Ecological Energetics in Early Homo

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Models for the origin of the genus Homo propose that increased quality of diet led to changes in ranging ecology and selection for greater locomotor economy, speed, and endurance. Here, I examine the fossil evidence for postcranial change in early Homo and draw on comparative data from living mammals to assess whether increased diet quality has led to selection for improved locomotor performance in other lineages. Body mass estimates indicate early Homo, both males and females, were approximately 33% larger than australopiths, consistent with archeological evidence indicating an ecological change with the origins of our genus. However, many of the postcranial features thought to be derived in Homo, including longer hind limbs, are present in Australopithecus, challenging the hypothesis that early Homo is marked by significant change in walking and running performance. Analysis of energy budgets across mammals suggests that the larger body mass and increased diet quality in early Homo may reflect an increase in the hominin energy budget. Expanding the energy budget would enable greater investment in reproduction without decreasing energy available for larger brains or increased activity. Food sharing and increased adiposity, which decrease variance in food energy availability, may have been integral to this metabolic strategy.

Introduction

In describing the first specimens of Homo habilis 5 decades ago, Leakey, Tobias, and Napier (1964) argued for two distinct grades within the hominin lineage. Australopithecus species of south and east Africa—with their large molars and ape-size brains—were viewed as more primitive in their cognitive abilities and behavior, while H. habilis—with its larger brain, smaller molars, and dexterous hands capable of making the earliest stone tools—marked the beginnings of modern human ability and behavior (Leakey, Tobias, and Napier 1964). While Leakey, Tobias, and Napier (1964:9) viewed Australopithecus and Homo as “two branches of Hominidae evolving side by side,” subsequent work has suggested that the origin of our genus marks an ecological shift in foraging behavior and diet from an earlier australopith strategy that persisted throughout much of the Pliocene (Aiello and Wheeler 1995; Bramble and Lieberman 2004; Conroy and Pontzer 2012; Leonard and Robertson 1997; O’Connell, Hawkes, and Blurton Jones 1999; Shipman and Walker 1989). In this review, I briefly outline current ecological models for the evolution of the genus Homo and examine whether the proposed changes in foraging behavior are consistent with comparative data from living mammals and the fossil evidence of postcranial anatomy and locomotor performance in Plio-Pleistocene hominins.

Researchers have long focused on foraging behavior in reconstructing hominin ecology and evolution (Bramble and Lieberman 2004; Dart 1949, 1957; Darwin 1871; Hawkes et al. 1998; Lee and Devore 1968; Lovejoy 1981). Unlike the other great apes, which travel modest distances each day in search of plant foods and must fend for themselves, human foragers range widely, hunt regularly, and share religiously (Marlowe 2005). Early models of hominin evolution proposed that these defining aspects of modern human foraging behavior arose early in the hominin lineage. Darwin (1871:40) offered that our species’ “preeminent success in the battle of life” was in large part due to our progenitors’ bipedal posture, which freed their hands and allowed them “to defend themselves with stones or clubs, to attack prey, or otherwise obtain food.” Dart’s (1949, 1957) osteodontokeratic interpretations of Australopithecus behavior followed, with the Man the Hunter paradigm emerging in the 1960s (Lee and Devore 1968).

As late as the 1980s, models of early hominin evolution suggested that Australopithecus, then the oldest hominin genus known, engaged in hunting and food sharing (Carrier 1984; Lovejoy 1981). However, over the past 3 decades, analyses of australopith dental and postcranial anatomy have typically portrayed them as semi-arboreal and vegetarian (Conroy and Pontzer 2012). Analyses of australopith locomotor anatomy, based largely on the A.L. 288 Australopithecus afarensis skeleton (e.g., Stern and Susman 1983; see Ward 2002), have
suggested that they were too arboreal and too inefficient on the ground—in essence, too apelike—to be plausible hunter-gatherers (but see Latimer 1991). Instead, recent models of hominin evolution have proposed that the roots of modern human foraging ecology lie in the origin of the genus *Homo*, recalling the distinction made by Leakey and colleagues nearly 50 years ago (Aiello and Wheeler 1995; Bramble and Lieberman 2004; Leakey, Tobias, and Napier 1964; O’Connell, Hawkes, and Blurton Jones 1999; Shipman and Walker 1989).

**Ecological Models for the Origin of *Homo***

Because of the inclusion of meat, underground storage organs (USOs), and cooking, the diet quality (i.e., kcal/g of food; see Leonard and Robertson 1997) of modern human foragers is greater than that of living apes, and most ecological models for the origin of *Homo* suggest that a shift toward modern human diet quality was instrumental in shaping the evolution of our genus (Aiello and Wheeler 1995; Bramble and Lieberman 2004; Leonard and Robertson 1997; O’Connell, Hawkes, and Blurton Jones 1999; Shipman and Walker 1989). However, current models differ in which aspects of modern human foraging behavior they view as seminal.

Many ecological models for the evolution of the genus *Homo* emphasize the adoption of hunting and scavenging (Aiello and Wheeler 1995; Bramble and Lieberman 2004; Shipman and Walker 1989). In these hunting and scavenging models, meat and marrow provided valuable energetic and nutritional rewards for early *Homo* while simultaneously creating selection pressure for locomotor and cognitive adaptations to pursue prey or monopolize fresh carcasses. These models often envision the pursuit of prey and carcasses occurring under the midday sun of equatorial Africa, producing additional selection pressure for effective thermoregulation (Bramble and Lieberman 2004; Ruff and Walker 1993; Walker 1993). Proponents of these hunting and scavenging models view the tall, long-limbed proportions of *Homo erectus* (epitomized by the KNM-WT 15000 skeleton) as evidence for improved running and thermoregulatory ability and the increase in brain size and reduction in tooth size as evidence for the inclusion of energy-rich meat/marrow into the diet (Aiello and Wheeler 1995; Bramble and Lieberman 2004; Shipman and Walker 1989).

Others have suggested that hunting and scavenging were of negligible importance in the evolution of our genus and have instead focused on the gathering of USOs, food sharing, and cooking (O’Connell, Hawkes, and Blurton Jones 1999; O’Connell et al. 2002; Wrangham et al. 1999). In these USO models for the origin of *Homo*, climatic changes leading to increased aridity in the early Pliocene led to an increased reliance on USOs, which are rich in calories and nutrients and available even in dry seasons (O’Connell, Hawkes, and Blurton Jones 1999). The difficulty in locating and harvesting these underground foods led to selection favoring the provisioning of children, which in turn resulted in longer female life spans and increased body size (O’Connell, Hawkes, and Blurton Jones 1999). In a variant of this model, the adoption of cooking plays a key role by unlocking otherwise indigestible carbohydrates in USOs and alters the social dynamics of early *Homo* by creating a home base where males and females would cook and share food (Wrangham 2009; Wrangham et al. 1999).

Several studies have modeled the energetic consequences of improved diet quality and larger body size of Pleistocene *Homo* (Aiello and Key 2002; Aiello and Wheeler 1995; Leonard and Robertson 1997; Steudel-Numbers 2006). Perhaps the most influential has been the expensive tissue hypothesis of Aiello and Wheeler (1995), which proposes that the addition of readily digestible and energy-rich meat into the diet of early *Homo* decreased their required gut size, freeing metabolic energy to fuel a larger brain. Other studies have focused primarily on differences in daily energy expenditure (DEE; kcal/day) between *Australopithecus* and *Homo*, suggesting that the larger body size in *H. erectus* and an increase in ranging activity associated with a higher-quality diet would have substantially increased daily energy requirements for Pleistocene *Homo* (Aiello and Key 2002; Leonard and Robertson 1997; Steudel-Numbers 2006). This increase in DEE is generally viewed as increasing the challenge of meeting food requirements in Pleistocene *Homo*, although one analysis by Steudel-Numbers (2006) has suggested that this increase in DEE would be partially offset by an improvement in locomotor economy due to increased hind-limb length in *Homo*.

**Testing Ecological Models for the Origin of *Homo***

The models briefly outlined above each provide a compelling reconstruction of the origin and evolution of our genus. Despite their differences, these models share a common logical framework and set of assumptions that can be tested using comparative data from living mammals as well as evidence from the hominin fossil record. Recent work in the hominin fossil record, locomotor energetics, ranging ecology, and the evolution of mammalian metabolic strategies provide the opportunity to reexamine these ecological models with new data.

In discussing the transition from *Australopithecus* to *Homo*, it is necessary to address the taxonomic placement of the oldest taxon in the genus *Homo*, *Homo habilis*. Wood and Collard (1999) have suggested that the primitive morphology of *H. habilis* more accurately places it within *Australopithecus*. Similarly, many of the ecological models discussed above view *Homo erectus* as the earliest species to exhibit the morphological and behavioral traits they view as critical and definitive of the genus. The ecological reconstruction and taxonomic placement of *H. habilis* affect the timing but not the nature of the proposed transition from *Australopithecus* to *Homo*; instead, the assessment of *H. habilis* affects whether it is viewed as a latest exemplar of the *Australopithecus* grade or...
the earliest exemplar of the Homo grade. This timing is discussed below.

For the purposes of this analysis, I use a simplified taxonomic scheme that combines specimens assigned to H. habilis and Homo rudolfensis into a single taxon, Homo habilis sensu lato, and similarly places specimens previously assigned to Homo ergaster into H. erectus. Given the difficulty in assigning postcranial elements to species and the grade-level focus of these analyses, further distinction seems unwarranted. Further, I focus only on gracile Australopithecus taxa (Australopithecus afarensis, Australopithecus africanus, Australopithecus garhi, and Australopithecus sediba) because the postcranial evidence for robust forms is poor and because current hypotheses (both phylogenetic and ecological) view robust forms as an evolutionary side branch rather than ancestral to Homo (Conroy and Pontzer 2012).

Ecological models of past evolutionary events are inherently complex. In order to organize and facilitate discussion, I have outlined five broad points on which current ecological models for the origin of Homo rest. Some points are more vital to some models than to others, but all draw on these five points to some degree. Points 1–3 concern the evolution of hominin postcranial anatomy and the biomechanical effects of these changes on locomotor performance. Points 4–5 concern proposed links between ecological change and evolutionary pressures on locomotor performance. I use this broad distinction to organize the analyses and discussion below.

1. The postcranial anatomy of early Homo (at least by early Homo erectus) shows significant departures from the postcranial anatomy of earlier hominins. All of the ecological models outlined above draw on fossil analyses indicating that the postcranial anatomy of early Homo differs from that of Australopithecus. Derived aspects of modern human postcranial anatomy thought to be evident in early Homo include larger body size (especially females), longer hind limbs, shorter forelimbs, a narrow pelvis, shorter phalanges, and a stiff springlike plantar arch. A long list of derived postcranial changes in early Homo was given by Bramble and Lieberman (2004), who viewed these traits as critical for long-distance running. As mentioned above, the earliest evidence for larger female body size and some derived postcranial morphology is often noted in early Homo erectus rather than Homo habilis.

2. Postcranial changes evident in early Homo are products of natural selection, not neutral processes such as drift. The ecological models discussed above view the ecological transition from Australopithecus to Homo as a selection event. The behavioral and morphological traits adopted by early Homo are viewed as a response to changing climatic conditions and the transition to a new foraging regime.

3. The derived postcranial characters evident in early Homo improve locomotor performance (speed, economy, endurance). Hunting and scavenging models typically emphasize the importance of derived postcranial traits in early Homo for running performance (Bramble and Lieberman 2004; Shipman and Walker 1989). Others have suggested these traits are adaptations for walking long distances to gather plant foods (Isbell et al. 1998; O’Connell, Hawkes, and Blurton Jones 1999).

4. Evolutionary increases in diet quality result in increased ranging activity. Ecological reconstructions of Plio-Pleistocene hominins suggest an increase in ranging activity as a consequence of changing foraging behavior in Homo (Antón, Leonard, and Robertson 2002; Leonard and Robertson 1997; Steudel-Numbers 2006). In hunting and scavenging models, the pursuit of prey or fresh carcasses requires increased running speed (Shipman and Walker 1989) or endurance (Bramble and Lieberman 2004). The USO models do not explicitly link the change in diet quality to an increase in ranging but suggest that increased ranging would be a consequence of the drier climate and decreased food availability (O’Connell, Hawkes, and Blurton Jones 1999).

5. Evolutionary increases in ranging activity lead to corresponding increases in locomotor performance (speed, economy, endurance) in mammals. Ecological models for the evolution of our genus view changes in foraging behavior (point 4) as resulting in a new set of selection pressures on locomotor performance (point 2). Hunting and scavenging models are typically very explicit in outlining the aspects of performance most affected. In discussing the evolutionary consequences of a transition to hunting and scavenging, Shipman and Walker (1989) emphasized the importance of running speed. More recently, Bramble and Lieberman (2004) argued that the critical aspect of performance for early Homo was running endurance, the ability to run at a moderate speed for long periods in order to exhaust prey or outpace other scavengers to distant carcasses. The USO models for the evolution of Homo suggest increased ranging would lead to improved economy and endurance as well, although these models typically emphasize walking performance (Isbell et al. 1998; O’Connell, Hawkes, and Blurton Jones 1999).

Postcranial Change in Homo (Points 1–3)

Ecological models for the evolution of our genus draw on postcranial differences between Homo and Australopithecus. Dozens of morphological features have been cited by previous studies as distinguishing the locomotor anatomy of australopithecines from modern humans (see Bramble and Lieberman 2004; Stern 2000; Ward 2002). Here, I focus primarily on morphological features that have been shown through experimental testing to significantly affect locomotor performance. The discussion below is organized by the demonstrated contribution of each trait to locomotor performance or foraging ecology beginning with traits known to have the greatest effect. The evolutionary forces shaping these changes (point 2) are briefly discussed afterward.
Body Size

The USO models for the evolution of Homo draw on the evidence for increasing body size—particularly female body size—reported for Homo erectus (McHenry 1994). Increased female body size is taken as evidence for delayed female life history schedules (i.e., later age at maturity and longer life span) associated with the advent of provisioning by post-reproductive females (O’Connell, Hawkes, and Blurrton Jones 1999). The cooking hypothesis also views increased female body size as evidence for increased diet quality and a changing social landscape that favored a decrease in sexual dimorphism (Wrangham et al. 1999).

Figure 1 shows estimated body masses for Plio-Pleistocene hominins. Body mass estimates were taken from the literature or calculated from reported femoral head diameters (or, for the MH-1 Australopithecus sediba tibia, from the tibial surface dimensions) using the intra-Homo least squares regression in McHenry (1992). Data and sources are shown in Table 1 and in the extended version of this table (Table A1 in CA+ online supplement A).

As reported previously (McHenry 1992, 1994), there is good evidence for an increase in body mass from Australopithecus to Homo. Mean body mass for the pooled sample of Homo specimens (48.8 kg, SD ± 11.3, n = 15) was 32% greater than in Australopithecus (36.8 ± 74, n = 24). Body masses for specimens identified as male in the Homo sample (56.4 ± 78, n = 9) were 34% larger than those in Australopithecus (42.2 ± 4.9, n = 13), and masses for purported females in the Homo sample (40.7 ± 9.3, n = 7) were 32% larger than those of Australopithecus (30.5 ± 3.7, n = 11). Given the inherent error in estimating mass and the small samples available, further parsing into individual species is statistically unpalatable. Indeed, sample sizes become so miniscule that the confidence intervals for mean male and mean female body mass overlap (see McHenry 1994). Recent finds, while consistent with the general conclusion of increasing body size in Homo, advise caution in estimating the degree of dimorphism in Homo habilis or early H. erectus. Small specimens from Gona and Dmanisi indicate that the range of body mass in early Pleistocene Homo may not have been substantially less than that of Australopithecus (fig. 1; see also Antón 2012; Antón and Snodgrass 2012).

As discussed in USO models for the origin of Homo, adult body size is correlated with life history schedules (Charnov and Berriant 1993; O’Connell, Hawkes, and Blurrton Jones 1999), and sexual dimorphism is correlated with mating and reproductive strategies in primates (Plavcan 2012; Wrangham et al. 1999). The DEE (kcal/day) also increases with body size (Leonard and Robertson 1997; Nagy, Girard, and Brown 1999; see also Antón and Snodgrass 2012). Body mass also has a direct effect on locomotor cost, discussed below, but notably has no apparent effect on running speed. Maximum running speed in mammals is independent of body mass for species greater than 10 kg (Garland 1983b).

Limb Length

Increased relative hind-limb length in Homo has been cited as evidence for increased cursoriality, improving both walking and (especially) running performance in our genus (Bramble and Lieberman 2004; Isbell et al. 1998; Jungers 1982; Ruff and Walker 1993). Indeed, limb length is one of four primary determinants of locomotor cost (kcal/m) in terrestrial animals, the others being body mass, the effective mechanical advantage (EMA) of the limb joints, and the fascicle lengths of limb muscles (Pontzer, Raichlen, and Sockol 2009). The metabolic cost of walking and running derives from the volume of muscle activated in each step to support body weight; consequently, larger animals spend more energy to walk and run (Kram and Taylor 1990; see Pontzer, Raichlen, and Sockol 2009). Limb length, EMA, and muscle length largely determine the volume of muscle activated to support each gram of body mass. Animals with longer limbs, greater EMA (i.e., more straight-legged postures), and shorter muscle fascicles use less energy per gram of body mass to walk and run (Pontzer 2007; Pontzer, Raichlen, and Sockol 2009; Roberts, Chen, and Taylor 1998). The effects of limb length and EMA are evident within our own species. Humans with longer hind limbs use less energy to walk and run (DeJaeger, Willems, and Heglund 2001; Steudel-Numbers and Tilkens 2004; Steudel-Numbers, Weaver, and Wall-Scheffler 2007), and our use of more flexed hind limbs while running decreases the EMA of our knee and hip joints such that the energy cost (kcal/m) of running is greater than the cost of walking (Biewener et al. 2004; Pontzer, Raichlen, and Sockol 2009). Notably, the number of limbs used in locomotion (e.g., whether a species
Table 1. Estimated body masses and femur and tibia lengths for Plio-Pleistocene hominins

<table>
<thead>
<tr>
<th>Species and specimen</th>
<th>Mass (kg)</th>
<th>Sex</th>
<th>Femur (mm)</th>
<th>Tibia (mm)</th>
<th>Source</th>
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<td>ARA-VP-6/500</td>
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<td>.</td>
<td>262.0</td>
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<td>M</td>
<td>.</td>
<td>.</td>
<td>Leakey et al. 1995</td>
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<td>M</td>
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<td>T. Holliday, personal communication</td>
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<td>281.0</td>
<td>241.0</td>
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<td>432.0</td>
<td>.</td>
<td>Steudel-Numbers and Tilkens 2004</td>
</tr>
<tr>
<td>OH 28</td>
<td>54.0</td>
<td>F</td>
<td>456.0</td>
<td>.</td>
<td>Steudel-Numbers and Tilkens 2004</td>
</tr>
</tbody>
</table>

* Not included in body mass comparisons of *Australopithecus* and *Homo*.

b Estimated adult mass.

is bipedal or quadrupedal) has no effect on locomotor cost (Pontzer 2007; Pontzer, Raichlen, and Sockol 2009; Sockol, Raichlen, and Pontzer 2007; Taylor, Heglund, and Maloiy 1982).

Longer limbs—both forelimb and hind limb—are also known to improve an individual’s ability to dissipate heat and thermoregulate in hot environments by increasing the ratio of surface area to body mass (see Tilkens et al. 2007 and references therein). Small increases in core body temperature can have catastrophic effects on the brain and other organs, making adaptations for heat dissipation critical in hot environments (Schmidt-Nielsen 1999). Overheating also curtails ranging activity, as animals must stop walking and running if the heat produced from muscle activity threatens to raise...
the body temperature. Thus, in addition to improving locomotor economy, longer hind limbs in early Homo would likely improve endurance by preventing overheating (Bramble and Lieberman 2004; Ruff and Walker 1993).

In assessing the evidence for increased hind-limb length in Homo, one must account for its correlation with body mass. Figure 2 shows estimated hind-limb lengths (femur + tibia) plotted against estimated body mass for Plio-Pleistocene hominins. A sample of modern humans (n = 110, including measurements of n = 24 Pygmy skeletons generously provided by W. Jungers), chimpanzees (n = 60), and gorillas (n = 22) is shown for comparison (data from Pontzer et al. 2010a). The non-Pygmy human sample is from the Hamman-Todd collection at the Cleveland Museum of Natural History and consists of adults who died in the Cleveland area in the 1900s. While detailed genealogical data are not available for the Hamman-Todd sample, 60% (n = 52) of the individuals in this data set are identified as “black,” while 40% (n = 34) are identified as “white.” Individuals identified as “black” had a greater crural index (tibia/femur length: mean 0.85 ± 0.03) than “white” individuals (0.82 ± 0.03), suggesting the “black” and “white” populations represent more equatorial (presumably African) and more northerly (presumably European) populations, respectively. However, while the difference in mean crural index was significant (P < 0.001, t-test) it was relatively small, and the ranges for these populations (“black”: 0.79–0.91, “white”: 0.76–0.90) largely overlap. Mean crural index for the Pygmy sample (0.85 ± 0.02, range 0.81–0.89) was similar to the “black” sample (P = 0.83, t-test).

Fossil dimensions were taken from the literature (except A.L. 333-3, A.L. 827-1, StW 99, and MH-1, which were generously provided by T. Holliday). Data and sources are given in table 1. Where only tibia or femur lengths are known (the case for most early hominins including early Homo), hind-limb length was estimated using a crural index (tibia/femur length) 0.85. This value (0.85) is equal to the mean crural index for fossil Homo sapiens in the sample (0.85 ± 0.03, n = 12) and near the means for the modern H. sapiens sample (0.84 ± 0.03, n = 110) and combined Pan and Gorilla sample (0.84 ± 0.02, n = 82). To account for potential variation in crural index among early hominins, an error range of ±25 mm was plotted with the estimated hind-limb length, equivalent to a range of crural indexes from 0.80 to 0.90 for these fossils; this range is equivalent to that of the “black” and Pygmy samples, which is appropriate because the specimens for which femur or tibia length was estimated are all African (table 1). For incomplete specimens, when a maximum and minimum estimated length were available, the error range plotted in figure 2 was further expanded to reflect this range of uncertainty.

Figure 2 includes the Ardipithecus ramidus skeleton (ARA-VP-6/500; Lovejoy et al. 2009), the recent Australopithecus afarensis skeleton from Ethiopia (KSD-VP-1/1; Haile-Selassie et al. 2010), Australopithecus garhi (BOU-VP-12/1; Asfaw et
al. 1999), A. sediba (MH1-1; Berger et al. 2010), and the larger adult H. erectus specimen from Dmanisi (Lordkipanidze et al. 2007). The range of body mass estimates for the A. garhi specimen (30–43 kg) was based on the male and female means for Australopithecus (see above). As with hind-limb length estimates, a range of ±5% of estimated body mass was plotted for early hominin specimens in figure 2 to reflect some degree of uncertainty in mass.

Recent finds strongly challenge previous reconstructions of Australopithecus as having short hind limbs. Previous assessments of australopith hind-limb length focused on A.L. 288 and Sts 14, the only Australopithecus specimens for which reliable estimates of limb length and body mass were obtainable (Jungers 1982; McHenry 1991, 1992; Pontzer et al. 2010a; Steudel-Numbers 2006). These specimens have shorter hind limbs than expected for a human of similar mass (fig. 2; see Jungers 1982). However, hind-limb lengths for these specimens are ambiguous because the range of limb lengths seen in modern humans overlaps considerably with that of African apes at body sizes below 30 kg (fig. 2). Inclusion of new specimens suggests hind-limb length in Australopithecus is in fact similar to modern humans. Hind-limb lengths for the large-bodied A. afarensis specimen (KSD-VP-1/1), A. sediba, and A. garhi all fall within modern human range, with KSD-VP-1/1 clearly distinguished from the African apes (fig. 2). These results are robust to error in hind-limb length and body mass estimation; australopith hind-limb lengths relative to body mass remain in the modern human range even when hind-limb length and body mass estimates are varied substantially (fig. 2).

Hind-limb length within the genus Homo warrants discussion. Contrary to reconstructions of H. habilis as having short hind limbs, specimens of H. habilis—including OH 62—fall clearly within the range of modern humans. The hind-limb proportions (relative to body mass) of H. habilis combined with evidence for a springlike plantar arch in this species (see Harcourt-Smith and Aiello 2004; and below) suggest the bipedal capabilities of H. habilis would have been similar to those of H. erectus. Late Pleistocene hominins exhibit a substantial degree of variation in relative hind-limb length (fig. 2). Several Neanderthal specimens, including all of the European specimens and two Middle Eastern specimens, are more than 2 SDs below the range for modern human hind-limb length. While their relatively short tibiae contribute to a shorter hind limb, it is their total hind-limb length, not their crural index, that places Neanderthals outside the modern human range: the range of crural indexes among the Neanderthal sample (0.76–0.81) falls within the observed range in the modern human sample, but their relative hind-limb lengths do not. As discussed by Weaver and Steudel-Numbers (2005), the short hind limbs of Neanderthals may have increased their daily foraging costs.

**Plantar Arch and Achilles Tendon**

During running, the limbs of terrestrial animals act like springs. With each step the ligaments, tendons, and muscles store energy as the limb flexes under body weight and then release this strain energy to help propel the body into the next step (Biewener et al. 2004). In modern humans, much of this springlike work is performed by the plantar arch and the Achilles tendon (Alexander 1991). Together, the plantar arch and Achilles tendon convert over 50% of the energy stored as strain into kinetic energy, reducing the amount of muscular work and metabolic energy needed to power our stride (Alexander 1991). A rigid midfoot also appears to improve walking economy by increasing the efficiency with which the foot pushes off the ground at toe off: when the rigidity of the foot is effectively compromised by walking over a soft surface, the energy cost of walking increases (Lejeune, Willems, and Heglund 1998). Bramble and Lieberman (2004) have argued that a springlike Achilles tendon and plantar arch evolved early in the genus Homo as adaptations for endurance running.

The evolutionary history of these traits is difficult to assess. The presence of an elongated, humanlike Achilles tendon cannot be discerned from fossil remains using current techniques. However, it is notable that gibbons have an elongate Achilles tendon (Payne et al. 2006), indicating that its presence need not coincide with habitual endurance running. The plantar arch is more amenable to measurement in the fossil record, although associated foot bones are rare. Previous analyses of A. afrensis and A. africanus foot morphology have suggested that these species lacked the derived tarsal morphology, particularly of the navicular and cuboid, associated with the springlike modern human plantar arch, and some have even argued that these species retained an opposable hallux (Harcourt-Smith and Aiello 2004). However, more recent work has provided evidence that australopiths may have had a plantar arch. The hominin footprints at Laetoli, usually attributed to A. afrensis, suggest a foot that is functionally similar in many ways to that of modern humans, with a stiff midfoot, adducted hallux, and at least some arching (Tuttle, Webb, and Baksh 1991). Ward, Kimbel, and Johanson (2011) have recently described a fourth metatarsal from Hadar, attributed to A. afrensis, that has a humanlike degree of torsion that along with its proximal articular morphology suggests the presence of an arch. Evidence of an arch appears less ambiguous in early Homo. Specimens of H. habilis (OH-8) and H. erectus (Dmanisi) show strong evidence for the presence of a plantar arch in these taxa (Harcourt-Smith and Aiello 2004; Pontzer, Raichlen, and Sockol 2009). Thus, while it remains plausible that the springlike plantar arch typical of modern humans arose with the genus Homo, recent morphological evidence as well as mechanical analyses of the Laetoli trackway suggest this morphology may extend back to Australopithecus.
Numerous changes in the size and morphology of the limb joints and inferred changes in the size of the muscles that stabilize the trunk have been argued to reflect an increase in terrestrial locomotion, particularly running, in Homo (see Bramble and Lieberman 2004; Stern 2000; Ward 2002). For example, Bramble and Lieberman (2004) have suggested that the larger hind-limb joints and inferred increases in the size of the erector spinae and gluteus maximus muscles in early Homo serve to improve trunk stability and reduce mechanical stress on the joints during long-distance running. While these traits may in fact distinguish Australopithecus from Homo, their effects on locomotor performance are difficult to assess; none have been tested experimentally. Further, in light of the evidence for larger body size in early Homo (fig. 1), it is possible that some of these changes are allometric effects of increased mass.

Bramble and Lieberman (2004) suggest that these traits improve endurance, implicitly defined as the ability to run at a moderate to high speed for a long period of time (up to 1 hour or more), by improving stability of the trunk and reducing mechanical stress and fatigue in the hind-limb joints. However, the only morphological traits known to affect running endurance across mammals are the mass and mitochondrial density of the limb muscles (Weibel et al. 2004); the capacity of the liver and limb muscles to store glycogen may also constrain endurance ability (see Rapoport 2010). Hind-limb muscle mass is greater in modern humans than in living apes (Payne et al. 2006), as expected given our bipedal posture, but it is unclear whether australopiths, which were similarly dependent on their hind limbs for weight support, had similar hind-limb muscle mass. Current techniques are not capable of assessing mitochondrial density in extinct hominins. More work is needed to assess hind-limb muscle properties in Plio-Pleistocene hominins and to determine the effect of other implicated anatomical variables on locomotor performance.

Interpreting Postcranial Anatomy in Early Homo

The evidence outlined above challenges the hypothesis that walking and running performance improved substantially with the origin of the genus Homo. The similarity in hind-limb length between Australopithecus and Homo suggests that the derived longer hind limb typical of modern humans was already present in australopiths nearly 4 million years ago. Similarly, while australopith foot anatomy remains a subject of debate, there is evidence of a rigid, possibly springlike, plantar arch in both the skeletal anatomy of the A. afarensis foot (Ward, Kimbel, and Johanson 2011) and the Laetoli trackway (Tuttle, Webb, and Baksh 1991). Analyses of the Australopithecus pelvis and the footprints at Laetoli as well as computer simulations of australopith gait have previously indicated that Australopithecus most likely used a relatively straight-legged walking gait similar to modern humans (Pontzer, Raichlen, and Sockol 2009; Raichlen et al. 2010; Sockol, Raichlen, and Pontzer 2007; Wang et al. 2004). Thus, with the possible exception of the plantar arch, the locomotor anatomy of Australopithecus, at least as it pertains to walking and running performance, appears to have been functionally equivalent to that of early Homo.

Perhaps the clearest signal for postcranial change in early Homo is an increase in body mass of roughly 33% compared with australopiths (fig. 1). However, while an increase in body mass may signal an ecological change (see below), experimental and comparative evidence suggest increased size would not have improved walking and running performance. Larger animals use more energy to walk and run (Taylor, Heglund, and Margo 1982), and the proportion of DEE spent on travel also tends to increase with body size (Garland 1983a). As noted above, maximum running speed among mammals is independent of body mass above 10 kg (Garland 1983b), although it should be noted that among modern human athletes, sprinters are generally taller and heavier than distance runners (Weyand and Davis 2005). Indeed, larger body size in early Homo, absent an increase in relative hind-limb length, may be particularly difficult to reconcile with endurance running models. Among modern human athletes, endurance running appears to favor shorter, lighter individuals, while sprinters are heavier and taller (Weyand and Davis 2005). Further, because larger body size tends to reduce the ratio of surface area to body mass (Ruff 1994), increased body size in early Homo would likely diminish its ability to shed heat, contra behavioral reconstructions suggesting intense activity in the heat of the day.

Evidence for increased body mass does provide some support for hypotheses suggesting a change in ecology in early Homo, but this support is tempered by three observations from the fossil and comparative record. First, with the inclusion of new specimens of early Homo (fig. 1), there is no evidence that female size increases more than male size, which indicates that an emphasis on increasing female size in Homo may be unwarranted. Second, while larger species tend to have slower life histories (Charnov and Berrigan 1993), there is a considerable degree of variation in this relationship, and analyses of hominin tooth formation suggest that growth rates and thus life history schedules in early Pleistocene Homo were similar to those of Australopithecus (Dean and Smith 2009; Dean et al. 2001), though perhaps somewhat slower in H. erectus (see Schwartz 2012). Third, while larger species tend to have larger energy budgets, there is also a considerable degree of variation in this relationship. Measurements of DEE across a broad range of taxa indicate a sixfold range of variation in DEE even after accounting for the effects of body mass and phylogeny (Nagy, Girard, and Brown 1999). This last point is discussed below.

These analyses have omitted discussion of forelimb length in Australopithecus and Homo because arm length has no known effect on walking or running performance (other than
its effect on body mass). However, it may be that the primary change in limb length with the genus *Homo* is shorter arms rather than longer legs (Holliday 2012). Analyses of the intermembral index of *Australopithecus* suggest substantially longer arms than in *Homo*, although whether this is a primitive retention or an adaptation to climbing remains a matter of debate (Ward 2002). *Homo habilis* has also been argued to have long arms, based primarily on the OH 62 specimen, although this reconstruction is debated (Haeseler and McHenry 2004). Thus, rather than an increase in walking and running performance, the origin of *Homo*, or perhaps *H. erectus*, may mark a decrease in arboreal ability. This scenario is consistent with shorter, straighter phalanges evident in *Homo* (Aiello and Dean 1990); with the pattern of limb robusticity in African *H. erectus* (but not OH-62; Ruff 2009); and perhaps with the larger body size evident in early *Homo*, but it warrants further scrutiny of the hominin forelimb. Here again the small body size of A.L. 288, the primary specimen used to calculate australopithec intermembral index, may confute the difference in proportions with a difference in size. Analysis of the large-bodied KSD-VP-1/1 specimen suggests that forelimb and hind-limb proportions of *A. afarensis* may be more similar to modern humans than previously thought (Haile-Selassie et al. 2010).

Given the evidence for postcranial change, or lack thereof, in the origin of *Homo*, it is important to address whether reported changes in locomotor anatomy may reflect neutral evolutionary processes rather than selection (point 2). Recent comparisons of the human and Neanderthal cranium provide an important reminder that differences in hominin skeletal anatomy often thought to reflect natural selection may in fact reflect neutral processes (Weaver 2009). With this in mind, it is notable that the majority of postcranial traits distinguishing *Australopithecus* from *Homo* have not been tested with regard to their effect on locomotor performance. Traits with known effects on walking and running performance, namely hind-limb length, appear to have remained stable over the past 4 million years of hominin evolution, perhaps changing in the transition from *Ardipithecus* to *Australopithecus* (fig. 2). Similarly, the reorganization of the hominin pelvis for bipedalism, a likely product of natural selection (Grabowski, Polk, and Roseman 2011), appears to predate the genus *Australopithecus* and the transition to *Homo*. Thus, it is difficult to reject the hypothesis that the hominin postcranial skeleton has largely been under stabilizing selection since the middle Pliocene, with neutral evolutionary forces leading to small changes in joint morphology over time. The strongest candidate for postcranial change under natural selection in the evolution of *Homo* may be body mass (fig. 1).

Foraging Ecology and the Evolution of Locomotor Performance (Points 4 and 5)

As discussed above, current ecological models for the evolution of the genus *Homo* envision an increase in diet quality (Bramble and Lieberman 2004; Leonard and Robertson 1997; O’Connell, Hawkes, and Blurton Jones 1999; Shipman and Walker 1989; Wrangham et al. 1999). In these models, particularly those emphasizing hunting and scavenging, higher-quality diet in early *Homo* provided the benefit of increased energy availability but required a substantial increase in ranging activity. The USO models generally frame this increase in ranging activity as an increase in the daily distance traveled (O’Connell, Hawkes, and Blurton Jones 1999; see also Isbell et al. 1998), while hunting and scavenging models emphasize not only increased travel distance but also the need to travel quickly to run down prey or monopolize carcasses (Bramble and Lieberman 2004; Shipman and Walker 1989). Increased ranging activity is in turn thought to increase DEE and to impose a new set of selection pressures on hominin locomotor performance (Bramble and Lieberman 2004; Leonard and Robertson 1997; Steudel-Numbers 2006).

Comparative studies of living mammals suggest that increased diet quality leads to increased daily travel distance. Carbone et al. (2005), in a phylogenetically controlled multivariate analysis of daily travel distance in 200 mammal species, showed that daily travel distance increases significantly with diet quality. While variation in ranging distance is considerable, faunivores travel farther, on average, than similarly sized frugivores, which in turn travel farther than herbivores (Carbone et al. 2005); on average, carnivores travel four times farther each day than similarly sized herbivores (Garland 1983b). An analysis by Antón and colleagues showed that home range size among primates increases with both body mass and diet quality (Antón, Leonard, and Robertson 2002). Applying results from extant primates to fossil hominins, they estimated that home ranges for *Homo erectus* would have been 10 times larger than those of *Australopithecus* (Antón, Leonard, and Robertson 2002).

Yet increased travel distance does not appear to result in improved locomotor economy, speed, or endurance. Comparative studies of locomotor cost indicate that the economy of carnivores is no different than that of artiodactyls or other herbivores (Taylor, Heglund, and Maloiy 1982). Further, limb length in “cursorial” species is no different than that of other mammals and is unrelated to daily travel distance (Harris and Steudel 1997; Steudel and Beattie 1993). Similarly, maximum running speed does not differ between carnivores and artiodactyls, even among predator-prey pairs (Garland 1983a; Shipman and Walker 1989). Maximum aerobic power, a reliable measure of endurance, has not been investigated to determine whether it correlates with diet quality or ranging ecology in mammals, but several herbivores, including *Antilocapra* and *Equus*, have relatively high maximum aerobic power for their body size (Weibel et al. 2004), suggesting that diet quality and aerobic performance are not strongly positively correlated.
Limitations of Current Ecological Models

The lack of correspondence between ranging activity and locomotor performance, particularly locomotor economy, runs counter to the expectations of most ecological models for the evolution of Homo. However, these ecological models rest on two critical assumptions that are not well supported by the available comparative evidence. The first is that selection for improved locomotor economy is a relatively strong force shaping locomotor anatomy, particularly in cursorial species. In fact, analysis of foraging efficiencies among modern mammals suggests that selection pressure for improved locomotor economy is probably quite low relative to other selection pressures in most species because they already obtain a high rate of energy return while foraging (Pontzer 2012). In an analysis of foraging return rates for 228 mammal species, the median estimated foraging efficiency was 56:1; or 56 calories of food energy obtained for every 1 calorie spent on locomotion (Pontzer 2012). With such high foraging efficiencies, even large reductions in locomotor cost have relatively small effects on net energy intake (i.e., gross energy intake minus travel cost). For an organism obtaining a foraging efficiency of 40:1, a 20% reduction in locomotor cost would yield only a 1%/gain in net intake (Pontzer 2012). Thus, given the myriad selection pressures acting on the hominin postcranial skeleton, it is likely that selection for improved economy remained relatively weak throughout the Plio-Pleistocene regardless of any changes in foraging ecology.

A second problematic assumption of many ecological models is that they generally view DEE in hominins and other lineages in a “zero-sum game” framework in which any increase in the energy spent on one activity must be matched by a corresponding decrease in the energy spent on another (e.g., Aiello and Wheeler 1995; Charnov and Berrigan 1993; Isler and van Schaik 2009). Zero-sum frameworks have had success in explaining large-scale trends in life history (e.g., Charnov and Berrigan 1993) and brain size among primates and other animals (Fish and Lockwood 2003; Isler and van Schaik 2006, 2009), although some studies have found little evidence for energetic trade-offs (Barrickman and Lin 2010; Bordes, Morand, and Krasnov 2011; Jones and MacLarnon 2004). In the context of foraging ecology, zero-sum game models predict that longer daily travel distances increase the portion of the daily energy budget spent on travel, which detracts from the energy spent on other activities and in turn leads to selection to improve locomotor economy and restore energy expenditure to those activities.

While this logic is compelling, it is not supported by data on locomotor cost or anatomy; as noted above, daily travel distance is not correlated with locomotor efficiency among mammals. In fact, humans themselves do not appear to fit the predictions of a zero-sum game framework, casting some doubt on the applicability of this approach to hominin evolution. Despite having the largest, most metabolically expensive brains and longest daily travel distances of any primate species, human foragers outpace all other hominoids in terms of reproductive output and maximum life span (Hawkes et al. 1998; Isler and van Schaik 2012).

Recent work on mammalian metabolic strategies offers an alternative to zero-sum game approaches. Nagy, Girard, and Brown (1999), in reviewing measurements of DEE in wild populations of 79 mammal species, noted that there is a sixfold range of variation in DEE among species even after controlling for body mass and phylogeny. This variation in DEE appears to reflect evolved strategies for energy throughput (McNab 1986; Pontzer and Kamilar 2009; Sibly and Brown 2007). In habitats where food is abundant, species may adopt high-throughput (i.e., high DEE) strategies that increase food requirements but also provide more energy for reproduction. Alternatively, in habitats where food availability is highly variable or where foraging increases the risk of predation, species may evolve a low-throughput strategy that reduces the energy requirements even at the cost of lower reproductive output. In a test of this hypothesis, Pontzer and Kamilar (2009) conducted a phylogenetically controlled multivariate study of daily travel distance and reproductive output in a sample of 110 mammal species. While there was considerable variation among species, daily travel distance was found to be positively associated with lifetime reproductive output among mammals, suggesting that species that travel farther generally do so as part of a high-throughput strategy of increased DEE and reproductive investment (Pontzer and Kamilar 2009). Rather than a zero-sum game framework in which DEE is relatively constant, these results suggest that species’ metabolic strategies are labile over evolutionary time, with DEE shrinking or expanding in response to environmental pressures.

Ecological Implications of Increasing Diet Quality and DEE

A dynamic view of mammalian metabolic strategies focusing on throughput rather than efficiency and trade-offs changes the way one interprets the evidence for increased diet quality and ranging activity in Homo. Rather than presenting an ecological or energetic cost, increased travel distance and body mass in early Homo may reflect an improved ability to procure food energy and a subsequent expansion of the energy budget. Indeed, comparisons with the limited data available for ape DEE suggests humans may have evolved larger energy budgets at some point in our lineage (Pontzer et al. 2010b), and as discussed above, modeling studies suggest this may have occurred with Homo (Aiello and Key 2002; Leonard and Robertson 1997; Steudel-Numbers 2006). Expansion of the daily energy budget would make more energy available for brain growth, reproduction, and other investments without necessarily resulting in increased selection for locomotor performance.

Greater DEE in early Homo would suggest an increase in
food availability either through an increase in abundance or a decrease in variability (McNab 1986; Pontzer and Kamilar 2009; Sibly and Brown 2007). Given the evidence for improved diet quality, particularly the inclusion of meat, an increase in abundance is unlikely because higher-quality foods are generally less abundant (Carbone et al. 2005), requiring larger home ranges (Antón, Leonard, and Robertson 2002). Instead, the combination of increased DEE and higher diet quality suggests that early Homo evolved strategies for decreasing variance in food intake. Decreased variability might be achieved in a number of ways, but one intriguing possibility is the advent of food sharing, which would reduce day-to-day variance in food availability. The USO and cooking models (O’Connell, Hawkes, and Blurton Jones 1999; Wrangham et al. 1999) and hunting and scavenging models proposing exploitation of large game (e.g., Bramble and Lieberman 2004; Bunn and Pickering 2010; Shipman and Walker 1989) all implicate food sharing as a key derived ecological feature of early Homo. Increasing adiposity, which is evident in modern humans, would also serve to buffer variability in food availability by providing energy reserves during periods of food shortage (see Wells and Stock 2007). If the increase in body size and diet quality in early Homo is read as evidence for increased energy throughput, it may indicate that provisioning and food sharing, and perhaps increased body fat, were critical early adaptations in the evolution of our genus.

Summary and Conclusion

Recent fossil discoveries provide a new perspective on ecological models for the evolution of our genus. Comparisons of postcranial morphology suggest that adaptations for improved walking and running performance predate the origin of Homo. Indeed, locomotor performance in Australopithecus may have been equivalent to that of early Homo, including Homo erectus. The strongest case for postcranial change in early Homo is an increase in body mass, but recent finds challenge previous reconstructions of decreasing dimorphism in H. erectus, suggesting instead that variation in body size remained substantial throughout the early Pleistocene. The evidence for increased body size is consistent with models of ecological change in early Homo, but the relative stasis in locomotor morphology runs counter to models suggesting a marked change in ranging behavior and locomotor performance between Australopithecus and Homo.

The increase in body size evident in early Homo suggests an increase in DEE as discussed by previous studies of energy expenditure in fossil hominins (Aiello and Key 2002; Leonard and Robertson 1997; Steudel-Numbers 2006). However, far from increasing the challenge of finding sufficient food, comparative studies of living mammals suggest an expansion of the daily energy budget would likely reflect an improved ability to obtain food energy reliably and an increase in reproductive investment. This view is consistent with models emphasizing the importance of provisioning in early Homo, which decrease variance in food availability. A cooperative foraging strategy would have pervasive effects on the social and nutritional ecology of early Homo (O’Connell, Hawkes, and Blurton Jones 1999; Wrangham et al. 1999). Food sharing could also mitigate the ecological risk of seeking high-value, high-risk foods such as meat, and indeed the earliest confirmed evidence of butchery is associated with Homo habilis. Future efforts to reconstruct the evolution of our genus should seek to examine evidence for food sharing in the early Pleistocene.

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