What Was The Environment of Evolutionary Adaptedness Like?

One of the bedrock principles of evolutionary science is that what we are today is the product of evolutionary forces acting upon our ancestors in the past. In the case of human cultural evolution, people might select cultural variants based on some guesses about the future. But our individual and collective ability to predict the future is quite limited. We are today largely what evolution in the past made of our lineage. Hence, the concept of an Environment of Evolutionary Adaptedness has great appeal. The assumption usually seems to be that the human EEA is roughly approximated by ethnographically know foragers or other contemporary small-scale societies, like the !Kung and the Yanomamo. Human evolutionist often point out that we spent more than 99% of our evolutionary history as hunter-gatherers, suggesting that human evolution was shaped by a relatively constant environment something like that of contemporary foragers for most of the Pleistocene.

The trouble with this picture is that it does not do justice to a much richer, more interesting and more problem-ridden human evolutionary history. In the last two decades paleoanthropologists, paleoclimatologists, and human geneticists have begun to paint a more detailed picture of the past and it looks nothing like the received view. The paleoenvironmental record is being read with increasingly accuracy and precision as well-funded paleoclimatologists avidly seek data about past environments in order to help answer questions about future climate. The changes have been stunning. Over the last 65 million years, the world's climate has become cooler and drier, culminating in the Plio-Pleistocene ice ages, starting about 2.6 million years ago. At that time, the climate shifted from being dominated by a relatively low amplitude 23,000 year cycle to being dominated by a higher amplitude 41,000 year cycle. Then, about 1 million years ago, the amplitude of climate fluctuation increased again. A 100,000 year cycle became the dominant component of the variation and the amplitude of this cycle increased further about half a million years ago. Paleoanthropologists have noted that the first members our genus *Homo* appeared not long after the shift to the 41,000 year cycle. Larger brained hominins, the fore-runners of Neanderthals and our own species evolved after the shift to the 100,000 year cycle, particularly after 500,000 years ago.

Exactly what these low frequency climate fluctuations imply about hominin evolution is not clear. For sure, they would have brought dramatic shifts in the ranges of hominins, and that of their competitors, their predators and their prey. But there is no reason to believe that this would have created a niche which favored hominins who had large metabolically taxing brains—the time scales of change are much too long. A clue about what might have favored big brains and the things that big brains can do came to light in the mid 1990s when exquisitely detailed cores covering about the last 80,000 year were raised from the Greenland Ice Cap. They revealed a stunning pattern of high frequency high amplitude variation. During the last Ice Age, dramatic climatic changes occurred on times scales ranging from the millennium to the decade. Compared to these fluctuations , the "The Little Ice Age," which caused such so much social and economic disruption between 1250 and 1850, is hardly perceptible. More recently, a number of other high resolution ice, lake, and ocean cores have confirmed the pattern observed in Greenland core; high amplitude millennial and sub-millennial scale variation characterized the last glacial period. Cores having records covering the last four to five glacial cycles have shown that all the glacial periods were highly variable, and the interglacial periods, like the present, were relatively calm.

Some recent cores suggest that the drumbeat of sub/millennial scale variation has increased over the last few glacial cycles.

Sub/millennial scale variation has obvious implications for the evolution of human brain size. In addition to temporal variation, rapid change probably created a chaotic out-of-equilibrium spatial variation in ecosystems, compared to the more orderly communities and biomes that have exist for the last 11,500 years. Whether big brains are mainly about deploying content rich cognitive modules, rapid individual acquisition of new information, fast cultural evolution to run up new adaptations, or some combination of all three, one can imagine how the rather high costs of big brains could be repaid in such variable environments. Humans are not unique in this response to Pleistocene environments. Harry Jerison's classic study suggests that many mammalian lineages had large increases in brain size at the same time as hominins.

Interestingly, hominins do not seem to have very common any time in the Pleistocene, with the partial exception of West Eurasia during the last glacial period. Human genetic diversity is low compared to chimpanzees. Neanderthals appear to have had even lower diversity than Anatomically Modern Humans. Humans either went through recent population bottlenecks, or were chronically rare. The genetic data do not yet speak with one voice about the details of our paleodemography, but the archaeological evidence seems quite consistent with chronic rarity. Site densities per unit time are low, and both Anatomically Modern Humans and Neanderthals made Mousterian/MSA tools of intermediate complexity until the middle of the last ice age. That is, both very big-brained species made comparatively simple stone tools for one whole interglacial glacial cycle with little sign of cultural progress. This is a vexing puzzle. Big brains are very costly, and it makes sense that fancy behavioral capacities could support such a brain. But the brains seem to have reached very large size in people who still made comparatively simple tools. Both big-brained hominins after the middle of the last glacial did begin making much fancier tools. Richard Klein has suggested that some favorable genetic mutation about 50,000 years ago provided the final cognitive modernization that made modern capacities for cultural elaboration possible. Perhaps. But there is as yet no direct evidence. In this scenario, the advanced Neandertal toolkits were acquired by trade or copying from Anatomical Moderns. Another possibility is that environmental changes were responsible for the changes around 50,000 years ago, either by directly unleashing culture or by favoring genes that supported cultural elaboration.

The evidence from Tasmania and other situations where Holocene populations were isolated and small suggests that cultural complexity increases with effective population size. Tasmanians had a reasonably complex toolkit in the early Holocene that became much simplified after the flooding of the Bass Straight isolated a few thousand Tasmanians from the hundreds of thousands of Australians on the mainland. It may be that Anatomical Moderns and Neanderthals made relatively simple tools because their populations were too small and disconnect to develop and maintain more complex technology, not because they were cognitively or socially inferior.

Like humans, cheetah and African wild dogs have low genetic diversity. These species are interesting because, like Pleistocene humans, they prey mainly on medium sized herbivores. This is a crowded ecological niche in Africa today and would have been crowded in Pleistocene Eurasia. Ecologists have come to suspect that wild dogs and cheetah are confined to marginal habitat by interference competition from lions, hyenas, and leopards. Hominin fossils often show signs of being victims of predation. One possible explanation for the apparent rarity of hominins, even late, large-brained, comparatively sophisticated hominins, is that we were only a marginally successful member of the predator guilds of Africa and Eurasia.

Why might humans have begun to be substantially more common and more sophisticated about 50,000 thousand years ago? One possibility is that the frequency and perhaps the amplitude of climatic variation increased substantially just before this critical time, broadening our access to the carnivore niche. Perhaps our ultra big brains enabled us to hunt more successfully that the slower responding competition when the climate become more variable.

Even so, the making of ultra fancy tools seems to have been confined to the Upper Paleolithic of west Eurasia and southwestern Siberia until nearly the end of the Pleistocene. This is also a vexing pattern. Have archaeologist just missed Upper Paleolithic analogs, say in West Africa and Southeast Asia? Perhaps; tropical forests are hard for archaeologists to prospect, although what has come to light so far is not encouraging. West Eurasia is environmentally unique in being the relatively mild maritime end of the Mammoth Steppe Biome that once stretched from Spain and France across Siberia over the dry Bering Strait to Alaska and northwestern most Canada. At least the eastern most part of this biome (Beringia) was free of humans until about 14,000 years ago. Much of northeastern Siberia may have been exploited lightly and humans might have been confined to far western refugia during the cold episodes of the sub/millennial scale variation. The lack of fuel-wood may have been a factor in surviving winters. The big game themselves were better adapted to cold winters and seem to have been numerous in the regions that people could not exploit. One problem with being a really sophisticated hunter, with a full kit of clever gear for capturing prey, is that such populations might have tended to be become superpredators, expanding, over-exploiting their prey, and causing in turn a collapse of human populations. In Africa, several industries with an Upper Paleolithic cast, such as the Howison's Poort and Still Bay of Southern Africa, seem to have arisen and disappeared in less than a thousand years. Perhaps they represent population booms that began to make fancy tools and then suffered a superpredator's collapse. The west Eurasians may have avoided a similar fate only because they had an inadvertent protected reserve on the eastern Mammoth Steppe that provided a westerly flow of game populations, or some other environmental advantage that allowed them to maintain large populations and, hence, complex culture.

In the Holocene, but not in the previous interglacial, human populations exploded by shifting their caloric demand to plants. Cultural innovations have led to a veritable adaptive radiation of Anatomically Modern Humans into a huge variety of hunting-and gathering, horticultural, agrarian, herding, fishing, trading, and manufacturing niches. Humans likely always consumed some plant resources, at least at lower latitudes, but even the plant rich hunter-gather lifestyle of the San, Ache, Australians, and Western North Americas is outside the range Pleistocene peoples, much less agricultural adaptations. Recent genetic studies indicate that humans underwent a burst of evolution as they adapted to new diets and to the new diseases brought about by denser populations and contact with domestic animals. Whether any genes related to behavior also came under selection in the Holocene is currently unknown, but some paleogeneticists expect to find such loci. At minimum, the EEA extended into the first half of the Holocene. After this bust of evolution, we became better adapted to the Holocene than we ever were to the Pleistocene, to judge by the vast increase in our biomass and cultural diversity. Our Holocene adaptations seem to have generally exhibited boom and bust dynamics, perhaps an extension of a pattern of recurrent excessive exploitation of resources that goes back to Pleistocene episodes of superpedation.

The conventional EEA concept seems to me to create more problems than it solves. Rob Boyd's and my gene-culture coevolution hypothesis would best fit a smooth, intimate relationship between anatomical modernization, especially brain size, and toolkit complexity. Allison Brooks and Sally McBrearty outlined such a scenario a decade ago, but, according to other observers, the record looks more punctuated to many observers. Ephemeral local episodes of tool sophistication, often with regression, are plausibly the rule in the late Pleistocene, rather than a steady march of increasing technological complexity . The most common Evolutionary Psychology hypothesis would be consistent with a long-continued, stable, Pleistocene to which humans successful adapted, followed by chaos in the Holocene. But even the patterns of variation changed during the Pleistocene. The remarkable success of Holocene humans compared to our ancestors seems to contradict the idea that we are not adapted to the Holocene. Somehow, a marginally successful Pleistocene predator turned out *pre-adapted* for spectacular successes in the Holocene. The mysteries and complexities of the actual EEA are much more interesting than the caricatures we once held. As JBS Haldane is supposed to have said "The world is not only queerer than we suppose, it is queerer than we can suppose!" Perhaps what we turn out to be able to do in the Holocene says as much about what we might have been up to in the EEA as vice versa.

For a fully referenced version see Richerson, Peter J., Robert Boyd, and Robert L. Bettinger. 2009. Cultural Innovations and Demographic Change. *Human Biology* 81: 211-235.