do not seem to be limiting except on short time scales. Perhaps when external environments change, some lineages will fairly rapidly evolve to fill every empty ecological niche created by the change. In the last 12,000 years, hundreds of new fish species apparently evolved from a handful of ancestors in Lake Victoria, giving us some idea how fast natural selection can fill new niches (Verheyen et al. 2003).

WHEN WILL SELECTION FAVOR BIG BRAINS AND FANCY CULTURE?

Consider a radically externalist picture. Vertebrate brains are all roughly scale models of one another, differing mainly in size and hence in raw processing power. Relatively few and simple changes may be needed to create larger brains and new functional units, such as vision processing areas, in these larger brains (Krubitzer 1995), contrary to one of the main arguments for the internalist hypothesis. This is especially so within an order, such as the primates (Striedter 2005). Selection can thus plausibly have increased the size of brains and brain components like the cerebral hemispheres of the large-brained birds and mammals in fairly short order. We allow that some time is necessary to fine-tune the functions of large

brains, but let us suppose that much can be accomplished in the order of a thousand generations (~25,000 years for humans). Animal breeding for such things as increased milk yield and very large and very small size in dogs get large responses to artificial selection in tens of generations, so if brain evolution is mostly scaling up and scaling down, a thousand generations is actually a generous allocation of time if selection is even moderately strong.

An important consideration is that brains are very expensive organs metabolically. The adult human brain consumes ~16% of total metabolism against perhaps 5% for mammals with average brain sizes and 1% for our smallest brained relatives (Aiello and Wheeler 1995). Humans have plausibly had to sacrifice gut size and hence digestive efficiency to support the evolution of our metabolically costly brain, since gut tissue is even more energy intensive than nervous tissue. All else being equal, selection will favor as small a brain as possible. Think dinosaurs and their famously small brains relative to their body size. If evolution is going to favor big brains, the reason must be that the relevant organisms must live in complex or variable environments that demand big brains. The fact that many lineages of mammals (and probably birds) have undergone recent increases in brain size (Jerison 1973) strongly suggests that a common external environmental change has driven this major macroevolutionary trend.

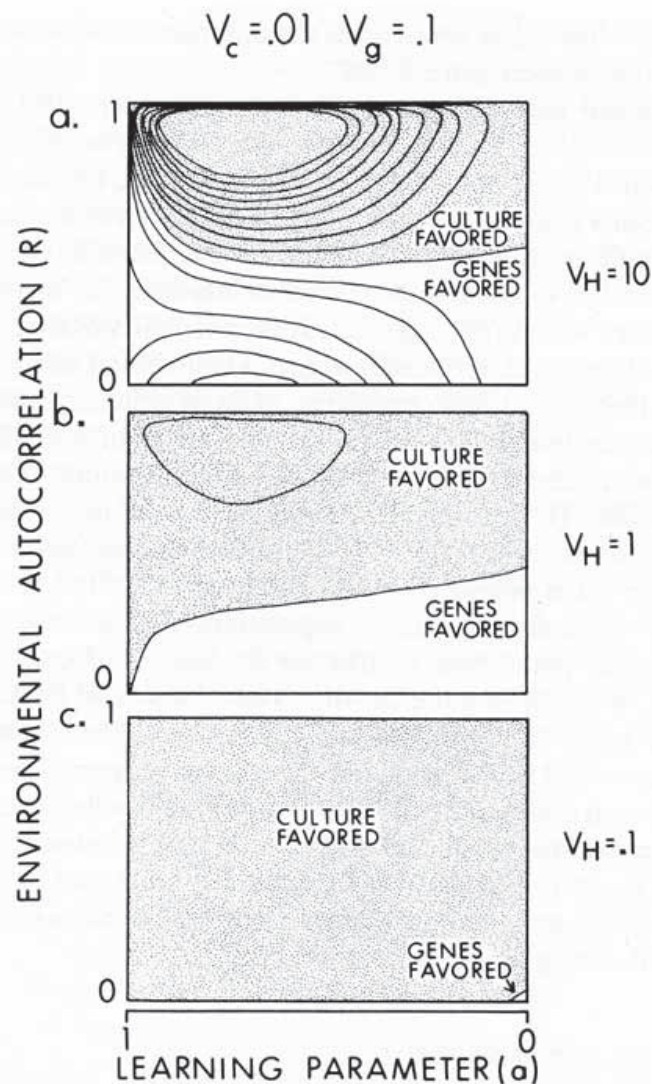
What sorts of selective pressures would drive the evolution of large brains and, in particular, the extraordinarily large brain and the associated complex culture of humans? Costly systems for phenotypic flexibility—individual learning and social learning are examples—are adaptations to cope with variable environments, as we will argue below. Organisms adapt to very slow environmental change by organic evolution and often to swifter change by range changes. Non-human large-brained animals—including other primates, and the crow and parrot families of birds—use large brains to learn how to cope with unpredictable environmental change (Reader and Laland 2002, Sol et al. 2005).

The effect of social learning is to leverage individual learning and decision-making using the inheritance of acquired variation. In a cultural system, a mother can transmit some of her accumulated wisdom to her offspring, sparing them the need to do as much costly trial and error learning as they would otherwise have to do. Many animals use simple systems of social learning to accomplish this trick (Heyes and Galef 1996).

Humans have evolved the capacity for an extremely sophisticated system of cumulative cultural evolution on this simple foundation (Boyd and Richerson 1985, Richerson and Boyd 2005, Tennie, Call, and Tomasello 2009). Humans are quite accurate imitators allowing us to acquire more complex behaviors from others than is possible with simpler forms of social learning not dependent on accurate imitation. Even something as simple as a stone-tipped spear draws upon complex wood-working and stone-working skills and the making of cordage and adhesives. Human individual learning is mainly applied to small improvements in already complex artifacts, leading to the cumulative improvements of toolkits over many generations. No one person invents a fancy skin boat like the Arctic kayak. Rather, kayaks probably evolved over a period of a thousand years or more to judge by the evidence from more durable artifacts (Dumond 1984). Aside from just passing on useful innovations, people can also shop in the marketplace of extant ideas. If we see our neighbors employing a superior new technique, we can borrow it from them, leading to the fairly rapid diffusion of new techniques over wide areas.

Mathematical models suggest that a costly cultural system is adapted to cope with fluctuations of less than a generation (horizontal borrowing of simple innovations) to many tens of generations for the buildup of whole new subsistence systems. On time scales beyond several hundred generations, or around 10,000 years, even humans will begin to respond to variation with genetic rather than cultural adaptations. Thus, humans have undergone massive cultural evolution in the past 10,000 years while the evolution of our genes amounted to some relatively minor tinkering, much of that in response to new diets and new diseases caused by agriculture supplying abundant starchy staples and by the dense populations supported by agriculture (Sabeti et al. 2006, Laland, Odling-Smee, and Myles 2010, Richerson and Boyd 2010). On a time scale of 100,000 years and longer, human populations in the past evolved genetically in ways that paleoanthropologists can easily see in their bones.

Figure 11.1 illustrates these principles with the results of a theoretical study (Boyd and Richerson 1985). Two different stylized populations were pitted against one another in three different environments. One population comprised basic animals that could learn individually and transmit the *starting* point of individual learning genetically. The second population was exactly the same, except that the cultural population transmitted the *end* point



11.1. The results of a mathematical contest between a model of genetic transmission plus individual learning and a model of cultural transmission plus individual learning. The panels should be read as contour plots measuring the difference in fitness of the two populations under different conditions. The learning parameter ' α ' measures the importance of inherited initial behavior relative to individual experience. When $\alpha = 1$, individuals don't learn individually but trust their inherited information completely. V_H is the environmental variation, rising in increments of 10 from the bottom to the top panel. The environmental autocorrelation, R , measures the degree to which the environmental variation is organized into multi-generational "waves" in which the parental and offspring environments statistically resemble one another. As is explained in the text, the conspicuous mound in the top panel, where the culture plus learning system is highly fit compared to its genes plus learning alternative, occurs in an environment with extreme, but fairly highly autocorrelated variation. Note that at even higher autocorrelations the genetic system is favored again. (From Boyd and Richerson 1985: chap. 4.)

of their learning to their descendants via social learning. The existence of social learning is one of the most basic differences between a cultural and a genetic evolutionary system. Culture includes the potential to inherit acquired traits and genes do not. The figure is in the form of a contour map that plots the difference in fitness of the two populations as a function of important evolutionary and environmental parameters. The a parameter across the bottom measures the importance of individual learning. When $a = 0$, individuals depend entirely upon their cultural or genetic inheritance and don't learn for themselves. When $a = 1$, they depend entirely upon their own learning and give no weight to what they inherit. The vertical axis is the effect of how organized the variable environment is. The world of the model is noisy, but the noise can be autocorrelated. That is, if $R = 0$, the environmental variation is simple random noise with a variance V_H . As R increases toward 1, a stronger and stronger statistical relationship exists between the environment of mom's generation and offspring's generation, holding the total amount of variation constant. The three panels illustrate the effect of three different amounts of total variance, V_H .

Note that the topography is very flat when the amount of environmental variance is small or moderate. In the model comparison, genes and culture do almost the same work when little evolution is required. If we added a cost to culture, like having a big brain, we would see no culture in the bottom two panels, or only the low-cost culture that many small-brained animals have. Culture has a very big advantage only in one region of the top panel. When the environmental variation is very high, but when that variation is fairly highly autocorrelated, culture is a big advantage. Also, notice that the peak in the top two panels is shifted to the left of center, indicating a substantial dependence on cultural transmission relative to the individual's own experience in the region where culture has its largest advantage. When culture is really important, you should take mom's advice pretty much to heart. If the autocorrelation is too low, listening to mom is not sensible; she is too likely to have lived in a different environment from you. In this situation it makes sense to depend heavily upon individual learning. Although not well displayed in the plot, there is a cliff at the top of each panel. As the environmental autocorrelation becomes very strong, the cultural system becomes a liability again. This result also makes sense. When R is very large, environmental change is very slow, and genes track slow changes under the influence of selection well enough to outweigh the extra costs of the cultural system.

The culture imagined in this model is not only simple but conservative. We allowed only gene-like vertical transmission from one generation to the next. Other aspects of the cultural system, like biased borrowing of useful techniques within a generation will have the effect of making culture useful in more rapidly changing, less autocorrelated environments. Qualitatively, we might say that the more conservative vertical components of culture, especially the building of complex adaptations by many piecemeal innovations, ought to be useful to adapt to changes with autocorrelation out to a few hundred generations. The less conservative mechanisms might be useful to spread new adaptive responses to step-like environmental changes horizontally down to time scales of less than a generation. The Anatomically Modern Human (AMH) cultural system, complete with languages that can accurately and rapidly communicate many ideas, looks like a “tunable” system that could be used to adapt to a broad range of variation from time scales of years to a few millennia. This modeling exercise was completed more than a decade before the climate variation described in the next section was discovered, so the models were not concocted to fit the data!

The human cultural system of adaptation may be thought of as a specific subtype of what Potts (1996, 1998) called “variability selection” (see also Calvin 2002). Potts imagined that a variety of genetic and behavioral adaptive systems would have been favored as environmental variability increased in the last few million years. He discusses environmental variability on a variety of time scales and is not specific about what mechanisms are adapted to which time scales. As the data reviewed below show, the last glacial had high rates of climate change on the millennial and submillennial time scales, exactly those that the theoretical study discussed above flags for special interest.

A reviewer sensibly objected that this explanation for human brain size fails to account for why our brain is so extremely large whereas other species still retain much smaller brains. In his classic study, Jerison (1973) noted that *distributions* of mammal brain sizes increased during the Cenozoic with many mammals retaining small brains. Evolutionary ecologists have long been interested in the effect of environmental variation on species diversity (e.g., Abugov 1982). The general effect is that environmental variation opens niches for “fugitive species” that evade more competitive species by growing quickly in unpredictable patches before superior competitors can build up a population to suppress them. Thus variability tends to increase

diversity by creating new ecological niches for species with adaptations keyed on variability.

We imagine that increasingly variable climates diversified niches such that smaller-brained species could still exploit the least variable part of variable environments. Larger-brained species began to use cleverer strategies to exploit windfalls and evade dearths to which smaller-brained species are unable to adapt. The high overhead cost of large brains (Aiello and Wheeler 1995) means that species that exploit resources to some degree protected from environmental fluctuations will be able to outcompete otherwise similar larger-brained species for more stable resources. Sol et al. 2005 provide evidence that the success of introductions of birds to novel environments is correlated with their brain size relative to body size. Reader and Laland's (2002) study of mentions of innovative behavior in the primatological literature finds a strong correlation between innovation and brain size. An increased diversity of brain sizes among otherwise similar taxa at evolutionary equilibrium thus seems a quite plausible result of more variable environments.

Humans in the Pleistocene might well count as a fugitive species exploiting a rather marginal niche. We are not aware of any paleoanthropological evidence that Pleistocene human populations were ever very abundant compared to our smaller-brained competitors. Estimates of effective human population sizes based on mitochondrial coalescence data suggest populations of a few thousand in Africa and perhaps 100,000 in South Asia after 40 kya (Atkinson, Gray, and Drummond 2008). Middle and Lower Pleistocene human abundances seem to have been low relative to competing species (Bobe and Leakey 2009). For example, at the Swartkrans site in South Africa, a large volume of material was excavated, dating between 1.8 and 1 mya. The minimum number of *Homo* individuals recovered was 3 compared to 39 australopithecines, 33 monkeys, 10 large cats, 13 hyenas, and 15 canids (Watson 2004). Given that this is a famous early human site, the number of *Homo* recovered seems rather modest compared to probably competing species, assuming that early *Homo* had an omnivorous diet. The relative abundance of *Homo* in a representative sample of Pleistocene fossil localities would be very interesting. *Homo*'s commitment to large brains and culture did not become a major evolutionary success story until late in our history.

Our stark externalist hypothesis can easily fail in the face of evidence that is currently accumulating regarding past climate variation. If the millennial and submillennial scale variation in the climate record has not changed as

the brain sizes and cultural sophistication have increased, allowing for only small lags on the order of at most a few tens of thousands of years, the radical externalist hypothesis is untenable. We can add back more and more internal constraints if lags prove to be longer. If the data eventually show no relationship at all between millennial and submillennial scale variation and the growth of brains and culture, or more decisively yet, an inverse relationship, our theoretical argument must be fatally flawed. Perhaps internal limitations are all that have regulated the growth of nervous systems since the first multicelled animals evolved in the Precambrian—the extreme internal hypothesis. That human brains and culture seem to have evolved in a time of high environmental variation could be a complete coincidence.

EVOLUTION OF THE EARTH'S CLIMATE SYSTEM


The global environment has changed radically over the last 80 million years (Fig. 11.2). Likely enough, environmental change has thrown up vast new ranges of adaptive peaks favoring big brains since the extinction of the dinosaurs (and the ancient small-brained mammals and birds that were their companions). These peaks have probably grown higher in the past few million years. The Holocene geological era (the last 10,000 or so years) has been graced with an unusually stable climate. The Little Ice Age, lasting from ~1100 CE until 1900 CE, turns out to be a polite hiccup compared to the robust climatic belches of the slightly deeper past, although the Little Ice Age hiccup blew a hard wind on some human societies (Fagan 2002). Ruddiman (2007) argues that the long quiet Holocene climate is unusual for an interglacial and that it is a product of gentle anthropogenic increases in atmospheric CO₂ and CH₄ due to releases of these gases from forest clearance and from rice paddies. He attributes the Little Ice Age to Eurasian farm abandonment and forest regrowth in the aftermath of the Bubonic Plague.

Geologists in the 19th century discovered the first hints of dramatically different past climates in the unmistakable signs of several large-scale ice ages in the latter part of the Pleistocene era. Classic geological methods gained a limited insight into these events because each succeeding glacial advance nearly wiped out the evidence of its predecessors. Ocean, lake, and ice coring in the 1960s and 70s, together with the development of dating methods and geochemical, geophysical, and biological proxy measures of past climates, revealed a much richer picture of climate deterioration over

the whole Cenozoic (“Age of the Mammals”) era (65 mya–present). Under favorable conditions, application of these methods to ice and mud cores enable paleoclimatologists to read a great deal from the material deposited layer by layer by the fall of sediment and snow.

Two of the many paleoclimate proxies are $\delta^{18}\text{O}$ and pollen grains (Bradley 1999). $\delta^{18}\text{O}$ is the ratio of the main natural heavy isotope of oxygen to the most abundant isotope ^{16}O , expressed as deviations from a standard sample in parts per thousand.

Modern mass spectrometers ionize samples containing isotopes and accelerate them toward an array of detectors in a magnetic field to separate isotopes based on their mass. Small variations in isotope ratios are measured quite accurately by such instruments. The deposition of oxygen isotopes in the shells of common marine amoebae called foraminifera is temperature dependent, providing a paleothermometer for the oceans. The foraminiferal thermometer is complicated by the fact that $\text{H}_2^{16/18}\text{O}$ water, being a bit heavier than $\text{H}_2^{16/16}\text{O}$, has a lower vapor pressure. This means that a given molecule of $\text{H}_2^{16/18}\text{O}$ is less likely than a molecule of $\text{H}_2^{16/16}\text{O}$ to escape from the ocean surface as water vapor and, if already a vapor molecule, more likely to condense into rain or snow. This condensation discrimination effect is temperature dependent, providing a paleothermometer measuring the temperature at which snow preserved in ice caps condensed.

During ice ages, isotopic discrimination makes the ocean’s waters systematically heavier as light water is disproportionately locked up in the glaciers, biasing the foraminiferal thermometer. Hence water vapor evaporated from the heavy oceans will be heavier than during ~~interglacials~~ too,  biasing the condensation thermometer. These biological and physical isotope discrimination processes have been intensively studied in an effort to calibrate the proxies in terms of actual temperatures. Often, the raw isotopic ratio in ocean carbonate skeletons or ice water is reported without conversion to a possibly problematic paleotemperature. Used in this way, $\delta^{18}\text{O}$ is mainly an ice-volume indicator, but ice volume is closely related to global temperature.

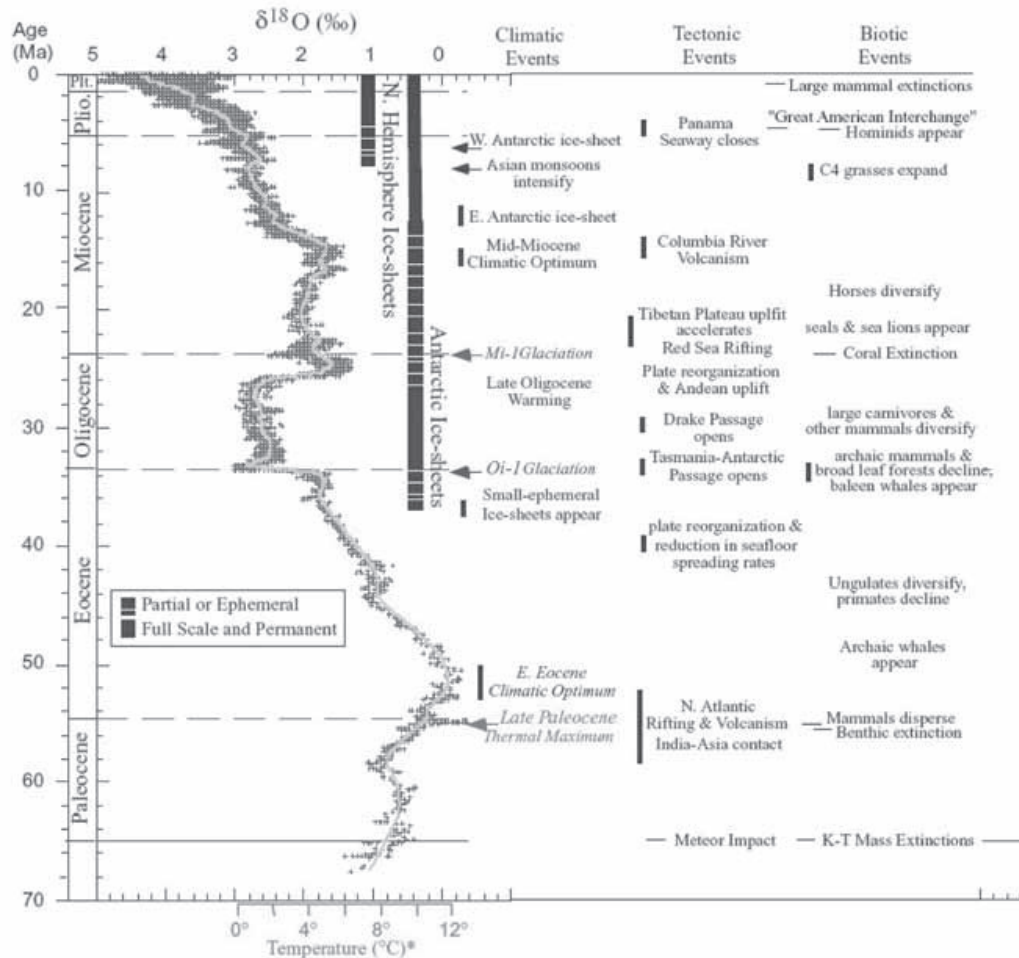
Pollen grains are representative of the many biological proxies that are used for inferring past terrestrial climates from lake and coastal ocean sediments. Many plants shed rather copious amounts of pollen, and pollen grains have characteristic cell walls that preserve well in lake- and ocean-bottom muds. As layers of mud accumulate, they roughly record the abun-

dances of pollen-shedding plants. Plants have more or less limited ranges today and the limits are often climatic. Given a suite of plants, and assuming that plants have not evolved much, we can infer past climates from the pollen found in cores. Aside from climate reconstructions, pollen spectra also help paleoecologists reconstruct past ecosystems. Climate and climate variation have direct impacts on human populations, but many of the most important impacts will be felt through impacts on ecosystems which furnish biotic resources to the humans that live in them.

The large-scale history of climates over the Age of the Mammals is that climates became cooler and drier in a series of steplike transitions, culminating in the Plio-Pleistocene ice ages after about 3 mya (Figs. 11.2 and 11.3). The Plio-Pleistocene ice ages themselves are a multistage deterioration that includes three shifts toward higher amplitude, lower frequency ice fluctuations. The first stone tools appear in the paleoanthropological record 2.6 mya, not long after the climate variation began to increase in the late Pliocene (Opdyke 1995). The first signs that hominins start their run toward our extraordinary brain sizes occur slightly later (McHenry and Coffing 2000) (Fig. 11.3). Around a million years ago, 100 ky-year-long glacial cycles of very great amplitude began, the last few wiping out all of the continental evidence of their predecessors. The amplitude of the 100 ky-year-cycles is greater for the last half of their dominance. Up until the advent of ocean core drilling in the mid-20th century, geologists had thus seen only the last three of these big excursions and knew nothing of the longer record.

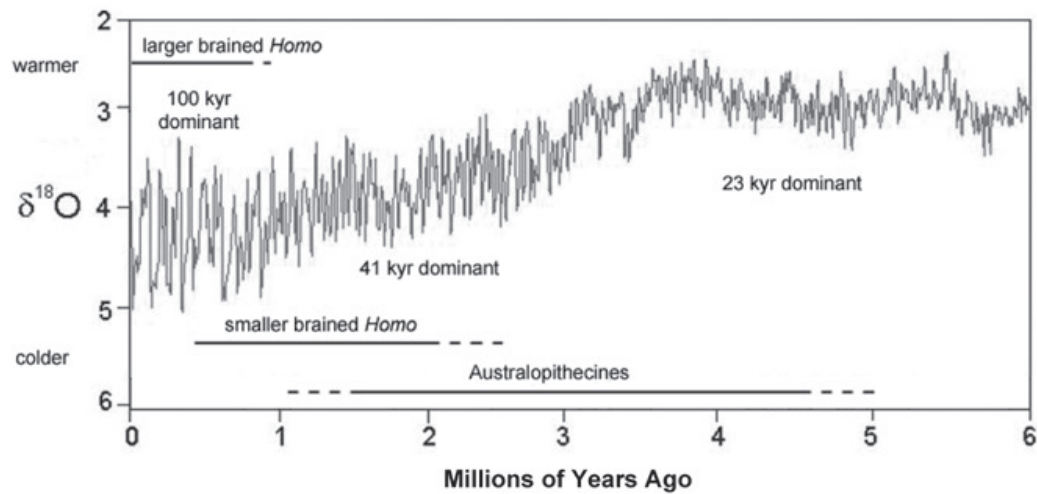
The low-frequency climate fluctuations are tuned to variations in the earth's orbit. The fluctuations that dominated the record in the late Miocene and early Pliocene (6–3 mya) have a period of around 20 ky and are tuned to the wobble of the earth's axis of rotation. The variation from the late Pliocene to the mid-Pleistocene (3–1 mya) was dominated by a 41 kyr cycle that is tuned to the variation of the inclination of the earth's axis of rotation. In the last half of the Pleistocene, the dominant mode of variation switched again, now to a 100 kyr cycle tuned to the variation in the earth's orbit from being more nearly circular to markedly elliptical.

The causes of this ongoing climate change were not the orbital parameters themselves, since these remain nearly constant for long periods of time. They also cause only relatively small redistributions in the amount of radiation from the sun as a function of latitude and season of the year. Rather, the earth's ocean-atmosphere-ice sheet system seems to have evolved to



11.2. The record of climate warmth over the last 69 million years based upon the ^{18}O isotope paleoclimate index. The envelope of gray points around the center trend line gives some idea of the increasing amplitude of variation about the trend. Other important events associated with climate change are indicated. The geological events include ones that caused reorganization of air and water flows that may have played a role in causing the climate change. Biotic changes are likely the evolutionary consequences of climate change. For example, as forests contracted because of increased aridity accompanying cooling at the end of the Eocene, archaic mammals were replaced by grazers adapted to more open country. The large carnivores that preyed upon the grazers also diversified. The Miocene expansion of the C4 aridity adapted grasses was probably a consequence of the spread of tropical savannas and temperate steppes. (Modified from Zachos et al. 2001. Reprinted with permission from AAAS.)

“tune in” different orbital frequencies and amplify them. Seafloor spreading has altered the positions of continents, closed seaways, raised mountain ranges, all having the effect of altering wind patterns and ocean currents.



11.3. A composite marine core record of climate deterioration since the mid-Miocene. During cold periods the oceans are enriched in the heavy ^{18}O isotope, a proxy for paleotemperature and ice volume. Periods during which different orbital quasi-cycles dominate the variation in $\delta^{18}\text{O}$ are indicated. The time lines for important groups of hominine taxa are indicated. Australopithecines include both gracile and robust forms from the early *Australopithecus ramidus* to the late *A. robustus*. The line for small-brained *Homo* includes *H. rudolfensis*, *erectus*, and *ergaster*. The line for large-brained *Homo* includes *H. heidelbergensis*, *neanderthalensis*, and *sapiens*. (Redrawn from Opdyke 1995; hominin time lines adapted from Klein 2009. See also deMenocal 2004.)

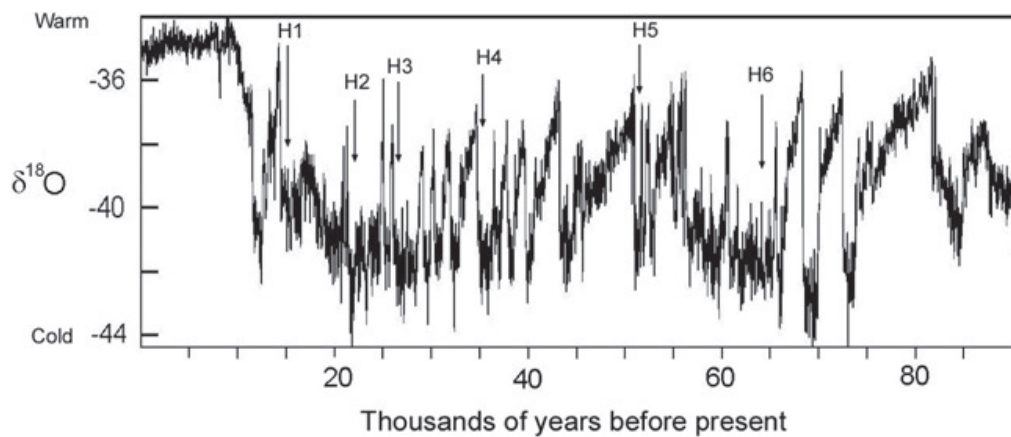
Ice particularly acts as a feedback mechanism. If cooling causes ice sheets to grow, their bright white surface reflects sunlight back to space, cooling the earth still further. No consensus yet exists on the exact mechanisms involved in the tuning process. The annotations on Figure 11.2 are a clue as to what is on paleoclimatologists' minds.

In the late 1980s and early 1990s two teams of paleoclimatologists, one mostly American (the Greenland Ice Sheet Project 2) and one primarily European (the Greenland Ice Core Project) drilled two 3 km long cores 20 miles apart through the middle of the Greenland Ice Cap (Alley 2000). These teams discovered that last-glacial climates varied sharply on quite short time scales (Fig. 11.4). The cores can resolve the seasons back more than 10 kya and the resolution at 80 kya is only a little more than a decade. Some of the changes in the ice core record are instantaneous within the limits of the record.

Events during the final episodes of warming at the end of the Pleistocene are well resolved in Greenland ice. For example, the Bølling transition

is the increase in temperature that produced the last high-amplitude spike before the final end of high amplitude millennial scale variation (just after H1 in Fig. 11.4). This sudden jump from rather cold conditions to interglacial warmth began about 14,650 years ago. The climate in Greenland seems to have warmed about 9°C in about 50 years (Severinghaus and Brook 1999). The most extreme event in the Holocene was a two-century-long cold snap about 8,500 years ago when Greenland cooled by about 2.8°C and Central Europe by about 1.7°C (von Grafenstein et al. 1998). This cold event was probably due to a pulse of meltwater from the remnants of the North American or European continental glaciers and can be seen as a sharp downward spike in Figure 11.4.

Exactly what process drove the high-frequency, high-amplitude variation during the last glacial is poorly understood. One of the main mechanisms thought to drive the millennial and submillennial scale variation in climate is variation in heat transport to high latitudes in the Northern Hemisphere by the so-called Atlantic Conveyor (Broecker and Denton 1989). The Atlantic Conveyor consists of the Gulf Stream and associated currents of warm, salty water that today flow north of Iceland. At these high latitudes, the



11.4. The Greenland ice paleotemperature proxy record. During periods of high ice volume ^{18}O is depleted in ice as it accumulates in the ocean. These data are filtered (averaged) using a 150-year low-pass filter so that variations on the time scale of 150 years and less are not portrayed. The Holocene is the little-varying last 11,000 years. The Heinrich events, when large volumes of ice-rafted debris from the North American Glacier were deposited in the western North Atlantic, are noted as H1-H6. (Redrafted after Ditlevsen, Svensmark, and Johnsen 1996 and Bond et al. 1993.)

warm water is cooled in winter by evaporation and conduction of heat to the cold air. It thus becomes sufficiently dense to sink in large volumes to form one of the two major sources of dense bottom water in the Holocene oceans (the other major source is Antarctic Bottom Water, formed in the Southern Ocean along the coast of Antarctica).

These deep-cycling currents are known as the earth's "thermohaline" circulation since the system is driven by temperature and salt effects on density, unlike shallow currents that are wind driven. The sinking of North Atlantic Bottom Water draws the warm water of the tropical and subtropical Atlantic poleward, warming the Northern Hemisphere at high latitudes, preventing continental glaciers from forming in North America and western Europe. During the ice ages, this circulation fails or is driven to lower latitudes, allowing the formation of northern continental glaciers.

One of the sources of instability in the thermohaline circulation is the discharge of fresh water into the North Atlantic. Fresh water is significantly less dense than salty ocean water. If the continental glaciers discharge large volumes of freshwater ice to the high North Atlantic, the conveyor will shut down or shift south. The striking fact is that the continental glaciers, particularly the North American one, discharged vast quantities of ice into the North Atlantic in spasms called Heinrich events (after the German oceanographer who first discovered them).

Icebergs calved from the glacier carried vast volumes of sand and pebbles that are recovered in ocean sediment cores and can be traced back to the geological formations over which the glacial parents of the icebergs traveled. Note in Figure 11.4 that much of the variation in the last glacial consists of warm peaks followed by relatively slow cooling punctuated by abrupt warming. Heinrich events are associated with the final part of the cooling in some of these "Bond cycles," followed within a few hundred years by an abrupt warming (Bond et al. 1993). Bundled within the Bond cycles are Dansgaard-Oeschger cycles, again named after the oceanographers who discovered them, with periods of about 1,000 years. Note that the variation is anything but a simple cycle; every Bond cycle has its unique features. Not all Bond cycles are associated with Heinrich events. A vivid picture of the difficulties of disentangling all the feedbacks that might be implicated in the generation of millennial and submillennial scale variation can be found in Broecker (1995).

Since higher latitudes are more affected by glacial variations in temperature than lower latitude regions, one might imagine that the latitudes rel-

evant to human evolution were little influenced by millennial and submillennial scale climate variation. This is clearly not the case. High-resolution lake and ocean cores have turned up considerable evidence that all latitudes were affected. At least in the Northern Hemisphere, the variation was driven by the same processes that affected the high Arctic. The Southern Hemisphere data are complex and controversial. The same sort of millennial and sub-millennial scale variation exists, but the peaks and troughs may not correspond to those in the Northern Hemisphere.

Some notable high-resolution data come from marine cores off the California coast (Hendy and Kennett 2000), the Arabian Sea (Schultz, von Rad, and Erlenkeuser 1998), the tropical Atlantic (Petersen et al. 2000), the South China Sea (Wang et al. 1999), and a lake core from Italy (Allen, Watts, and Huntley 2000). A lake core from Lake Tanganyika in the African Rift resolved some of the millennial and submillennial scale features seen in other cores (Stoltz et al. 2003). In the case of the California coast, the temperature variation between stadials (colder periods) and interstadials (warmer periods) in the last glacial was about 7° C, whereas during the entire Holocene variations have stayed within a 2° C envelope. So far, most of the high-resolution data available are restricted to the last glacial, but reasonably high resolution data for the last several glacial cycles are becoming available (Martrat et al. 2007, Loulergue et al. 2008). These records suggest that glacial epochs have highly variable climates and that interglacials have less, just as in the last glacial cycle. Larrasoña et al. (2003) report from a dust record from the Eastern Mediterranean that millennial scale variation increased sharply after the shift of the low frequency variation to dominance of the 100 ky cycle.

Much of the evolutionary trajectory toward modern humans transpired in the last 500 ky or so (Klein 2009, McBrearty and Brooks 2000). An extreme externalist hypothesis postulating short lags between selection and response to selection would require ongoing increases in environmental variability to drive ongoing human evolution between 500 kya and about 50 kya, by which time the paleoanthropological record indicates that humans were cognitively completely modern. The complexity of durable artifacts and the quality of artistic productions from the Upper Paleolithic in western Eurasia (the best-studied region) are on the same level as those collected from living hunter-gatherers.

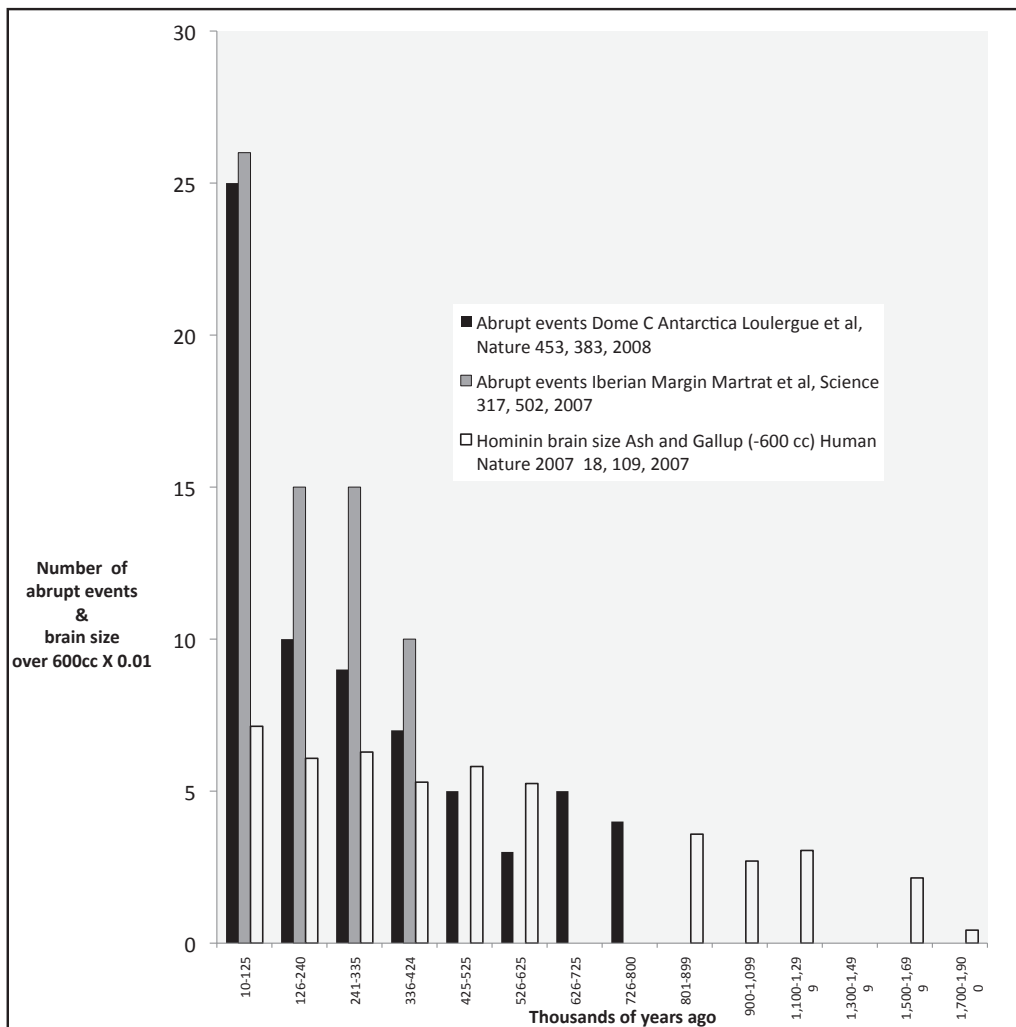
According to McBrearty and Brooks (2000), during the Middle Paleolithic period, brains got very large and our material culture began to add

fancier and fancier elements, culminating in the Upper Paleolithic of western Eurasia. Klein and Edgar (2002) propose a much more abrupt shift from the Middle to Upper Paleolithic cultures, perhaps deriving from a fortuitous mutation enabling symbolic behavior about 50 kya. Could this part of the human evolutionary story have been driven by ongoing increases in high-frequency environmental variation, or was the final modernization a result of internal limitations causing a lag in responses to climate change that occurred earlier, perhaps with the shift to the dominance of the 100 ky glacial cycle beginning about a million years ago?

We currently have two cores with relevant data. One core from the eastern Atlantic off Iberia offers a high-resolution glimpse of the last 420 ky (Martrat et al. 2007). The other is the EPICA Dome C ice core from Antarctica, which samples the last 800 ky (Loulergue et al. 2008). The last glacial cycle was considerably more variable than the second- and third-to-last. Martrat et al. (2007) count 25 stadial-interstadial sub-cycles in the last glacial cycle compared to 15 in the previous two. The earliest glacial cycle in their record counts only 10 sub-cycles. The stadial-interstadial cycles are especially tightly packed between 50 kya and 11 kya. Loulergue et al.'s (2008) core suggests a similar increase in abrupt millennial scale variation over the last 8 glacial-interglacial cycles (Fig. 11.5). This figure includes the data on human brain size increase in the same glacial-cycle time bins based on the data compiled by Ash and Gallup (2007). The fit between the increasing numbers of abrupt climate change events per glacial cycle and brain size increase is as good as one could expect of the so far limited and noisy data.

The big event in human history that occurred about 50 kya was the movement of AMH out of Africa to the rest of the Old World accompanied by the shift from less complex artifacts of the Middle Paleolithic to the more complex ones of the Later Stone Age/Upper Paleolithic. Importantly, *ephemeral* indications of sophisticated artifacts appear in Africa well before 50 kya (Jacobs et al. 2008) and Africa and eastern Eurasia apparently lacked tool traditions of Upper Paleolithic complexity until much after 50 kya (Richerson, Boyd, and Bettinger 2009).

Perhaps the abrupt evolutionary change that Klein and Edgar (2002) postulate was not so much a fortuitous internal event as evolution in response to the up-tempo beat of the Dansgaard-Oeschger cycles after 60 kya, as the two long high-resolution cores indicate. If McBrearty and Brooks (2000) are correct that the evolution of modern behavioral capacities was



11.5. Number of abrupt events per glacial cycle and human brain size increase. Gray bars: Sea-surface temperature in the Eastern Atlantic off Iberia (Martrat et al. 2007). Black bars: Atmospheric methane concentration estimated from bubbles trapped in the EPICA Dome C ice core from Antarctica (Louergue et al. 2008). Number of abrupt events indicated by original authors in both cases. Open bars: Human brain size increase above ape baseline of 600 cc. Sample sizes per time bin range from 2 to 27. A single outlier in the 726–800 bin not plotted (Ash and Gallup 2007).

stretched out over a longer period in Middle Paleolithic times, the shift from relatively few Dansgaard-Oeschger cycles in the fourth and fifth glacial to more in the second and third might explain a slower pattern of modernization, but one still driven by ongoing environmental deterioration.

We might also imagine that people were biologically, including cognitively, modern for some time before 50 kya, as indicated by brain size, and

that the emergence of Upper Paleolithic industries was more a cultural evolutionary than a genetic evolutionary response to the increase in Dansgaard-Oeschger cycles and also to the ecological peculiarities of western Eurasia (Richerson, Boyd, and Bettinger 2009). Perhaps the increasingly variable environment gave highly cultural AMH a decisive competitive advantage over Neandertals and other archaic hominin species living in temperate and colder Eurasian environments. Neandertals and AMH apparently coexisted in the Levant for tens of thousands of years. Perhaps because Neandertals were cold-adapted and AMH a tropical form, AMH remained restricted to what was essentially a subtropical African outpost in far southwestern Asia. Both species apparently made indistinguishable Middle Paleolithic/Mousterian tools during this period (Klein 2009). A highly variable environment might have tipped the competitive balance in favor of the more cultural AMH. Despite their tall lean body form better adapted to lose heat than to retain it, they could use tailored clothing and sophisticated shelters to mitigate this disadvantage while adapting better to variable environments.

The high-resolution paleoclimate evidence currently in hand is still quite sketchy, and the paleoanthropological record could always stand improvement. However, the existing record is certainly sufficient to make a tentative case that increased rapid environmental variation could have driven increased cultural capacities in humans, and increasingly sophisticated cultural systems based on those capacities, over the last few glacial cycles. If the increasing amplitude of the low-frequency climate record outlined in Figure 11.3 was also accompanied by increasing high-frequency variation, then the whole of human evolutionary history might have been driven rather closely by the increasing frequency and amplitude of Dansgaard-Oeschger cycles and higher frequency components of climate. Indeed, the theory illustrated by Figure 11.1 suggests that brain size might itself be a useful paleoclimate index that is sensitive to high-frequency climate change, and that the evolution of human culture in particular evolved in response to Dansgaard-Oeschger cycles and related high-frequency climate variation. The evolution of small-brained members of our own genus, *Homo*, from australopiths coincides roughly with the onset of glacial cycles at the 41 ky-time scale.

The first knapped stone tools also appear in the paleoanthropological record about this time, 2.6 mya. The evolution of larger brained and culturally more sophisticated *Homo* apparently began sometime around 500 kya, perhaps associated with the increase in amplitude of the 100 ky glacial

cycle. The bone record and the stone tool record—some index of cultural sophistication—do not match up perfectly. Such evidence as we have (e.g., Fig. 11.5) suggests a degree of independence of the Dansgaard-Oeschger cycles from the glacial cycle period. Clearly, we have much more to learn.

One interesting puzzle is what happens during interglacials. In the cores just reviewed, the last interglacial had long periods of modestly variable environments. If humans are especially adapted to highly variable environments, our hypothesis suggests that interglacials should disfavor humans. In the present interglacial, humans have invented agriculture and become the earth's dominant organism (Richerson, Boyd, and Bettinger 2001), a result contrary to this hypothesis. On the other hand, previous interglacials saw no conspicuous human florescence. Human populations presumably responded to the glacial-interglacial cycle, but these responses are so far unresolved by paleoanthropologists.

RECONSTRUCTING PALEOECOLOGY

Paleoclimate reconstructions are only half the battle in reconstructing the environments and environmental variation that might have affected human evolution. Both the Neandertals and AMH of the last 250 ky appear to have based their subsistence on hunting large mammals, although the Upper Paleolithic people had access to a suite of difficult-to-catch small game that Middle Paleolithic people could not exploit (Stiner et al. 1999). Upper Paleolithic AMH differed from some latest Pleistocene and many Holocene people in that apparently nowhere did they make heavy use of plant resources (Richerson, Boyd, and Bettinger 2001). The transition to the Holocene ushered in climates that were warmer, wetter, and much less variable, and which had higher carbon dioxide concentrations. Such climates apparently favored a higher reliance on plant resources in many parts of the world and the intensification of the use of plant resources led to agriculture in many areas, which in turn spread slowly over the Holocene to most parts of the world (Richerson, Boyd, and Bettinger 2001). Because the climates of the Holocene are so different from the Pleistocene glacial episodes, ethnographically known hunter-gatherers are imperfect models of Pleistocene peoples (Bettinger 2001).

The glacial climatic regimes supported very different plant and animal communities in the last glacial compared to the Holocene (Graham and

Lundelius 1984, Guthrie 1984). Last glacial communities were structured by different forces from those in the Holocene and have no precise analogs in the ecosystems we know from the present. This is so even though the species involved are mostly the same. The difference is in the way species were arranged on the landscape.

Jackson and Williams (2004) review the methods and some of the most significant findings regarding Pleistocene plant communities. Graham et al. (1996) provide a similar review focused on mammals. Both plants and mammals exhibit what were originally termed “disharmonious distributions.” In particular, species that today occur in different *biomes* (sub-continental scale biogeographic units) lived in the same biomes in the Pleistocene. In North America, for example, conifers that today live in boreal forests mainly in Canada coexisted with deciduous forest species that today live mainly south of the Canadian border. Animal distributions were similar. As Guthrie (1984) put it, the pattern of the last glacial world was “plaid,” while that of the Holocene is “stripes.” In the plaid world local diversity was higher, whereas in the stripes world of today species are restricted to their “own” biome, and local community diversity is lower. In the 1980s, paleoecologists attempted to explain disharmonious distributions in terms of less seasonality or less environmental variability of other kinds, allowing local diversity to build up by fine-tuning interactions among species. Since the discovery of millennial and submillennial scale climate variation, explanations have shifted to the hypothesis that plaid distributions reflect out-of-equilibrium conditions.

Allen and Huntley (2000) provide a comparison of the unusual pollen record from Lago Grande di Monticchio in southern Italy with other western European records. The Monticchio record exhibits the pattern of millennial and submillennial climate variation seen in Figures 11.3, 11.4, and 11.5, but the short stadials and interstadials are not reflected in most pollen records. Allen and Huntley argue that Monticchio was near the local forest-grassland community boundary during the last glacial and that the rugged topography surrounding the lake meant that refuge populations of many species existed locally. Hence the pollen rain into the lake could reflect short time scale increases in population density of many species. In other records, long-range dispersal would be required for species favored at any one instant to be reflected in the pollen rain. Coope (1979) showed that fossil beetles whose diets are not tied to specific plants provide a much more sensitive climate indicator than plants normally do. The beetles disperse by

flight more rapidly than the plants can manage by more passive means and thus reflect more ephemeral environmental events. Pollen flora normally average over ecological variation that was probably quite relevant to the lives of Pleistocene humans.

The picture that emerges is that the plant and animal communities of last-glacial times were often far out of equilibrium with the climate of the moment. Ranges were expanding or contracting. Ill-adapted species might persist for a bit because they faced no effective competition from better-adapted species that had yet to expand their range into a given location. Woody species might persist for long periods of time in relic stands, diversifying the environment for animals. Ecologists have long suspected that temporal heterogeneity can drive up species diversity. A recent review of this phenomenon suggests that environmental variability can feed variance into chaotic mechanisms that tend to generate endogenous variation even in stable environments (Scheffer et al. 2003). Models of multi-species predator-prey systems suggest that ecological dynamics are often chaotic. Thus, ice age ecosystems were probably highly and unpredictably dynamic. Such environments would have imposed novel constraints on hunter-gatherer adaptations.

Elsewhere we argue that such environments are not conducive to intensive use of plant resources because a focus on plants implies dietary and processing specializations that require thousands of years to perfect; a span of time far longer than any plant assemblage would persist in a last-glacial plaid world (Richerson, Boyd, and Bettinger 2001). Consistent with this notion, Middle and Upper Paleolithic people seem to have been big game specialists, although Upper Paleolithic peoples were certainly skilled at taking small game and fish and would have no doubt used high quality plant resources, such as fruits and nuts, when available. Perhaps even relatively low quality plant resources would have been used when unusually abundant or during times of shortages of better resources (Kislev, Nadel, and Carmi 1992).

Poor quality plant resources, such as grass seeds, can be harvested and made palatable using generalized technologies such as beating ripe seeds into a basket and parching the seeds by tossing them on a tray with live coals (popcorn is a parched-seed product). Holocene peoples used more specialized techniques to acquire large quantities of seeds (agriculture in many cases) and preparation techniques that increase the nutrients our short gut can absorb from low-quality plant resources (typically, fine grinding and

thorough cooking). Evidence for heavy use of these specialized techniques is restricted to the Holocene.

Aside from the *variability* of ice age environments, their *productivity* is also important to understanding Pleistocene hunter-gatherer adaptations. Because ice age environments were on average drier and colder, and had lower carbon dioxide concentrations, than interglacial ones, terrestrial plant productivity must on average have been lower. Indeed, carbon isotope ratio data suggest that this was the case (Beerling 1999).

The data on plant productivity are, however, misleading. The most productive plant communities are closed canopy forests. But forest leaves are held well off the ground and are often defended from browsing by mechanical or chemical means. Hence, forests are much like deserts in terms of the production of animal biomass, particularly large herbivore biomass. By contrast open forests support large browsers like mastodons. Moist grasslands can have almost as high plant production as forests, but the above-ground biomass is all within reach of grazers, making these ecosystems the highest producers of large herbivore biomass. Colder tundra-type vegetation and drier steppe grasslands and shrublands support significant large herbivore biomass despite low plant productivity because what vegetation exists is subject to grazing and browsing.

Thus, in the deserts and arid shrublands of the American West, cattle and sheep ranching are major industries and feral donkeys and horses are abundant enough to be considered pests. Based mainly on the abundance of grazing herbivore fossils, Guthrie (2001) proposed that northern Eurasia was covered by what he called the “Mammoth Steppe” Biome during glacial periods. He reasoned that even when mean temperatures were much like tundra and boreal forest today, the climates were actually much different than these Holocene biomes. Mainly, they were more arid and hence sunnier. They were also at lower latitudes, leading to a longer and warmer summer growing season. Floristically, they were dominated by grasses, sedges, and low shrubs in the sage family. Incidentally, these dominants produce pollen that is not diagnostic at the species level, and they are very diverse groups with species adapted to a very wide variety of habitats. Hence palynology is of relatively little help in reconstructing them. The animal fossil record, dominated by woolly mammoth, horses, and bison, is abundant, consistent with considerably higher herbivore production than would be the case for modern tundra.

Huntley and Allen (2003) make a similar but more general point. Ice age cold and low carbon dioxide concentrations would limit trees more than low growing plants. Ground hugging vegetation benefits from heating of the boundary layer next to the ground even when the air above is cold and soil respiration during the growing season would increase CO₂ in the same microhabitat. Hence, the ice age plaid environment would tend to have many patches with low vegetation of perhaps moderate productivity but very exposed to grazing. At temperate and tropical latitudes, large areas may have been very dry Sahara-like deserts at some points in time. Hyper-arid deserts that sustain little or no human life seem often to be punctuated by wetter “pluvials” with ample surface water and productive grasslands and even forest. Kusimba (1999) gives a scenario for such climate and ecosystem variation in East Africa during Late Stone Age times.

Huntley and Allen (2003) attempted to model the impact of climate on vegetation in last glacial Europe. One might hope to use climate reconstructions to drive a regional climate simulation for Europe and then to reconstruct the vegetation living under the climate. This proved impossible to do as the simulated climates during the example stadial used were not cold enough to account for the floras implied by the palynology. They do provide a reconstruction based on the pollen data.

The pollen data indicate that closed canopy forests were of limited distribution in both warm and cold events. They infer that warm events favored more moisture-adapted plants and the cold events more area with plants adapted to arid conditions. Hence plant productivity was higher during warm events and, given that forest expansion was modest, herbivore productivity was probably higher as well. Of course, these reconstructions are quite limited in area. For most of Asia and Africa, even this crude synthetic picture of vegetation dynamics is not yet possible. Clearly, even in the best-studied corner of the world, a high-resolution picture of large herbivore productivity variation in time and space is well beyond our current understanding.

IMPLICATIONS FOR HUMAN EVOLUTION

The Pleistocene Epoch was very different from the Holocene. At least during the glacial phases of the last few glacial-interglacial cycles, high-amplitude millennial and submillennial scale variation was much greater than during the Holocene. Our picture of how this variation evolved is still

quite incomplete. It may have become progressively more intense over the last million years. It may have become especially intense in the last glacial, especially after 50 kya when African AMH began to replace more archaic forms like Neandertals in Eurasia. It is potentially correlated with the well-resolved low-frequency orbital scale (Milankovich) variation, which became more intense in three steps dating back approximately 500 kya, 1 mya, and 2.6 mya. The main events of human evolution map onto these events reasonably well. Theoretical models of cultural evolution suggest that culture is adaptation to millennial and sub-millennial scale variation. Two long, high-resolution cores support the hypothesis that increasing climate variation drove the evolution of our brain size right into the last glacial. Decisive tests of the extreme externalist hypothesis will be forthcoming as our understanding of past environmental variation improves.

Paleoecological reconstruction is best developed for Europe for the last glacial cycle, although even there it is much sketchier than we would like. “Disharmonious distributions” with high local diversity suggest that ice age Mammoth Steppe Biomes in northern Eurasia were radically different from those of the Holocene. Closed canopy forest was much reduced and grassy, open biomes dominated most of the area. These open biomes differed greatly in composition under the influence of gradients of temperature and aridity. They were very likely composed of highly dynamic out-of-equilibrium communities whose intrinsic tendency to chaotic variation was pumped by climate variation on time scales too short for range adjustments to lead to Holocene type biomes that are closer to equilibrium.

On the other hand, such open environments, except the very coldest and driest, had medium to very high herbivore productivity. Such sketchy data as are available from lower latitudes also suggest very dynamic ecosystems, a reduction in forest cover, and an expansion of arid grasslands and deserts.

The highly dynamic, but more productive, glacial environments would present three adaptive challenges for big-herbivore hunters. The first would be the ability to take large herbivores on a routine basis. This problem was solved in Middle Paleolithic (MP) times by Mousterian toolmakers. The second would be to cope with the uncertainty of a very noisy environment. Food security on time scales ranging from weeks to years would likely have been more severe than for most ethnographically known hunter-gatherers. Upper Paleolithic/Late Stone Age (UP/LSA) populations were evidently

much higher in Europe and Southwest Asia than were the preceding Middle Paleolithic (MP) populations faced with the same suites of game. UP/LSA people must have found solutions to the food security problem that escaped MP people. Social systems for risk reduction are one candidate for such adaptations in accord with evidence for social complexity at least among some UP 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 very small populations they may be lost by chance. The famous case is the Tasmanians, whose toolkit simplified after they were cut off from Australia by rising sea level (Henrich 2004; see also Shennan 2001, Powell, Shennan, and Thomas 2009, Kline and Boyd 2010).

The population on Tasmania at contact times numbered a few thousand. The much more complex mainland toolkit was maintained by a population at contact times of a few hundred thousand. O'Connell and Allen (2007) review evidence that AMH in Australia during the Pleistocene lived at very low population densities and maintained MP style stone tools. (See also Brumm and Moore 2005.) AMH populations in Africa and Southwest Asia also made MP tools for tens of thousands of years leading up to the UP/LSA. The same seems true of South Asia (James and Petraglia 2005) even though the absolute population of southern Asians seems to have been larger than elsewhere after 50 kya (Atkinson, Gray, and Drummond 2008).

On some accounts, more and less complex industries, all made by AMH, coexisted in Africa for several tens of thousands of years (McBrearty and Brooks 2000). Some good evidence suggests that more sophisticated tools were made during brief episodes in Africa (Jacobs et al. 2008). (But equally qualified commentators see a much more abrupt transition from MP to UP/LSA artifacts [Klein 2009].) An artifact assemblage resembling that of the west Eurasian UP does not occur in Australia until the mid Holocene, although we have no reason to think that Australian people were in any way primitive biologically. Some authors interpret the early UP Châtelperronian industry to be a product of diffusion from AMH to Neandertals but some good evidence suggests it to be an indigenous product of Neandertal invention (Zilhão et al. 2010). Perhaps toolkit complexity waxed and waned with

the demographic fortunes of populations subject to highly variable conditions and cannot be interpreted uncritically as indicating the raw cognitive sophistication of the toolkit makers.

Populations so small that they lose complex tools would also have a less responsive cultural evolutionary system. Perhaps over a wide range of herbivore productivities, human population densities were bistable. A high population density equilibrium would generate a fancy technology and rapid evolutionary response to millennial and submillennial scale variation. Hence it could maintain high population density. A small population in the same conditions would have a simple toolkit 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 while an especially poor one would reduce a complex population to simplicity. Perhaps in good times in good places AMH (and Neandertals?) could achieve population sizes adequate to sustain more complex toolkits whereas in poorer times and places they could only sustain simpler technologies.

If environments remained poor enough long enough, a population that had achieved UP complexity might suffer a Tasmanian style loss of complexity and drop back to the MP 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 change, it will jump to the other equilibrium where it will again persist under environmental conditions where the other equilibrium could be sustained but cannot be attained. This would explain the coexistence of technologies with a LSA cast with those of a MP appearance in Africa during much of the last glacial. AMH appeared in Africa between 200 and 160 kya (White et al. 2003, McDougall, Brown, and Fleagle 2005), long before fully modern suites of artifacts were produced for sustained periods of time.


The ability of AMH to displace (or assimilate; Green et al. 2010) archaic hominin species like the Neandertals may have depended less upon differences in innate abilities and more upon 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 MP equilibrium. Human populations could well have imposed their own chaotic dynamics on ice age systems.

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 australopiths to the UP. Slight increases are evident at each major change of taxa with one major exception. UP people had an old/young adult ratio of about 2.1, while the European Neandertals had a ratio of only 0.35. In Southwest Asia, where Neandertals and AMH coexisted using Mousterian technology, the small dental sample suggests that both populations had an old/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 individually acquired knowledge. Culturally more sophisticated societies can support larger populations which will also tend to conserve a more sophisticated cultural repertoire. Caspari and Lee's analysis lends weight to the idea that large-brained hominins of the late Pleistocene had bistable population dynamics.

LARGE-SCALE "ORDERLY ANARCHY"?

The Upper Paleolithic of western Eurasia is theoretically important because the artifacts these people made, such as their famous ivory carvings, cave paintings, and sophisticated stone, bone, and ivory tools, suggest that they were innately essentially identical to ourselves, especially as regards their intelligence and other cognitive attributes. This was the final set of Environments of Evolutionary Adaptedness that shaped human nature, save only whatever fine tuning occurred in the Holocene. Of course, western Eurasia was not the set of environments in which modern behavior arose; that happened in Africa or possibly an African outpost in the Levant. However western and northern Eurasia still have the best archaeological data and hence furnish us with the best picture of what UP/LSA people were capable of. Klein (2009) provides a very useful summary of the available paleoanthropology. In triangulating on the sorts of social systems that might have evolved in the latest Pleistocene, culminating in the evolution of modern artifact kits that characterized the people that spread out of Africa, one useful exercise is to reflect upon the demands a highly variable climate might have made upon social organization. The very different environments of the Pleistocene compared to the Holocene, and the fact that the late Holocene hunter-gatherers were almost all highly specialized in

one way or another, means that UP peoples likely lay outside of the envelope of ethnographically known societies. We here attempt to guess in what direction UP peoples might have departed from the ethnographically known sample.

The reader is warned that attempts to guess the social organization of Pleistocene peoples from the archaeological record is a rather speculative enterprise. Social organization leaves few and ambiguous traces. Other scholars have reached very different conclusions from those argued here. For example, Owens and Hayden (B. Hayden, pers. comm. 1997) compared  UP cave art, and its possible use in rituals involving adolescents, with similar practices among ethnographically known hunter-gatherers. They concluded that UP societies were “transegalitarian.” By this they meant that UP societies were fairly complex politically and had entrepreneurial leaders with higher status than ordinary members of society. Among other things, this analogy requires that UP societies were sufficiently sedentary to accumulate material surpluses that leaders used in competition for status. Their ethnographic analogs are people like the Northwest Coast salmon fishing people that lived in permanent plank-house villages of some size.

We argue below that highly variable climates would have prevented UP people from being sedentary, though they may have been politically complex despite being mobile. In general, we think that analogies between UP and Holocene hunter-gatherers are fraught because last glacial environments were dramatically different from those of the Holocene. Given that the environments of the last glacial were far outside the envelope of Holocene environments, we imagine that social adaptations were likewise probably outside the ethnographic envelope. For other notable attempts to reconstruct UP lifeways see Gamble (1999) and Boehm (2012).

Highly dynamic but locally diverse, disharmonious environments would, in principle, mean that small groups could find a favorable bit of mosaic and settle down and defend it, secure that the variety of resources available in a small area would support a band-sized unit with reasonable security. People using such a strategy might have to have been prepared to move fairly frequently as the mosaic shifted, but perhaps patches would tend to remain more or less the same for a few years or a few generations. Perhaps that is what Neandertals and other makers of MP tools did. They may have chased niches where big game and vulnerable small game were locally unusually abundant as such niches shifted across the landscape.

Studies of the movement of raw materials found in particular camps suggest that either MP people moved little and/or traded little compared to UP people in the same environments. In very arid or otherwise spare environments, such as Australia, AMH at very low densities with small, widely separated bands exploiting unusually favorable environments would have been restricted to toolkits of only MP complexity due to the Tasmanian Effect.

The big game that made up the bulk of the herbivore biomass in the size ranges preferred by humans—antelope, red deer, caribou, bison, and horses—were likely very mobile in the last ice age. Certainly the living versions of these species move on a large scale. These animals were probably moving about the landscape to exploit favorable grazing opportunities, avoid humans and other predators, and escape extreme weather. UP people apparently hunted them more effectively than MP people, in part probably because the UP people had access to a broader variety of fall-back resources than MP people (Stiner, Munro, and Surovell 2000). Compared to Neandertals and other Mousterians, UP people could rely on local sedentary resources if their luck failed while they pursued high-risk but high-mean-return migratory big game. Gamble et al. (2004) argue that a difference like this led to a decisive competitive advantage of AMH people over Neandertals in Europe after about 45 kyrs ago. If it proves true that Neandertals were also capable of UP technology and if the evidence for Neandertal genes in Eurasian AMH populations is confirmed, a more complex story of the end of the Neandertals will have to be told.


A possible picture of the UP people at relatively high population densities in western Eurasia is that they were something like the American Great Basin Shoshone (Murphy and Murphy 1986), but with larger bands focused on big game hunting. The Shoshone exploited plant and animal resources in their temperate desert environment, mainly traveling in small independent family groups. The Shoshone did aggregate into multifamily camps in the winter, where they conducted cooperative activities such as rabbit drives, antelope hunts, and ceremonial activities. On the northern edge of their range, they violently contested access to the bison herds with the Blackfeet and their allies. Early accounts state that sometimes as many as 200 warriors were massed for such fights. Leadership for cooperative activities was *ad hoc*.

Because of the simplicity of the Shoshone social system, it is sometimes taken as representing the ancestral state of AMH (Steward 1955). However,

Murphy and Murphy (1986) stress that this system was sophisticated as much as simple. Lone families, often with a store of food that took hundreds of hours to produce, would have been easy prey for larger bands that might want to rob them. Family mobility, and the lack of strong systems of extended kinship often so important in hunter gatherer social structure, meant that winter encampments might contain many strangers. Murphy and Murphy analogize Shoshone life to a modern nation in the sense that highly mobile citizens of these states can move freely within the borders of the state and attach themselves to open task groups wherever they pitch up. To do so required institutions that, among other things, recognized that people had rights to what they produced. Interestingly, the Northern Shoshone were allied with the Bannock, speakers of a mutually unintelligible language. It speaks to the political sophistication of these peoples that they could have an alliance with the Bannock while having a hereditary conflict with the Blackfoot. Yet they had no formal leadership or decision-making institutions.

The Shoshone cannot be considered a direct analogy to UP people, much less a homology. Bettinger (2001) points out that the Shoshone, like most ethnographically known hunter-gatherers, are late Holocene people with a high dependence on plant resources compared to Pleistocene analogs, and even their immediate Holocene predecessors in the Great Basin. But the variable environments faced by the Shoshone and their consequent flexibility and opportunism might have some parallels with UP peoples. Shoshonean family bands would have been too small to deal efficiently with big game, so probably kinship- and friendship-based bands built around 5–10 skilled hunters would have been the basic social units of UP people (Hill et al. 2011). The ethnographic sample of big game hunters is dominated by bands of this sort. Hunting with spear throwers requires a collective team of about this size to be effective and a fair number of people are required to eat up a large game carcass before it spoils (Bettinger 2009). In an emergency these basic bands could fission further to exploit small game and plants. In the case of big windfalls or an opportunity to conduct large-scale drive hunts, several bands might aggregate either to exploit the concentrated resource more effectively or to use a windfall to subsidize collective social activities.

The UP focus on big game as a primary target is a little like the late horse-mounted hunters of bison on the American Plains. The mounted bison hunters moved mainly as modest-sized bands much as we infer for UP people, but were prone to fission into family foraging groups at lean times

of year and to aggregate opportunistically when large herds were located (Oliver 1962). ~~(Oliver 1962)~~. Interestingly, a group of Shoshone, famously  known as the Comanche, very successfully adapted to mounted hunting with minimal changes in their ancestral Shoshone social institutions (Hämäläinen 2008). The UP people were pedestrian, limiting their ability to locate and pursue wide-ranging migratory herds. On the other hand, they enjoyed a quite diverse fauna rather than specializing in one major species. A “plaid” Pleistocene world would likely have sustained a diversity of game with diverse aggregation sizes, whereas a “striped” world would tend to larger, unispecific aggregations. Foot mobility might have sufficed to exploit the sort of ephemeral aggregations existing in a plaid environment. Also a plaid environment with broken woodlands and brushlands in the mosaic would provide the cover needed to deploy ambush tactics based on teams of men using spearthrowers. Excavated UP middens often have a heavily disproportionate representation of the bones of a single species as if UP people often focused on a migration choke-point or other situations where they could harvest game windfalls. Stiner, Munro, and Surovell’s (2000) point that UP hunters could take small fleet game using clever tricks probably also implies that they used clever strategies to take large game, for example, using drives and pounds.

Ice age peoples using both MP and UP/LSA technology must have faced severe problems of food security in a dynamic, unpredictable environment. Most likely, MP people could only hope to exploit the less risky of these environments, while UP people likely used intrinsically riskier strategies. For example, UP people pushed further north and east in Eastern Europe and Siberia than Neandertals, eventually reaching North America as the climate warmed at the end of the Pleistocene (Klein 2009: chap. 7; Hoffecker and Elias 2007). The cooperative big game hunting adaptation in ethnographic food foragers relies upon social institutions for risk pooling to mitigate risks of food shortfalls (Winterhalder 1986, Hawkes, O’Connell, and Blurton Jones 2001, Wiessner 2002). If we are correct that climate variability fed through ecosystem processes to create high variation in subsistence resources, UP peoples at population densities necessary to evade the Tasmanian Effect must have had more sophisticated risk management institutions than perhaps any ethnographically known foragers.

One of the interesting features of Shoshone social institutions according to Murphy and Murphy (1986) is that the constituent family bands could

move about opportunistically on the landscape with reasonable confidence that they were safe from violence by other Shoshone and Shoshone allies and confident that any resources they produced would not be expropriated by a stronger band. R.L. Bettinger (pers. comm.) has termed this sort of social organization “orderly anarchy” because, in the hunter-gatherer case, it is managed by social institutions other than those of formal leadership. In ethnographic California, orderly anarchy facilitated trade and made armed conflict infrequent at population densities that elsewhere exhibited intense conflict and a tendency for hierarchical political office to arise. Orderly anarchy is a theoretically neglected form for managing social complexity, despite its high profile as a component of modern mobile societies (Putnam, Leonardi, and Nanetti 1993, Ostrom 1990). Imagine the Shoshone with larger constituent bands and perhaps more elaborate social institutions for organizing expedient cooperation in multi-band aggregations.

If large concentrations of game were found, several bands might be recruited for a pound or drive or just for a celebration to help a band eat up a windfall. Young men can run formidable distances carrying messages. If an ever-shifting collection of bands kept in touch with each other in an organized way, the steppe telegraph could probably support a sophisticated fission-fusion system that efficiently found concentrations of big game, assembled the bands needed to exploit them fully, and fissioned to again seek new concentrations of big game, all insured by an ability to exploit small game and plants as necessary, and to receive help from successful bands if a band’s subsistence luck failed. Marshack (1971) argued that abstract ladder-like designs inscribed on bone plaques were calendrical devices. Although this suggestion is controversial, we might imagine that bands planned meetings by one means or another.

Some aspects of the paleoanthropological record are consistent with the complexity via orderly anarchy reconstruction. The main named traditions of western and northern Eurasia, the Aurignacian and Gravettian, are very widely distributed in time and space compared to the scale of named archaeological traditions and ethnographically known social systems in the Holocene (van Andel, Davies, and Weninger 2003). These cultural phenomena, marked by both symbolic artifacts like the famous Gravettian “Venus” figurines and utilitarian ones such as Aurignacian split base antler points, are distributed from the Urals to the Atlantic and from the Mediterranean to the highest latitudes from which occupations have been recorded (White

2006). In time, these phenomena last for 10 ky or more. Interestingly, the last glacial record of northwest China does not show any of the distinctive markers of the west Eurasian record (Brantingham et al. 2001). However, Upper Paleolithic people did leave a record even farther north in Baikalian Siberia (Hoffecker and Elias 2007). The west Eurasians were perhaps one ethnic group that met other ethnic groups only somewhere in central Eurasia, making the UP transition the original European Union.

Aside from providing scope for operating a highly opportunistic fission-fusion resource acquisition strategy, common ethnicity over a wide area would increase the effective population size for the acquisition and conservation of culture against the Tasmanian Effect. Bocquet-Appel et al. (2005) estimate Upper Paleolithic populations for all of Europe to be in the range of only a few tens of thousands of people. Maintaining the complexity of the UP toolkit with such small populations perhaps required UP Europe to be one society to boost effective population size up to the numbers necessary to support that sophistication (Powell, Shennan, and Thomas 2009).

Indeed, the Upper Paleolithic of western and northern Eurasia looks on present evidence to be unique. Perhaps the combination of a large area of productive Mammoth Steppe with a considerable area of maritime climates in the far west supported uniquely dense human populations in this region. In times of warmer climates at least, UP peoples could spread into areas such as the Levant that might have been too dry in colder times to sustain significant populations, and far to the north and east where stadials might have been too cold to permit human occupation. Hoffecker and Elias (2007) argue that a lack of fuelwood would have limited human expansion into northeastern Siberia and Beringia during the colder episodes of the late Pleistocene. Perhaps the sustained sophistication of the west Eurasian UP existed because the eastern part of the Mammoth Steppe Biome acted as a protected area that prevented sophisticated hunters from causing the collapse of exploited species (Richerson, Boyd, and Bettinger 2009).

The Later Stone Age peoples of Africa may prove to have cultures as complex as the Upper Paleolithic (Henshilwood et al. 2003), but on current evidence many diagnostic UP features are episodic in the African late Pleistocene.

Perhaps the analog of the maritime west Eurasian center of cultural complexity in Africa was in equatorial western Africa, an area now covered by tropical forest (Dupont et al. 2000). Southeast Asia might harbor a simi-

lar phenomenon as biome reconstructions there also suggest widespread grasslands and dry forests in regions now characterized by wet tropical forests (Hope et al. 2004). These regions have few archaeological sites, perhaps due in part to difficult and hence inadequate exploration. Recent evidence from East Kalimantan (Borneo) suggests that Pleistocene peoples made cave art there (Chazine 2005).

Paleolithic art may contain some information about the social organization of its producers. For example, Owens and Hayden (1997) argue, based on ethnographic analogies, that painted caves were the sites of initiation rites of juveniles into the secret societies of social stratified “transegalitarian” societies. Similarly, Lewis-Williams (2002) uses ethnographic analogies to argue that cave art records the experiences of shamans in altered states of consciousness. Barton, Clark, and Cohen (1994) argue that cave art was produced to symbolically mark group territories during climate downturns when competition for territory became acute in the mild western refuges of UP peoples. However, this interpretation is hardly consistent with the apparent stylistic unity of the Aurignacian and Gravettian traditions noted above. Other students of Paleolithic art are much more skeptical of extracting social information from these productions (Conkey et al. 1997, Bahn and Vertut 1997, Nowell 2006).

Dale Guthrie, the paleontologist who invented the concept of the Mammoth Steppe, is the latest person to attempt a comprehensive analysis of Paleolithic art (2005). Aside from a detailed knowledge of the animals depicted by UP artists, Guthrie is an artist and big game hunter by avocation. He conducted allometric studies of human hands in order to interpret hand and foot prints associated with art in caves. He argues that much UP Pleistocene art, especially the relatively crude pieces, was made by adolescent boys. Many of the hand stencils in caves are the size and shape of those of adolescent males. On Guthrie’s interpretations, many of the images are of testosterone-charged themes including naked or provocatively adorned women, crudely rendered vulvas, and big game animals, often big game fatally struck by projectiles and coughing up blood.

Remarkably, no scenes of warfare are present in the rather large corpus of UP art Guthrie reviews, although such scenes are not uncommon in Holocene hunter-gatherer rock art and in the drawings of modern adolescents. Drawings of men carrying shields are also absent from the UP record but are present in Holocene rock art. Warfare is all but universally present

among Holocene hunter-gatherers (Otterbein 1985) and shields or parry sticks are very common warriors' gear.

The duration of the Aurignacian and Gravettian traditions in time suggests that the pressure for the generation of stylistic variation was comparatively weak. Guthrie argues that the UP art was dominated by highly naturalistic images (though often crudely rendered images when produced by inexpert juveniles) that incorporate little if any arbitrary stylistic variation. Across the whole UP, art has been impossible to periodize for this reason. This is utterly different from the Holocene where point styles, pottery decoration, and the like are used as time markers on a quite fine scale. The use of symbols to mark group differences leads to distinctive differences in art styles while stylistic similarity and syncretism signal the unity or union of groups (Logan and Schmittou 1998). In Guthrie's interpretation, in striking contrast to that of Lewis-Williams, little if any UP art expresses supernatural themes, and supernatural belief systems typically code symbolic markers of group identity. Since stylistic variation in the Holocene often marks the boundaries between competing social systems, the apparent fact that art was used as a form of personal expression in the UP, but not in its common Holocene function of group badging (Wiessner 1984), suggests that the social organization of UP peoples was strikingly different from those of Holocene hunter-gatherers.

CONCLUSION

The paleoclimatological and paleoecological evidence suggests that Pleistocene people faced very different challenges than did Holocene hunter-gatherers, especially the late, specialized hunter-gatherers of the ethnographic sample. The paleoanthropological and archaeological evidence says much the same thing. Unfortunately, neither body of evidence is sufficient to nail a description (or descriptions) of Paleolithic social life.

We can see fairly clearly that Middle Paleolithic and Upper Paleolithic social systems were quite different. Population densities seem to have increased across the MP/UP transition and raw materials began to be moved impressive distances by UP peoples. Whether the institutions involved in the change took the form of orderly anarchy, transegalitarian leadership and stratification, and/or other social innovations is difficult to verify. Given that ice age climates and biotic environments were clearly outside the en-

velope of Holocene ones, simple parallels to well-described ethnographic cases are unlikely to be correct.

The puzzle that the stones and the bones of the paleoanthropological record are so weakly correlated illustrates the basic problems of deciphering Late Pleistocene lifeways. Since AMH participated in both MP and UP technologies, a case can be made that cultural differences, driven by something like our bistable population hypothesis or directly by environmental productivity, rather than genes were responsible for the complex interdigitation of MP and UP lifeways. That the Châtelperronian industry, with clear UP elements, might have been made by Neandertals suggests that Neandertals could at least acquire UP traits by diffusion from AMH (Klein 2009:592).

On the other hand, a late, anatomically cryptic modernization of human cognition, perhaps even by a single mutation, might explain the UP “revolution” (Klein [2003a] does not accept that African industries, which seem to some paleoanthropologists to be approaching the UP in complexity, are actually materially different from MP industries). A simple externalist hypothesis invoking genetic evolution is that the onset of high-frequency Dansgaard-Oeschger climate variation after 70 kya favored parallel increases in the innate capacity for culture in both Neandertals and AMH.

One possible picture that seems to be consistent with much of the data is that people could exploit variable Pleistocene environments at low population densities using necessarily simple social and technical strategies by seeking the most stable and most productive environments available. This was perhaps the MP strategy that even quite late AMH used in poor environments. The best-studied case of AMH using MP-level artifacts for prolonged periods is Australia. Alternatively, in environments with high mean herbivore productivity, AMH, and perhaps Neandertals as well, could exploit riskier big game resources using better technology and fancier social organization to increase game take and mitigate risk. Both strategies are potentially self-reinforcing via the Tasmanian effect. MP strategies are too few to sustain the complex technology the UP strategy requires. An unusual, sustained runup of a MP population would be required to transition to the UP strategy. The palimpsest of MP and UP industries in Africa and Southwest Asia suggests a complex story of gains and losses of the UP strategy during the first half of the last glacial.

Once UP population densities are achieved, complex culturally transmitted technology and social organization can maintain high effective pop-

ulation sizes by sophisticated social institutions (Wiessner 2002, Yengoyan 1968) in the face of considerable environmental variability and at low absolute population densities. At least in western Eurasia the UP strategy was sustained from ca. 40 kya until the onset of the Holocene began to transform hunter-gatherer lifeways. Australians and the peoples of northwestern China seem to have retained MP-level tools much longer, perhaps because of aridity-enforced low effective population sizes.

Our rapidly developing knowledge of ancient climates is working a revolution in how we understand our own past. Quite conceivably, a Plio-Pleistocene pattern of increasing high-frequency climate variability may have driven the pattern of increase in cognitive and cultural sophistication revealed by the paleoanthropological record. At any rate, externalist hypotheses are accumulating some real evidence in their favor.

It is important to note that these are the early days of high-resolution paleoclimate and paleoecological reconstructions. The paleoanthropological record, frustratingly ambiguous about social organization at best, has temporal and spatial gaps that may well mislead us. While we should be modest about any particular hypothesis, it is hard to believe that high-frequency, high-amplitude climate variation played no role in human evolution.