

# Transitions in Prehistory

Essays in Honor of Ofer Bar-Yosef



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Edited by

John J. Shea and Daniel E. Lieberman



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## THE TRANSITION FROM AUSTRALOPITHECUS TO HOMO

Daniel E. Lieberman, David R. Pilbeam, and Richard W. Wrangham

### **Preamble**

This paper is in honor of Ofer Bar-Yosef's seventieth birthday and his remarkable career. One of Ofer's many admirable qualities is his enjoyment of a friendly exchange over speculative hypotheses. In this spirit, we offer a perhaps typically "Harvard-dogma" approach to the origins of the archaeological record and the behavioral transition from *Australopithecus* to *Homo*. We are mindful of the lack of data available to test our model, but we hope it will be received as intended: as a springboard for speculating about one of the most fundamental transitions that occurred in human evolution.

### **Introduction**

Of the various transitions that occurred during human evolution, the transition from *Australopithecus* to *Homo* was undoubtedly one of the most critical in its magnitude and consequences. As with many key evolutionary events, there is both good and bad news. First, the bad news is that many details of this transition are obscure because of the paucity of the fossil and archaeological records. The oldest known archaeological sites from 2.6 million years ago (Semaw et al. 1997; Dominguez-Rodrigo et al. 2006) provide, at best, a sparse and incomplete glimpse of early hominin behavior (see Stern 1993). In addition, it is unclear who made the oldest tools, and the fossil record itself leaves much to be desired. The genus *Homo* is probably at least 2.3 million

years old (Kimbrel et al. 1997), but most of the fossil evidence for early *Homo* comes from the period between 1.9 and 1.6 million years ago from just a few localities in the East African Rift Valley. In addition, fossils attributed to *H. habilis* are poorly associated with inadequate and fragmentary postcrania (Johanson et al. 1987), no fossils attributed to *H. rudolfensis* are associated with any postcrania, and the earliest material attributed to *H. erectus* is highly variable, and contemporary with *H. habilis* and *H. rudolfensis* (Spoor et al. 2007). Finally, the relationship between the oldest *Homo* from Africa and Eurasia (at Dmanisi) remains murky because of their morphological variability and nearly contemporary ages (Lieberman 2007). When we discuss early *Homo*, we do not know for sure how many species we are dealing with and how different they are.

But there is good news: although we lack many details about exactly how, when, and where the transition occurred from *Australopithecus* to *Homo*, we have sufficient data from before and after the transition to make some inferences about the overall nature of key changes that did occur between australopiths such as *A. afarensis* and unambiguous *H. erectus*. When viewed from a distance, it is evident that the transition involved some increase in body size, an increase in absolute brain size, a substantial diminution of tooth and face size, and a shift to a much more human-like body shape, including relatively longer legs (see Wood and Collard 1999;

Lieberman 2007). An important caveat, however, is that some or all of these shifts may not have been as dramatic and rapid as once thought. Body mass and stature range from 30 to 50 kg and 100 to 150 cm, respectively, in australopiths and from 50 to 70 kg and 160 to 185 cm in early African *H. erectus* (McHenry 1988; Anton 2003); however, *H. erectus* fossils from Dmanisi range from 40 to 50 kg and 145 to 160 cm (Lordkipanidze et al. 2007). In addition, some early African *H. erectus* fossils appear to have been quite small, though not as small as females from Dmanisi (Spoor et al. 2007). Moreover, although absolute brain size does increase across the transition, larger brains in early *Homo* apparently scale with body size, so that encephalization quotients (EQs) in the early African and Georgian *H. erectus* individuals are not much different from those of australopiths (Anton 2003; Rightmire 2004; Lordkipanidze et al. 2007).

Regardless of the tempo of the transition, and whether the fossils commonly assigned to *H. erectus* sample two species (one smaller and the other larger), the general suite of changes that we observe suggests increased locomotor efficiency, the appearance of endurance-running capabilities, the loss of many arboreal locomotor capabilities, and an increased ability to thermoregulate in hot, arid conditions (see Wheeler 1991; Ruff 1991; Bramble and Lieberman 2004; Anton et al. 2002; Pontzer 2007). These transitions were almost certainly related to a profound behavioral shift characterized by an increase in meat acquisition through scavenging and/or hunting, and the regular manufacture of stone tools designed for regular extracting and processing (Shipman and Walker 1989; Schick and Toth 1993). Moreover, it is reasonable to infer that these observable changes probably reflect behavioral transitions, such as

increased cognitive capacities, more food sharing and central-place provisioning, a sexual division of labor, larger day ranges, and so on.

However, not all aspects of *H. erectus* biology were like those of recent humans. For example, *H. erectus* life history was apparently much like that of chimpanzees and australopiths (Dean et al. 2001; Dean 2006); they may not have had a full capacity for language, and the extent to which they were able to extract versus collect resources may have been limited. Nevertheless, it is reasonable to infer that at least some of the essential elements of the hunter-gatherer way of life were present – albeit in a nascent form – in early *H. erectus*.

Here we ask to what extent the many diverse aspects of this momentous transition were integrated. Although it is common and often necessary to consider the origins of derived features such as toolmaking, meat-eating, or endurance running in isolation, it is widely assumed, often implicitly, that these and/or other derived aspects of hominin biology are partially linked. This is a reasonable assumption because natural selection operates on heritable aspects of an organism's phenotype that improve reproductive success. Many aspects of phenotype are non-independent in terms of how they are selected because they operate in the context of a combined set of strategies that affect fitness in particular environmental conditions. Put differently, natural selection often operates on suites of traits, behavioral and morphological, that function as a system. This begs the question, What was the system? In the case of the genus *Homo*, we are not alone in hypothesizing that many of the shifts evident in both the fossil and the archaeological records across this transition are part of a broad trophic-level shift related most fundamentally to energetics (see, for example, Shipman and Walker 1989; Aiello and Key

**Table 1.1 Life history comparisons for chimpanzees, *Australopithecus*, African *H. erectus*, and modern humans**

Species	Age of completed neural growth	Age of completed somatic growth	Age of first reproduction	Age of last reproduction	IBI	% infant and juvenile mortality
<i>Pan troglodytes</i>	3.5 years	10-11 years	13-14 years	30 years	5-6 years	65%
<i>Australopithecus</i>	3-4 years	<b>11-12</b>	<b>14-15 years</b>	?	?	?
<i>Homo erectus</i>	4.5 years	<b>11-13</b>	<b>14-15 years</b>	?	?	?
Old World human foragers (nonequestrian)	6-7 years	16-18	18-20 years	37-42 years	3-4 years	35%

Chimpanzee and forager data from Goodall 1986; Kaplan et al. 2000; Hill et al. 2001; Marlowe 2005; Brewer-Marsden et al. 2006. Hominid estimates from Dean 2006. Bold numbers indicated educated guesses.

2002; Anton et al. 2002). In particular, *H. erectus* evolved to occupy a novel niche by accomplishing an unusual physiological trick: increasing body size and reproductive rates while shifting to a higher-quality diet. For a primate, this switch involved combining foraging with being a diurnal social (partial) carnivore, a shift that favored an integrated suite of physiological, anatomical, and behavioral changes.

### The Problem: A Shift in Maternal Energetics

Before considering the relationships among derived traits such as toolmaking, increased body size, food processing, endurance running, and tooth reduction that coevolved somehow over the *Australopithecus-Homo* transition, it is useful to begin by thinking about how such traits may relate to fitness, and hence to natural selection.<sup>1</sup> For many reasons, it makes sense to focus on the life history and reproductive strategies of females, the “ecological sex” (Wrangham 1980). A few key variables proximately determine a given female’s fitness: her age at first reproduction, her interbirth interval (IBI), her reproductive lifespan, and her offspring’s mortality rate. Table 1.1 summarizes these variables for chimpanzees (data from

Goodall 1986; Kaplan et al. 2000; Hill et al. 2001; Brewer-Marsden et al. 2006), for non-equestrian, Old World human foragers (data from Kaplan et al. 2000; Marlowe 2005), and for fossil hominins based on what little we know from analyses of dental and somatic maturation (see Smith and Tompkins 1995; Dean et al. 2001; Dean 2006). These data highlight how human foragers have evolved an unusual but successful life-history strategy compared to chimpanzees, and presumably the last common ancestor of chimpanzees and humans. Of particular importance, human foragers have extended the duration of ontogeny, delaying the age at first reproduction but substantially decreasing the interbirth interval (IBI). Such a strategy is likely made possible by the combination of lower rates of infant and juvenile mortality and by increasing the length of the reproductive years (for a detailed discussion see Charnov and Berrigan 1993; Kaplan et al. 2000). However, as Table 1.1 also indicates, this strategy is not shared by all species of the genus *Homo*. Analyses of fossil dentitions and skeletal maturation patterns suggest that the rate of ontogeny in *H. erectus* was perhaps only slightly delayed compared to that of *Australopithecus* and chimpanzees, and that early

**Table 1.2 Energetic comparison of chimps, humans, and hominins**

Species	Male body mass	Male DEE	Female body mass	Female DEE	Female DEE gestating	Female DEE lactating	Female expenditure per IBI
<i>Pan troglodytes</i>	40	1332	30	1175	1469	1671	3.27 Mcal
<i>A. afarensis</i>	45	1610	30	1175	1469	1671	3.27 Mcal*
African <i>Homo erectus</i>	63	2087	52	1807	2269	2487	4.74 Mcal*
Old World human foragers (nonequestrian)	70	2259	57	1931	2414	2665	2.66 Mcal*

Key: \* assuming chimpanzee-like IBI, \* assuming human forager-like IBI, DEE = daily energetic expenditure, IBI = inter-birth interval. Data from Pusey et al. 2005; Aiello and Key 2002.

*Homo* was much more like chimpanzees than like later hominins such as Neanderthals or modern humans in terms of the rate of maturation (Dean 2006; see also Machiarelli et al. 2006).

At this point, there is not enough information to assess empirically if IBIs, mortality rates, and the average age of last reproduction were different in *H. erectus* than they were in australopiths or chimpanzees. Yet, even though *H. erectus* did not have a modern-human-like rate of ontogeny, Table 1.2 summarizes several lines of evidence that suggest that this species' life-history strategy was fundamentally different in ways that would have favored a shorter IBI. Most importantly, body mass and brain size are generally larger in African *H. erectus* than in any species of *Australopithecus* (although not universally, as once thought, given that body size in the Dmanisi sample is smaller than in the African sample). African *H. erectus* apparently attained a human-like body mass at an earlier age than modern humans did, and thus grew faster, requiring a higher rate of energy during growth. A larger body incurs considerable added metabolic costs, especially for mothers. As shown by Key and Ross (1999), across primates, daily energetic expenditure (DEE) is a simple metabolic scaling function ( $DEE = 93.3W^{0.75}$ , where W is body mass in kg) (see also Leonard

and Robertson 1997). In addition, daily energetic expenditure costs during gestation are on average 25 percent higher (Coelho 1986), and daily energetic expenditure costs during lactation are on average 37–41 percent higher (Oftedahl 1984). These equations, with slight adjustments for scaling effects, were applied by Aiello and Key (2002) to predict energetic costs for African *H. erectus* females during lactation, gestation, and nonreproductive periods. Aiello and Key's extrapolations to estimates of body mass indicate that a typical African *H. erectus* female would have had approximately 50 percent higher daily energetic expenditure costs than an *A. afarensis* female. Critically, if the *H. erectus* female had a chimpanzee-like IBI of approximately 5 years, then not only would she have had fewer offspring, but also each offspring would have cost 45 percent more, an extra 1.47 Mcal! This whopping extra cost per infant signifies that there would have been a strong selective advantage for *H. erectus* females to decrease their IBI. If *H. erectus* females had a human-forager-like IBI (about 3 years), then their cost per infant would have been about 20 percent less than the cost in australopiths, in spite of their higher daily costs. In other words, a shorter IBI would have increased fitness relative to cost in larger-bodied hominins.

Note additionally that *H. erectus* had a bigger brain than *A. afarensis* had, both absolutely and relatively. It is difficult to be sure about mean brain sizes of *H. erectus* females given a poor fossil record and uncertainty about which fossils are males and which are females, but it is reasonable to estimate that early African *H. erectus* females had brains somewhere in the ballpark of 600–700 cm<sup>3</sup>, about 20–30 percent smaller than those of males.<sup>2</sup> Brain size matters because brain is an expensive tissue: an adult human brain uses about 20–30 percent of the body's metabolic energy when at rest, approximately 400–650 calories per day for a typical adult (Clark and Sokoloff 1999). If, as suggested by Aiello and Wheeler (1995), there was a trade-off between brain mass and gut mass, then total daily energetic expenditure estimates in *H. erectus* are probably correct.

In short, absolutely bigger bodies and absolutely larger brains in *H. erectus* required a shift in energetics. *H. erectus* individuals, especially mothers, had higher daily energetic requirements than australopiths had. These increased requirements may have correlated with decreased IBIs (a hypothesis that requires testing). In this respect, it makes sense that early *H. erectus* retained the ancestral rapid rate of ontogeny present also in australopiths and chimpanzees, because a high-energy strategy posed two challenges for *H. erectus* mothers. First, *H. erectus* mothers needed reliable and plentiful sources of food to pay for basic metabolic and reproductive costs. In addition, if they were weaning their offspring earlier than australopiths were, then they also needed to provision weaned yet still immature offspring at higher rates than australopiths did. All of this means that, fundamentally, the shift from *Australopithecus* to *Homo* required greater access to energy from food.

How, then, did *H. erectus* females get the extra energy? In theory, there are three nonexclusive

strategies for an organism to acquire more energy from its diet. The first is to change what foods are eaten, the second is to change how the food is acquired, and the third is to change how the food is processed. Various lines of evidence suggest that *H. erectus* employed all three strategies. Indeed, our argument is that changes in all three types of strategies may be intrinsically linked. Simply put, a savanna-dwelling primate such as *H. erectus* could not and did not augment its daily energetic intake without becoming partially carnivorous, which, in turn, required a new set of behavioral strategies that combined running, division of labor, and food processing. Together, these connections may help account for many of the derived features of the archaeological and fossil record that occurred more or less as an ensemble during the shift from *Australopithecus* to *Homo*. We begin with carnivory, then discuss food acquisition, and then food processing and social organization.

### **Was *H. erectus* an Obligate, Frequent Carnivore?**

Adding meat to the hominin diet was not a novel strategy of *Homo*, given the presence of meat, albeit at low levels, in the chimpanzee diet and the likelihood that meat was sometimes a part of the australopith diet (Goodall 1986; Sponheimer et al. 2005; Lee-Thorp and Sponheimer 2006). However, many researchers have pointed out various reasons to suspect that meat was a much more important component in the diet of early *H. erectus* than in the diet of *Australopithecus* (e.g., Milton 1999; Bunn 2001; Aiello and Wheeler 1995). One line of evidence is the unusual combination in *H. erectus* of increased body and brain size with smaller teeth and faces. In general, variations in body size correlate with dietary quality: larger animals eat

lower quality foods (as measured by the percentage of fiber in the diet). Although larger-bodied animals, including primates, need absolutely more food, they need relatively fewer calories per unit of body mass and can afford longer gut passage times (hence more fermentation and absorption) and thus process larger quantities of higher-fiber foods (for reviews, see Gaulin 1979; Lambert 1998; du Toit and Yetman 2005). This relationship (the Jarman-Bell principle) helps account for many dietary differences observed among hominoids: smaller-bodied apes such as gibbons feed on much-higher-quality resources (almost exclusively fruit), whereas larger-bodied apes such as gorillas have a much higher component of fiber in their diets.

*H. erectus* clearly does not obey the predictions of the Jarman-Bell principle. Compared to *Australopithecus*, *H. erectus* has considerably smaller and more thinly enameled molars and premolars, combined with a relatively smaller face. Large, thick postcanine teeth perform better than small, thinly enameled ones at breaking down tough, fibrous foods that require repetitive, high forces (for review, see Lucas 2004). Thus from a functional perspective, the smaller, thinner postcanines of *H. erectus* make sense only if the species was chewing a higher-quality diet that was neither particularly tough nor stiff. Smaller, thinner postcanine teeth also match the smaller face of *H. erectus*, which has a less robust mandible, narrower zygomatic arches, and other features that indicate that the species was less able to produce and resist high bite forces typically associated with a tough, fibrous diet (Demes and Creel 1988; Hylander 1988). In addition, skeletal reconstructions suggest that *H. erectus* had a relatively narrow waist, which would have been incompatible with a large gut typical of species that ferment high-fiber foods

(Aiello and Wheeler 1995; Bramble and Lieberman 2004; Jellema et al. 1993). Finally, microwear analyses of *H. erectus* tooth wear suggest that the species chewed foods that were less tough than those of australopiths (Teaford and Ungar 2000; Ungar et al. 2006).

Anatomical evidence for a shift to high-quality foods, including meat, in the early *Homo* diet accords with the ecological and archaeological evidence. Although the process of aridification that occurred prior to the Pleistocene was complex and variable (Behrensmeyer et al. 1997; Bobe et al. 2002), *H. erectus* in particular and early *Homo* in general are associated with climatic shifts to more open, xeric habitats. Paleontological and geological evidence from a variety of sites, including the Turkana Basin and Olduvai Gorge, indicate an expansion of grasslands in the environments in which *H. erectus* lived around 1.9–1.7 Ma (Cerling and Hay 1986; Potts 1998; Feibel et al. 1991; Rogers et al. 1994; Cerling 1992; Reed 1997). Since fruits are not abundant in such habitats, particularly during the dry season, two major types of foods would most likely have permitted *H. erectus* to increase body mass without resorting to low-quality bulk foods: meat and underground storage organs (USOs). The latter were probably critical for australopiths (Hatley and Kappelman 1980; Hawkes et al. 1997; Ungar 2004), perhaps as fallback foods (Laden and Wrangham 2005), and they were probably also important for *Homo*. Indeed, Wrangham and colleagues (1999) suggested that cooked USOs might have been a critical component of early *Homo* diets (see also Wrangham 2006). The cooking hypothesis has neither been supported nor disproved empirically, but has been criticized because of a lack of definitive evidence for cooking (see below) and because of archaeological evidence for access to meat – the other potential source of high-quality food in the

savannah. As is well known, Early Stone Age (ESA) sites dating back to more than 2.5 Ma include bones with cut and fracture marks indicative of flesh removal and marrow extraction, along with stone tools with wear from cutting meat (Schick and Toth 1993; de Heinzelin et al. 1999; Semaw et al. 1997; Semaw 2000). Which hominins left these traces, and to what extent and how frequently they scavenged or hunted remains debated. However, by the time that *H. erectus* appears circa 1.9 Ma, there is evidence that hominins were actively hunting medium- to large-sized mammals (for reviews see Potts 1998; Bunn 2001; Dominguez-Rodrigo 2002). Significantly, meat and other animal tissues such as marrow provide high-quality sources of calories that are low in fiber, combined with proteins and fats.

In short, anatomical, physiological, ecological, and archaeological evidence suggest that the higher energetic demands of *H. erectus* were met to some extent by a dietary shift involving more meat in addition to other foods, such as USOs. Meat would also have been important as a source of protein and fat. Leaving aside the issue of how such foods were processed and shared (see below), regular access to meat requires a major trophic shift in which *Homo* became a carnivore of some sort.

### **How Did Early *Homo* Compete as a Carnivore with an ESA Technology?**

Joining the carnivore guild, even as a partial member, must have posed a serious challenge for hominins. Carnivores have to not only kill their prey but also compete with other carnivores in the context of competition for a kill (Van Valkenburgh 2001). Carnivores compete and hunt through a combination of strength, speed, stealth, and cooperation. If early humans were carnivores, then how did they manage to kill

their prey and/or compete with other carnivores over access to prey? This was not a trivial problem for early *Homo*, because hominins lack the natural weaponry of cursorial predators, such as claws and fangs, and cannot sprint fast enough to capture most prey. The fastest human sprinters can run approximately 10 m/sec for only about 20–30 seconds; in contrast, most African mammals that were apparently hunted by *Homo* can run at least twice as fast for several minutes (Garland 1983; Bramble and Lieberman 2004).

Most scenarios of early human hunting and scavenging assume that early *Homo*, like modern humans, managed to hunt and compete with other carnivores by relying heavily on technology. In scavenging, 85 percent of the carcass weight that the Hadza scavenge is acquired by driving off or killing the initial predator, mostly lions, using spears, and bows and arrows (O'Connell et al. 1988). In addition, modern hunter-gatherers often have to fend off hyenas from a kill using weapons (Potts 1998; Bunn and Ezzo 1993). They also use a variety of technologies to hunt, primarily the bow and arrow, poison, nets, hunting dogs, and the spear-thrower (Binford 1984; Churchill 1993; Marlowe 2005). Importantly, all these forms of weaponry were invented after the origin of modern *H. sapiens* (Shea 2006a). In addition, hafted stone spear points are less than 300,000 years old in the archaeological record (Shea 2006a). Other ESA tools, Acheulian handaxes and spheroids, have been proposed as hunting weapons (O'Brien 1981; Clark 1955), but this is unlikely (Shea 2006b). Handaxes perform poorly as projectiles (Whittaker and McCall 2001), and it is untrue that spheroids (putative bola stones) are found at ESA sites in clusters of two or three (cf. Cole 1963:148). Thus, modern hunter-gatherers such as the Hadza and the Bushmen, who hunt with

bows and arrows as well as other weapons such as poison, tipped spears, and dogs, are not useful analogues for how *H. erectus* would have hunted.

How then did *H. erectus* hunt and/or scavenge armed only with an ESA technology? One possibility is using spears or clubs, which might have been manufactured by *H. erectus* well before their oldest instance of preservation (at Schoeningen, approximately 400,000 years old). Even so, ethnographic studies suggest that hunting with spears would have posed very serious risks to ESA hunters. According to Binford (1984) and Churchill (1993), recent hunters employ five different strategies to kill prey: (1) disadvantaging, in which prey are first immobilized using traps, water, or hunting dogs; (2) ambushing, in which hunters hide until prey come close enough to kill using projectiles; (3) approach, in which hunters stalk free-moving animals until they are within projectile range; (4) encounter, in which hunters kill prey that happen to be within range as they encounter them by chance; and (5) pursuit, in which hunters chase an animal until it is within range or collapses from exhaustion. Importantly, Churchill (1993) has shown that spears are rarely used in ambush, approach, or encounter hunting, but instead are used primarily to dispatch prey that have been disadvantaged or incapacitated by pursuit. There are two reasons for the limited utility of spears. First, the killing range of *hafted* spears is only  $7.8 \pm 2.2$  m (Churchill 1993), a distance that would be considerably less for *untipped* spears. Stone, bone, or metal points greatly increase the effectiveness of the spear because they are much sharper, thereby enabling the spear to penetrate hair and skin with more energy, and to either cause hemorrhaging of internal organs or lame the animal. Thrown, untipped spears have a lower, possibly negligible, probability of mortally wounding or disabling an animal.

The second reason that recent hunter-gatherers use sonnet- or metal-tipped spears to kill only disadvantaged animals is to minimize risk to the hunter. Although one can safely kill small animals such as gazelles or duikers at close range by stabbing or clubbing them, getting within a few meters of any medium- to large-sized animal is seriously risky because such animals can kick or butt with great force. Rodeo athletes, who regularly interact at close quarters with large mammals, frequently incur injuries such as broken legs that would have killed or disabled early humans (Berger and Trinkaus 1995). It follows that ESA hunters would have faced significant and considerable challenges in trying to kill medium- to large-sized mammals using untipped spears without a reliable method of disadvantaging their prey. Put differently, evidence that ESA hunters were able to hunt mammals such as zebra, wildebeest, and various other antelopes (e.g., Bunn and Kroll 1986; Potts 1998; Dominguez-Rodrigo 2002) suggests an ability to get close enough to prey to kill them with crude, nonprojectile weapons without serious risk of injury.

In the absence of bows and arrows, tipped spears, and technologies by which recent hunter-gatherers disadvantage large animals, the most likely method by which *H. erectus* was able to hunt safely and effectively was persistence hunting (PH). PH is a type of pursuit hunting in which humans use endurance-running (ER) capabilities to chase animals during the midday heat, driving them into hyperthermia and exhaustion so they can be safely killed. PH has not been considered much for the ESA because it is practiced only rarely by recent hunter-gatherers, including the Bushmen (Schapera 1930; Marshall 1958; Washburn 1960; Liebenberg 1990, 2006), the Tarahumara of Mexico

(Bennett and Zingg 1935; Pennington 1963; Balke and Snow 1965; Groom 1971), the Navajo and Paiutes of the American Southwest (Nabokov 1981), and Australian aborigines (McCarthy 1957). This makes sense: PH is now rare because modern hunter-gatherers have dogs, bows and arrows, and other technologies at their disposal. However, several sources of physiological, anatomical, and ethnographic evidence suggest that PH is probably the most likely way that ESA hunters were able to become effective (low-risk and reliable) predators of large animals.

The first is that humans are among the best endurance runners of the mammalian world, having capabilities that surpass those of most mammals and which appear to be a derived feature of the genus *Homo*. Humans have a wide range of musculoskeletal features that improve ER performance, many of which are biomechanically unrelated to walking and which first appear in the genus *Homo*. These include an enlarged *gluteus maximus*, larger anterior and posterior semicircular canals, elongated tendons in the legs, a narrow waist, decoupling of the head and shoulder, and so on (Bramble and Lieberman 2004; Lieberman et al. 2006, in press). In addition, humans have specialized thermoregulatory capabilities including plentiful sweat glands, loss of fur, and various brain-cooling mechanisms. Humans may be comparatively poor sprinters, but they can easily run long distances (>5 km) in extreme heat at speeds greater than the trot-gallop transition of most mammals. This is an important point because most mammals can thermoregulate adequately via panting when walking or trotting, but not when galloping. Galloping requires a 1:1 coupling of locomotion with respiration, thereby preventing quadrupeds from panting and galloping at the same time (Bramble and Jenkins 1993; Entin et

al. 1999). The only nonhuman mammalian endurance runners – all social carnivores – can only trot during cool conditions in either temperate habitats, or at night, dawn, and dusk (for review, see Bramble and Lieberman 2004).

Second, ethnographic evidence indicates that humans use their ER capabilities to practice PH in precisely the kinds of habitats and contexts we know existed for African *H. erectus* and in ways that capitalize on human ER advantages over quadrupeds (Carrier 1984). PH is primarily used in relatively open habitats during the day when it is hot. In the Kalahari, for example, most persistence hunts occur in temperatures of 39–42°C (Liebenberg 2006). Once hunters spot a target prey, usually a large mammal such as a kudu, they chase the animal above the prey's preferred trot speed at a gallop. Making the prey gallop (preferably at a nonpreferred speed) is critical because, as noted above, most mammals become hyperthermic when galloping long distances in the heat because they cannot thermoregulate adequately via panting. Also, unlike humans, most quadrupeds have an optimal speed for trotting and galloping (Hoyt and Taylor 1981), so running at an intermediate speed elevates its cost, hastening its rate of fatigue. When chased, most prey typically gallop away from the hunter, and try to cool down while the hunter catches up (Carrier 1984; Liebenberg 1990; Heinrich 2002). Because most animals cannot lose heat fast enough between bouts of pursuit, their core body temperature rises, eventually leading to heat stroke and exhaustion. The less the animal can rest, the faster it reaches a state of hyperthermia. Even kangaroos, which can sweat fairly well, reach lethal core body temperatures after one to two hours of running (Dawson et al. 1974).

Third, despite many preconceptions to the contrary, ER is not very costly compared to

walking for humans and would yield high returns for PH. Various experiments (e.g., Margaria et al. 1963; Cavagna and Kaneko 1977) have shown that the cost of walking at optimal speed (1.3 m/s) is approximately 0.16 l O<sub>2</sub>/kg/km, only 30 percent lower than the cost of running, which is 0.21 l O<sub>2</sub>/kg/km. In addition, the cost of running is invariant with respect to speed below approximately 5–6 m/s, which is above the trot-gallop transition of most mammals. Walking 15 km costs about 750 Kcal, but running the same distance at any ER speed costs only approximately 980 Kcal. These costs indicate that PH would have been very rewarding when hunting large mammals, even if the hunts are only 50 percent successful, as reported by Liebenberg (2006). Running down a 200 kg mammal such as a wildebeest over 15 km and then walking home with the meat would cost an ESA hunter approximately 1,730 Kcal. If we assume, very approximately, that the average caloric yield of the animal is 2000 kcal/kg (based on caribou [USDA 2006]), and that 60 percent of the animal is edible, then the hunter will have acquired a potential total of 240,000 Kcal! The same effort to kill even a 13 kg duiker would yield 15,600 Kcal.

In short, *H. erectus* could have hunted medium to large mammals effectively, economically, and safely during the ESA, despite the lack of any projectile technology, by using endurance running to perform persistence hunting. Because PH takes advantage of derived human thermoregulatory advantages, the strategy would probably have been useful only in tropical, equatorial habitats, or possibly in semitemperate zones in higher latitudes during just the summer. Note also that ER would also have been advantageous for scavenging. Regardless of whether hominins scavenged in open habitats, or in riparian habitats where competition with hyenas was probably lower

(Blumenschine 1986, 1987), ER would help any scavenger compete effectively for carcasses, which are ephemeral resources. As reported by O'Connell and colleagues (1988:357), when Hadza see a scavenging opportunity, often by sighting circling vultures in the distance, they “abandon other activities and move quickly to the spot, often at a run [emphasis added].”

### Cognitive, Social, and Technological Correlates of Being a Diurnal, Social, Carnivorous Primate

So far, we have argued that *H. erectus* was able to pull off a physiological trick: increasing body size and maybe also decreasing IBIs by regularly obtaining high-quality resources, especially meat. Human endurance capabilities would have made persistence hunting reasonably effective and safe for ESA hominins despite their lack of technology, allowing them to participate in the carnivore guild in a new way, as diurnal carnivores. However, such a subsistence strategy has several constraints that relate to other aspects of the archaeological and paleontological records associated with the transition from *Australopithecus* to *Homo*.

The first constraint to consider is cognitive. One key characteristic of PH is the need to track prey. As documented by Liebenberg (1990, 2006), tracking requires a hunter to distinguish various kinds of animal tracks and to predict an animal's movements to some extent. The faster a hunter using PH can track an animal, the quicker the prey becomes hyperthermic. Recently, Pickering and Bunn (2007) have argued that PH in early *Homo* is unlikely because their smaller brains imply a lack of cognitive abilities necessary to track. Yet many carnivores manage to “track” using olfactory and visual cues despite having smaller brains, and tracking would have been necessary for *H. erectus* hunters regardless of

whether they walked or ran (Lieberman et al. 2007). Although we cannot document when the cognitive capacity necessary for tracking first evolved, it is plausible to hypothesize that tracking abilities were present in *H. erectus* given its relatively larger brain along with other indications of complexity such as the ability to make symmetrical tools that required some mental template.

A second constraint is social. Over the long term, PH is a high-yield subsistence strategy, but it is apparently successful only about 50 percent of the time among the Bushmen (Liebenberg 2006). For this reason, most carnivores are social and rely on kin networks for sharing. The need to share would have particular importance in hominins (Isaac 1978). Hominin females may have been able to participate in some hunting and scavenging occasionally, especially in acquiring small mammals (for example, see Shostak 1981:93, 101–102), but PH of large game was probably not feasible for pregnant or nursing females. Since such females have the highest energetic demands (see above), then it is likely that they would have been provisioned, at least occasionally, by males. Ethnographic data have limited utility for predicting ESA behaviors, but among foragers such as the Hadza, meat from large game is typically shared widely within a camp (Kelly 1995; Hawkes and Bird 2002). Moreover, Marlowe (2005) has shown that Hadza males bring back significantly more meat when their wives are nursing, the period when their energetic needs are the highest and their foraging productivity is the lowest. Higher male contribution to the diet in foraging societies is associated with younger ages of weaning, indicating that male provisioning can be an important component of reproductive success (Marlowe 2001). These data also highlight an important social correlate of male provisioning and food sharing

among hunter-gatherers: a sexual division of labor, especially in tropical habitats (Kuhn and Stiner 2006). Gathered foods (typically gathered by females) usually have lower yields than hunted or extracted foods, but they are more predictable and require less risk and energy to acquire.

A third and final set of constraints is technological. To rely on meat and other animal products, small-toothed creatures such as *H. erectus* would have required a simple technology such as the Oldowan for extracting marrow and cutting meat. More important, hominin carnivory would also have required some form of food processing. One basis for this reasoning is the trade-off between time and energy for both males and females when one combines a sexual division of labor with a diet that includes a substantial proportion of meat and other shared foods. For example, a hunter (or group of hunters) who spend many hours per day in pursuit of prey or carcasses does not have a guarantee of acquiring meat. Admittedly some of his foraging time may be spent gathering opportunistically, and sometimes hunts are abandoned when other high-value resources, such as honey, are located, so he may be able to acquire some calories during the day. Nevertheless, on days when a hunter returns to camp without having been able to feed himself, he depends on food gathered by females and/or other more successful hunters. This means that he must ingest a substantial part of his daily caloric intake in an evening meal. Evening meals are routinely described as being the main meal of the day in hunter-gatherers, and we suspect they are a hunter-gatherer universal.

The reason that such a food-sharing system would be facilitated by, and indeed may depend on, food processing is that unprocessed diets would take too much time to eat and digest in an evening meal. For example, even though

chimpanzees eat a high proportion of fruits, their diet is 30–40 percent fiber (Conklin-Brittain et al. 2002), requiring them to spend about 50 percent of the day chewing, refilling their stomachs about every two hours (Wrangham 1977). Constant feeding throughout the day is obviously incompatible with the human strategy of PH. A male cannot spend half the day feeding yet still engage in persistence hunting (or any other kind of hunting). Nor can he come back to camp hungry and then eat like a chimpanzee, refilling his stomach every two hours for 12 hours. Time may be less of a constraint for females, who can eat as they go more easily than males, but nonetheless, they would benefit from the ability to rapidly process and digest high-quality foods, such as meat, especially if it is not available until the evening. Even chimpanzees cannot chew unprocessed raw meat rapidly (Wrangham and Conklin-Brittain 2003), so it is unlikely that *Homo erectus* would have been able to either.

Tubers have less fiber than many chimpanzee fruits and piths, and thus may have been an important component of an intermediate, “transitional” diet between that of chimpanzees and *Homo* (Conklin-Brittain et al. 2002; Laden and Wrangham 2005; Wrangham 2005). Yet, even moderate fiber diets, probably much lower in fiber than acquired by Paleolithic hunter-gatherers, pose significant challenges to human digestive physiology. Modern “raw-foodists,” who do not cook but instead use advanced technologies (e.g., blenders) to process highly domesticated, low-fiber foods, find it difficult to meet their nutritional needs without cooking (Wrangham and Conklin-Brittain 2003). If ESA hunter-gatherers did not cook (see below), then they must have supplemented their moderate fiber diets with meat. Yet, raw meat also poses substantial digestive challenges because its high collagen

content makes the tissue both tough and elastic. Human and chimpanzee teeth lack shearing crests necessary to comminute raw, tough meat effectively. A chimpanzee can spend as many as 11 hours consuming a few kilograms of colobus monkey, yielding a meager return of approximately 380–400 Kcal/hr, similar to eating fruits (Goodall 1986; Wrangham and Conklin-Brittain 2003). Preliminary experiments involving Harvard undergraduates (Lieberman, unpublished data) also indicate that raw meat is difficult to chew for humans, requiring more force per chew and more chews per unit of mass to break down into pieces small enough to swallow.

The obvious solutions to these challenges are mechanical processing, in which tools are used to pound or otherwise alter food before chewing, or cooking, in which heat is applied to food by roasting or other means (see Wandsnider 1997). Such processing has multiple consequences depending on the specific foods, but we suggest there are two important general effects.

First, the foods become easier to chew. This means that individuals are required to spend such little time eating (perhaps chewing one hour a day, compared to about six hours for a chimpanzee) and that they can use the evening meal to satisfy a major part of their caloric needs. The gain in time would free many hours for alternative activities such as hunting. Processing can thus be seen as facilitating the sexual division of labor.

Second, while food processing can have diverse consequences such as improved detoxification, reduced handling time, and extended storage life, we suggest that a key result is to increase the net energy gain per fresh weight eaten. For meat items, this can be expected to occur as a result of reduced energetic costs of digestion (thanks to reduced structural integrity of meat) and increased protein digestibility (as a

result of denaturing). For starch-containing items, it can be expected to follow partly from reductions in particle size and hydration of starch grains (Wrangham 2006).

It is not known when cooking was first invented. Wrangham and colleagues (1999) have suggested that cooking evolved with *Homo erectus*, based on its energetic benefits combined with reduction in posterior tooth crown area in early *Homo* compared to *Australopithecus* (McHenry 1988; Wood 1991). As shown by Lucas (2004), a 50 percent reduction in food toughness would allow hominins to chew with teeth that are 80 percent smaller in area. In line with the prediction of cooking by *Homo erectus*, control of fire has been suspected in at least six Lower Paleolithic sites from South Africa to Israel (Wrangham 2006). For example, there are traces of what appear to be anthropogenic fire at Gesher Benot Ya'aqov at 750,000 years ago (Goren-Inbar et al. 2004), as well as at a few late Middle Paleolithic and early Middle Paleolithic sites such as Hayonim and Kesem (Meignen et al. 2002; Karkanas et al. 2007). It seems reasonable to conclude that fire became a part of hominin technology between 750,000 and 250,000 years ago, and did not become common in Middle Paleolithic sites until about 250,000 years ago (James 1989; Brace 1995).

If absence of evidence is indeed evidence of absence (a debatable premise), then early *Homo* such as *H. erectus* did not cook. If we assume this is so, then it is likely that energy-needy *H. erectus* hunter-gatherers solved the trade-off between time and diet by including a substantial component of intensely processed meat. Food processing would improve digestibility not only of USOs and other gathered foods, but also of meat. As any cook knows, pounding effectively tenderizes meat, making even the toughest cut of meat

easier to chew. A spheroid would have made an excellent meat tenderizer (alternatively, using a cobblestone to tenderize lots of meat, would eventually turn it into a spheroid).

In short, regardless of whether *H. erectus* had the technology to cook, any diet with substantial quantities of meat must have required a unique combination of cognitive, social, and technological adaptations. These include tracking, tool manufacture, food sharing, a sexual division of labor, and some degree of food processing.

### Conclusion: The Package Deal

The above account is a “story,” in the sense that we have attempted to integrate the fossil and archaeological evidence, combined with a few reasonable conjectures, to consider what sort of selective pressures might have favored the transition from *Australopithecus* to *Homo*. Briefly put, we think the transition depended on a new strategy for acquiring and using energy in open habitats. Regardless of what triggered the transition, bigger brains and larger bodies combined with smaller teeth and faces required *H. erectus* to enter the carnivore guild, at least in part. Being a carnivore permitted early humans to augment energy intake in an unusual habitat for an ape and may have allowed *H. erectus* to lower IBIs. Yet, becoming a carnivore – which means not only killing animals but also competing with other carnivores – must have been a substantial challenge for ESA hominins, whose most sophisticated weapon was probably a sharpened wooden stick. To meet this challenge, *H. erectus* probably combined a series of traits including running for PH, social division of labor, food sharing, and food processing. The fundamentals for the modern hunter-gatherer way of life, thus, may be as old as the genus *Homo*, although they have been elaborated by other, later technological

improvements such as cooking and projectile weapons.

Much is needed to test these ideas. One obvious prediction is that meat contributed a much higher proportion of the diet for *H. erectus* than for any species of *Australopithecus*. While this inference is not incompatible with existing data (Teaford and Ungar 2000), better methods are needed to quantify the contribution of meat to hominin diets. Another prediction is that food processing was a critical application of Oldowan technology. Testing this hypothesis will require new methods to identify the presence of pounding and other processing techniques from archaeological and paleontological materials. We need new techniques to detect the presence of primitive methods of cooking, such as roasting over a very simple campfire without a hearth. We need better data on the ways early hominins hunted and the extent to which ESA technologies could have permitted reliable scavenging or hunting using methods such as PH. Finally, although the ethnographic record remains a critical source of data about the hunter-gatherer way of life, we must also look beyond the ethnographic record, whose limitations severely constrain our ability to propose hypotheses about ancient behaviors. A good example may be persistence hunting, which may be a rarely practiced remnant of an ancient way to hunt, perhaps from a time before cooking, before projectile weapons, and before modern humans. The next time we sit down for a meal and discuss how we got it, we may be doing something quintessential to the genus *Homo*.

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### Notes

1. Please note we are not arguing that the transition from *Australopithecus* to *Homo* derived from an increase in fitness between species, but that any shifts need to be interpreted in terms of their effects on differences in relative fitness within a species.
2. The estimate derives from comparisons of smaller crania attributed to *H. erectus* such as D2700 (600 cc), D2282 (625 cc) and KNM-42700 (691 cc), which are presumably females, with larger crania such as KNM-ER 3733 (804 cc), 3883 (848 cc), KNM-WT 15000 (900 cc), and D2280 (750), which are presumably males.

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