

The First Humans - Origin and Early Evolution of the Genus *Homo*

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Chapter 8

Brains, Brawn, and the Evolution of Human Endurance Running Capabilities

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The Evolutionary Question Posed by Human Running Capabilities

Theories about hominin evolution are often connected intimately with notions of what it is to be human. Such ideas have had a particularly strong influence on thinking about the definition and origin of the human genus (see Landau, 1993; Wood and Collard, 1999; Wood, 2009). Many, if not most scenarios for the evolution of the genus *Homo* emphasize the importance of quintessentially human traits such as large brains, tool-making, and complex cognition. Usually these derived features have been interpreted, explicitly or implicitly, as a suite of novel strategies that emphasize cognitive over athletic means of competing with the rest of nature (“red in tooth and claw”). Most animals compete with each other to a significant extent using athletic capabilities such as strength, power, agility and speed. Obviously, humans compare poorly with other mammals, including African apes, in these characteristics: we are weak, slow, and awkward

creatures. Even though male chimpanzees weigh less than a typical adult modern human, they can produce much more force, can sprint more rapidly, and are obviously more agile during locomotion (Stedman et al., 2004). Yet, although no human alive could match a chimpanzee in hand-to-hand combat, our cognitive capacities are extraordinarily better developed. Accordingly, it seems reasonable to focus on evolutionary scenarios for the genus *Homo* that explain the triumph of brains over brawn.

Interestingly, the idea that humans are poor athletes is demonstrably wrong in one crucial respect. While humans have comparatively poor performance capabilities in terms of power and strength, we are unusually specialized endurance athletes, with surprisingly impressive aerobic performance capabilities. These capabilities are particularly remarkable for endurance running (ER), defined as running long-distances (>5 km) using aerobic metabolism. These capabilities, which have been reviewed in depth by Carrier (1984) and Bramble and Lieberman (2004), compare extremely well to other mammals, especially primates, in terms of several performance criteria such as speed and distance, especially in hot conditions.

Speed

Human ER speeds range from 2.3 to 6.5 m/s. While the latter are elite performance speeds for world-record holders, many amateurs without special training are easily capable of sustained running at 5 m/s. Such speeds are fast compared to the endurance speeds of specialized quadrupedal cursors. A dog of similar body mass to a human (65 kg) has a trot-gallop transition speed of 3.8 m/s, and can sustain a gallop at 7.8 m/s under ideal climatic conditions for only 10–15 min (Heglund and Taylor, 1988). Dogs and other quadrupedal cursors cannot gallop for long periods, especially when it is hot (see below). Thus, while a large dog can outrun a human over short distances of a kilometer or two, most fit humans can outrun any dog over longer distances. As detailed by Bramble and Lieberman (2004), humans also have remarkable endurance

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capabilities even in comparison to larger cursors such as ponies and horses. The latter offer a useful, extreme example because they have been bred intensively via artificial selection for running. Horses can easily outrun humans with a maximum gallop speed of 8.9 m/s for a 10 km race, but their sustainable galloping speed declines dramatically for runs longer than 10–15 min; in repeated runs over long distances, horses are constrained to about 5.8 m/s for approximately 20 km per day, above which they can sustain irreparable musculoskeletal damage (Minetti, 2003). By these standards, human ER capabilities are quite impressive, and explain why humans can sometimes best horses in long distance races such as marathons (e.g., <http://www.man-v-horse.org.uk/>).

Distance

Human ER capabilities are also comparable to the best quadrupedal cursors in terms of distance. Fit amateur humans can easily run 10 km or more a day, and are capable of far longer distances such as marathons and ultramarathons (although rarely on a daily basis!). Only a few other mammals, such as wolves, hunting dogs and hyenas, are known to habitually run long distances of 10–20 km a day (Pennycuik, 1979; Holekamp et al., 2000). These animals, notably, are all social carnivores in which natural selection has favored capabilities for running as a critical part of their hunting or scavenging strategy. Like humans, these cursorial specialists can also run distances greater than 10–20 km, but only when forced to do so by humans, and they are all restricted to a trotting gait, or, in the case of hyenas and wildebeest, a canter (a slow gallop just above the trot–gallop transition). Some dogs, for example, can be forced to trot as much as 100 km in cool conditions (e.g., with fans blowing air on them, or in the arctic winter), but these feats are unnatural and often cause severe physiological distress (Dill et al., 1933; see below). Alaskan huskies are perhaps the extreme example of an animal specially bred for endurance: these dogs can run in packs up to 50 km in frigid conditions at a lope (a slow gallop), but for longer distances they must switch to a trot (Hinchcliff et al., 1998); in addition they cannot perform these feats in warm weather.

Environmental Context

While a few mammals can trot long distances, comparable to those that humans can run, they cannot run long distances *while galloping* in hot conditions without becoming hyperthermic. This major constraint derives from two aspects of mammalian biology. First, the thermogenic effects of exercise

increase in proportion to the number and rate of cross-bridges that are activated during muscular contractions. In humans for example, running can generate as much as tenfold more heat than walking (Cheuvront and Haymes, 2001), and a sprinting cheetah generates so much heat that it must stop after approximately 1 km (Taylor and Rowntree, 1973). Second, the major mechanism by which most mammals cool themselves, panting, is problematic during galloping. Panting occurs via shallow breaths, about ten times the normal rate of respiration, in the dead space of the upper pharynx without any gas exchange occurring in the lungs (Schmidt-Nielson, 1990). Panting mammals, however, cannot satisfy their respiratory demands for oxygen during galloping, and the 1:1 coupling of locomotion with respiration that occurs during galloping is biomechanically incompatible with panting (Bramble and Jenkins, 1993; Entin et al., 1999).

Humans, however, have evolved a number of specialized modifications for effectively dissipating copious quantities of heat while running in hot, arid conditions. For one, humans do not have to couple respiration with stride (Bramble and Carrier, 1983). In addition, humans are considerably derived in terms of the number of eccrine sweat glands and the loss of almost all fur. Sweating is an effective means of cooling (evapotranspiration of 1 ml H₂O requires 580 cal of heat [Schmidt-Nielson, 1990]), but is ineffectual with fur, which traps air and moisture at the skin's surface, thereby considerably reducing convection (McArthur and Monteith, 1980). Therefore, other tropical cursorial mammals such as hyenas and hunting dogs that can run long distances are constrained to do so at night or during the dawn and dusk when the days are hot. Humans alone are capable of ER during midday heat. Human sweating, however, imposes high water demands, requiring as much as 1–2 l/h in well-conditioned athletes (Torii, 1995).

In short, humans are comparatively superb endurance athletes, particularly in hot, arid conditions that are conducive to heat-loss from sweating. In fact, humans appear to occupy a rare extreme in the general trade-off between aerobic and anaerobic capabilities (Wilson and James, 2004). Natural selection often favors speed over endurance because of the dynamics of predator–prey interactions: slower animals typically have lower fitness. Animals built for speed and power are rarely good at endurance and *vice versa*, in part because of muscle fiber composition. In most mammals, there is a predominance of Type IIb (fast-glycolytic) and Type IIa (fast oxidative) relative to Type I (slow oxidative) muscle fibers. The former fast-twitch fibers can produce several times more force but are anaerobic and fatigue quickly. Slow-twitch fibers have higher aerobic capacity, but produce less force. Most human leg muscles have about 50% of each type (McArdle et al., 1996), but can increase slow-twitch fiber content to about

80% through aerobic endurance training. They can also increase fast-twitch fiber content to between 70–80% through power training (Thayer et al., 2000). Such training effects for fast twitch fibers are more common in humans with a novel form of the ACTN3 gene that predisposes individuals to have a high fast twitch muscle fiber content (Yang et al., 2003). In general, quadrupedal cursors have higher percentages of fast-twitch fibers in hind limb extensor muscles than humans, with cheetahs having the highest known-values (Armstrong et al., 1982; Acosta and Roy, 1987; Williams et al., 1997).

Human endurance capabilities raise two questions. First, when did they evolve? Second, why did they evolve? Accordingly, we first review a few points about the evidence for ER capabilities in the genus *Homo* and its relationship to walking. We then consider some alternative hypotheses about the sort of conditions that might have led to selection for ER capabilities.

When Did ER Capabilities Evolve?

The derived ER capabilities of humans must have evolved sometime after the split of the human and chimpanzee lineages. Other primates rarely engage in any kind of running. Even patas monkeys (*Erythrocebus patas*), which have several typical cursorial specializations such as long, digitigrade limbs, sprint rarely and then only for short distances (Isbell, 1998). Importantly, running is also rare among chimpanzees; it comprises less than 1% of their locomotor repertoire (Hunt, 1992). Moreover, when chimpanzees run during hunting or chasing, they typically sprint rapidly for about 100m, fatigue quickly, and then pant heavily while resting to cool down (R. Wrangham, personal communication).

Given that ER capabilities are derived in hominins, there are three alternative possibilities about their evolutionary origins. First, ER and walking capabilities might have coevolved with the origins of upright, habitual bipedalism. Second, ER capabilities might have evolved sometime around the morphological transition between *Australopithecus* and *Homo*. Third, ER capabilities may have evolved sometime more recently than earliest *Homo*, perhaps in *H. erectus*, *H. heidelbergensis* or *H. sapiens*. As emphasized by Bramble and Lieberman (2004), testing these hypotheses is a challenge because many of the physiological and anatomical features that improve ER performance do not fossilize. In addition, many features, such as long legs, that improve running performance capabilities also improve walking performance capabilities (e.g., Pontzer, 2005, 2007; Steudel-Numbers and Tilkens, 2004; Steudel-Numbers et al., 2007). However, several criteria may be useful for evaluating the extent to which morphological

features evident in the fossil record may be adaptations for ER. The most useful of these derive from the biomechanical differences between running and walking.

Running Versus Walking

Running is biomechanically unlike walking in several crucial ways that can help specifically diagnose ER capabilities. Most importantly, walking is modeled as an inverted pendular gait in which the body's center of mass (COM) vaults over a relatively extended leg during stance. Potential energy is stored as the COM rises during the first half of stance; this energy is then released as kinetic energy as the COM falls during the second half of stance. During walking, kinetic and potential energy are thus out of phase. In contrast, kinetic and potential energy are in-phase during running, which saves energy in a completely different way via mass-spring mechanics. In this system, the COM falls during the first half of stance, storing elastic energy in collagen-rich tendons and ligaments in the leg; these structures then recoil during the second half of stance, as the COM rises, propelling the body into an aerial phase (see Alexander, 1991). Therefore, derived features in the human body relevant to mass-spring mechanics are evidence for selection for improving running, not walking, capabilities.

Another aspect of biomechanics in which running differs critically from walking is stabilization, primarily of the head and trunk. Walking is an inherently more stable gait than running, especially in upright, relatively stiff-legged bipeds such as humans. During walking, the human trunk is held upright above the hips, and the COM is rather stable with fluctuations of about 4–5 cm in the vertical and horizontal planes (Saunders et al., 1953). In contrast, running is somewhat like a controlled fall, in which the trunk and head are more flexed than during walking, each by approximately 10° in a typical runner (Thorstensson et al., 1984). In addition, ground reaction forces (GRFs) are more than twice (often as much as four times) as high in ER than walking (Keller et al., 1996). Since human bipeds have comparatively extended, stiff legs and upright axial columns compared to quadrupeds, the high GRFs generated at foot strike are transmitted as a rapid shock wave – the heel strike transient (HST) – up the legs, axial skeleton and into the head. GRFs in humans rise again more slowly after the HST, peaking at mid-stance when the COM reaches its nadir.

Maintaining stability is important to prevent a fall in all running animals, but is a special challenge for intrinsically unstable bipeds such as humans in which falls are more likely to cause serious injury. Running humans thus must stabilize the trunk and head in response to destabilizing forces at heel

strike as well as at midstance. Trunk stabilization, which is needed to keep the body from falling over, is primarily achieved by contractions of the gluteus maximus (Lieberman et al., 2006). Head stabilization is more complex but no less important, because of the need to stabilize gaze via the vestibulo-ocular reflexes (VORs) which sense angular accelerations of the head and adjust eye movements to stabilize images on the retina. Because the head is not balanced, forces that are generated during running have the tendency to cause rapid pitching. These movements are problematic if they exceed 200°/s, the threshold above which the VORs decrease in performance, causing significant losses of balance and visual acuity (Gauthier et al., 1984; Maas et al., 1989; Cromwell et al., 2001). Other quadrupedal and bipedal cursors have somewhat horizontally oriented necks and cantilevered heads, which enable them to stabilize the head through flexion and extension of the neck. Humans, however, must stabilize the head by other means, because our necks are vertical and emerge from near the center of the cranial base (see below).

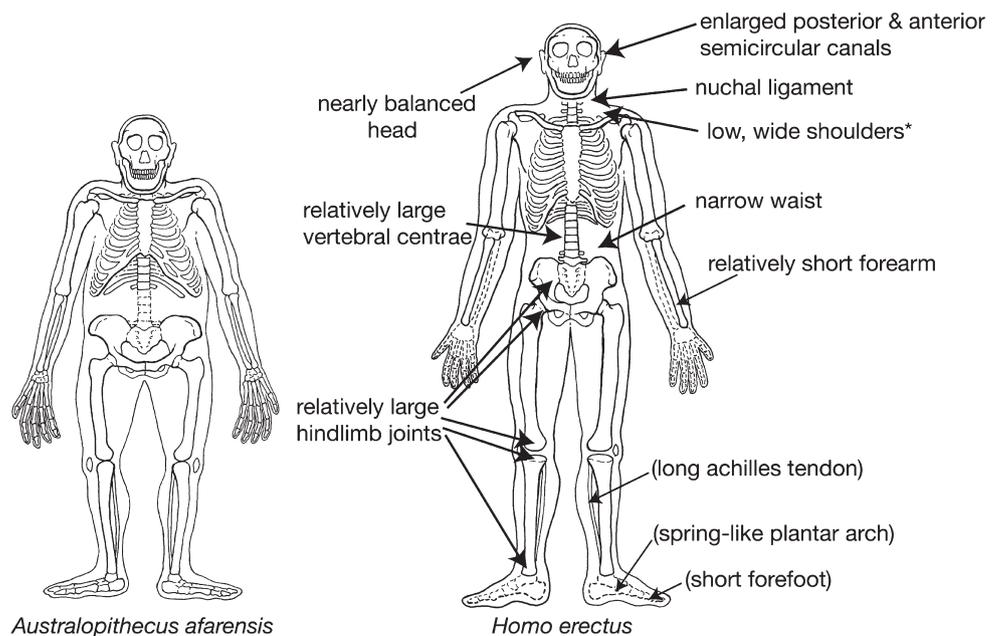
Finally, running and walking differ in the intensity of the thermoregulatory and mechanical demands they impose. As noted above, GRFs, hence joint reaction forces (JRFs), are several times higher during running than walking. In addition, running generates as much as an order of magnitude more heat than walking. It follows that adaptations for thermoregulation are considerably more limiting for running than walking. Both walking and running in hot, midday, arid conditions would have benefited from derived human sweating capabilities (Wheeler, 1991), but it is reasonable to conclude that running would not be possible without them. In

addition, the lack of adaptations such as sweating and hair loss in other African mammals, all of whom cannot run for long in hot conditions, lends extra support to the hypothesis that ER was a factor that led to their evolution and/or elaboration in humans (eccrine glands are a derived feature of catarrhines, but are vastly more numerous in humans than other primates [Jablonski, 2006]).

Evidence for Skeletal Features That Improve ER Performance

Based on these criteria, several lines of fossil evidence suggest that ER capabilities first emerged in the genus *Homo*. These features are discussed at length in Bramble and Lieberman (2004), but a few that are illustrated in Fig. 8.1 merit brief mention here. First, while there are some indications in the skeleton of morphological specializations related to the mass-spring mechanics of running, features related to stabilization are more prevalent. In terms of trunk stabilization, the cranial portion of the gluteus maximus, which plays a critical role in running but not walking, has a considerably expanded origin in *H. erectus* relative to *Australopithecus* (Rose, 1984; Lieberman et al., 2006). The gluteus maximus also acts in concert with the erector spinae to stabilize the trunk, and the sacroiliac trough in which the latter originates may be considerably expanded in *Homo* compared to *Australopithecus* (see Lovejoy, 1988). Even more concrete evidence of derived mechanisms for stabilization relevant only to running is in the head. As shown by Spoor et al.

Fig. 8.1 Illustration of basic body shape differences between *A. afarensis* (left) and *H. erectus* (right) highlighting features discussed in the text that are derived in *H. erectus* and which would improve endurance running performance. Features in parentheses are as yet unknown (in the foot) or hypothetical reconstructions (e.g., Achilles tendon length). Note that shoulder position (indicated with an *) in *H. erectus* is unresolved (Modified from Bramble and Lieberman, 2004).



(1994), the diameters of the anterior and posterior semicircular canals relative to body mass, which influence their sensitivity to head pitching accelerations, are first expanded in early *Homo* compared to *Australopithecus* and *Pan*. The vestibular system is fully formed prior to birth (Jeffery and Spoor, 2004), and is not significantly challenged during walking. It is difficult to think of any human activity other than running that would have selected for increased sensitivity to head pitching.

The anatomical relationships between the shoulder and the head comprise another set of derived features of *Homo* that are absent in *Australopithecus* and which have key roles in head stabilization during running. During walking, the head is stabilized in minor ways by inertia, the viscoelastic properties of the ligaments and muscles that connect the head to the axial skeleton, and by contractions of the head extensors (Hirasaki et al., 1999; Winter et al., 1990). During running, however, the heelstrike transient imparts such a rapid and substantial pitching impulse to the head that it needs to be stabilized almost instantly to avoid vestibular overload. Humans do so by a novel mechanism (a mass-damping system), in which the long axis accelerations of the arm counter pitching accelerations of the head via an out-of-phase elastic linkage (Bramble et al., 2009). A critical component of this system is an almost complete decoupling of the head and shoulder so they can act as linked masses. In chimpanzees, the shoulder and head are tightly connected by a massive trapezius, the rhomboideus, and the atlanto-clavicularis (Aiello and Dean, 1990). These connections have all been lost in humans with the exception of the cleidocranial portion of the trapezius (CCT). This muscular strap between the shoulder and midline occiput interdigitates with another novel feature in humans, the nuchal ligament (NL). This tendon-like structure originates on the midline of the occiput and connects with the upper trapezius as well as a deeper fascial septum that attaches to the cervical spines (Mercer and Bogduk, 2003). A NL is present in other cursors such as canids, equids and bovids, as well as in a few species with massive heads (Dimery et al., 1985; Bianchi, 1989). In running, but not walking, the CCT fires before HS on the stance side arm, linking the mass of this arm with the head in the midsagittal plane via the NL. Critically, evidence for this linkage is first present in the fossil record of early *Homo* (all *H. erectus* skulls as well as KNM-ER 1813) because the NL leaves a trace on the skull in the form of a sharp, everted, median nuchal line that is not present in *Australopithecus* or *Pan*. While apes and australopiths sometimes have a rounded ridge in the midline of the occipital, this ridge lacks the everted contour indicative of a NL.

Other derived changes in *Homo* relevant to stabilization during running but not walking may be evident in the shape of the waist, thorax and neck. Leg swing during the aerial

phase of running causes substantial angular momentum, which, unchecked, would cause the body to rotate around a vertical axis before heel strike. Humans counteract this momentum not only by swinging the arms in opposition to the legs, but also by rotating the thorax independently of the hips and head (Hinrichs, 1990). Such rotations, which are neither important nor particularly marked during walking, are made possible by two zones of separation: a relatively narrow, tall waist; and a relatively tall neck with low, wide shoulders. Although the waist in *Australopithecus* was probably as tall as in *Homo*, it was relatively wider as judged by the greater bi-iliac breadth of the australopithecine pelvis (Lovejoy, 1988; Schmid, 1983). A narrow waist in *Homo* may reflect smaller guts (Aiello and Wheeler, 1995), but it would also have improved running performance by reducing resistance between the pelvis and ribcage, and decreasing inertial moments for thorax rotation.

The second rotational zone of separation, between the upper thorax and neck, is harder to assess in early *Homo*. Whether the thorax of *Australopithecus* was funnel-shaped, as in apes, or barrel-shaped, as in humans, is debated (Schmid, 1991; Ward, 2002), but most evidence suggests that a barrel-shaped upper thorax is first present in the KNM-WT 15000 skeleton (Jellema et al., 1993). The primitive condition of a narrow upper thorax in combination with more muscular connections between the shoulder and head would have no effect on walking performance capabilities. They are useful for helping generate torque in the shoulder for orthograde climbing (Larson, 1993), but would decrease the ability to stabilize the head during running. It is interesting to speculate that selection for running capabilities may have come at the expense of adaptations for climbing, explaining why *Homo* is the first non-arboreal primate. However, Larson et al. (2007; see also Larson, 2009) have suggested that the KNM-WT 15000 shoulder was somewhat narrow with a relatively short clavicle and a glenoid fossa that faced anteriorly in order to accommodate a low degree of humeral torsion. A humerus from Dmanisi (D2700) also has a low degree of humeral torsion (Lordkipanidze et al., 2007). It is hard to interpret these data in part because both KNM-WT 15000 and D2700 are juveniles. The clavicle (which grows intramembranously) is the last bone in the human body to attain adult size, and both skeletons have clavicles that fall in the range of humans at equivalent ontogenetic stages (Scheuer and Black, 2000). Without better reconstructions of the upper thorax itself, it is difficult to assess the relative breadth and position of the shoulders in these specimens, one of which (KNM-WT 15000) has evidence for axial pathologies that may have affected upper thoracic anatomy. Regardless, low humeral torsion in *H. erectus* would have compromised its ability to throw effectively (Larson et al., 2007; Larson, 2009), raising questions about how the species was able to hunt (see below).

As noted above, it is much harder to document elastic structures in the skeleton relevant to the mass-spring form of energy exchange used in running but not walking. The most important anatomical components of the system are extensive tendons, especially the Achilles, which are substantially longer in humans relative to chimpanzees or gorillas. The size of the Achilles tendon insertion in the Hadar calcanei (Susman et al., 1984) suggests that they had an ape-like configuration, but such inferences must remain speculative without evidence of some relationship between tendon length and tendon insertion morphology. A more promising anatomical region for evidence of mass-spring anatomy that requires further study is the foot, especially the plantar arch. Some form of arch is useful in bipedal walking in order to act as a windlass to stiffen the foot for effective toe-off (Kappel-Bargas et al., 1998), but in running the arch functions quite differently as a spring, storing and releasing approximately 17% of the energy generated during each impact of the foot with the ground (Ker et al., 1987). Although australopithecines clearly had some form of plantar arch, there are several indications that the arch had a different configuration in *Homo*. In particular, the navicular in apes and australopithecines has a relatively expanded medial tuberosity, suggesting that it was a weight-bearing element (Harcourt-Smith, 2002). In addition, the first hominin fossil with a close-packed calcaneo-cuboid joint (as evident by an expanded medial flange on the proximal cuboid) is OH 8, a specimen attributed to early *Homo* (Lewis, 1989; Susman, 2008). Together, these novel features – along with an unequivocally adducted big toe and a relatively shorter forefoot (see Susman et al., 1984; Aiello and Dean, 1990) – hint that elastic storage mechanisms in the foot necessary for running may be derived features of the genus *Homo*.

Finally, it is important to note that there are more than a dozen other derived skeletal features of the genus *Homo*, particularly in *H. erectus*, which improve performance for both walking and running (summarized in Bramble and Lieberman, 2004). Given that hominins were habitual bipeds for at least 4 million years before the origin of *H. erectus* with little evidence for any major change in postcranial anatomy (reviewed in Ward, 2002), it is difficult to imagine that selection for walking alone was responsible for the derived features of *Homo*. The most likely scenario is that *H. erectus* was the first hominin with a substantially expanded diurnal day range made possible by both walking and running. Indeed, both gaits are important ways to travel long distances, and one can expect that hominins would have walked rather than run whenever possible (see below). Thus, the extent to which selection acted on running versus walking is impossible to assess, as both would have been important. That said, it is worthwhile noting that the considerably more extreme thermoregulatory and mechanical demands of running might have imposed a greater selective benefit on

performance capabilities in running than walking. In addition, many ancestral features of australopithecines that improve climbing performance, such as long forearms and heavily muscled shoulders, do not conflict with the biomechanical demands of walking, but may impede the ability to stabilize the head. Selection for running capabilities may thus have selected against arboreal capabilities in *Homo*.

Put together, there is much evidence that *H. erectus* but not *Australopithecus* was capable of ER. However, this inference does not imply that *H. erectus* was necessarily as good as modern humans or even later archaic *Homo* at ER. Some modern human features that improve ER performance may have evolved since early *H. erectus*. In addition, there are some hints that *H. habilis* may have possessed some ER capabilities, but the evidence is sparse and equivocal (see Bramble and Lieberman, 2004). While it is possible that ER capabilities had evolved by the time of *H. habilis*, it is premature to be definitive, and there are theoretical reasons to hypothesize that such capabilities, if they existed, were not as developed as in *H. erectus*. Natural selection tends to take advantage of existing variations in the context of some fitness benefit. Thus, it is unlikely that selection would have favored the evolution of ER-related features if hominins had not already been engaged to some extent in a form of ER. One potential scenario is that early *Homo* during the Oldowan started to scavenge and/or hunt to a limited extent. At some point, hominins that were better at ER for various reasons (longer legs, larger anterior and posterior semicircular canals, and so on) had a slight fitness benefit, leading to the evolutionary changes that we observe in *H. erectus*.

Why Did Endurance Running Capabilities Evolve?

Given the above evidence that ER capabilities are derived in the genus *Homo*, and that they were probably present to some extent in *H. erectus*, the final question to address is why these capabilities evolved in the first place. Answering this question, however, is a challenge because it is obvious that humans today – including contemporary hunter-gatherers – no longer need to practice ER (although it remains a potentially useful component of some hunter-gatherer subsistence strategies). Thus, answers need to be sought primarily in past rather than present behaviors. Nevertheless, ethnographic studies of recent humans provide several lines of evidence which suggest that ER would have significantly improved performance in scavenging and/or hunting activities prior to the invention of sophisticated projectile technology such as the bow and arrow. In order to explore these hypotheses, we first outline several alternative ways in which ER may have been useful for scavenging versus hunting during the Early

Stone Age, and we evaluate the recent ethnographic and paleoenvironmental evidence relevant to both forms of meat procurement.

Endurance Running and Scavenging

The debate about scavenging in human evolution is long and contentious, largely because it is difficult to prove that the animal bones found in early archaeological sites were procured by scavenging or hunting (for reviews, see Bunn, 2001; Dominguez-Rodrigo, 2002). Another point of contention has been the challenge of evaluating how reliably or effectively early *Homo* would have been able to scavenge in various habitats. Regardless of the extent to which scavenging occurred, the most likely source of scavenged carcasses would have been lion kills, because lions, unlike hyenas, do not consume all their prey, but instead leave behind marrow, brains and sometimes flesh (Blumenschine, 1987, 1988). Leopard and sabertooth tiger kills might have been additional possible sources of edible animal tissue (Cavallo and Blumenschine, 1989; Marean, 1989), but it is unclear how common such carcasses would have been, and how much of the carcass sabertooths would have consumed (Van Valkenburgh, 2001). In any event, early *Homo* might have used two general strategies to scavenge from lion kills. One possibility is that hominins scavenged opportunistically when they happened to come across carcasses in the course of their daily foraging activities. Alternatively, or additionally, hominins might have sought out scavenging opportunities strategically by searching for carcasses through long range cues, the most common of which is seeing vultures circling in the air from a distance.

Apart from whether hominins were scavenging opportunistically or strategically, to do so effectively they would have faced two considerable challenges, both of which are relevant to ER. First, carcasses are comparatively rare and ephemeral resources, largely because of hyenas, which are impressively efficient at finding kills. According to Cooper (1991), hyenas in Kruger Park typically arrive at lion kill sites within 30 min of a kill, even at night. Given that a large percentage of kills occur at night, it is probable that only a fraction of kills, notably those made during the day, were available for scavenging by diurnal hominins. In addition, it is often argued that hominins in environments such as the Serengeti would have been most effective at scavenging in riparian habitats where the density of hyenas is lower and scavengeable carcasses survive for longer (Blumenschine, 1986, 1987). In wetter, less seasonally arid environments (e.g., the Parc National des Virunga), carcasses might have been more available in more open habitats, but they still would have been rare and rapidly consumed (Tappen, 2001).

The second serious challenge that hominins would have faced while scavenging is competition. To become scavengers (or hunters), they would have entered the carnivore guild, which means competing with other carnivores. In fact, most interspecific interactions between carnivores occur in the context of competition for a kill (Van Valkenburgh, 2001). Carnivores compete through a combination of strength, speed, stealth, and cooperation, and the risk of mortality associated with these interactions is quite high. Human hunters are no exception to this competition: a high percentage of scavenging opportunities observed among modern hunter-gatherers are classified as “competition” or “power” scavenging in which groups of foragers drive off lions or hyenas from a kill using weapons (O’Connell et al., 1988; Potts, 1988; Bunn and Ezzo, 1993). According to O’Connell and colleagues (1988), 85% of the total carcass weight that the Hadza scavenged was acquired by driving off or killing the initial predator (mostly lions). Since it is probable that early *Homo*, like modern humans, was neither strong nor powerful, but also lacked the sophisticated weapons available to modern foragers, it is debatable to what extent they would have been able to engage in competition scavenging. It may strain credulity to imagine hominins successfully driving off a pack of lions or hyenas armed only with stones and sharpened sticks, but Hadza foragers seem to be able to do just that with relatively simple weapons. It must be remembered, however, that the Hadza’s armature includes projectile weapons, and the carnivores in question have undergone thousands (perhaps millions) of years of natural selection for avoiding encounters with groups of well-armed humans.

The combination of ephemerality and competition has led many researchers to suggest that scavenged meat was not a commonly available resource for early hominins (e.g., Bunn, 2001; Tappen, 2001; Dominguez-Rodrigo, 2002). However, it is possible that ER provided an additional means to improve access to this potentially very valuable resource. In particular, hominins during the day in open habitats would be able to identify scavenging opportunities by seeing vultures in the distance, often many kilometers away. If they just walked to the kill site, it is likely that little meat would be left to scavenge, and/or there would be considerable competition with hyenas. But, as demonstrated above, early *Homo* might have been able to run the few kilometers necessary to get to the kill *before* other scavengers. Since hyenas face the same thermoregulatory constraints as other non-human mammals for running long distances in extreme heat (they run primarily at night and during the dawn or dusk), hominins would have had a competitive advantage over hyenas for getting to diurnally available carcasses, particularly in the dry season. Whether and to what extent hominins did this is debatable, but modern ethnographic evidence provides some support for this potential strategy. As reported by O’Connell et al. (1988: 357), when Hadza believe they have a scavenging

opportunity, they “abandon other activities and move quickly to the spot, *often at a run* [emphasis added].” In another example, a !Kung bushwoman, Nisa (Shostak, 1981: 93), recounts an instance in which she used ER to secure quickly an opportunistically discovered carcass before it is lost to other scavengers:

I remember another time, when I was the first to notice a dead wildebeest, one recently killed by lions, lying in the bush. Mother and I had gone gathering and were walking along, she in one direction and I a short distance away. That’s when I saw the wildebeest... She stayed with the animal while I ran back, but we had gone deep into the mongongo groves and soon I got tired. I stopped to rest. Then I got up and started to run again, following along on our tracks, ran and rested and then ran until I finally got back to the village. It was hot and everyone was resting in the shade... My father and my older brother and everyone in the village followed me [back to the wildebeest]. When we arrived, they skinned the animal, cut the meat into strips, and carried it on branches back to the village.

In short, ER might have opened a new niche for scavenging that was previously unavailable.

Endurance Running and Hunting

Another key, perhaps even more important role for ER in *H. erectus* and possibly earlier *Homo* may have been during hunting. As noted above, a wide array of evidence suggests that hominins were actively hunting, at least by the time that *H. erectus* appears circa 1.9Ma (for reviews see Potts, 1988; Bunn, 2001; Dominguez-Rodrigo, 2002). The evidence for hunting includes a large proportion of bones with cut-marks indicative of flesh removal from regions of shafts that would not have had flesh had they been scavenged. In addition, many of these bones are from medium- to large-sized mammals. One question that arises from these findings is how early humans managed to kill their prey? Humans not only lack the natural weaponry of cursorial predators such as claws and fangs, but also cannot run fast enough to capture most prey by sprinting. The fastest human sprinters can run approximately 10m/s for about 20–30s; in contrast, most African mammals that were apparently hunted by *Homo* can run approximately twice as fast for several minutes (Garland, 1983). Thus, most scenarios of early human hunting posit, not unreasonably, that humans managed to hunt only with the aid of various forms of technology.

The reliance of human hunters on technology poses an interesting quandary relevant to ER, because the extremely limited, simple technology of the Early Stone Age (ESA) has led some researchers to doubt that early *Homo* was capable of hunting (e.g., Binford, 1984; Brain, 1981). Stone tools, namely Acheulian handaxes and spheroids are viewed by some researchers as possible hunting weapons (O’Brien, 1981; Clark, 1955), but the evidence that they were

specifically designed for such tasks is weak or equivocal (Shea, 2006b). Handaxes perform poorly as thrown projectiles (Whittaker and McCall, 2001), and it is a myth that spheroids (putative bola stones) are found at ESA sites in groups of two or three (cf., Cole, 1963: 148). More plausible ESA weapons might have included sharpened wooden spears, such as those recovered from Middle Pleistocene contexts (ca. 400ka BP) at Schöningen, Germany, although it is unlikely that early *Homo* spears would have been as sophisticated as the Schöningen example (Theime, 1997). Importantly, even if we assume that ESA hunters made spears, there is no evidence that they made stone-tipped or bone-tipped spears, which are capable of inflicting serious damage from a distance. The most effective Paleolithic technologies for hunting, the bow and arrow and the spear thrower (atlatl), were not invented until quite recently, probably after the origin of modern *H. sapiens* (Shea, 2006a). In this crucial respect, modern hunter-gatherers such as the Hadza and the Bushmen, who have bows and arrows as well as other weapons such as poison and tipped spears, are not particularly useful analogues for how early *Homo* would have hunted (see Lieberman et al., 2007). Moreover, as noted above, Larson (Larson et al., 2007; Larson, 2009) has suggested that *H. erectus* lacked a modern shoulder configuration, which would have compromised the species’ ability to throw projectiles effectively.

In spite of the deficiencies of the ethnographic record, studies of recent hunters suggest that the lack of any sophisticated projectile technology during the ESA would have presented early hominin hunters with several significant challenges, especially prey encounter, and risk of injury. According to analyses by Binford (1984) and Churchill (1993), hunters typically employ five general strategies to kill prey: (1) disadvantaging, in which prey are first immobilized by mechanisms such as traps, mud, water, and hunting dogs, and then killed; (2) ambushing, in which hunters hide (often behind a blind) until prey come close enough to kill; (3) approach, in which hunters stalk free moving animals until they are within weapon 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. In a review of ethnographic and ethnohistoric literature from 96 recent human groups, Churchill (1993) has shown that the bow and arrow and atlatl are by far the most common weapons used to hunt for most of these strategies, and the Hadza and Bushmen are no exception. Spears, which might have been available (albeit in crude form) to ESA hunters, are rarely used in ambush, approach or encounter hunting, but instead are used primarily to dispatch disadvantaged prey that have been immobilized or incapacitated. In addition, modern hunters not only use stone- or bone-tipped spears that ESA hunters did not have, but also usually use

them after they have disadvantaged their prey using dogs or other recent technologies (e.g., boats, snares, nets) that were probably also unavailable to ESA hunters.

There are two reasons that hunters use spears primarily to kill only disadvantaged prey. First, the killing range of spears is very limited. Experiments with replicas of the Schöningen spears by trained athletes suggest they may be effective out to 15 m (Rieder, 2003), but the controlled conditions of an athletic field do not precisely replicate the conditions of hunting large dangerous mammals at close quarters and/or in dense vegetation or on uneven terrain. The mean distance from which ethnographic throwing spears are cast at their targets is only 7.8 ± 2.2 m ($n = 14$) (Churchill, 1993). Moreover, it is important to note that the ability of ESA hunters to kill with spears would have been considerably less than observed in modern hunters because ESA spears, if they existed, lacked stone or bone points. These points greatly increase the effectiveness of the spear because they are much sharper than a wooden tip, enabling the spear to penetrate hair and hide. In addition, the major way by which spears disable or kill prey is from causing hemorrhaging of an animal's internal organs, or by laming the animal. Thus, thrown wooden spears have a much lower, possibly negligible probability of mortally wounding or disabling an animal. The differential lethality of wooden vs. stone- or bone-tipped weapons is intuitively obvious, but imprecisely quantifiable. Some measure of support for this hypothesis can be seen in the strong association in ethnographic contexts between the use of stone projectile points and the hunting of large dangerous mammals and warfare. In a nutshell, people use stone and bone-tipped armatures to improve penetration and to minimize the chances that their target can either recover or retaliate. The main cost of this strategy lies with the considerable time and effort needed to haft stone or bone armatures (or their modern metal counterparts) to wooden shafts. Such weapons are frequently among the most complex subsistence aids used by recent hunter-gatherers (Oswalt, 1976). Simple wooden spears, on the other hand, can be made quickly, repaired easily, and unlike bone- or stone-tipped weapons, they retain considerable functional versatility. Moreover, given their short effective range, hunters using such simple spears are unlikely to miss their targets. In contrast, the effective ranges of the atlatl and the bow and arrow are approximately 40 and 26 m, respectively (Churchill, 1993). Moreover, these weapons have a much greater chance of causing internal bleeding and death, and are thus much more effective. The countervailing cost of such projectile weapons are that, as noted, they require considerable time and energy to build and maintain, and using them requires the learning and practice of specialized skills (Blurton-Jones and Marlowe, 2002). The bow and arrow and atlatl have completely changed human hunting practices since their invention in the Late Pleistocene (Cattelain, 1997; Shea, 2006a).

The other reason of relevance that hunters use spears mostly to kill disadvantaged large prey is to minimize risk to themselves. It is possible to kill small animals, such as gazelles or duikers, at close range by stabbing or clubbing them, but getting within a few meters of any medium- to large-sized animal is clearly very risky. Understandably, we have no data on injury rates for humans who try to kill such animals at close quarters with ESA technology because rational humans apparently will not attempt such feats on large, non-disadvantaged animals. But it is reasonable to assume that such behaviors would be extremely hazardous. It is doubtful that any reader of this paper would be willing to try to sneak up on a wildebeest or kudu and kill it with a sharpened wooden stick: one well-aimed kick or impact with the animal's horns could cause serious, potentially fatal injury! American rodeo athletes, who regularly interact at close quarters with large, dangerous mammals, frequently incur injuries, such as broken legs, that would have killed or disabled a Pleistocene hominin (Berger and Trinkaus, 1995). It follows that ESA hunters would have faced significant and considerable challenges in their efforts to kill prey using untipped spears without some reliable method of disadvantaging their prey. Put differently, evidence that ESA hunters appear to have been able to hunt medium- to large-sized mammals such as wildebeest, zebra, waterbuck and various other antelopes (e.g., Bunn and Kroll, 1986; Potts, 1988), strongly suggests that they were somehow able to get close enough to their prey to kill them with crude, non-projectile weapons without serious risk of injury. Given the absence of dogs, nets, and other technologies typically employed by recent hunter-gatherers to disadvantage large animals, the most likely method by which this occurred was persistence hunting (PH), a form of pursuit hunting in which humans use ER during the midday heat to drive animals into hyperthermia and exhaustion so they can be easily killed. Although ethnographic evidence indicates that PH is practiced relatively rarely by recent hunter-gatherers, PH is not only a low-risk method by which ESA hunters could become effective predators, but is also surprisingly low in terms of energetic cost.

PH has been observed among a variety of recent human groups, all in tropical, arid habitats. Among others, PH has been documented for the Kalahari Bushmen (Schapera, 1930; Marshall, 1958; Washburn, 1960; Liebenberg, 1990, 2006), the Tarahumara of Northern Mexico (Bennett and Zingg, 1935; Balke and Snow, 1965; Groom, 1971; Pennington, 1963), the Navajo and Paiutes of the American Southwest (Nabokov, 1981), and Australian aborigines (McCarthy, 1957). In all these cases, PH has three basic characteristics that make it an effective, albeit time-consuming and intensive method of hunting for a poorly-armed human. First, PH primarily occurs during the day when it is hot - often during the hottest time of the year and the day. In the Kalahari, for example, most persistence hunts occur in temperatures of 39–42°C

(Liebenberg, 2006). Second, once hunters spot a target prey animal, they chase the animal at a run, preferably between the prey's preferred trot and gallop speeds. This speed is significant because, as noted above, most mammals cannot gallop long distances, but instead quickly become hyperthermic because of their inability to thermoregulate fast enough via panting. In addition, and in contrast to humans (and kangaroos), most prey have a U-shaped cost of transport (COT, the energy per unit body weight to go a given distance) and thus prefer to trot and gallop only at those speeds that minimize cost (Hoyt and Taylor, 1981). Running at an intermediate speed therefore elevates the animal's cost, hastening its rate of fatigue. When chased at such speeds, prey typically gallop away from the hunter, and try to cool down and rest while the human catches up (Carrier, 1984; Liebenberg, 1990; Heinrich, 2002). Since the animal usually cannot lose heat fast enough during this interval, core body temperature in the prey rises until the animal suffers from heat stroke and exhaustion. Even a kangaroo, which is capable of sweating and has a speed-independent COT, reaches lethal core body temperatures after 1 to 2 h of running (Dawson et al., 1974).

The third key characteristic of PH is the need to track the animal. As noted by Liebenberg (1990, 2006), tracking is a considerable skill that requires the hunter to be able to distinguish tracks in the ground, but also to think like the animal. Tracking is often done while walking, but the faster the hunter can track his/her prey, the quicker the prey becomes hyperthermic. When the cognitive capacity necessary for tracking first evolved is impossible to document, but it seems reasonable to hypothesize that tracking abilities were present in *H. erectus* given its relatively larger brain not to mention its ability to make symmetrical tools that required some mental template (Wynn, 2002). Tracking is also a skill that has to be taught and learned in the field and on the go. In the context of an ER-based hunting strategy, juveniles and/or adolescents would have to have been able to keep up with adults while learning tracking skills.

Viewed from the perspective of ESA hunting technologies and hominin ER capabilities, PH via ER has several key advantages. First, this method of hunting is low risk, and comparatively easy for any human capable of ER and who has the ability to track animals. Second, PH has a relatively high success rate. Approximately 50% of the persistence hunts documented by Liebenberg in the Kalahari were successful, leading to an approximately 70% higher yield of meat per day than hunting using a bow and arrow (Liebenberg, 2006). Third, PH has a surprisingly low metabolic cost. Although PH has frequently been discounted as an unlikely strategy for hunting because the metabolic cost of human running is about 50% higher than an average quadrupedal mammal's after adjusting for body mass, closer inspection of the evidence reveals that the actual cost of ER is not that high, particularly compared to the potential pay-off. The

COT of ER in humans is approximately $0.211 \text{ O}_2/\text{kg}/\text{km}$ (Margaria et al., 1963; Cavagna and Kaneko, 1977), about 30–40% higher than the minimal cost of O_2 ($0.161 \text{ O}_2/\text{kg}/\text{km}$) consumed during walking. In addition, while the COT for walking is U-shaped, with an optimal speed (about 1.3 m/s or 5 km/h), the COT for running is independent of speed in humans. In other words, a running human consumes the same amount of energy per unit distance running at a slow jog (3 m/s) or a competitive pace (6 m/s). Assuming an average conversion rate of 4.8 kcal/l O_2 , then running 15 km at any ER speed costs approximately 980 Kcal, whereas walking the same distance at an optimal speed costs 750 Kcal. Put in everyday terms, running 15 km to kill a large antelope requires fewer calories than the 1,040 Kcal consumed from a Big Mac® and a medium-sized french fries at McDonald's (http://www.mcdonalds.com/app_controller.nutrition.index1.html)! Since a large antelope weighs more than 200 kg and contains several orders of magnitude more calories than McDonald's can manage to pack into one of its meals, one can easily appreciate that the pay-off is clearly worthwhile, even if the chances of success are only 50%.

A final, possibly important advantage of PH is that it does not require any sophisticated technology other than the simplest weaponry such as a spear or club. Hunting is generally a male activity in recent hunter-gatherer societies, but older children and women (the latter unaccompanied by children or infants) who were good at ER would also have been effective persistence hunters with little risk. Again, Nisa provides an excellent example of this point (Shostak, 1981: 101–102):

Another day, when I was already fairly big, I went with some of my friends and with my younger brother away from the village and into the bush. While we were walking, I saw the tracks of a baby kudu in the sand. I called out "Hey, Everyone! Come here! Come look at these kudu tracks." The others came over and we all looked at them.

We started to follow the tracks and walked and walked and after a while, we saw a little kudu lying quietly in the grass, dead asleep. I jumped up and tried to grab it. It cried out "Ehnnn... ehnnn..." I hadn't really caught it well and it freed itself and ran away. We all ran, chasing after it, and we ran and ran. But I ran so fast that they all dropped behind and I was alone, chasing it, running as fast as I could. Finally, I was able to grab it, I jumped on it and killed it... I gave the animal to my cousin and he carried it. On the way back, one of the other girls spotted a small steenbok and she and her older brother ran after it. They chased it and finally her brother killed it. That day we brought a lot of meat back to the village and everyone had plenty to eat.

Despite the many advantages of PH, it also has some disadvantages that probably account for its comparative rarity among modern hunter-gatherers with dogs, bows and arrows and other such recently invented (or domesticated) technologies. First, PH is clearly more demanding metabolically and physically than other methods of hunting. It is difficult to imagine why any recent human since the invention of the bow and arrow would regularly engage in PH if other, less

grueling forms of obtaining meat were available. PH is also not an option for old or infirm individuals. That said, peak ER performance, as judged by marathon times, is achieved by humans in their 30s; individuals in their 40s typically run long distances such as marathons within 10–20% of their peak performance time (Noakes, 2003). Another cost of PH is that humans require considerable quantities of water in order to thermoregulate adequately during these feats. According to Liebenberg (2006), Kalahari Bushmen always precede a persistence hunt by drinking as much water as they possibly can; carrying water in a gourd or some other form of bottle also improves a hunter's chances. Finally, long distance ER requires dietary sources of salt, which is lost at high rates in sweating, as well as high concentrations of glycogen and triglycerides that can be stored in both the muscle and liver and hydrolyzed into free fatty acids (for review, see Coyle, 2000). Although "carbohydrate-loading" increases these stores, the capability to store glycogen and free fatty acids is highly labile in response to training and does not require diets that are abnormally high in simple carbohydrates (Tsintzas and Williams, 1998).

Another requirement, although not a disadvantage, of PH is that, like other forms of hunting, it requires a cooperative social system in which individuals share food. When an unsuccessful hunter returns to camp, he or she still needs to consume enough calories to pay not only for normal metabolic costs but also for the additional costs of running (at most 50% more than walking). This can only be accomplished by social networks based on food-sharing, and division of labor (Isaac, 1978).

Habitats and Endurance Running

A final consideration relevant to the evolution of ER is habitat. ER, whether for scavenging or for persistence hunting, is obviously an activity suited primarily to relatively open habitats, especially short grass savannas such as the Serengeti ecosystem, as well as more open, arid habitats such as the semi-desert Kalahari or the scrubland of the Turkana Basin. ER is also possible in lacustrine and open woodland zones that lack dense ground vegetation, but is not practicable in tall grass savannas, dense woodland, forest, or marshes and swamps. Although open habitats are a prerequisite for ER, we do not suggest that hominins capable of ER lived exclusively in such zones. Like humans today, early *Homo* almost certainly exploited a wide range of environments. In addition, PH and/or scavenging were probably seasonal behaviors. Thus, our hypothesis is that open habitats in combination with ER capabilities may have provided an important new niche for diurnal scavenging and/or hunting that was one component of their food procurement strategy.

When the open, semi-arid grassland habitats that are now so common in East Africa originated has been the subject of much debate. One theory is that open savannas emerged rapidly during the Pliocene, sometime between 2.8 and 2.5 Ma, as demonstrated by the evolution and prevalence of grazing bovid species such as alcelaphines (e.g., wildebeest, hartebeest and topi) and antelopes (e.g., gazelle) (Vrba, 1995). However, it seems more probable that the process of aridification that occurred prior to the Pleistocene was complex, highly variable, and not as radical as originally suggested (Behrensmeyer et al., 1997; Bobe et al., 2002). Xeric habitats were present prior to 1.8 Ma, for example at Laetoli, which was a dry savanna circa 3.2 Ma (Hay, 1987), but such habitats were probably not widespread until about 1.8 Ma (for review, see Potts, 1988). Thus, regardless of whether earliest *Homo* had evolved ER capabilities (see above), the degree to which habitats conducive to ER were prevalent prior to 1.8 Ma, just after *H. erectus* first appears in the fossil record, is unresolved.

Several lines of evidence suggest that *H. erectus* was probably the first hominin species regularly able to exploit open, hot and arid savanna environments conducive to ER. One source of evidence is the body form of *H. erectus* itself, whose long limbs and narrow thorax is ideally suited to thermoregulating in the midday sun (Ruff, 1991). More importantly, paleontological and geological evidence from a variety of sites, including the Turkana Basin and Olduvai Gorge, indicate that grasslands were present in the environments in which *H. erectus* lived. In the Turkana Basin, for example, a major environmental change occurred around 1.9 Ma when a lake formed in the central portion of the basin in place of the meandering Omo River, and there was a coincident expansion of open habitats (Feibel et al., 1991; Rogers et al., 1994). At this time, oxygen isotopes from soil samples record a major increase in the percentage of C4 grasses, and faunal assemblages indicate an increased percentage of open habitat grazers (Feibel et al., 1991; Cerling, 1992). By 1.7 Ma, the lake in the Turkana basin had gone, but the region continued to host a diverse range of environments, in which the marginal zones of the basin had "open woodland along ephemeral drainages, giving place laterally to scrub, thicket and dry grassland" (Feibel et al., 1991: 334). These latter habitats would probably have been ideal for PH during dry seasons, and have been present ever since, including around 1.5 Ma when the Nariokotome boy lived (Feibel and Brown, 1993; Harris and Leakey, 1993).

Olduvai Gorge presents a similar picture. According to Cerling and Hay (1986), Lower Bed I of Olduvai was a wet, marshy habitat, but by the top of Bed I (approximately 1.8 Ma), the environment was more open and arid. At the top of Bed II, which is dated to approximately 1.7 Ma, there is a prevalence of dry vegetation and open habitats (Cerling and Hay, 1986). For example, oxygen isotope analyses of soils

indicate that C4 vegetation went from between 20–40% to between 60–80% around 1.8Ma, for a phase that lasted at least 50,000 years (Hay, 1976). Although conditions at Olduvai and elsewhere certainly fluctuated considerably throughout the Pleistocene (see Potts, 1998), it is reasonable to conclude that within the general region of the Gorge there was an abundance of open habitats after about 1.75Ma that would have been conducive either to scavenging or hunting by ER.

A relationship between ER and open-country adaptations by *H. erectus* may also be involved in the marked shift in the quality of evidence for hominin dispersal into temperate Eurasia after 0.9Ma. Prior to this time, evidence for hominin occupation is sparse, but afterwards there is clear and consistent evidence of such occupation (Dennell, 2003). The onset of Middle Pleistocene glaciations after 0.9Ma, and the increasingly open-steppic landscapes throughout much of Eurasia may have made this region a more hospitable venue for *H. erectus*' ER-based hunting adaptation.

Conclusion

In conclusion, humans have a surprisingly impressive ability to run long distances at relatively high speeds and in extremely hot conditions compared to other specialized cursors. In many respects, these capabilities can also exceed those of the few other mammals – all social carnivores – known to engage in ER. In addition, human ER capabilities are all the more special because other primates generally eschew running other than occasional sprinting, and they lack endurance capabilities.

If humans are so good at ER, then why have these capabilities received so little attention in the history of research on human evolution? There have been countless articles and numerous books on the evolution of bipedalism in hominins, yet, with the exceptions of Carrier (1984) and Bramble and Lieberman (2004), none have considered running in any depth (see also Bortz, 1985; Heinrich, 2002). There are three major reasons for this lack of attention. First, what is out of sight is often out of mind: humans no longer need to run very much, and do so now primarily for pleasure or health. Second, we consistently underrate our abilities as athletes, primarily because we tend to focus on aspects of athleticism related to speed and power in which humans are pathetic compared to most mammals. The idea that brains have triumphed over brawn is so deeply engrained that it rarely receives much consideration.

Finally, students of the fossil record of human evolution have, understandably, focused on the origins of walking. There is substantial evidence that the earliest hominins were bipedal (Haile-Selassie, 2001; Galik et al., 2004; Zollikofer

et al., 2005; Richmond and Jungers, 2008), and that walking was a key part of the transition that set early hominins off on a strikingly different evolutionary trajectory than chimpanzees (Darwin, 1871). There has been much debate over the extent to which early hominins were arboreal and whether these capabilities compromised their ability to walk optimally (Lovejoy, 1988; Stern, 2000; Ward, 2002), but few doubt that australopithecines were capable, habitual bipeds. However, it is important to note that the biomechanics of running and walking are substantially different, especially for a biped. In addition, the physiological demands of ER are quite different from those of sprinting or walking. Thus, evidence for walking capabilities in early hominins is not necessarily evidence for ER capability. Instead, a diverse array of comparative functional morphological and physiological evidence (Carrier, 1984; Bramble and Lieberman, 2004) suggests that human ER capabilities are not a byproduct of selection on bipedal walking alone. It follows that human ER capabilities demand some explanations for when and why they evolved.

Unfortunately, we cannot pinpoint precisely when ER first evolved. As outlined above and by Bramble and Lieberman (2004), the majority of the fossil evidence points to *H. erectus* as the first endurance runner. But, as also noted, we cannot rule out the possibility that *H. habilis* had some ER capabilities, nor can we rule out the hypothesis that later hominins had better performance capabilities than early *H. erectus*. More definitive answers require more evidence and more research. That said, the available evidence suggests that *Australopithecus* lacked many, if not most, of the derived features of *Homo* that improve ER performance. Some of these derived features, such as relatively large anterior and posterior semicircular canals, and the nuchal ligament, are specific to running. Other derived features, such as long legs, would have benefited both running and walking. Thus it is reasonable to speculate that selection for ER occurred in the context of selection for *both* walking and running long distances.

If there has been any skepticism about the ER hypothesis, then it has been with regard to why ER evolved (see, for example, comments in Carrier, 1984; also Pickering and Bunn, 2007). Because modern humans, including recent hunter-gatherers, no longer require ER in their daily lives, it is hard for many scholars to imagine how ER would have been selected for in the distant past. However, such reliance on the ethnographic present – what Wobst (1978) has referred to as the “tyranny of ethnography” – is problematic since recent inventions (such as the bow and arrow and the domestication of the dog) have substantially changed human hunting strategies in precisely those aspects that relate to ER. Critically, these innovations allow humans to hunt and kill animals from a distance without getting close to large prey. But for most of the history of the genus *Homo*, it appears that

hominins have been able to kill large, prime age, adult prey that would have posed serious risks to any hunter armed solely with an untipped spear. ER, however, would have changed that equation by allowing hunters in the hot, arid and open habitats that have existed in Africa since at least 1.9 Ma, to run their prey into exhaustion, thereby disadvantaging them sufficiently to be slain with minimal risk and a high probability of success. While ER-based persistence hunting would have required the cognitive skills to track an animal combined with abundant access to water, the energetic costs are surprisingly low in comparison to walking, and well worthwhile in terms of the payoff. Like other methods of hunting, ER and PH would also have required social groups with food-sharing.

Although the extent to which scavenging was an important behavior among early hominins is still debated, it is likely that scavenging played some component of early *Homo* subsistence strategies, just as it now does among the Hadza and Bushmen. Since carcasses are an evanescent resource in which early access improves the chance of getting something to eat and minimizing competition with other carnivores, then it would have benefited from ER capabilities.

In short, there is a compelling case to be made that ER would have given early *Homo* the ability to create a new niche within the carnivore guild: that of a diurnal predator within the increasingly open habitats in Africa by 1.9 Ma. In particular, ER would have provided ESA hunters with various means of getting meat at comparatively low risk and low cost. Observations that ER is rare among modern hunter-gatherers who possess weapons (such as the bow and arrow and atlatl) are not disproof of the hypothesis. Instead, the persistent, albeit rare, use of ER in scavenging and persistence hunting by modern hunter-gatherers such as the Bushmen, the Tarahumara and others are testaments to the importance of running in hunting in general, and the effectiveness of persistence hunting in particular, despite the invention of technologies that have made these athletic feats obsolete.

Finally, it is fun to conclude by speculating on a possible scenario for the evolution of ER in the genus *Homo*. Natural selection works by tinkering (Jacob, 1977). That is, selection can work only by taking advantage of small-scale heritable variations that somehow improve performance within a particular fitness context. One can well imagine circumstances in which the earliest members of the genus *Homo* or perhaps australopithecines began to scavenge or possibly hunt a little. In such a context, individuals with variations such as larger anterior and posterior semicircular canals, longer legs, narrower waists, more sweat glands, and so on might have enjoyed some fitness benefit because their improved performance in long distance running and/or walking that helped them acquire more meat. Over time – depending on factors

such as the strength of selection, how much variation was available, and population size – modern ER capabilities, along with a modern-shaped body evolved, probably first in *H. erectus*. These capabilities apparently enabled *H. erectus* to kill medium- to large-sized animals in the hot, open habitats of Africa in the Early Pleistocene without any weaponry more sophisticated than a sharpened wooden stick. After the ESA, more sophisticated projectile technologies evolved (e.g., stone- and bone-tipped spears, bows and arrows, spear throwers and nets) that gave hunters other, less grueling options to bring home the bacon. As a result, persistence hunting has become less important. In addition, many hominins started to move out of Africa into temperate zones where PH was no longer possible. But the traces of our ancestry persist in a body well-suited to ER, a behavior that nowadays serves primarily as a means of relaxation and a way to stay healthy.

References

- Acosta, L. Jr, Roy, R.R., 1987. Fiber-type composition of selected hindlimb muscles of a primate (cynomolgus monkey). *Anatomical Record* 218, 136–141.
- Aiello, L., Dean, M.C., 1990. *An Introduction to Human Evolutionary Anatomy*. Academic, London.
- Aiello, L., Wheeler, P., 1995. The expensive tissue hypothesis: the brain and digestive system in human and primate evolution. *Current Anthropology* 36, 199–221.
- Alexander, R.M., 1991. Elastic mechanisms in primate locomotion. *Zeitschrift für Morphologie und Anthropologie* 78, 315–320.
- Armstrong, R.B., Saubert, C.W. 4th, Seeherman, H.J., Taylor, C.R., 1982. Distribution of fiber types in locomotory muscles of dogs. *American Journal of Anatomy* 163, 87–98.
- Balke, B., Snow, C., 1965. Anthropological and physiological observations on Tarahumara endurance runners. *American Journal of Physical Anthropology* 23, 293–301.
- Behrensmeyer, A.K., Todd, N.E., Potts, R., McBrinn, G.E., 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278, 1589–1594.
- Bennett, W.C., Zingg, R.M. 1935. *The Tarahumara: an Indian Tribe of Northern Mexico*. University of Chicago Press, Chicago, IL.
- Berger, T.D., Trinkaus, E., 1995. Patterns of trauma among the Neandertals. *Journal of Archaeological Science* 22, 841–852.
- Bianchi, M., 1989. The thickness, shape and arrangement of the elastic fibres within the nuchal ligament from various animal species. *Anatomischer Anzeiger* 169, 53–66.
- Binford, L., 1984. Bones of contention: a reply to Glynn Isaac. *American Antiquity* 49, 164–167.
- Blumenshine, R.J., 1986. Early Hominid Scavenging Opportunities: Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. *British Archaeological Reports International Series*, 283, Oxford
- Blumenshine, R.J., 1987. Characteristics of an early hominid scavenging niche. *Current Anthropology* 28, 383–407
- Blumenshine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *Journal of Archaeological Science* 15, 483–502.
- Blurton-Jones, N.G., Marlowe, F.W., 2002. Selection for delayed maturity: does it take 20 years to learn to hunt and gather? *Human Nature* 13, 199–238.

- Bobe, R., Behrensmeyer, A.K., Chapman, R.E., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution* 42, 475–497.
- Bortz, W.M., 1985. Physical exercise as an evolutionary force. *Journal of Human Evolution* 14, 145–155.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago, IL.
- Bramble, D.M., Carrier, D.R., 1983. Running and breathing in mammals. *Science* 219, 251–256.
- Bramble, D.M., Jenkins, F.A.J. Jr., 1993. Mammalian locomotor-respiratory integration: implications for diaphragmatic and pulmonary design. *Science* 262, 235–340.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432, 345–352.
- Bramble, D.M., Lieberman, D.E., Raichlen, D.A., Whitcome, K., 2009. Passive head stabilization in running humans. *Science* (in review).
- Bunn, H.T. 2001. Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene *Homo*. In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-Eating and Human Evolution*. Oxford University Press, Oxford, pp. 199–218.
- Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science* 20, 365–398.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27, 431–452.
- Cattelain, P., 1997. Hunting during the Upper Paleolithic: bow, spearthrower, or both? In: Knecht, H. (Ed.) *Projectile Technology*. Plenum, New York, pp. 213–240.
- Cavagna, G.A., Kaneko, M., 1977. Mechanical work and efficiency in level walking and running. *Journal of Physiology* 268, 467–481.
- Cavallo, J.A., Blumenshine, R.J., 1989. Tree-stored leopard kills: expanding the hominid scavenging niche. *Journal of Human Evolution* 18, 393–399.
- Carrier D.R., 1984. The energetic paradox of human running and hominid evolution. *Current Anthropology* 24, 483–495.
- Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 97, 241–247.
- Cerling, T.E., Hay, R.L., 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. *Quaternary Research* 25, 63–78.
- Chevront, S.N., Haymes, E.M., 2001. Ad libitum fluid intakes and thermoregulatory responses of female distance runners in three environments. *Journal of Sports Sciences* 19, 845–854.
- Churchill, S.E., 1993. Weapon technology, prey size selection and hunting methods in modern hunter-gatherers: implications for hunting in the Palaeolithic and Mesolithic. In: Peterkin, G.L., Bricker, H.M. Mellars, P.A. (Eds.), *Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia*. Archeological Papers of the American Anthropological Association No. 4, pp. 11–24.
- Clark, J.D., 1955. The stone ball, its associations and use by prehistoric Man in Africa. In: L. Balout (Ed.), *Actes du Congrès Pan-Africain de Préhistoire*, Ile session, Alger, 1952. Arts et Métiers, Paris, pp. 403–407.
- Cole, S., 1963. *The Prehistory of East Africa*. Mentor, New York.
- Cooper, S.M., 1991. Optimal hunting group size: the need for lions to defend their kill against loss to spotted hyenas. *African Journal of Ecology* 29, 130–136.
- Coyle, E.F., 2000. Physical activity as a metabolic stressor. *American Journal of Clinical Nutrition* 72, 512S–20S.
- Cromwell, R.L., Newton, R.A., Carlton, L.G., 2001. Horizontal plane head stabilization during locomotor tasks. *Journal of Motor Behavior* 33, 49–58.
- Darwin, C., 1871. *The Descent of Man*. John Murray, London.
- Dawson, T.J., Robertshaw, D., Taylor, C.R., 1974. Sweating in the kangaroo: a cooling mechanism during exercise, but not in the heat. *American Journal of Physiology* 227, 494–498.
- Dennell, R., 2003. Dispersal and colonisation, long and short chronology: how continuous is the Early Pleistocene record for hominids outside East Africa. *Journal of Human Evolution* 45, 421–440.
- Dill, D.B., Bock, A.V. Edwards, H.T., 1933. Mechanism for dissipating heat in man and dog. *American Journal of Physiology* 104, 36–43.
- Dimery, N.J., Alexander, R.M., Deyst, K.A., 1985. Mechanics of the ligamentum nuchae of some artiodactyls. *Journal of Zoology*, London 206, 341–351.
- Domínguez-Rodrigo, M., 2002. Hunting and scavenging by early humans: the state of the debate. *Journal of World Prehistory* 16, 1–54.
- Entin, P.L., Robertshaw D., Rawson R.E., 1999. Effect of locomotor respiratory coupling on respiratory evaporative heat loss in the sheep. *Journal of Applied Physiology* 87, 1887–1893.
- Feibel, C.S., Brown, F.H., 1993. Microstratigraphy and environments. In: Walker, A., Leakey, R.E.F. (Eds.) *The Nariokotome *Homo erectus* skeleton*. Harvard University Press, Cambridge, MA, pp. 21–39.
- Feibel, C.S., Harris, J.M., Brown, F.H., 1991. Palaeoenvironmental context for the late Neogene of the Turkana Basin. In: Harris, J.M. (Ed.): *Koobi Fora Research Project*, Vol. 3. Clarendon, Oxford, pp. 321–370.
- 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.
- Garland, T., 1983. The relation between maximal running speed and body mass in terrestrial mammals. *Journal of Zoology* 199, 1557–1570.
- Gauthier, G.B., Piron, J.P., Roll, J.P., Marchetti, E., Martin, B., 1984. High-frequency vestibulo-ocular reflex activation through forced head rotation in man. *Aviation, Space and Environmental Medicine* 55, 1–7.
- Groom, D., 1971. Cardiovascular observations on Tarahumara Indian runners – the modern Spartans. *American Heart Journal* 81, 304–314.
- Haile-Selassie, J., 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412, 178–181.
- Harcourt-Smith, W.E.H., 2002. Form and function in the hominoid tarsal skeleton. Ph.D. thesis, University College London, London.
- Harris, J.M., Leakey, M., 1993. The faunal context. In: Walker, A., Leakey, R.E.F. (Eds.), *The Nariokotome *Homo erectus* skeleton*. Harvard University Press, Cambridge, MA, pp. 54–60.
- Hay, R.L., 1987. Geology of the Laetoli area. In: Leakey, M.D., Harris, J.M. (Eds.), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon, Oxford, pp. 23–47.
- Hay, R.L., 1976. *Geology of the Olduvai Gorge*. University of California Press, Berkeley.
- Heglund, N.C., Taylor, C.R., 1988. Speed, stride frequency and energy cost per stride. How do they change with body size and gait? *Journal of Experimental Biology* 138, 301–318.
- Heinrich, B., 2002. *Why We Run: a Natural History*. Harper Collins, New York.
- Hinchcliff, K.W., Shaw, L.C., Vukich, N.S., Schmidt, K.E., 1998. Effect of distance traveled and speed of racing on body weight and serum enzyme activity of sled dogs competing in a long-distance race. *Journal of the American Veterinary Medicine Association* 213, 639–44.
- Hinrichs, R.N., 1990. Upper extremity function in distance running. In: Cavanagh, P.R. (Ed.) *Biomechanics of Distance Running*. Human Kinetics Books, Champaign, IL, pp. 107–133.
- Hirasaki, E., Moore, S.T., Raphan, T., Cohen, B., 1999. Effects of walking velocity on vertical head and body movements during locomotion. *Experimental Brain Research* 127, 117–30.

- Holekamp, K.E., Boydston, E.E., Smale, E., 2000. Group travel in social carnivores. In: Boinski, S., Garber, P. (Eds), *On the Move: How and Why Animals Travel in Groups*. University of Chicago Press, Chicago, IL, pp. 587–627.
- Hoyt, D.F., Taylor, C.R., 1981. Gait and the energetics of locomotion in horses. *Nature* 292, 239–240.
- Hunt, K.D., 1992. Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *American Journal of Physical Anthropology* 87, 83–105.
- Isaac, G.L., 1978. Food sharing and human evolution: archaeological evidence from the Plio-Pleistocene of East Africa. *Journal of Anthropological Research* 34, 311–325.
- Isbell, L.A., Pruetz, J.D., Lewis, M., Young, T.P., 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. *American Journal of Physical Anthropology* 105, 199–207.
- Jablonski, N., 2006. *Skin: a Natural History*. University of California Press, Berkeley.
- Jacob, F., 1977. Evolution and tinkering. *Science* 196, 1161–1166.
- Jeffery, N., Spoor, F., 2004. Prenatal growth and development of the modern human labyrinth. *Journal of Anatomy* 204, 71–92.
- Jellema, L.M., Latimer, B., Walker, A., 1993. The rib cage. In: Walker, A., Leakey, R. E.F. (Eds), *The Nariokotome Homo erectus Skeleton*. Harvard University Press, Cambridge, MA, pp. 294–325.
- Kappel-Bargas, A., Woolf, R.D., Cornwall, M.W., McPoil, T.G., 1998. The windlass mechanism during normal walking and passive first metatarsalphalangeal joint extension. *Clinical Biomechanics* 13, 190–194.
- Keller, T.S., Weisberger A.M., Ray J.L., Hasan S.S., Shiavi R.G., Spengler D.M., 1996. Relationship between vertical ground reaction force and speed during walking, slow jogging, and running. *Clinical Biomechanics* 11, 253–259.
- Ker, R.F., Bennett, M.B., Bibby, S.R., Kester, R.C., Alexander, R. McN., 1987. The spring in the arch of the human foot. *Nature* 325, 147–149.
- Landau, M., 1993. *Narratives in Human Evolution*. Yale University Press, New Haven.
- Larson, S.G., 1993. Functional morphology of the shoulder in primates. In: Gebo, D.L. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, Dekalb, pp. 45–69.
- Larson, S.G., 2009. Evolution of the hominin shoulder: early *Homo*. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds), *The First Humans: Origin and Early Evolution of the Genus Homo*. Springer, Dordrecht, pp. 65–75.
- Larson, S.G., Jungers, W.L., Morwood, M., Sutikna, T., Jatmiko, Saptomo, E.W., Due, R.A., Djubiantono, T., 2007. *Homo floresiensis* and the evolution of the hominin shoulder. *Journal of Human Evolution* 53, 718–731.
- Lewis, O.J., 1989. *Functional Morphology of the Evolving Hand and Foot*. Oxford University Press, Oxford.
- Liebenberg, L., 1990. *The Art of Tracking: The Origin of Science*. David Philip Publishers, Claremont (South Africa).
- Liebenberg, L., 2006. Persistence Hunting by Modern Hunter-Gatherers. *Current Anthropology* 47, 1017–1025.
- Lieberman, D.E., Raichlen, D.A., Pontzer, H., Bramble, D.M., Cutright-Smith, E., 2006. The human gluteus maximus and its role in running. *Journal of Experimental Biology* 209, 2143–2155.
- Lieberman, D.E., Bramble, D.M., Raichlen, D.A., Shea, J.J., 2007. Endurance running and the tyranny of ethnography: a reply to Pickering and Bunn. *Journal of Human Evolution* 53, 439–442.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.
- Lovejoy, C.O., 1988. The evolution of human walking. *Scientific American* 259, 118–125.
- Maas, E.F., Huebner, W.P., Seidman, S.H., Leigh, R.J., 1989. Behavior of human horizontal vestibulo-ocular reflex in response to high-acceleration stimuli. *Brain Research* 499, 153–156.
- Marean, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. *Journal of Human Evolution* 18, 559–582.
- Margaria, R., Cerretelli, P., Aghemo, P., Sassi, G., 1963. Energy cost of running. *Journal of Applied Physiology* 18, 367–370.
- Marshall, J., 1958. Man as hunter. *Natural History* 72, 291–309, 376–395.
- McCarthy, F.D., 1957. *Australian Aborigines: Their Life and Culture*. Colorgrature Publications, Melbourne.
- McArdle, W.D., Katch, F.I., Katch, V.L., 1996. *Exercise Physiology: Energy, Nutrition and Human Performance*. 4th edition. Lea and Febiger, Philadelphia, PA.
- McArthur, A.J., Monteith, J.L., 1980. Air movement and heat loss from sheep. I. Boundary layer insulation of a model sheep, with and without fleece. *Proceedings of the Royal Society of London, Part B, Biological Sciences* 209, 187–208.
- Mercer, S.R., Bogduk, N., 2003. Clinical anatomy of ligamentum nuchae. *Clinical Anatomy* 16, 484–493.
- Minetti, A.E., 2003. Physiology: efficiency of equine express postal systems. *Nature* 426, 785–786.
- Nabokov, P., 1981. *Indian Running: Native American History and Tradition*. Ancient City Press, Santa Fe, NM.
- Noakes, T., 2003. *The Lore of Running*. 4th Edition. Human Kinetics, Champaign, IL.
- O'Brien, E.M., 1981. The projectile capabilities of an Acheulean handaxe from Olorgesailie. *Current Anthropology* 22, 76–79.
- O'Connell, J.F., Hawkes, K., Blurton-Jones, N.G., 1988. Hadza scavenging: implications for Plio-Pleistocene hominid subsistence. *Current Anthropology* 29, 356–363.
- Oswalt, W., 1976. *An Anthropological Analysis of Food-Getting Technology*. Wiley, New York.
- Pennington, Campbell W., 1963. *The Tarahumara of Mexico, Their Environment and Material Culture*. University of Utah Press, Salt Lake City.
- Pennycuik, C.J., 1979. Movements of the migratory wildebeest population in the Seregeti. In: Sinclair, A.R.E., Norton-Griffiths, M. (Eds), *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago, IL, pp. 164–184.
- Pickering T.R., Bunn, H.T., 2007. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *Journal of Human Evolution* 53, 438–442.
- Pontzer, H., 2005. A new model predicting locomotor cost from limb length via force production. *Journal of Experimental Biology* 208, 1513–24.
- Pontzer, H., 2007. Limb length and the scaling of locomotor cost in terrestrial animals. *Journal of Experimental Biology* 210, 1752–1761.
- Potts, R., 1988. Environmental hypotheses of human evolution. *Yearbook of Physical Anthropology* 41, 93–136.
- Richmond, B.G., Jungers, W.L., 2008. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* 319, 1662–1665.
- Rieder, H., 2003. Der Große Wurf der frühen Jäger: Nachbau altsteinzeitlicher Speere. *Biologie im Unserer Zeit* 33, 156–160.
- Rogers, M.J., Feibel, C.S., Harris, J.W.K., 1994. Changing patterns of land use by Plio-Pleistocene hominids in the Lake Turkana Basin. *Journal of Human Evolution* 27, 139–158.
- Rose, M.D., 1984. A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. *American Journal of Physical Anthropology* 63, 371–378.
- Ruff, C.B., 1991. Climate, body size and body shape in hominid evolution. *Journal of Human Evolution* 21, 81–105.
- Saunders J.B.D.M., Inman, V.T., Bresler, B., 1953. The major determinants in normal and pathological gait. *Journal of Bone and Joint Surgery* 35A, 543–555.

- Schapera, I., 1930. The Khoisan Peoples of South Africa: Bushmen and Hottentots. Routledge and Kegan Paul, London.
- Scheuer, L., Black, L., 2000. Developmental Juvenile Osteology. Academic Press, London.
- Schmid, P., 1983. Eine Rekonstruktion des skelettes von A.L. 288-1 (Hadar) und deren Konsequenzen. *Folia Primatologica* 40, 283-306.
- Schmid, P., 1991. The trunk of the australopithecines. In: Coppens, Y., Senut, B. (Eds), *Origine(s) de la Bipédie chez les Hominidés*. Presses du CNRS, Paris, pp. 225-234.
- Schmidt-Nielsen, K., 1990. *Animal Physiology: Adaptation and Environment*. 4th edition. Cambridge University Press, Cambridge.
- Shea, J.J., 2006a. The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. *Journal of Archaeological Science* 33, 823-846.
- Shea, J.J., 2006b. What stone tools can (and can't) tell us about early hominin diets. In: Ungar, P. (Ed.), *Early Hominin Diets: The Known, the Unknown and the Unknowable*. Oxford University Press, Oxford, pp. 321-351.
- Stedman, H.H., Kozyak, B.W., Nelson, A., Thesier, D.M., Su, L.T., Low, D.W., Bridges, C.R., Shrager, J.B., Minugh-Purvis, N., Mitchell, M.A., 2004. Myosin gene mutation correlates with anatomical changes in the human lineage. *Nature* 428, 415-418.
- Shostak, M., 1981. *Nisa: The Life and Words of a !Kung Woman*. Harvard University Press, Cambridge, MA.
- Spoor, F., Wood, B., Zonneveld, F., 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* 369, 645-648.
- Stern, J.T., 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. *Evolutionary Anthropology* 9, 113-133.
- Studel-Numbers, K.L., Tilkens, M.J., 2004. The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins. *Journal of Human Evolution* 47, 95-109.
- Studel-Numbers, K.L., Weaver, T.D., Wall-Scheffler, C.M., 2007. The evolution of human running: effects of changes in lower-limb length on locomotor economy. *Journal of Human Evolution* 53, 191-196.
- Susman, R.L., 2008. New evidence bearing on the status of *Homo habilis* from Olduvai Gorge. *American Journal of Physical Anthropology* 135 (S46), 203.
- Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatologica* 43, 113-156.
- Tappen, M., 2001. Deconstructing the Serengeti. In: Stanford, C.B., Bunn, H.T. (Eds), *Meat-Eating and Human Evolution*. Oxford University Press, Oxford, pp. 13-32.
- Taylor, C.R., Rowntree, V.J., 1973. Temperature regulation and heat balance in running cheetahs: a strategy for sprinters? *American Journal of Physiology* 224, 848-851.
- Thayer, R., Collins, J., Noble, E.G., Taylor, A.W., 2000. A decade of aerobic endurance training: histological evidence for fibre type transformation. *Journal of Sports Medicine and Physical Fitness* 40, 284-289.
- Theime, H., 1997. Lower Paleolithic hunting spears from Germany. *Nature* 385, 807-810.
- Thorstensson, A., Nilsson, J., Carlson, H., Zomlefer, M.R., 1984. Trunk movements in human locomotion. *Acta Physiologica Scandinavica* 121, 9-22.
- Torii, M., 1995. Maximal sweating rate in humans. *Journal of Human Ergology (Tokyo)* 24, 132-152.
- Tsintzas, K., Williams, C., 1998. Human muscle glycogen metabolism during exercise. Effect of carbohydrate supplementation. *Sports Medicine* 25, 7-23.
- Van Valkenburgh, B., 2001. The dog-eat-dog world of carnivores: a review of past and present carnivore community dynamics. In: Stanford, C.B., Bunn, H.T. (Eds), *Meat-Eating and Human Evolution*. Oxford University Press, Oxford, pp. 101-121.
- Vrba, E.S., 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. 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. 385-424.
- Ward, C.V., 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yearbook of Physical Anthropology* 35, 185-215.
- Washburn, S.L., 1960. Tools and human evolution. *Scientific American* 203, 169-181.
- Wheeler, P.E., 1991. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. *Journal of Human Evolution* 21, 107-115.
- Whittaker, J.C., McCall, G., 2001. Handaxe-hurling hominids: an unlikely story. *Current Anthropology* 42, 566-572.
- Williams, T.M., Dobson, G.P., Mathieu-Costello, O., Morsbach, D., Worley, M.B., Phillips, J.A., 1997. Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. *Journal of Comparative Physiology, Part B* 167, 527-535.
- Wilson R.S., James R.S., 2004. Constraints on muscular performance: trade-offs between power output and fatigue resistance. *Proceedings of the Royal Society, Biological Science* 271 Supplement 4, S222-225.
- Winter, D.A., Ruder, K.G., MacKinnon, C.D., 1990. Control of balance of upper body in gait. In: Winters, J.M., Woo, S.L.Y. (Eds), *Multiple Muscle Systems: Biomechanics and Movement Organization*. Springer, New York, pp. 534-541.
- Wobst, M., 1978. The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology. *American Antiquity* 43, 303-309.
- Wood, B.A., 2009. Where does the genus *Homo* begin, and how would we know? In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds), *The First Humans: Origin and Early Evolution of the Genus *Homo**. Springer, Dordrecht, pp. 17-28.
- Wood, B.A., Collard, M., 1999. The human genus. *Science*, 284, 65-71.
- Wynn, T., 2002. Archaeology and cognitive evolution. *Behavioral and Brain Science* 25, 389-402.
- Yang, N., MacArthur, D.G., Gulbin, J.P., Hahn, A.G., Beggs, A.H., Eastal, S., North, K., 2003. ACTN3 genotype is associated with human elite athletic performance. *American Journal of Human Genetics* 73, 627-631.
- Zollikofer, C.P., Ponce de Leon, M.S., Lieberman, D.E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature* 434, 755-759.