Chapter 6

Primate Models for Human Evolution

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SYNOPSIS

While many models have been developed to depict the behavior and ecology of our earliest relatives, the Man the Hunter model has been the most widely accepted view of human evolution. Many human traits (e.g., bipedalism, tools, and fire) are often linked to this perspective. Theories of human aggressive hunters abound but are rarely based on evidentiary approaches. Here is outlined a methodology using the fossil record and extant primate ecology and behavior. Data on fossil humans, modern primates, and rates of predation indicate that Man the Hunted may be the most accurate descriptor of our earliest relatives.

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MODELS OF HUMAN EVOLUTION

What kinds of evidence should be used in attempts to reconstruct the behavior of our earliest ancestors? The best evidence of early hominin behavior must include careful examination and understanding of the actual skeletal remains of the creatures. However, evidence of behavior also includes other substantiation (such as tools or footprints) left by the creatures, and other fossil materials that give us clues about the environment in which they lived (such as fauna, flora, or water sources). These fossils provide the most important data for an accurate reconstruction. Interestingly, some past reconstructions of early human behavior lacked a critical examination of the fossil evidence. We might say they were virtually fossil-free.

Besides fossils, any other types of secondary evidence used in reconstructions are less reliable, but nonetheless offer insights. These are ranked in the following order as far as applicability to developing models of early hominin lifestyles: (1) The behavior of nonhuman primates living under ecological conditions similar to those of our earliest ancestors (see also Elton, 2006). However, these conditions are different for different ancestors. Hominins likely began as edge species but moved onto the savanna about two million years ago (Conroy and Pontzer, 2012), and there were often several species living simultaneously. (2) The behavior of our genetically closest primate relatives, such as chimpanzees, bonobos, and gorillas (McGrew, 2010). However, the behavior of the great apes is very diverse and each species is unique, so simple analogs are not very useful. Yet, some behavioral characteristics may remain conservative within a taxonomic group. For example, monogamous pair bonds among the lesser apes (gibbons including siamangs), or upright posture among the great apes, might be considered phylogenetically conservative traits shared by all species within a taxon. (3) Characteristics shared by certain (or all) modern humans that also might be similar in our earliest ancestors. Modern foragers (see the chapter by Little and Blumler in the present volume), however, are just as advanced and evolved within their own culture and environment as any Western urban dwellers. Our least confident recommendation is (4) the behavior of other animal species that might be living under similar conditions or share some aspects of the lifestyle of early humans, such as certain carnivore or prey species. A cat is still a carnivore even if it eats some grass; early hominins opportunistically included a few vertebrates in their diet, but they cannot legitimately be compared to obligate meat eaters (Hladik et al., 1999; McDougall, 2003).

In using any of these types of secondary evidence, if we are not extremely careful (because in many cases similar-looking behaviors are not the same), we can end up comparing apples with oranges, lions with hominins, or even strangler figs with purse snatchers! Obviously, words with loaded meaning for humans—war, rape, murder, infanticide, and genocide to name a few—must be used with extreme caution when referring to the activities of nonhuman species. In this regard, Jonathan Marks (2002, p. 104) warns against "a science of metaphorical, not of biological, connection."

We cannot necessarily impute correlation, therefore, between human ancestors and data based on extant carnivores, modern human foragers, or great apes. For example, even the concept of hunting in chimps and humans is quite different. Present-day human hunters purposely search for prey, but chimpanzees do not: "Instead, they forage for plant foods and eat prey animals opportunistically in the course of looking for fruits and leaves" (Stanford, 1999, p. 48). Even though they do hunt for prey occasionally, they are basically frugivorous (Hladik, 1977; Milton and Demment, 1989; Boesch and Boesch-Achermann, 2000). Furthermore, reconstructions must always be compatible with the actual fossil data—the fossils are real but the models we construct are hypothetical and must constantly be tested and reconfirmed. Lastly, when attempting to construct models of our early ancestors' behavior, it is necessary to be precise about timing (Tattersall, 2010). If we say our earliest human ancestors (those who lived seven million years ago; see the chapter by Hunt) behaved in a certain way, we cannot use fossil evidence from two million years ago.

For example, could hunting by early hominins have occurred without tools? The first evidence of stone tools comes from around 2.6 million years ago (mya) (Semaw, 2000) (see chapter by Toth and Schick). The earliest hominin fossils, however, date from almost 7 mya, at least 4 million years before the first stone tools. In fact, when we look at the fossil evidence, hunting may have come quite late to our human family. Interpretations of hominin behavior, therefore, should be conservative and cautious, as stated by Jurmain et al. (2003) (Figure 1):

> *The mere presence of animal bones at archaeological sites does not prove that hominids were killing animals or even necessarily exploiting meat. Indeed, as was the case in the earliest South African sites, the hominid remains themselves may have been the meal refuse of large carnivores.*

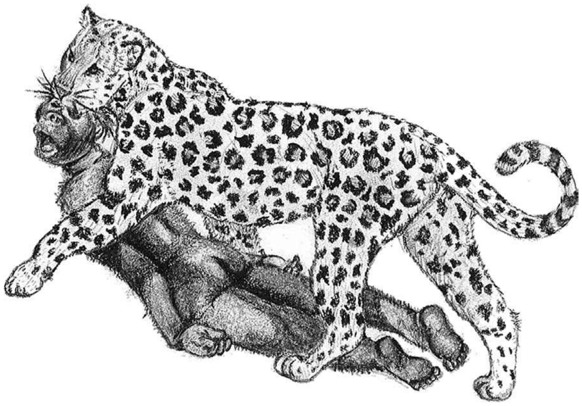

FIGURE 1 Predation by leopards on our earliest ancestors.

In examining one of the most accepted models of human evolution, the "Man the Hunter" model, we can see how fossil evidence may have been misused. The transition to hunting as a dominant way of life does not appear to have started until after the appearance of our own genus, *Homo*, and may not have even begun with the earliest members of our genus. *Homo erectus* has been given credit in the past for existing as a large animal hunter, with dates as far back as 1.75 mya hypothesized for such a lifestyle (Klein, 1999). But if a conservative approach to this subject is taken, looking only at facts and fossils, the first indications of hunting are amazingly recent. In fact, according to some paleontologists, the first unequivocal evidence of large-scale systematic hunting by humans is available from only 60,000–80,000 years ago (Binford, 1992; Klein, 1999). The earliest hominin fossils, therefore, existed almost 7 million years before the first factual evidence of systematic hunting by humans.

No actual fossil evidence of tools designed for hunting exists earlier than approximately 400,000 years ago—that evidence is a finely shaped wooden spear excavated at Schöningen, Germany (Dennell, 1997; Theime, 1997). Well-known sites in Spain, dated at 500,000 years ago, contain a huge number of large mammal bones and were thought to represent unquestionable evidence of megafauna killed by Pleistocene hunters. Now these sites are being reconsidered in light of better archaeological analysis. Elephant bones in situ could just as likely represent natural deaths or carnivore kills as the remains of human hunting (Klein, 1999; Klein et al., 2007). Further, no hominins were large-scale hunters before they had the use of fire (because of their dentition and alimentary tract, points we elucidate below), although insects, small vertebrates, lizards, and birds likely were eaten opportunistically. The best evidence for the controlled use of fire appears around 800,000 years ago in Israel (Goren-Inbar et al., 2004). Klein (1999, p. 160) states: "The assumption of consistent hunting has been challenged, especially by archaeologists who argue that the evidence does not prove the hunting hypothesis … it is crucial to remember (although not as exciting) that probably the majority of calories [came] from gathering plant foods."

DENTITION AND DIET

Whether *H. erectus* or any other hominin before 800,000 years ago hunted or scavenged may be a moot question. Hunting would only be an activity undertaken if early hunters could eat what they killed, and to eat raw meat it is necessary to have teeth capable of processing it.

Obviously, Man the Hunter models of human evolution assume that a significant portion of our earliest ancestors' diets must have come from killing and eating meat from relatively large mammals. By comparing the characteristics of the dental and jaw morphology of various living primates with those of fossils, we can make inferences about the diets of early hominins. Teaford and Ungar (2000), Ungar (2004) carried out such a comparison. Using the features of tooth size and shape, enamel structure, dental microwear, jaw biomechanics, occlusal slope, and relief of lower molars, they found that the earliest humans had a unique combination of dental characteristics and a diet different from those of modern apes and modern humans.

Australopithecus afarensis, who lived between 3.6 and 2.9 mya (and possibly as far back as 5 mya) (see the chapter by Ward), is characterized by thick jawbones, with comparatively small incisors and canines in relation to molars (Teaford and Unger, 2000). The molars, by comparison with other primates, are huge, flat, and blunt, show less slope and relief, and lack the long shearing crests necessary to mince flesh. *Australopithecus afarensis* also had larger front than back molars. The dental enamel is thick, and microwear on the teeth is a mosaic of gorilla-like fine wear striations (indicating leaf eating) and baboon-like pits and microflakes (indicating fruits, seeds, and tubers in the diet). This evidence all points away from meat eating.

In studies of mid- to large-sized primates such as macaques, baboons, chimpanzees, and modern human foragers for which the amount of time spent obtaining animal protein has been quantified, the total time is very low, usually making up less than five percent of time spent feeding (Garber, 1987; Sussman, 1999). Given these facts, we hypothesize that early humans were able to exploit a wide range of dietary resources, including both hard, brittle foods (e.g., tough fruits, nuts, seeds, and pods) and soft, weak foods (e.g., ripe fruits, young leaves and herbs, and flowers and buds). They may also have been able to eat abrasive objects, including gritty plant parts such as grass seeds, roots, rhizomes, and underground tubers. As stated by Teaford and Unger (2000, pp. 13508–13509), "this ability to eat both hard and soft foods, plus abrasive and nonabrasive foods, would have left early hominids particularly well suited for life in a variety of habitats, ranging from gallery forest to open savanna." Dental morphology indicates that the earliest hominins would have had difficulty breaking down tough pliant plant foods such as seed coats and mature leaves. Another tough pliant food that our early ancestors would have had difficulty processing was meat. Teaford and Unger state (2000, p. 13509): "The early hominids were not dentally preadapted to eat meat—they simply did not have the sharp, reciprocally concave shearing blades necessary to retain and cut such foods."

Both modern chimpanzees and humans have alimentary tracts that are specialized for the eating of neither leaves nor animal protein, but instead are more generalized and similar to those of the majority of primates who are omnivorous and eat a mixture of food types (Martin et al., 1985; Martin, 1990). Modern humans, especially in Western cultures, think of themselves as meat eaters. For Americans and many other cultures, meat defines that ephemeral status of wealth for which we strive. Because they themselves were rooted in these cultural stereotypes, anthropologists egregiously misnamed the modern forager cultures as hunter-gatherers and initially emphasized the contributions of male hunters. Nevertheless, more than two-thirds of modern-day foragers' food comes from gathering of plant foods by women, who in the process opportunistically capture small mammals and reptiles. Less than one-third of the diet (the meat portion brought in by male hunters) serves to supplement their foraged nutritional intake, except in cold climates or where fishing is prevalent (Marlowe, 2005).

Lastly, we believe that hominins did not hunt on a large scale before the advent of controlled fire. Again, we have neither the dentition nor the digestive tract of a carnivore. Our anatomy and physiology did not particularly suit us for digesting meat until the mastery of cooking solved the problem. Our intestinal tract is short, and predigestion by cooking with fire had to precede any major meat eating. As stated above, the oldest known hearths with good evidence for controlled use of fire are around 800,000 years old.

LOCOMOTION

By far the best known australopith is *A. afarensis*. Collections from Hadar, Ethiopia alone have yielded 250 specimens, representing at least 35 individuals, and there are a number of other East African sites with remains of this species (Kimbel and Delezene, 2009). Specimens include the famous Lucy (dated 3.2 mya), the most complete adult skeleton from this time period, and fossil footprints from Laetoli, Tanzania (dated 3.6 mya). Most hypotheses concerning human evolution position *A. afarensis* as a pivotal species from which all other later hominins, including *Homo*, evolved (Fleagle, 1999; Tattersall, 2010; Conroy and Pontzer, 2012). Given the above facts, we see *A. afarensis* as a good species to examine when attempting to develop models of early human behavior (Figure 2).

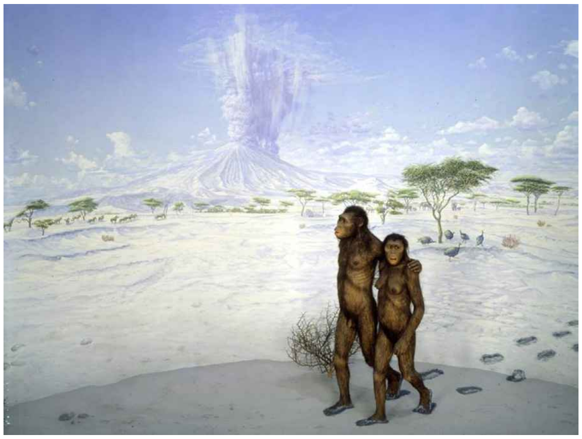

FIGURE 2 A reconstruction of two *Australopithecus afarensis* (used by permission of American Museum of Natural History AMNH Library 4936[2]). (See color plate section).

Terrestrial bipedalism is a hallmark of the fossil hominin family. This mode of locomotion can be inferred from fossil specimens that are nearly seven million years old (Galik et al., 2004—but see the chapter by Hunt for full explanation). It appears long before the vast growth of open grasslands in Africa and before the expansion of human brain size and recognizable stone toolmaking. Besides the fossilized bones, direct evidence of early bipedalism comes from the fossilized footprints at Laetoli (White, 1980; Tuttle, 1985). Looking at the skeletal evidence, however, the locomotion of these early hominins was not exactly identical to ours.

Australopithecus afarensis seems to have been a primate equally at home in the trees and on the ground, as indicated by several factors. First, the limb proportions are different from those of modern humans. The arms are similar in proportion to those of modern humans, but the legs are relatively shorter and more apelike, implying the use of suspensory locomotion in trees (Kimbel et al., 1994). Other aspects of the upper limbs retain features indicating an ability to move easily in the trees. The wrist and hand bones are quite chimpanzee-like, and the finger and toe bones are slender and curved as in apes, giving *A. afarensis* grasping capabilities compatible with suspensory behaviors. The toe bones are relatively longer and more curved than in *Homo sapiens*, and the joints of the hands and feet, as well as the overall proportions of the foot bones, reinforce evidence for climbing adaptations and arboreal activity. Nevertheless, the relative thumb length of these hominins is closer to that of modern humans than it is to chimpanzees (Susman et al., 1984; Conroy and Pontzer, 2012). The pelvis and lower limbs of *A. afarensis* are a mixture of humanlike and apelike features. Overall, Rak (1991, p. 283) summarizes: "Although clearly bipedal and highly terrestrial, Lucy evidently achieved this mode of locomotion through a solution of her own."

It appears that the combination of skeletal characteristics found in *A. afarensis* enabled these hominins to be quite versatile. They were able to use the ground and the trees equally and successfully for a very long time. We believe these early hominins were well adapted to their environment and not in the least inhibited by switching back and forth from bipedalism on the ground to quadrupedalism in the trees.

There have been several models proposed to account for the evolution of human bipedalism, each using specific behavioral or morphophysiological traits (e.g., tool using, carrying, vigilance, heat dissipation, and energy efficiency). Each model has some merit, but none of the theories seem to catch the significance of switching a method of locomotion. Furthermore, there are many other primates who spend most of their time on the ground, yet none has developed bipedalism, even though each of the theorized advantages presumably also could have accrued to them.

It is difficult to separate consequence from causation. We cannot conclude that any of the suggested models above caused hominins to become bipedal (again, see the chapter by Hunt). None of the theories may be causative; instead, all the theoretical causes may be results of a preadaptation to being bipedal. All the great apes are preadapted to bipedalism. When our ancestors came down from the trees, bipedalism was possible because of body proportions and suspensory adaptations—longer arms and shorter legs that allow gibbons, orangutans, and chimpanzees to hang from trees and forage for fruit. All apes have varying capacities for erect posture and are able to walk upright; bonobos, especially, will stride upright with humanlike posture. Further, we propose that when the earliest hominins began using the ground for a major portion of their activities, their body proportions were more suited for bipedalism than for other forms of locomotion. As stated by Fleagle (1999, p. 528):

> *Although it is important to see early hominids in the context of hominoid evolution, it is equally important to realize that in the same way that they were not little people, they also were not just bipedal chimps, but the beginning of a new radiation of very different hominoids. It is this uniqueness that makes reconstructing hominid origins so difficult. Thus although early hominids and their bipedal adaptations are certainly derived from an African apelike ancestry, human bipedalism is morphologically and physiologically different from the occasional facultative bipedal behaviors occasionally seen in other primates. The morphological and behavioral commitment to bipedalism that characterized early hominids suggests unique ecological and historical circumstances as well.*

Some primate species are intrinsically adapted to edge habitats and therefore able to take advantage of changing environments. We hypothesize that the earliest hominins were edge species (see below), and that they exploited a terrestrial habitat due to a developing mosaic environment that included climate change. Rather than seeking the factors that *caused* early human ancestors to become bipedal, we propose that it was a preadaptation that already existed, and it was efficient in a new habitat; the successes or added advantages were simply by-products.

Besides bipedalism and limb use, there are solid conjectures of what our earliest ancestors were like as far as body build, height, weight, and brain capacity.

From various *A. afarensis* specimens and by examining the skeleton of Lucy, it seems that there was a considerable size difference between males and females. Although the canines of both sexes were relatively small and not at all daggerlike, they were larger and longer in the males than in the females. The range of body size for *A. afarensis* individuals is estimated to be 30–45 kg (Fleagle, 1999). The height of the adults has been estimated at 1.0–1.7 m (Klein, 1999). Lucy stood slightly over 1 m tall and weighed around 30 kg (she was definitely on the small side) (Conroy and Pontzer, 2012). If these weights are accurate, we can extrapolate that female *A. afarensis* were the size of male baboons, and males were the size of female chimpanzees.

The cranial capacity of these hominins is estimated at 400–500 cubic centimeters—about the size of a modern chimpanzee, but twice as large as early, Miocene fossil apes. On average, australopiths and modern chimpanzees have brains that are two to three times larger than those of similar-sized mammals, whereas the modern human brain is six to seven times larger than that of other mammals.

Looking at brain size relative to body size, using the encephalization quotient as a measurement, the brain of *A. afarensis* was slightly larger in relation to its body than that of modern chimpanzees (EQ = 2.4 for *A. afarensis* vs. 2.0 for chimpanzees) (Boaz, 1997). Thus, our ancestors were midsized to relatively large-sized primates with brains that were slightly larger than that of any nonhuman primate, although only a fraction bigger than those of modern chimpanzees.

HABITAT OF OUR EARLIEST ANCESTORS

Although many early theories of human evolution stress the importance of arid, savanna environments, these seem to have become primary habitats beginning only about 2 mya (see chapter by Sept for complete discussion). The African climate was becoming more arid in the time between 12 and 5 mya, and equatorial forests were undoubtedly shrinking (Conroy and Pontzer, 2012). However, the process that led to this climatic phenomenon also greatly enlarged transitional zones between forest and adjacent savanna. Closed woodland forests were still widespread in East Africa 3.5 mya, whereas the proportion of dry shrub to grassland habitats began to increase around 1.8 mya (Schekleton, 1995).

It is in these transitional zones that the behavioral and anatomical changes were initiated in early hominin evolution. The flora and fauna remains found in association with fossil hominins of this time period indicate a mixed, mosaic environment—ecologically diverse and subject to seasonal and yearly changes (Potts, 1996; Wolpoff, 1998; Conroy and Pontzer, 2012). These environments were wetter than those in which later fossil hominins are found, and most fossil sites of this time period contained water sources such as rivers and lakes (WoldeGrabriel et al., 2001; Wrangham et al., 2009).

Thus, the earliest hominins appear to be associated with variegated fringe environments or edges between forest and grassland (Sept, 2013). These habitats usually contain animal and plant species of both the forest and the grassland, as well as species unique to the borders between the two, often referred to as *edge* species. During these earliest times, it appears that hominins began to take advantage of the growing fringe environments, lessening competition with their sibling ape species that were better adapted to exploit the dense forest, thus partitioning the niche occupied by the parent species of both apes and hominins into two narrower and less overlapping adaptive zones (Klein, 1999; Lee-Thorp et al., 2003; Reed, 2008; Conroy and Pontzer, 2012).

From available evidence, we speculate that our early ancestors were able to exploit a great variety of food resources but were mainly fruit eaters, probably supplementing this diet with some young leaves and other plant parts, social insects, and a small number of opportunistically captured small vertebrate prey—lizards, small snakes, birds, and mammals. They also likely exploited some freshwater and marine resources (Cunnane and Stewart, 2010).

Several other primate species are intrinsically adapted to edge habitats and thus can also take advantage of changing environments. Madagascan ring-tailed lemurs, African baboons and vervet monkeys, and some Asian macaques and langurs are nonhuman primate examples. Not coincidentally, these are some of the most common and numerous of all living nonhuman primates. The macaque genus (*Macaca*), for example, has the widest geographical distribution of any nonhuman primate in Asia. Many macaque species in Asia are endangered, but the ones that have the healthiest populations (e.g., long-tailed macaques, *Macaca fascicularis*, and rhesus macaques, *M. mulatta*) are edge-adapted.

Certain ecological niches may breed certain behavioral repertoires. Many argue that the closer the DNA comparison, the more similar the behaviors between two related species (McGrew, 2010). In that case, chimps and bonobos would be the best prototypes for early human ancestors. However, if ecology is paramount, chimps and bonobos may be less suitable prototypes (although some traits between these close relatives may still be important and phylogenetically conservative), and the best models for early humans may be edge species.

Nearly 40 years ago, Robin Fox (1967, p. 419) declared:

> *But the problem of taking the great apes as models lies in the fact of their forest ecologies. Most modern students of primate evolution agree that we should pay close attention to ecology in order to understand the selection pressures at work on the evolving primate lines. This has been shown to be crucial in understanding … evolution.*

Even if one were to learn everything about the hominin-ape common ancestor, many of the most crucial questions about distinctively hominin evolution would remain unanswered. Although there is a fairly impressive record of human fossils during the period of 7 to 2 mya, there is a lack of great ape fossils at these early sites. Therefore, it seems likely that chimpanzee and gorilla ancestors did not inhabit these fringe environments and were instead restricted to closed forest ecosystems—areas where fossils are less likely to be preserved (Stewart, 2010). Some populations of chimpanzees moved into more mosaic, open habitats relatively recently, long after humans had moved into these environments. Furthermore, modern chimpanzees do not live in habitats in which modern humans lived in the past or are found today. The historical geographic range of chimpanzees is quite restricted, probably more restricted than even that of early humans before leaving Africa.

In our opinion, the best primate models to use as a basis for extrapolation about behavioral characteristics of our earliest ancestors are modern primate species living in edge habitats. Macaques can be extremely good colonizers of edge habitats. The macaque genus spread throughout Asia before humans reached that continent (Delson, 1980). By the time *Homo erectus* arrived in Asia 1.8 mya, most hominins were no longer edge species—our more recent ancestors were exploiting more open habitats by this date (Tattersall, 2010)—so hominins likely did not displace macaques. We propose that the macaques, true "weed" species, are excellent models for reconstructing how our earliest ancestors lived. Many of the features of the behavior and ecology of macaques are very similar to those of other primates living in similar habitats. In our opinion, it is these shared characteristics that make this such a strong model. After all, it is the environment in which species find themselves that determines many of their evolutionary adaptations.

THE MACAQUE MODEL

Long-tailed macaques (*M. fascicularis*) are small edge-dwelling species that spend a good proportion of time both in the trees and on the ground. They are omnivorous and very versatile in their locomotion, although mainly quadrupedal. The most widespread of any Southeast Asian monkey, they occur from Burma through Malaysia and from Thailand to Vietnam, while offshore populations are found on Java, Borneo, and numerous smaller islands as far east as the Philippines and Timor. Throughout this area, broadleaf evergreen and other forest types are interspersed with secondary and disturbed habitats, and it is the latter that long-tailed macaques prefer. They are most commonly found in secondary forest habitat, preferably near water (Sussman et al., 2011). The success of the long-tailed macaque throughout its Asian distribution is widely credited to its being an "adaptable opportunist" (MacKinnon and MacKinnon, 1980, p. 187). Researchers emphasize that these monkeys are extremely adaptable and able to flourish in highly disturbed land (Figure 3).

These are slender, active monkeys; average weight is 4–5 kg for females and 6–7.75 kg for males. Long-tailed macaque society is organized around matrilineal hierarchies. There are always one or two dominant males within the group, as well as some lower-ranking adult males, plus the adolescent and subadult male offspring of the females. At sexual maturity, males migrate to a new group. Female offspring are philopatric, but mate with unrelated males who join their group (Jamieson, 1998).

In most primates adapted to edge environments, it is the males who migrate. However, in the closest genetic relatives of humans, the African great apes, females normally change

FIGURE 3 Long-tailed macaques (*Macaca fascicularis*). (See color plate section).

groups when they mature. This appears to be a phylogenetically conservative characteristic among hominoids, which makes it possible that among our earliest ancestors, females rather than males migrated between groups. However, among most modern human foragers, individuals reside with their maternal relatives at times and with their paternal relatives at other times, or sometimes with neither (Marlowe, 2005).

The ability of edge species to exploit a wide variety of environments is accompanied by substantial behavioral flexibility. Long-tailed macaques appear to be primarily arboreal where suitable vegetation exists, but they come to the ground along riverbanks, seashores, and in open areas—and in some portions of their recently colonized range, such as Mauritius, they are highly terrestrial (Sussman and Tattersall, 1981). They are eclectic omnivores with a distinct preference for fruit. But the variety of habitat they exploit is reflected in a wide selection of food items—leaves, grasses, seeds, flowers, buds, shoots, mushrooms, water plants, gum, sap, bark, insects, snails, shellfish, bird eggs, and small vertebrates (Sussman et al., 2011). Human-disturbed habitat or proximity to human settlements is not avoided; rather, they tend to live in proximity to humans throughout their range, which results in crop raiding of sugar cane, rice, cassava, and taro fields.

Long-tailed macaques live in large multimale, multifemale groups of up to 80 individuals, although in some areas groups are much smaller. They show distinct flexibility in structure; the large basic social unit tends to split into smaller subgroups for daytime foraging activities. Subgroups may be all males, but most often consist of adult males accompanying females and their young. The number and size of subgroups vary with season and resource availability (Jamieson, 1998). The entire troop re-forms each evening and returns to the same sleeping site each night, usually on the edge of a water source. Because of their unique behavior of returning to a home base each night, long-tailed macaques are referred to as "refuging" species.

FOSSILS AND LIVING PRIMATES

Looking at the fossil evidence, it is apparent that human ancestors living from 7 to 2.5 mya were intermediate-sized primates not smaller than male baboons or larger than female chimpanzees. Given their relative brain size, they were at least as clever as the great apes of today. They had diverse locomotor abilities, exploiting both terrestrial and arboreal habitats. They used climbing and suspensory postures when traveling in the trees and were bipedal when on the ground. We believe that their bipedalism was a preadaptation, but walking on two feet freed the arms and hands and proved to be advantageous in many ways.

Given their relatively small size and small canines, there is no reason to think that our early ancestors were any less vulnerable to predation than are modern monkeys—some of which have yearly predation rates generally comparable to those of gazelles, antelopes, and deer (Hart, 2000; Hart and Sussman, 2009). Indeed, edge species can be highly vulnerable to predation, and because of this usually live in relatively large social groups with many adult males and adult females; adult males often serve as sentinels and provide protection against predators. Because a primate group with only one male and 10 females can have the same reproductive output as a group with 10 males and 10 females, often the male role in primate groups is to act as a first line of defense; if he gets eaten there are other males to take his place. If a sexually mature female gets eaten, then she and all her potential offspring are lost.

We propose that, like long-tailed macaques, our hominin ancestors may have lived in multimale, multifemale groups of variable size that were able to split up depending on the availability of food and re-form each evening at home base refuges. However, certain facts such as the exact size of the groups and subgroups, whether males or females migrated from the group when they reached sexual maturity, the internal structure of the group (whether matrilineal or formed along male kinship lines), are impossible to determine accurately. Indications of these social parameters cannot be found in the fossil record and are quite variable even in closely related living primates.

In sum, the best archetype of early hominins may be multimale, group-living, midsized, omnivorous, quite vulnerable creatures living in an edge habitat near a large water source. These primates may well have been a refuging species returning to the same well-protected sleeping site each night. Most modern foragers are considered central-place foragers focusing their activities around a principal location, as are many birds, social carnivores, and primates (Marlowe, 2005). These creatures were adept at using both the trees and the ground, but when they exploited the terrestrial niche, they had upright posture and were bipedal. They depended mainly on fruit, including both soft fruits and some that were quite brittle or hard, but also ate herbs, grasses, seeds, and gritty foods such as roots, rhizomes, and tubers. A very small proportion of their diet was made up of animal protein, mainly social insects (ants and termites) and occasionally small vertebrates captured opportunistically. These early hominins did not regularly hunt for meat and could process it neither dentally nor in their digestive tracts.

Like all other primates, especially ground-living and edge species, these early hominins were very vulnerable to predators and this trait did not diminish greatly over time. Fossil evidence to this effect exists from South Africa, the Zhoukoudian cave in China (Boaz et al., 2004), skulls uncovered at Dmanisi in the Republic of Georgia, and a fossil found at Olorgesailie, Kenya (Hart and Sussman, 2009).

MAN THE HUNTED

Given that the earliest hominin ancestors were medium-sized primates without any inherent weapons to fight off the many predators that lived then—and given that they lived in edge environments that incorporated open areas and wooded forests near rivers—they were vulnerable to predation like other primates were. Because of this, we hypothesize that rates of predation were just as high in our early ancestors as they are in modern species of primates, and our origins are those of a hunted species (Hart and Sussman, 2009).

Protection from predation is one of the most important aspects of group living, and we believe that this was true of our earliest ancestors. Based on the long-tailed macaque model, social groups of early hominins may have been organized in a way that allowed efficient exploitation of a highly variable and changing environment and also protected its members from predators. Thus for early hominins, we propose several strategies for protection from predators based on the behavior and social organization we observe in long-tailed macaques.

- Relatively large groups of 25–75 individuals: Since safety lies in numbers, a main reason that all diurnal primates live in groups is for predator protection. In his research on modern human foragers, Marlowe (2005) found that the median group size is 30 individuals.
- Versatile locomotion that exploits both arboreal and terrestrial milieus: The major advantage of agility in the use of diverse habitats is safety in trees and dense underbrush. An added advantage of upright posture is the ability to scan for predators.
- Flexible social organization: Gathering scarce resources in small groups, but reuniting as a larger group when predation requires strength in numbers, allows small groups to quickly disperse and hide while large groups can mob and intimidate predators. Again, modern human foragers fit this pattern of flexibility (Marlowe, 2005).
- Multimale social structure: This provides more male protection when traveling through open areas and when the group settles in the evening or at midday. When large groups break into subgroups, females and young are accompanied by one or more larger males.
- Males as sentinels: Males are usually larger in these species. Upright posture adds to the appearance of large size and also allows for better vigilance and improved ability to wave arms, brandish sticks, and throw stones. Males mob or attack predators, since they are the more expendable sex.
- Careful selection of sleeping sites: Refuging species bring the whole group together at night in a safe area. During daytime rest periods, staying in very dense vegetation is essential. Males stay on high alert during these inactive periods and when the group is on the move.
- Remain one step ahead of predators: Intelligence endows primates with the ability to monitor the environment, communicate with other group members, and implement effective antipredator defenses (Hart and Sussman, 2009).

Our reconstruction of the behavior and ecology of our earliest hominin ancestors reflects the pervasive influence of large ferocious predatory animals throughout human evolution. Many circumstances have been proposed as a catalyst for the evolution of the human species—competition for resources, intellectual capacity, male–male conflicts, and hunting. But looking at our primate relatives and the fossil record, predation pressure was probably one of the most critical components in shaping human evolution.

REFERENCES

Binford, L., 1992. Subsistence—a key to the past. In: Jones, S., Martin, R., Pilbeam, D. (Eds.), Cambridge Encyclopedia of Human Evolution. Cambridge University Press, Cambridge, pp. 365–368.

Boaz, N., 1997. Eco Homo. Basic Books, New York.

Boaz, N., Ciochon, R., Xu, Q., Liu, J., 2004. Mapping and taphonomic analysis of the *Homo erectus* loci at locality 1 Zhoukoudian, China. Journal of Human Evolution 46, 519–549.

Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of Tai Forest: Behavioural Ecology and Evolution. Oxford University Press, Oxford.

Conroy, G.C., Pontzer, H., 2012. Reconstructing Human Origins: A Modern Synthesis, third ed. W. W. Norton & Company, New York.

Cunnane, S.C., Stewart, K.M. (Eds.), 2010. Human Brain Evolution: The Influence of Freshwater Fish and Marine Resources. John Wiley & Sons, New York.

Delson, E., 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: Lindburg, D.G. (Ed.), The Macaques: Studies in Ecology, Behavior and Evolution. Van Nostrand-Reinhold, New York, pp. 10–30.

Dennell, R., 1997. The worlds oldest spears. Nature 385, 787–788.

Elton, S., 2006. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in paleoanthropology. Journal of the Royal Anthropological Institute 12, 19–38.

Fleagle, J., 1999. Primate Adaptation and Evolution, second ed. Academic Press, New York.

Fox, R., 1967. In the beginning: aspects of hominid behavioural evolution. Man 2, 415–433.

Galik, K., Senut, B., Pickford, M., Gommery, D., Treil, J., Kuperavage, A.J., Eckhardt, R.B., 2004. External and internal morphology of the BAR 1002’00 *Orrorin tugenensis* femur. Science 305, 1450–1453.

Garber, P.A., 1987. Foraging strategies among living primates. Annual Review of Anthropology 16, 339–364.

Goren-Inbar, N., Alperson, N., Kislev, M., Simchoni, O., Melamed, Y., Ben-Nun, A., Werker, E., 2004. Evidence of hominin control of fire at Gesher Benot Ya’aqov, Israel. Science 304, 725–727.

Hart, D., 2000. Primates as Prey: Ecological, Morphological, and Behavioral Relationships between Primate Species and Their Predators (Ph.D. thesis). Washington University, St. Louis.

Hart, D., Sussman, R.W., 2009. Man the Hunted: Primates, Predators, and Human Evolution, expanded ed. Westview Press, New York.

Hladik, C., 1977. Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In: Clutton-Brock, T. (Ed.), Primate Ecology: Studies of the Feeding and Ranging Behaviour in Lemurs, Monkey and Apes. Academic Press, New York, pp. 481–501.

Hladik, C., Chivers, D., Pasquet, P., 1999. On diet and gut size in nonhuman primates and humans. Is there a relationship to brain size. Current Anthropology 40, 695–697.

Jamieson, R.W., 1998. The Effects of Seasonal Variation in Fruit Availability on Social and Foraging Behavior in *Macaca fascicularis* in Mauritius (Ph.D. thesis). Washington University, St. Louis.

Jurmain, R., Kilgor, L., Trevathan, W., Nelson, H., 2003. Introduction to Physical Anthropology, ninth ed. Wadsworth/Thomson Learning, California.

Kimbel, W., Delezene, L.K., 2009. “Lucy” redux: a review of research on *Australopithecus afarensis*. Yearbook of Physical Anthropology 52, 2–48.

Kimbel, W., Johanson, D., Rak, Y., 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. Nature 368, 449–451.

Klein, R.G., 1999. The Human Career: Human Biological and Cultural Origins, second ed. University of Chicago Press, Chicago.

Klein, R.G., Avery, G., Cruz-Uribe, K., Steele, T.E., 2007. The mammalian fauna associated with an archaic hominin skull cap and later *Acheulean artifacts* at Elandsfontain, Western Cape Province, South Africa. Journal of Human Evolution 52, 164–186.

Lee-Thorp, J.A., Sponheimer, M., van der Merwe, N.J., 2003. What do stable isotopes tell us about hominid dietary and ecological niches in the Pliocene? International Journal of Osteoarchaeology 13, 104–113.

MacKinnon, J.R., MacKinnon, K.S., 1980. Niche differentiation in a primate community. In: Chivers, D.J. (Ed.), Malayan Forest Primates. Plenum Press, New York, pp. 167–190.

Marks, J., 2002. What it Means to Be 98% Chimpanzee: Apes, People, and Their Genes. University of California Press, Berkeley.

Marlowe, F.W., 2005. Hunter-gatherers and human evolution. Evolutionary Anthropology 14, 54–67.

Martin, R.D., 1990. Primate Origins and Evolution: A Phylogenetic Reconstruction. Princeton University Press, Princeton.

Martin, R.D., Chivers, D.J., MacLarnon, A.M., Hladik, C.M., 1985. Gastrointestinal allometry in primates and other mammals. In: Jungars, W.L. (Ed.), Size and Scaling in Primate Biology. Plenum Press, New York, pp. 61–90.

McDougall, J., 2003. Meat in the human diets. The McDougall Newsletter. 2 (7). www.drmcdougall.com.

McGrew, W.C., 2010. In search of the last common ancestor: new findings on wild chimpanzees. Philosophical Transactions of the Royal Society B 365, 3267–3276.

Milton, K., Demment, M., 1989. Features of meat digestion by captive chimpanzees *(Pan Troglodytes)*. American Journal of Physical Anthropology 18, 45–52.

Potts, R., 1996. Evolution and climate variability. Science 273, 922–923.

Rak, Y., 1991. Lucy’s pelvic anatomy: its role in bidpedal gait. Journal of Human Evolution 20, 283–290.

Reed, K.E., 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. Journal of Human Evolution 54, 743–768.

Schekleton, N.J., 1995. New data on the evolution of Pliocene climatic variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 242–248.

Semaw, S., 2000. The world’s oldest stone artifacts from Gona, Ethiopia: their implication for understanding stone technology and pattern of human evolution between 2.6–1.5 million years ago. Journal of Archaeological Science 27, 1197–1214.

Sept, J., 2013. Plants and proto-people: paleobotanical reconstruction and modeling early hominin ecology. In: Sponheimer, M., Lee-Thorp, J.A., Reed, K.E., Unger, P. (Eds.), Early Hominin Paleoecology. Boulder: University Press of Colorado, pp. 355–396.

Stanford, C., 1999. The Hunting Ape: Meat Eating and the Origins of Human Behavior. Princeton University Press, Princeton.

Stewart, K.M., 2010. The case for exploitation of wetlands environments and foods by presapiens hominins. In: Cunnane, S.C., Stewart, K.M. (Eds.), Human Brain Evolution: The Influence of Freshwater Fish and Marine Resources. John Wiley & Sons, New York, pp. 137–171.

Sussman, R.W., 1999. The species-specific dietary patters in primates, and human dietary patterns. In: Sussman, R.W. (Ed.), The Biological Basis of Human Behavior: A Critical Review. Prentice Hall, New Jersey, pp. 143–157.

Susman, R.L., Stern Jr., J.T., Ungars, W.L., 1984. Arboreality and bipedality in the Hadar hominids. Folia Primatologica 43, 113–156.

Sussman, R.W., Tattersall, I., 1981. Behavior and ecology of *Macaca fascicularis* in Mauritius: a preliminary study. Primates 22, 192–205.

Sussman, R.W., Shaffer, C.W., Guidi, L.M., 2011. *Macaca fascicularis* in Mauritius: implications for macaque-human interactions and for future research on long-tailed macaques. In: Gumert, M.D., Fuentes, A., Jones-Engel, L. (Eds.), Monkeys on the Edge. Cambridge University Press, New York, pp. 207–235.

Tattersall, I., 2010. Macroevolutionary patterns, exaptation, and emergence in the evolution of the human brain and cognition. In: Cunnane, S.C., Stewart, K.M. (Eds.), Human Brain Evolution: The Influence of Freshwater Fish and Marine Resources. John Wiley & Sons, New York.

Teaford, M., Ungar, P., 2000. Diet and the evolution of the earliest human ancestors. Proceedings of the National Academy of Sciences 97, 13506–13511.

Theime, H., 1997. Lower Paleolithic hunting spears from Germany. Nature 385, 807–810.

Tuttle, R.H., 1985. Ape footprints and Laetoli impressions: a response to the SUNY claims. In: Tobias, P.V. (Ed.), Hominid Evolution: Past, Present and Future. Alan R. Liss, New York, pp. 129–130.

Ungar, P., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. Journal of Human Evolution 46, 605–622.

White, T.D., 1980. Evolutionary implications of Pliocene hominid footprints. Science 208, 175–176.

WoldeGrabriel, G., Haile-Selassie, Y., Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B., Heiken, G., White, T., 2001. Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. Nature 412, 175–181.

Wolpoff, M., 1998. Paleoanthropology, second ed. McGraw Hill, New York.

Wrangham, R., Cheney, D., Seyfarth, R., Sarmiento, E., 2009. Shallow-water habitats as sources of fallback foods for hominins. American Journal of Physical Anthropology 140, 630–642.