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Man the Hunter and Other Stories

It is necessary to remember that fossils were alive when they were important.

S. L. Washburn,
in *Anthropology Today* (1967)

Around five or six million years ago, a hairy, one-meter tall creature that looked much like an upright chimpanzee left the security of the woodlands for life on the open savannahs of eastern Africa. Physically defenseless but gifted with a sharp mind, the species had carved a niche for itself by becoming bipedal, allowing the creatures to travel efficiently for long distances over open ground. Its members ate mostly fruits and leaves but also included increasing quantities of meat, both hunted and stolen from animal carcasses that they found on the savannah. Eventually they learned to modify stones into tools, which over time became effective butchering implements, and perhaps also weapons. Intelligence and sociability were their most valuable assets in coping *with the risks of a dangerous world. They therefore lived in social groups or perhaps in monogamous pairs for the safety of numbers. These first hominids flourished, and their descendents became ever larger-brained and more human, eventually evolving into modern Homo sapiens.*

The above account of human origins has been the standard version that students of human origins as well as the public have learned and recited for many years, but you should not find it very convincing. Our knowledge of what the earliest members of our hominid family were like is itself still evolving. The evidence for bipedalism arising in a fairly treeless savannah niche is, for example, considered tenuous.[1] Did the earliest hominids (members of the human family) hunt, or did they scavenge to obtain their meat? What precise factors brought about the dramatic expansion in brain size? For every simplistic portrait of human origins such as the one above, there are dozens of researchers eager to tackle other untested assumptions. Some of these debates over our origins are quite fierce and have profound implications for understanding who we are.

The study of human origins is like the plot of the Japanese film *Rashomon*. A brutal crime has been committed and observed by a number of eyewitnesses. A suspect is apprehended, but each eyewitness account of the crime in question differs in some critical way. Even though the facts have been established, the police are unable to reconstruct the event to their satisfaction. The crime is clear but the lines of evidence do not converge due to the prism of circumstance and perspective through which the observers' differing accounts pass. This is the situation in which scientists studying human origins find themselves; the bits of evidence from primate behavior, fossils, and other sources do not always build a consensual picture. Instead, they often point to a variety of possible scenarios, all of which probably contain important elements of the truth.

This Old House

The difficulty in studying human origins lies in our narrow view of the ancient world. We are constrained by our firsthand knowledge only of the present, in which the why and wherefore of the past are lost. Go into an old house and look around. If, like most older homes, it has been remodeled and refurbished many times over its long life, you will be confronted with a jumble of architectural and furnishing styles. The Victorian fixtures in the living room, the Craftsman sideboard in the dining room, and the 1960s kitchen remodel all coexist in one place. Modern heating and wiring systems are built on top of the original, and beneath the wallpaper there are other layers from previous chapters in the house's life. These changes obscure the original appearance quite effectively. Today the house is a mosaic reflecting a long history of styles and decors, *none of which could have been predicted by the previous generation's designers*. A casual observer can no more look back from the 1990s to see the house clearly in its original form than he could have stood in the kitchen in the 1890s and predicted the course the house would take in the century to come.

The lesson of the old house is a good one for those who theorize about the primate origins of our own behavior and anatomy. Each piece of furniture and each component of the floor plan is one part of the jigsaw puzzle of evolutionary function and form that natural selection molds. What's more, the puzzle is internally interactive. That is, when a new piece is added, other pieces have to accommodate and be accommodated. When bipedal posture is adopted, the circulatory system, the spinal column, the diet and foraging behavior, and even the mode of social interaction also change. This makes assembling the puzzle retrospectively an enormous challenge. In constructing theories of our origins, we amass diverse evidence from fossils, modern human behavior, the behavior and anatomy of living primates, and from genetic studies to develop conceptual models of what our earliest ancestors were like. But in the end we often create scenarios that rely heavily on the behavior of just one closely related species, which becomes an analogy for the form that our ancestors may have taken.

The chimpanzee model has long been foremost among these analogous models due to its obvious appeal. We are physically very similar to these apes and studies show our DNA sequences to be about 98.4 percent the same; this makes chimpanzees more closely related to us than they are to gorillas. But the 1.6 percent different DNA is enough to make us distinct, having followed our separate evolutionary paths for 6 million years. We can easily see how different modern humans are from our ancestors. Modern chimpanzees, on the other hand, appear to have remained more similar to our common ancestor. But it would be a mistake to assume that early humans were very similar to chimpanzees simply because they looked more like chimps than like modern people. There have been, in effect, 12 million years of evolution (6 along each prong of the fork) separating humans and chimpanzees—long enough for profound changes to have occurred. The ape and the human were quite similar at the earliest stages of the early hominid-chimpanzee ancestor branching, when the lines had been going their own way for no more than 2–3 million years. We must compare the modern chimpanzee with the likely anatomy and behavior of our early common ancestor that lived before the node occurred in our families' branches. It is this gap that we are trying to span when reconstructing our family roots.

What is a model of human evolution? Primatologist Jim Moore distinguishes a model from a theory. A model is an explanation that uses one member of an analogous pair as a point of reference in understanding the bigger picture.[2] Thus craters on the moon can be used to model the way in which celestial objects crash into celestial bodies in our solar system. We can study the moon in detail because of its proximity and then use a lunar model for crater formation. In time, space probes may prove this model to be completely wrong if, for instance, we learn that craters on other moons in the solar system are formed by other means. The lunar model is an analogic model; it uses one well-known example to predict conditions elsewhere. A theory, by contrast, should be an intellectual construct that uses facts from disparate sources to build a prediction about some natural phenomenon. For instance, one might theorize that based on studies of the velocity and impact rates of meteors that have been recorded throughout the solar system, the appearance of craters on celestial bodies everywhere should be similar. This is different from the lunar model of crater formation because it casts its net more widely for relevant data to test the hypothesis about craters. Moore points out, however, that, in practice, models and theories are often treated as one and the same.

A theory ought to have predictive power. In the physical sciences, researchers claim they have proved the existence of objects, whether elementary particles or celestial bodies, that have never been observed visually. Showing theoretically that a black hole or brown dwarf ought to exist is enough to provoke other researchers to take up the search. This is because of the consistent and predictive laws of the physical world. Human evolutionary scientists hypothesize retrospectively what extinct creatures may have been like, choosing from a wide range of possible adaptations. Researchers have attempted to create predictive theories, plausible scenarios, or even simply stories that contain some well-informed guesses about a long-gone reality. But in truth, evolutionary models are, in spite of their tremendous power to explain past history, not predictive. Models of the evolutionary process can describe and explain the history of organic change in a lineage even though they could never have predicted that those changes would occur.

Primate Models of Early Humans

When we want to build a model of something that no one has ever seen, it helps a great deal to have another structure on hand that is similar to what is being modeled. However, having that similar-but-not-the-same model handy may mislead us in important ways. We could use the principles of primate ecology combined with what we know about the relationship between anatomy and behavior to reconstruct the social lives of early hominids. This approach, however, is fraught with uncertainties. If the solitary-living orangutan were not alive today, primatologists examining ancient orangutan skeletons would be perplexed to note that males were dramatically larger than females, which is typical of polygynous, group-living primates but completely unexpected for solitary ones. Similarly, no primatologist could determine the behavioral differences between the chimpanzee and the bonobo based on the animal's anatomy without having a fully fleshed version to study in life as well. In fact, if the chimpanzee and bonobo existed only as fossils they might be mistaken for one species because of their anatomical similarity. These are important reminders of the limitations in modeling the behavior of extinct animals. When a researcher constructs a grand conceptual model of early human evolution, she or he has no choice but to resort at some point to the use of a strong analogy with some living, well-studied primate relative.[3] There are four great apes, and any one of them could be a good analog for the human ancestor. But of course the human ancestor was not exactly like any of them, and perhaps was so different that to use any as exemplars may be counterproductive.

We can construct a portrait of a hominid ancestor based on the behavior of one or a few living and highly analogous species. Most models that attempt to use empirical evidence from a range of disciplines implicitly use a chimpanzee model as the psychological starting point. Primatologist Richard Wrangham has argued that of the four great apes, the chimpanzee is the best model of our own origins because it has more features that link it with gorillas and humans than with bonobos. He posits the chimpanzee as the direct best analogic model for the last common ancestor, citing molecular, anatomical, and behavioral links between chimpanzees and gorillas that leave bonobos as an outgroup.[4] Because we know that we are more closely related to chimpanzees than to gorillas, the former would then be the last living word on our ancient selves. Adrienne Zihlmann and her colleagues, meanwhile, have long proposed the bonobo as the best model for an early hominid, citing morphological similarities in this ape to the human bipedal adaptation.[5] Other researchers have seen these similarities only as interesting but coincidental parallelisms; the apparent adaptation to bipedal posture may be an adaptation to an arboreal lifestyle.[6] Bonobos are probably not a more appropriate model for the last common ancestor with hominids than chimpanzees.

It is impossible to overstate the role of the chimpanzee and bonobo in the evolution of theories about human origins. Understanding the lives of extinct forms represented only by bones would be vastly more difficult in a world in which paleoanthropologists had access only to the newly discovered hominoid fossil and had never seen living individuals. Live animals provide us with examples of the range of possible adaptations for feeding, ranging, territoriality, mating, offspring rearing, and a variety of other behaviors without which there would be no starting point for reconstructing hominid lifeways. Not surprisingly, most self-proclaimed conceptual models have settled on a very chimpanzee-like creature as the presumed common ancestor of all the hominids.[7] Only by comparing the ecological and anatomical features of the living apes can we hope to distinguish the range of possible adaptations from those that the extinct species was likely to have had. The problem of extrapolating from living to extinct forms is compounded by the absence of fossil African apes that would provide physical evidence of the evolution of the chimpanzee-bonobo lineage after their divergence from the shared ape ancestor.

Perhaps the greatest misconception about the use of a chimpanzee model of human evolution is the often repeated notion that using a chimpanzee analogy limits our perspective of the unique traits that early hominids would have possessed. Andrew Hill speaks for many paleoanthropologists in stating that "pretending that the very early hominids are almost exactly like modern chimpanzees, or any other particular animal, seems to me a dead end. Work is then devoted to confirming this view of the past, and this practice prevents the detection of differences."[8] Hill is mistaken: if anything, using a chimpanzee model keeps us from forming a cardboard view of any extinct hominid species. The earliest primate researchers used to speak of "the monkey" to refer to all primates, in the days before we appreciated the dramatic diversity of mating systems and other behaviors among the primate order. Likewise, William McGrew has chastised us for thinking of "the chimpanzee" by pointing out that the degree of cultural diversity among chimpanzee populations across Africa prevents us from generalizing about the species' tool-use capabilities, hunting styles, and so on. And in the same way, paleoanthropologists err when they speak of "the australopithecine" as though each species of early human was monolithic. In all likelihood, there were populations of *Homo habilis* that hunted avidly for small mammals, and other populations living at the same time 100 kilometers away that were scavengers. This is the nature of the diversity of chimpanzee societies, and there is good reason to think it would have characterized early human populations as well.

Other theorists have used great ape societies as referent points for reconstructing aspects of the earliest hominid's social behavior and ecology. These models have focused on different aspects of species-specific traits as critical features also present in the common ancestor. Richard Wrangham compared the social systems of the African apes to ascertain the behavioral ecology of the common ancestor; he concluded that polygynous, male-bonded kin groups were the core of the common ancestor's society. He found inconclusive evidence about territoriality and male philopatry.[9] Michael Ghiglieri conducted a similar analysis using only the chimpanzee and bonobo and considered male reproductive strategies and intense male kin group-enforced territoriality to be the core features around which a model of the stem hominid should be built.[10] These papers focused on male bonding in relation to male reproductive strategies, because the emerging consensus on the nature of both chimpanzee and bonobo society is that they are composed of male-bonded kin groups. Only a few researchers have considered female *Pan* behavior in such models of early hominids. William McGrew posited the female chimpanzee as a prototype of an early hominid female; he saw active mate solicitation in a polygynous setting as evidence of females that were active reproductive strategists rather than passive receptacles for males' reproductive ambitions.[11]

Models are of course only as well supported as the information on wild apes that is used to build them. In the 1970s, when a debate over whether early humans were hunters and scavengers was brewing, the archaeologist Glynn Isaac built a seminal model of early human behavior based on the sharing of food after butchering the carcasses of savannah ungulates. Isaac rejected the behavior of modern chimpanzees in building this model. He did not know then that meat consumption by chimpanzees is as frequent as we know it is today. Isaac considered chimpanzee hunting to be more similar to what we would call gathering in traditional human societies because it involved only small packages of protein.[12] We know today that the cumulative amount of meat can be quite high because of the tendency for chimpanzees to capture several monkeys in a single hunt. Chimpanzees share meat nepotistically but they do not store food for later consumption; hand to mouth is the rule. Isaac would have been forced to frame the sharing hypothesis differently had he known of the more recent discoveries about chimpanzee behavior.

Analogic models do not necessarily have to be built upon the biology of our very closest relatives. The first modern use of a referent species for early humans was in fact a monkey, the savannah baboon. Irven DeVore and Sherwood Washburn published a series of papers in the early 1960s that focused on the role of the male baboon and its status-seeking, mate-guarding, and sometimes meat-eating nature. These findings held sway for many years in modeling our view of what the most important factors driving primate societies were. Eventually it was pointed out that female baboon behavior is as interesting and important as that of males, but male behavior continued to dominate the research agenda on baboons until recent decades. We saw ourselves as baboon-like, and so our models of our ancestors suggested baboon traits.

Hunting and meat eating by baboons was studied by Shirley Strum in a troop nicknamed the Pumphouse Gang at Gilgil in Kenya. Strum has now studied these animals for more than twenty-five years, but in the early 1970s she observed their hunting behavior in particular. Her study of meat eating showed that the Gilgil baboons ate meat more frequently—once per day—than any other known population of nonhuman primates. The exact pattern of both hunting and sharing varied depending on the individuals involved in each hunt, but the baboons at Gilgil were more sophisticated in their hunting behavior than any other baboons that have been studied. Strum reported cooperation, particularly when a particular adult male was involved in the hunt. This male appeared to be a catalyst who promoted hunting by other males, females, and even juveniles. The Gilgil baboons thus provide a model for a cultural basis of hunting; they suggest that aside from any energetic concerns about the rate of return in hunting by baboons, meat eating is a learned tradition that may be exterminated or initiated depending on the composition of the group. Past experience, observation, and imitation of others dictated much of the meat-eating behavior of the Pumphouse Gang. Individuals did not scavenge carcasses unless they had some prior experience with the carcass or could watch another group member eating from it.[13] Why one population of baboons scavenges while another does not may be due to experience and learning opportunities. This hallmark of complex social behaviors, including hunting, certainly applies to chimpanzees as well. In the Taï forest of the Ivory Coast, the majority of adult males who did the hunting in Christophe Boesch's long-term study of chimpanzees recently died from an outbreak of the ebola virus. Learned traditions of hunting may have died with them. If there can be a silver lining in such a tragedy, it will be to observe whether and how the hunting tradition reemerge as a new crop of young male hunters matures without the benefit of observing their elders.

Meanwhile, in the forests of Latin America there is another, much smaller primate that also hunts and eats meat voraciously whenever it has the chance. This primate is a monkey much smaller than a baboon, and in addition to its carnivorous habits it is also the most adept tool user among the New World monkeys. The capuchins of the genus *Cebus*, found across South and Central America, hunt as avidly and as successfully as chimpanzees. They engage in relay chase hunts that resemble those reported for both baboons and chimps. They also employ tools more than any other monkey. Their brain-to-body size ratio is very high, as is true of chimpanzees. Studies of captives have shown capuchins to be active and strategic food sharers as well. It has only been in the last several years that any attention has been focused on their hunting prowess and sharing behaviors. This lack of attention is in turn due to the general lack of interest anthropologists have shown in the smaller-bodied Neotropical monkeys as models of human evolution.

Meat eating, tool use, and large relative brain size therefore occur in two distantly related primate groups—apes and New World monkeys—and meat eating and related behaviors are also known in an Old World monkey, the baboon. Is this a random evolutionary convergence, or has natural selection driven the coevolution of these traits? These animals are exemplars of how effective nonhuman primates can be as hunters. They are just three of two hundred primate species, so one might argue that meat eating was not a fundamental factor in the rise of the human species. The coincidence of traits among these species, however, is striking.

Other Origins

Finally, there is no good reason to limit ourselves to primates when using living animals to reconstruct the origins of intelligence and complex social behavior. Anthropologists study prosimians such as bushbabies and lorises because they are our primate kin, but they are so distantly related that what we are likely to learn from them about the origins of human behavior is extremely limited. If an anthropologist were to turn to the cetaceans—the dolphins and whales—for answers about the origins of humanness, he would risk ridicule. However, if we are interested in how complex social systems arose, then comparing how the Darwinian process has molded unrelated highly intelligent species may be more informative than comparing two more related but fundamentally different animals.

It is hard to imagine mammals living in more different worlds than a dolphin and a chimpanzee. And yet these two creatures are representatives of the only two evolutionary lines of the billions that have ever lived to produce big-brained, socially sophisticated, and highly intelligent beings. Their social convergence may be due to ecological factors. Dietary and foraging constraints on the two species may be similar. For dolphins, the food resource is fish, which are unpredictable in occurrence and widely dispersed. This patchy resource promotes foraging in small, fluid social units, paralleling chimpanzee society, which is structured around the patchy distribution of their favored fruits in African forests. Male chimpanzees form long-lasting bonds based on kinship, and these coalitions attempt to control females in order to obtain matings. Male bottlenose dolphins in a landmark study in Shark Bay, Western Australia, have also been reported to form long-lasting alliances that cooperatively coerce females to mate with them. This cooperative behavior is also valuable in driving off predatory sharks, and possibly in finding schools of fish.[14] Both species are highly communicative, with vocalizations that show regional dialectical variation and a strongly learned basis. These parallel social adaptations suggest that the social complexity and brain size increase that we see in ourselves have their roots in the social and ecological environment in which our ancestors found themselves.

The Missing Link Is Neither

The idea of a missing link in human evolution is deeply instilled in all of us. No matter how complete the evolutionary sequence of human fossils becomes, there will always be those who demand a missing link. By definition, the missing link is the most recent common ancestor of both humans and great apes, which must have lived immediately before the split of these two lineages in the late Miocene or earliest Pliocene era. But in reality, there is no such thing as a missing link or even a most recent common ancestor. The concept of a common ancestor is just a metaphor for the enormously complex process of speciation that preceded the emergence of the hominids.

Consider the process by which two modern primate species might form. A vast river changes its course in the Amazon basin, splitting what was once a population of monkeys into two smaller populations. Over millennia, each population goes its own evolutionary way due to an accumulation of mutations that do not penetrate into the other, now disjunct population. The result will be multiple new populations that are genetically, morphologically, and behaviorally different enough that we consider them separate species. The criteria we use to recognize the populations as distinct species depends on which concept of species we use. Initially, there was not a single different population that gave rise to other, daughter populations. Rather, there were a number of populations, each with its own set of slight genetic and morphological and behavioral differences. We see this variation in geographically distinct populations today in many animal species. It is a gross oversimplification to imagine that there was one or even just a few populations of ape ancestors that gave rise to the hominids. In reality, there may have been numerous ones, and they may have differed substantially in morphology and behavior from one another, and had periodic contact during which their genes mixed. To invoke the missing link by calling any one of these populations the founder of our gene pool is almost certainly wrong. But because we are so limited in our knowledge of the fossil record, and even more in understanding what the fossil record can inform us about behavior, we employ the common ancestor logic in trying to model early hominid behavior.

Early Hominids as Weaklings

One of the most indelible images in our depiction of early humans is that they were weaklings. As humans became human, they lost two adaptations that characterize the great apes: climbing ability and long canine teeth. The usual depiction of these nascent humans suggests that they were not particularly well adapted to either their new grassland environment or to the forest habitat they are said to have left. We see them traveling warily across the savannah, armed with only their brains against the carnivores that eagerly preyed on them. Often, their gait is depicted as a shuffling, inefficient form of semibipedalism, as though the creatures had some half-formed ability to walk. This caricature is pervasive even among human evolutionary scientists—indeed, it was present in both a recent widely watched documentary on human evolution and a recent book about human nature. The image of early humans taking up bipedalism after a long ancestry of ape quadrupedalism is implicitly that of people who take up a sport late in life—that, because it is not their lifelong habit, they will take time to do it well and may never be really proficient. This is nonsense, since at each stage of the evolutionary process natural selection molded a means of moving about that was efficient enough to be favored and perpetuated. There was no way to predict, nor any a priori reason to think, that evolutionary change in the way apes moved would ultimately produce an upright walker. We do not know why hominids became bipedal, but we can explain many of the consequences, such as greatly enhanced energetic efficiency over the ape's knuckle walking.[15] Nevertheless, the shuffling protohominid is a mainstay of popular and scientific accounts of early humans. The depiction of early humans as weaklings is also odd considering that we do not see apes in this light; what could be more gracefully agile than a chimpanzee? Even when chimpanzees travel on the ground, they are hardly defenseless, mobbing dangerous animals such as leopards and driving them away through joint effort.

Our ancestors may not have had huge canines, but they certainly may have been highly efficient killers and predators. During the years I conducted research at Gombe there was one elderly male chimpanzee, Evered, who was an accomplished hunter even though in his last years he had lost the muscle tone needed for treetop agility as well as nearly all of his teeth! Even modern people who lack anatomical adaptations to tree living but who live in forested environments have a tree-climbing ability far beyond that of anyone raised in Western society. Neither chimpanzees nor humans have any anatomical traits that specifically adapt them to a predatory way of life. Instead, both use their ability to hunt socially and cooperatively to compensate for a lack of such adaptations. One of the arguments against a hunting ancestry for early hominids has been that they lacked such adaptation and therefore were forced to scavenge for carcasses as their sole source of meat. This is a highly implausible scenario, in part because early hominids could make a living on the numerous small and medium-sized mammals with which they shared their habitat.

Our deep preconceptions influence and constrain the ways in which we theorize about the early nature of humanity. These preconceptions change, but they are always constrained by the limitations of our evidence and by the prevailing biases of the day. The extent to which these models reflect reality versus our own reflections of ourselves is embodied in some of the influential models of human origins that follow.

Man the Hunter

In 1966 about fifty anthropologists who studied the life ways of traditional foraging people gathered in Chicago for a conference to examine the status of the world's hunter-gatherers.[16] Perhaps the foremost scientific conclusion that came out of the meeting was that the importance of meat in the diets of foraging people had been exaggerated. This was deeply ironic, since the most influential and ultimately notorious perspective to emerge from the meeting came to be known as "Man the Hunter." Sherwood Washburn, the most prominent and listened-to biological anthropologist of his day, and Chet Lancaster contributed a paper called "The Evolution of Hunting." It set out to explain how and why the human brain had experienced a 3.5-fold increase in size and complexity since the dawn of humanity. Washburn and Lancaster claimed that "our intellect, interests, emotions, and basic social life—all are evolutionary products of the success of the hunting adaptation"[17] (p. 293). They were referring mainly to our more recent human ancestors during the Pleistocene. In their view, hunting for game animals was at the soul of the human experience. However, they noted that the sexes had different roles in many traditional societies when it came to acquiring meat. Men, according to Washburn and Lancaster, hunt, while women gather. This view put men in the important role of obtaining the highest-quality nutrients and the calories that their households would use. Hunting requires communication and coordination of action among the hunters. This placed an evolutionary premium on intelligence and communicative ability in order to successfully track and hunt down potentially dangerous prey. Men did this, and women did not. Moreover, Washburn and Lancaster linked the deep human love of hunting to the equally deep human love of going to war and to acts of aggression in general. The fact that it is almost always males who carry out these acts served to reinforce the idea that men had a natural right to occupy the glamor role of clever-minded forager, meat provider, and conqueror in human societies. Ever since, theories of human evolution have focused on male activities rather than female as the core human adaptations.

In principle, the evolutionary logic on which Man the Hunter was based was sound. It was an analogy based on the behavior of traditional foragers that employed a model of cognitive evolution equating a fundamental change in human anatomy and behavior that was carried out by one sex only—men. However, we know of many cases in which, due to genetic linkages called "pleiotropic effects," one sex exhibits traits that natural selection clearly produced in the other sex only. Male nipples are an obvious example. The serpentine neck of the giraffe, long thought to be the product of natural selection favoring those giraffes that could reach high branches to forage more effectively than short-necked neighbors, was probably not the result of natural selection for neck length. Male giraffes use their necks to combat for females, twisting and thumping each other in a dominance struggle. Longer-necked males have greater mating success, though at the same time they suffer greater mortality from predators than smaller males.[18] All else being equal, natural selection would favor shorter necks. But not only male giraffes have long necks; females do, too, because of pleiotropic effects. In the same way, the early hominid brain could have increased in both males and females even if only males were hunting for meat.

The intellectual stakes were higher in Man the Hunter, however, since it was about the roots of human gender relations, not giraffe necks. The response to Man the Hunter was angry and its impact long lasting. Many anthropologists were angered by the suggestion that a hallmark in our ancestry was effected by natural selection for male cognitive abilities, implying that women were merely carried along in some genetic linkage. Anthropologists Adrienne Zihlmann and Nancy Tanner pointed out that in some of the traditional societies that are most vaunted for the man's role in hunting, up to 85 percent of the animal protein obtained by a household came not from men at all, but from the less glamorous role of women gathering foods such as nuts, tubers, and small animals.[19] The role of human females had been neglected in Man the Hunter, according to the anthropological community, due to the gender politics of scientific advances and partly due to the failure to appreciate the role of women in foraging.

In the largest cross-cultural database that exists—a survey of 179 societies that examines how labor is divided in human groups—men alone hunt in 166, both men and women hunt in 13, and in not one do women alone do the hunting. Women, on the other hand, are the main gatherers of plant foods in about two-thirds of societies in the same survey.[20] So the reality of male predominance as hunters and of women as gatherers is not in dispute. Instead, anthropologists began to realize that although men hunt, they often fail to catch enough prey to sustain the family, and this task falls to women. Men might kill one giraffe and talk about it around the fire at night for a year until another is killed. In the reaction to Man the Hunter, the fact was lost that while meat may not be the *valuable* food resource it had been assumed to be, it is nevertheless the most *valued* food resource in most human groups, including among foraging people.

The backlash to Man the Hunter permeated all fields of anthropology. In the study of nonhuman primates, it contributed to a reappraisal of the way in which the field was practiced. Observers had always tended to focus more on the behavior of males than females, because they are often bolder and therefore more visible.[21] The practice of observational primatology was made more systematic when it was recognized that females also played a central role in the primate group. More recent theoretical advances made it clear that females rather than males are often the central players around which the mating system is structured.[22] Man the Hunter's backlash eventually led to an engendering of the field of archaeology; it was recognized that the role of women in early human societies had long been ignored in favor of the often more visible role of men. Stone tools made for butchering carcasses will preserve in the fossil record, while the implements of gathering made and used by women might not. Women nevertheless performed critical tasks and occupied spheres of influence in antiquity that went far beyond where the largely male archaeological community had considered them for decades.[23] Archaeologists today refer to the failure of an earlier generation of scholars to consider the role of women as a "Paleolithic glass ceiling."

A Good Story

A good model of human origins should provide a number of hypotheses about our ancestors' behavior and anatomy that interweave in a sensible way. That is, the model must be both internally and externally consistent. It must explain the origins of those traits that are uniquely human above all else, since other traits that we share with the great apes are likely primitive ones that we possess simply due to a common ancestry. What is left after these are stripped away is those traits that define our humanness. To retrospectively build a human ancestor requires that we consider the roots of the key components. Some models make wonderful stories; like a novel they may be internally consistent even though they do not overall accord well with physical evidence. For example, the idea that humans passed through an aquatic phase in prehistory has been advocated and accepted in some popular accounts,[24] even though the specific lines of evidence in the model have no support.[25] It is simply an attractive, internally consistent story about who we are and how we came to be human.

The key adaptations that we must consider will vary depending on what stage of human evolutionary history we are thinking about. For instance, when imagining the common ancestor of all hominids, the key character is bipedalism, arising at least five million years ago and exhibited by no other primate. Our very large and complex brains, our tool-using capabilities, the increased amounts of meat in our diet, and our unusual social system all evolved at much later dates—2.5 million years for stone tool use and less than 200,000 years ago for a modern level of brain-size increase. The theories of hominid origins that have gained the most attention and notoriety have been those that have woven the greatest number of human traits together in an internally consistent way, even though we will see that these often become houses of cards by virtue of the number of variables they seek to link. In the following sections I discuss some key adaptations and how they fit into a portrait of early hominid behavior.

Key Adaptations

bipedalism

No aspect of modern humans has been speculated about more than our unique bipedal posture and locomotion. Whatever the protohominid's mode of travel, bipedalism would probably have evolved only if it had increased the efficiency of movement in the emerging new species. For instance, Karen Steudel of the University of Wisconsin has analyzed the energetic efficiency of bipedalism in order to assess the hypothesis that early humans became more efficient travelers when they became bipedal; she disputes this widely held notion.[26] In the 1970s, studies of chimpanzee walking patterns led researchers to claim that bipedalism required no less an output of energy per unit of distance than quadrupedalism.[27] Later, anthropologists Peter Rodman and Henry McHenry found the opposite result; they reported that bipedalism must have arisen due to its far greater efficiency over the knuckle walking of apes.[28] Steudel argues that while bipedal walking is more efficient than knuckle walking, it is not likely to have been more efficient in its earliest incarnations than the quadrupedal alternatives available at that time. In other words, natural selection probably did not favor the continued evolution of bipedal locomotion in emerging hominids due to its efficiency unless our common ancestor with chimpanzees was a knuckle-walker. Ruling out improved energetics as the primary stimulus for bipedalism leaves a number of other reasons that have been promulgated. For example, here are some published explanations, along with at least one piece of contradictory information:

1. Being upright gives a height advantage to intimidate predators and other hominids.[29] *Problem*: Why is it important to be permanently upright? Standing upright for just a few seconds would achieve the same result.
2. Being upright allows an early grassland hominid to see over tall grass.[30] *Problem*: Same as above, plus the doubt over whether early hominid evolution really occurred in grassland versus woodland habitats.
3. Being upright reduces one's exposure to intense tropical sun and heat, thereby reducing heat stress on the savannah.[31] *Problem*: Again, the evidence that this key period of evolution took place on the savannah is now considered shaky.
4. Being upright is not about walking, but rather about posture when foraging. The bipedal posture may have evolved to allow apes to pull down low-hanging, fruit-laden branches,[32] or to allow for better tree-climbing ability on vertical trunks.[33] *Problem*: Neither of these receives strong support from the behavior of modern quadrupedal chimpanzees.
5. An upright walker has its hands freed for carrying food, offspring,[34] or tools.[35] I will deal with this last scenario below, for it incorporates some of the most widely held assumptions that have recently dogged models of human origins.

BIPEDALISM AND MEAT EATING

In 1981 physical anthropologist Owen Lovejoy published a paper that proved an influential but controversial model of human origins. He suggested that we should look at both bipedalism and the unusual reproductive system of humans to establish the likely social behavior of the earliest hominids as well as why they became bipedal. Unlike chimpanzees and bonobos, in which females possess large fluid-filled swellings when ovulating, human females conceal their ovulation. Lovejoy saw the roots of female manipulation of male behavior in the concealment of ovulation; unable to time the exact period of ovulation, male protohominids would have had to remain near the female in order to mateguard against the possibility of cuckoldry. At the same time, increased use of savannah habitat led to efficient bipedal walking. Lovejoy hypothesized that male provisioning of stay-at-home females resulted. Males used their newfound freedom of the hands to carry meat back to females. They thereby enhanced females' nutritional status, enabling an increased reproductive rate that was good for both sexes.

Unfortunately for Lovejoy's model, there is no reason to think that advertisement of ovulation has ever been a part of hominid biology. Chimpanzees and bonobos had a common ancestor with other great apes, and probably evolved their swellings after their lineage had split with other apes. This is the most parsimonious explanation and would explain why none of the other apes or humans possess swellings while both the chimpanzees and bonobos do. The concealment of ovulation in women is simply the retention of a widespread primitive primate feature. The swelling is a chimpanzee-bonobo feature that evolved sometime between 5 and 2.5 million years ago. Moreover, we have little reason to assume that early hominids would have been monogamous, any more than all modern human societies are (the majority are polygynous). Some form of polygyny, the social system of three of the four great apes and of the majority of human societies, is the probable social organization of our common ancestor with the apes. Lovejoy's model is thus internally consistent but fails in the face of the evidence.

Karen Steudel argues that bipedalism is not likely to have replaced quadrupedalism on energetic grounds alone.[36] So we might consider the existence of an early bipedalism and a later bipedalism. This is speculative since we as yet have no fossil that exhibits a clearly different, unknown form of bipedal walking than ourselves.[37] However, it must have existed, since bipedalism arose over thousands of generations with each intermediate form molded by natural selection serving some useful purpose of its own. We do not know if the common ancestor of humans and great apes was a knuckle walker. Since all of the four great apes walk either on their knuckles or on the sides of their fists (orangutans), it is possible that there was a knuckle-walking stage in human evolution, as proposed many years ago by Sherwood Washburn and others.[38] If bipedalism arose for reasons other than enhancing walking efficiency, however, then the concern that it is more efficient than knuckle-walking but not more than quadrupedalism is unnecessary. But an early type of bipedalism, whether it arose from knuckle walking or not, could certainly have characterized the earliest hominids. The cause of this bipedalism could have been any of the hypotheses I presented earlier, or one that has yet to be proposed. The more modern form of bipedalism that we see in both ourselves and our known ancestors could have arisen later and been enhanced for energetic reasons.

One of the most striking differences between the foraging behavior of chimpanzees and that of humans is that chimpanzees crave the meat of other animals but do not search for it. Instead, they forage for plant foods and eat prey animals opportunistically in the course of looking for fruits and leaves. Certainly they are skilled hunters, particularly when in large groups. They could presumably obtain much larger amounts of meat if they actively searched for it. Yet there is little evidence that chimpanzees search for meat.[39] The only factor that could reasonably account for the chimpanzees' failure to search for food is that the return rate on their energy expenditure is not enough to do so. A biped can walk longer distances in search of desired food compared to a knuckle walker. Thus, if there was a knuckle-walking stage of hominid evolution through which early hominids passed, it would have precluded searches for unpredictable, moving sources of meat. Once bipedalism had evolved to a point of energetic efficiency, active searching could become justifiable, and meat would increase as a percentage of the diet.

Any model that seeks to explain human evolution must explain the enormous increase in the size of the neocortex of the brain in humans. I have already argued that, based on the behavior of chimpanzees, hominids ate meat much more frequently and at an earlier stage in their evolution than is commonly thought. This meat eating probably increased as early hominids began to use larger-sized animals as prey and as they began to use tools to make use of the carcasses. As the size of the brain increases during such a trend, one of the body's metabolically most expensive organs to maintain must be nourished. Where does the energy come from to nourish such a large brain? Leslie Aiello and Peter Wheeler have hypothesized that the energy to nourish an increasingly larger brain came from a metabolic trade-off in which the size and scope of the metabolic investment in the gut were reduced.[40] They suggest that in the course of primate evolution, the size of the brain has coevolved in inverse relation to the size of the digestive tract. This would partially explain why fruit-eating and meat-eating primates have shorter guts; these foods are more easily digested, allowing more energy to be devoted to increasing brain size. We know that leaf-eating animals sometimes have smaller brains and lower basal metabolic rates than fruit eaters of comparable body size. This relationship holds true among primates as well. Aiello and Wheeler suggest that the australopithecines improved the quality of food in their diet over that of their forerunners and thereby enabled a continued degree of encephalization. Likewise, among living primates the capuchin monkeys have among the highest brain-to-body-size ratio and also one of the highest-quality diets. This diet includes a high percentage of vertebrate animal protein. The implication of Aiello and Wheeler's "expensive tissue hypothesis" is that in a wide range of animal groups, those species that eat a high-quality diet should show greater brain development than those with a poor-quality diet. This has yet to be shown. But the notion that a high-quality diet frees the metabolism of an evolving hominid to develop a larger and larger brain is extremely appealing because it would explain both the trend toward greater encephalization and toward more meat in the diet of the evolution of the human lineage.

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