



CHICAGO JOURNALS



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Reviewed work(s):

Source: *Current Anthropology*, Vol. 53, No. S6, Human Biology and the Origins of Homo (December 2012), pp. S479-S496

Published by: [The University of Chicago Press](#) on behalf of [Wenner-Gren Foundation for Anthropological Research](#)

Stable URL: <http://www.jstor.org/stable/10.1086/667692>

Accessed: 09/02/2013 15:47

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Origins and Evolution of Genus *Homo*

New Perspectives

by Susan C. Antón and J. Josh Snodgrass

Recent fossil and archaeological finds have complicated our interpretation of the origin and early evolution of genus *Homo*. Using an integrated data set from the fossil record and contemporary human and nonhuman primate biology, we provide a fresh perspective on three important shifts in human evolutionary history: (1) the emergence of *Homo*, (2) the transition between non-*erectus* early *Homo* and *Homo erectus*, and (3) the appearance of regional variation in *H. erectus*. The shift from *Australopithecus* to *Homo* was marked by body and brain size increases, a dietary shift, and an increase in total daily energy expenditure. These shifts became more pronounced in *H. erectus*, but the transformation was not as radical as previously envisioned. Many aspects of the human life history package, including reduced dimorphism, likely occurred later in evolution. The extant data suggest that the origin and evolution of *Homo* was characterized by a positive feedback loop that drove life history evolution. Critical to this process were probably cooperative breeding and changes in diet, body composition, and extrinsic mortality risk. Multisystem evaluations of the behavior, physiology, and anatomy of extant groups explicitly designed to be closely proxied in the fossil record provide explicit hypotheses to be tested on future fossil finds.

Recent fossil and archaeological finds have complicated our interpretation of the origin and early evolution of genus *Homo*. It now appears overly simplistic to view the origin of *Homo erectus* as a punctuated event characterized by a radical shift in biology and behavior (Aiello and Antón 2012; Antón 2012; Holliday 2012; Pontzer 2012; Schwartz 2012; Ungar 2012). Several of the key morphological, behavioral, and life history characteristics thought to first emerge with *H. erectus* (e.g., narrow bi-iliac breadth, relatively long legs, and a more “modern” pattern of growth) seem instead to have arisen at different times and in different species. Further, accumulating data from Africa and beyond document regional morphological variation in early *H. erectus* and expand the range of variation in this species. These new finds also make the differences between *H. erectus* (s.l.) and *Homo habilis* (s.l.) less stark and suggest that regional variation in the former may reflect local adaptive pressures that result from inhabiting diverse environments in Africa and Eurasia. The mosaic nature of these acquisitions and the greater range of intraspecific variation, especially in *H. erectus*, call into question previous inferences regarding the selective factors behind the early evolution of our genus and its eventual dispersal from Africa.

They also raise questions about when a modern pattern of life history might have emerged and what role, if any, it played in our early evolution.

Modern humans have diverged in numerous ways from the life history patterns seen in other primates, and this “human package” seems linked to our ability to support larger brains and to disperse widely. Our unique suite of life history traits includes altricial birth, a large energy-expensive brain, long juvenile dependency with relatively late reproduction, short interbirth intervals (IBIs) with high fertility, and a long post-reproductive life span (Bogin 1999; Flinn 2010; Hill and Hurtado 1996; Kaplan et al. 2000; Leigh 2001). With this package we appear to have been able to circumvent several of the key constraints that affect other species. Many of the life history traits that define modern humans serve to decrease age-specific reproductive value (i.e., the contribution to the growth of the population) early in life and greatly increase the costs of reproduction and somatic maintenance. What is most striking about contemporary human biology is that we are able to produce numerous high-quality offspring that experience relatively low mortality, grow slowly, and live long lives. In essence, we are able to “have our cake and eat it too” by avoiding some of the life history trade-offs seen in other mammals and having a life history pattern that is both “fast” and “slow” and that emphasizes quantity and quality (Kuzawa and Bragg 2012).

This life history shift in humans was almost certainly facilitated by substantial behavioral and cultural shifts, including (1) cooperation in foraging (e.g., hunting/division of labor), which maximizes the ability to obtain a stable, high-

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quality diet; and (2) cooperation in reproduction (e.g., alloparenting and midwifery), which allows the compression of the IBI and the consequent stacking of offspring as well as the care for and provisioning of the secondarily altricial offspring necessitated by our unique obstetrical dilemma (Trevaathan 1987). Several key questions about these behavioral shifts remain unanswered, including when these traits emerged, whether they evolved together as a package or piecemeal in different hominin species, and the particular selective pressures that drove their evolution.

To address these distinct data sets, we bring together ideas raised at the Wenner-Gren workshop “Human Biology and the Origins of *Homo*” in Sintra, Portugal, 2011. To the papers presented in this special issue we add new data and perspectives, summarize the fossil and archaeological records (tables 1, 2), and consider what research on contemporary primate life history trade-offs, developmental plasticity, and regional adaptive patterns can help us infer about behavioral and cultural changes in early *Homo* (tables 3–5). These data give us a fresh perspective on three important shifts in human evolutionary history: (1) the emergence of genus *Homo*, (2) the transition between non-*erectus* early *Homo* and *H. erectus*, and (3) the appearance of regional morphological variation in *H. erectus* (including *Homo ergaster*). Using this integrated data set, we consider the implications for understanding the changing selective pressures that led to the transition to and evolution of early *Homo*.

How What We Now Know from the Hard Evidence Differs from What We Thought We Knew

Over the past several decades, a consensus had emerged that the shift to humanlike patterns of body size and shape—and at least some of the behavioral parts of the “human package”—occurred with the origin of *Homo erectus* (e.g., Antón 2003; Shipman and Walker 1989). This was seen by many researchers as a radical transformation reflecting a sharp and fundamental shift in niche occupation, and it emphasized a distinct division between *H. erectus* on the one hand and non-*erectus* early *Homo* and *Australopithecus* on the other.¹ Earliest *Homo* and *Australopithecus* were reconstructed as essentially bipedal apes, whereas *H. erectus* had many of the anatomical and life history hallmarks seen in modern humans. To some, the gap between these groups suggested that earlier species such as *Homo habilis* should be excluded from *Homo* (Collard and Wood 2007; Wood and Collard 1999).

Recent fossil discoveries paint a picture that is substantially more complicated. These discoveries include new fossils of

1. While it is recognized that *Australopithecus* may be paraphyletic, for the purposes of the comparisons in this paper, the genus is considered to exclude *Paranthropus* species but to include the best-represented species commonly assigned to *Australopithecus*, i.e., *A. anamensis*, *A. afarensis*, *A. garhi*, *A. africanus*, and *A. sediba*. When the data for specific comparisons come from a single species, that species is indicated by name.

H. erectus that reveal great variation in the species, including small-bodied members from both Africa and Georgia (Gambunia et al. 2000; Potts et al. 2004; Simpson et al. 2008; Spoor et al. 2007), and suggest a previous overreliance on the Nariokotome skeleton (KNM-WT-15000) in reconstructions of *H. erectus*. Additionally, reassessments of the Nariokotome material have concluded that he would have been considerably shorter than previous estimates (~163 cm [5 feet 4 inches], not 185 cm [6 feet 1 inch]; Graves et al. 2010), younger at death (~8 years old, not 11–13 years old; Dean and Smith 2009), and with a life history pattern distinct from modern humans (Dean and Smith 2009; Dean et al. 2001; Thompson and Nelson 2011), although we note that there is substantial variation in the modern human pattern of development (Šešelj 2011). Further, the recent discovery of a nearly complete adult female *H. erectus* pelvis from Gona, Ethiopia, which is broad and has a relatively large birth canal, raises questions about the narrow-hipped, Nariokotome-based pelvic reconstruction and whether *H. erectus* infants were secondarily altricial (Graves et al. 2010; Simpson et al. 2008).²

In addition to recent changes in our understanding of *H. erectus*, new discoveries and reanalyses have complicated the picture of earliest *Homo* by documenting its diversity and emphasizing underappreciated differences and similarities with *H. erectus* (Blumenshine et al. 2003; Spoor et al. 2007). Finally, a new view of *Australopithecus* has begun to emerge in which it shares many postcranial characteristics with *Homo*, including a somewhat large body and relatively long legs (Haile-Selassie et al. 2010; Holliday 2012; Leakey et al. 2012; Pontzer 2012). These results suggest a previous overreliance on the very small “Lucy” (A.L.288-1) skeleton to characterize that species/genus.

Brains, Bodies, and Sexual Dimorphism

Although recent discoveries reveal a larger *Australopithecus afarensis* and a smaller, more variable *H. erectus* than previously known, there still appear to be important differences between the species. Even when including the largest of the new *Australopithecus* fossils and the smallest of the new early *Homo* fossils, estimates suggest an average increase in body mass of 33% from *A. afarensis* to early *Homo* (in this case *H. habilis* + *Homo rudolfensis* + early *H. erectus*; Holliday 2012; Pontzer 2012). The difference is more modest—on the order of 10%—when comparing *A. afarensis* to only non-*erectus* early *Homo* (table 1). The fossil record also suggests a body mass increase of ~25% between early non-*erectus* *Homo* in East Africa and early *H. erectus* (Africa + Georgia). This expanding fossil record documents marked regional variation, with early African *H. erectus* being ~17%–24% larger on average than Georgian *H.*

2. We note that there is some disagreement regarding the specific status of the Gona pelvis, including suggestions that it may not be *Homo* (Ruff 2010). Nonetheless, other reconstructions of the KNM-WT 15000 pelvis were narrower than the original, suggesting that its breadth may not be a strong anchor point for neonate head size.

erectus of approximately the same geological age (table 1; Antón 2012).

Recent fossil evidence and reinterpretation of known specimens also documents a more mosaic pattern of evolving limb proportions, which has implications for locomotor reconstructions. New work shows that despite absolute size differences and contrary to conventional wisdom, relative hind-limb length does not differ from *Australopithecus* to *Homo* or among *Homo* (Holliday 2012; Holliday and Franciscus 2009; Pontzer 2012). The forelimb, however, is relatively stronger and slightly longer in both *Australopithecus* and non-*erectus* early *Homo* than it is in *H. erectus* (Ruff 2009). Further, the Georgian forelimb is slightly shorter than in early African *H. erectus*, which may reflect a temporal, climatic, or even secular shift (Holliday 2012; Pontzer 2012).

Cranial capacities show an increase of >30% from *A. afarensis* (mean = 478) to non-*erectus* early *Homo* (i.e., 1813 + 1470 groups; mean = 629 cm³). This marks the first time that hominin cranial capacity expands beyond the range of variation seen among great apes (Schoenemann 2006). Also, although the ranges overlap, average cranial capacity increases by ~25% from early non-*erectus* *Homo* to early *H. erectus* in Africa and Georgia (combined mean = 810 cm³) or by >30% when compared with just early African *H. erectus* (mean = 863 cm³). Among regional samples, both early African *H. erectus* and early Indonesian *H. erectus* are ~25% larger on average than Georgian *H. erectus* of about the same geological age, a similar difference as for body size (tables 1, 2).

Despite the problems of assigning sex to individual fossils, preliminary patterns of sexual dimorphism can be considered for different species using brain and body size estimates (Antón 2012; Plavcan 2012). The ratio of male to female mean values for brain and body size suggests that *H. erectus* is modestly less dimorphic than is *A. afarensis*. However, sex is hard to estimate for fossils, and the degree of dimorphism inferred depends on the particular variable considered, the means of comparison, and the specimens included in the sample (table 1; Plavcan 2012). For example, *A. afarensis* and early *H. erectus* show no difference in size variation (CVs) for body mass or endocranial capacity (table 1; and see table 3 in Antón 2012). By other measures, *H. habilis* (exclusive of 1470) is more dimorphic in body mass estimates than *Australopithecus* but less dimorphic in brain size (table 1; Plavcan 2012). And *H. erectus* is more dimorphic than *H. habilis* in brain size but less dimorphic in body size. Unfortunately, *H. habilis* values are particularly suspect given the small samples and uncertainty regarding numbers of included species. These data are equivocal as to the degree of dimorphism present but do not provide strong support for decreasing dimorphism in *H. erectus* (see Plavcan 2012).

Teeth, Development, and Diet

Examination of dental evidence such as tooth size, microwear, and developmental pattern can provide a window onto key

transitions in early *Homo*. As has been well documented, posterior teeth decrease in average size and increase in occlusal relief from *Australopithecus* to *Homo* (Ungar 2012). The trend is somewhat more pronounced in *H. erectus*, which shows substantial third molar reduction (Gabunia et al. 2000; Indriati and Antón 2008; Spoor et al. 2007). There is, however, substantial size overlap in jaw and tooth size among all early *Homo* (Antón 2008). In contrast, preliminary evidence suggests that incisor row length may be larger in non-*erectus* early *Homo* than in *Australopithecus* and intermediate in size in *H. erectus* (Ungar 2012). This may suggest dietary differences relating to incisal preparation.

Dental topography and microwear for all early *Homo* are more complex than in *Australopithecus*. Although early *Homo* likely ate a fairly generalized diet, this signal suggests they also consumed less brittle foods (Ungar and Scott 2009; Ungar et al. 2012). *Homo erectus* shows more variation and more small features than non-*erectus* early *Homo*, indicating greater dietary breadth in the former (Ungar and Sponheimer 2011). The signal is similar across regional samples of *H. erectus*. Thus, dental morphology suggests consumption of a generalized diet in early *Homo* but with a modestly increased dietary breadth compared with *Australopithecus*.

Although sample sizes are extremely small, there is some evidence that the emergence of the first permanent molar (M1), a variable that correlates with many life history traits, occurs about a year later in *H. erectus* than in *A. afarensis* (Dean et al. 2001; Schwartz 2012). This finding is consistent with a recent analysis that documents relatively minor growth and life history differences in *H. erectus* compared with earlier hominins and living African apes (Thompson and Nelson 2011). However, the pattern of skeletal and dental development in Nariokotome is not much outside the range of “tall” modern human children (Šešelj 2011), hinting perhaps at the modularity (i.e., independence) of developmental systems. Unfortunately, there are no data for M1 emergence for non-*erectus* early *Homo*, and we caution that M1 development can be decoupled from somatic growth rates (Dirks and Bowman 2007; Godfrey et al. 2003). Thus, life history reconstructions suggest a pattern of growth modestly different from *Australopithecus* yet distinct from later *Homo* species such as Neanderthals and modern humans.

Climate and Environment

Although populations of early *Homo* likely lived in a variety of specific environments, Potts (2012) reviews how multiple independent paleoclimatic records show an increase in the amplitude of the climate shifts and an increasing unpredictability in their timing during the origin and early evolution of *Homo*. He suggests that this inherent variation in climate placed a premium on developmental plasticity—the capacity for developing individuals to respond phenotypically to environmental conditions (Lasker 1969; Wells 2012)—and likely behavioral plasticity as well. The result of developmental plas-

Table 1. Differences that may relate to life history inferences compared between *Australopithecus* and *Homo* and within early *Homo* species based on hard evidence

	<i>Australopithecus afarensis</i> vs. early <i>Homo</i> ^a	<i>A. afarensis</i> vs. <i>Homo erectus/Homo ergaster</i> ^b	African <i>H. erectus</i> vs. <i>Homo habilis/Homo rudolfensis</i> ^c
Average brain size (cm ³ ; Antón 2012)	<i>Homo</i> larger: 629 vs. 478	<i>H. erectus/H. ergaster</i> larger: 810/863 vs. 478	<i>H. erectus</i> larger: 863 vs. 629
Average body mass (kg; Holliday 2012; Pontzer 2012)	<i>Homo</i> larger: 44 vs. 40	<i>H. erectus/H. ergaster</i> larger: 52/55 vs. 40	<i>H. erectus</i> larger: 52/55 vs. 44
BMR (kcal/day) ^d	<i>Homo</i> larger: 1,191.7 vs. 1,134	<i>H. erectus/H. ergaster</i> larger: 1,308–1,351 vs. 1,134	<i>H. erectus</i> larger: 1,308–1,351 vs. 1,192
TDEE (kcal/day) ^d	<i>Homo</i> larger: 2,026–2,264 vs. 1,927–2,153	<i>H. erectus/H. ergaster</i> larger: 2,224–2,568 vs. 1,927–2,153	<i>H. erectus</i> larger: 2,224–2,568 vs. 2,026–2,264
Humerofemoral strength proportions (Ruff 2008, 2009)	Both similar to <i>Pan</i>	Relatively less strong humerus in <i>H. erectus/H. ergaster</i>	Relatively less strong humerus in <i>H. erectus</i>
Humerofemoral length proportions (Holliday 2012; Pontzer 2012)	Same	Same	Same
Hind-limb length relative to body mass (Holliday 2012; Pontzer 2012)	Same	Same	Same
Sexual dimorphism:			
Brains:			
Male/female average brain size (sex designations as per Antón 2012)	<i>Homo</i> less dimorphic: 1.05 (♂625; ♀590) vs. 1.3 (♂507; ♀400)	<i>H. erectus/H. ergaster</i> less dimorphic: 1.15/1.2 (♂840/924; ♀730/770) vs. 1.3 (♂507; ♀400)	<i>Homo erectus</i> more dimorphic: 1.2 (♂924; ♀770) vs. 1.05 (♂625; ♀590)
CVs (Antón 2012)	<i>Homo</i> less dimorphic: 12.2 vs. 15.7	No difference: 17.8/15.9 vs. 15.9	<i>H. erectus</i> more dimorphic: 17.8/15.9 vs. 12.2
Bodies:			
Male/female mean:			
Using associated skeletons (Antón 2012)	<i>Homo</i> more dimorphic: 1.39 (♂46; ♀33) vs. 1.32 (♂39; ♀29.5)	<i>H. erectus/H. ergaster</i> less dimorphic: 1.06/1.0 (♂50/51; ♀47/51) vs. 1.39 (♂46; ♀33)	<i>H. erectus</i> less dimorphic: 1.06/1.0 (♂50/51; ♀47/51) vs. 1.39 (♂46; ♀33)
Using sex estimates of Pontzer (2012)	<i>Homo</i> more dimorphic: 1.77 (♂56.7; ♀31.9) vs. 1.32 (♂39; ♀29.5)	<i>H. erectus/H. ergaster</i> less dimorphic: 1.20/1.25 (♂55.8/60.4; ♀46.2/48.2) vs. 1.32 (♂39; ♀29.5)	<i>H. erectus</i> less dimorphic: 1.20/1.25 (♂55.8/60.4; ♀46.2/48.2) vs. 1.77 (♂56.7; ♀31.9)
CVs:			
Of body mass data (Antón 2012)	<i>Homo</i> more dimorphic: 33 vs. 20.2	No difference: 19.3/18.5 vs. 20.2	<i>H. erectus</i> less dimorphic: 19.3/18.5 vs. 33
Of femur length data (Antón 2012)	<i>Homo</i> more dimorphic: 13 vs. 16.3	<i>H. erectus/H. ergaster</i> less dimorphic: 8.7/5.8 vs. 16.3	<i>H. erectus</i> less dimorphic: 8.7/5.8 vs. = 13

Tooth size and shape (Ungar 2012)	Larger I's than <i>A. afarensis</i> ; less bunodont M's with more occlusal relief than <i>A. afarensis</i> ; overlapping ranges but smaller average M's than <i>A. afarensis</i>	Larger I's than <i>A. afarensis</i> ; less bunodont M's with more occlusal relief and thinner enamel than <i>A. afarensis</i> ; smaller M's than <i>A. afarensis</i>	<i>H. erectus</i> I's intermediate between <i>H. habilis</i> and <i>A. afarensis</i> ; thinner? enamel than <i>H. habilis</i> ; smaller M's than <i>H. habilis</i> with third molar reduction
Dental microwear (Ungar 2012; Ungar et al. 2012)	Unremarkable M surface complexity	Unremarkable M surface complexity with substantial variation and more small features	Unremarkable M surface complexity with substantial variation and more small features
Age at M1 eruption (Schwartz 2012)	<i>H. habilis</i> unknown; <i>A. afarensis</i> = 2.9–3.6 years	Later in <i>H. erectus</i> . 4.4–4.5 vs. 2.9–3.6 years	<i>H. habilis</i> unknown; <i>H. erectus</i> = 4.4–4.5 years
Site distribution (area/home range; Swisher et al. 1994)	Similar?	<i>H. erectus</i> across Old World by 1.6 Ma	<i>H. erectus</i> across Old World by 1.6 Ma
Stone transit distances? (Braun et al. 2008; Potts 2012)	<i>H. habilis</i> 10s to 100s of m from 2.5 to 2.3 Ma and possibly farther after 1.95 Ma; <i>A. afarensis</i> probably does not move stone	<i>H. erectus</i> and possibly <i>H. habilis</i> after 1.95 Ma transport rock 12–13 km; <i>A. afarensis</i> does not	Similar? <i>H. erectus</i> perhaps transports rock farther?
Cut-marked/percussion-marked bone (Potts 2012)	Ubiquitous after 2.5 Ma; one possible occurrence with <i>A. afarensis</i>	Ubiquitous after 2.5 Ma	Similar? Ubiquitous after 2.5 Ma
Tool technologies (Lepre et al. 2011; Semaw et al. 2003)	None before 2.6 Ma when Oldowan appears	Oldowan + Acheulean after 1.76 Ma	Similar tools or divided by taxon?

^a *Australopithecus afarensis* is used for comparative purposes because its cranial capacities (Holloway and Yuan 2004) and body mass (Pontzer 2012) values are greater than those for *A. africanus* and thus provide a conservative comparison for differences in size. Cranial capacity of KNNM-ER 1470 is excluded.

^b Given the small size of the Georgian remains, where available, *H. erectus* values are presented as the combined means for Georgian and early African *H. erectus* as a conservative comparison with *A. afarensis* followed by the early African *H. erectus*-only values. Age at M1 eruption is available only for the early African remains.

^c *Homo rudolfensis* is not included in brain size estimates, but postcrania assigned to the *Homo* sp. that may be *H. rudolfensis* are included in body size estimates.

^d Basal metabolic rate (BMR) is calculated by using the Oxford equations for prime adults (18–30 years) and the average body weight of each species. The average of male (16 × weight + 545) and female (13.1 × weight + 558) equations is reported. Total daily energy expenditure (TDEE) range is calculated as TDEE = BMR × physical activity level (PAL). A range of PALs from apelike (1.7; Pontzer and Kamilar 2009) to humanlike (1.9, being the mean of male, 1.98, and female, 1.82, averages for subsistence populations; Snodgrass 2012:368) are used. Lower mean values for *Pan* have been reported (1.5; Schroepler, Hare, and Pontzer 2012), but given the high range of variation, we opt for the more conservative values previously published.

Table 2. Regional differences between early *Homo erectus* samples related to important variables of life history

	African <i>Homo erectus</i> / <i>Homo ergaster</i> (1.8–1.5 Ma) ^a	Georgian <i>H. erectus</i> / <i>H. ergaster</i> (1.8–1.7 Ma) ^b	Asian <i>H. erectus</i> (>1.5 Ma) ^c
Average brain size (cm ³)	X = 863 (n = 5)	X = 686 (n = 3)	908 (n = 1)
Average body size (kg)	X = 57 (n = 4); X = 54 (n = 5)	X = 46 (n = 3)	?
BMR (kcal/day) ^d	1,352	1,221	?
TDEE (kcal/day) ^d	2,298–2,568	2,075–2,319	?
Sexual dimorphism:			
Brains (male/female mean values)	?1.2 (♂ = 924, ♀ = 770)	?1.07 (♂ = 700, ♀ = 655)	? (♂ = 908)
Bodies (male/female mean values)	1.0/1.25 (♂ = 51/60.4, ♀ = 51/48.2)	?1.21 (♂ = 48.8 [1], ♀ = 40.2 [1])	?
Age at M1 eruption (years)	4.4 (KNM-WT 15000)	?	4.5 (n = 1)
Forelimb to hind-limb length proportions	Similar to earlier hominins or a little shorter	Georgian has slightly shorter forelimb	?
Forelimb and strength proportions	Less strong relative to hind limb than in <i>H. habilis</i>	?	?
Tooth size/shape (Antón 2008; Indriati and Antón 2008; Ungar 2012)	<i>H. erectus</i> / <i>H. ergaster</i> I's intermediate between <i>Homo habilis</i> and <i>Australopithecus</i> ; smaller average M's than <i>H. habilis</i> or <i>Australopithecus</i> and with M3 reduction	?; largest of the <i>H. erectus</i> / <i>H. ergaster</i> teeth, smaller than <i>H. habilis</i> and with M3 reduction	?; larger than African, slightly smaller than Georgian, with M3 reduction
Tooth microwear (Ungar 2012; Ungar et al. 2012)	Unremarkable M surface complexity with substantial variation and more small features	Unremarkable M surface complexity with substantial variation and more small features	?
Transit distances?	12–13 km	?	?

^a Cranial capacities for KNM-ER 3733, 3883, 42700, KNM-WT 15000, OH 9; body mass values for KNM-ER 736, 737 1808, KNM-WT 15000 (n = 4) and BSN49/P27 (n = 5). Sexes are unknown; however, KNM-ER 1808, 3733, 42700, and BSN 49/P27 are presumed females for this table; KNM-ER 736 and 737 are not assigned to sex. Two sex dimorphism estimates are provided for body size: the first calculates body mass for male skeleton KNM-WT15000 and female skeletons KNM-ER 1808 and BSN 49/P27; the second follows Pontzer's sex designations for postcranial elements, includes more specimens, and moves KNM-ER 1808 to male. South African *H. erectus* do not preserve endocranial capacity. Body mass data for South African *H. erectus* are not included, but the few that are available are comparable to East African *H. erectus* and would not change the results here (see Antón 2012).

^b Cranial capacities for D2280, 2282, 3444; body mass values for large and small adult and D2021. Sexes are unknown; however, D2282 and the small adult are presumed females for this table; D2021 is unsexed.

^c Statements reflect Asian *H. erectus* older than 1.5 Ma only. Cranial capacity for Sangiran 4; dental dimensions for Sangiran 4 and S27; M1 emergence from Dean et al. (2001). While some postcranial size estimates have been made for mid-Pleistocene Asian *H. erectus* (Antón 2003), no postcranial fossils are available from the early Pleistocene.

^d BMR (basal metabolic rate) and TDEE (total daily energy expenditure) calculated as in table 1, using an average African *H. erectus* weight of 55 kg as per table 1.

ticity is seen in recent secular trends in size in humans (e.g., Boas 1912; Bogin 1999; Kaplan 1954; Shapiro 1939; Stinson 2012) and is a critical means by which humans balance the high costs of growing large-brained offspring while adjusting to environmental change at the generational or multigenerational timescale (Kuzawa and Bragg 2012; Walker et al. 2006; Wells 2012). If developmental pattern, particularly plasticity, is the target of selection (Kuzawa and Bragg 2012), a means of assessing how to visualize this pattern in the skeletal record of extant taxa is needed to lay a foundation for doing so in the fossil record. A similar means is needed for identifying behavioral plasticity from the archaeological record.

Material Culture

The archaeological record provides evidence of several key behaviors—including changes in dietary niche, ranging, and cognition—that are often associated with the rise of genus *Homo*. The manufacture and use of stone tools has long been

thought to signal a foraging shift and to be associated with the origin of *Homo* (Leakey, Tobias, and Napier 1964). The first unambiguous tools appear at 2.6 Ma, with cut-marked animal bone ubiquitous in sites after this time (Potts 2012); however, one occurrence of cut-marked bone has been argued to occur before the emergence of *Homo* (McPherron et al. 2010, 2011; but see Domínguez-Rodrigo, Pickering, and Bunn 2010, 2011). Although the Oldowan is linked to carcass processing, other uses related to plant food processing are important (Roche, Blumenschine, and Shea 2009). This emerging picture is consistent with dental evidence and supports a modest dietary shift to more carnivory in *Homo* and increased dietary breadth compared with *Australopithecus*.

A second noteworthy change occurs at approximately 1.95 Ma with an increase in stone transport distances that suggests the movement of rock over ~12 km intervals (Braun et al. 2008; Potts 2012). Further, by 1.76 Ma, Acheulean tools appear in the record (Lepre et al. 2011). These changes are often

attributed to *H. erectus* and are used to suggest increased range, although it is worth noting that this temporal association may be coincidental and that increased transit distances may be characteristic of all post-2.0-Ma *Homo*. Certainly after 1.6 Ma, *H. erectus*, but not other *Homo*, is distributed across the Old World, suggesting even greater ranging.

What Changes in Fossil *Homo* May Mean for Energetics

Changes in brain and body size and ranging have important implications for daily energy expenditures that must in turn be balanced by shifts in energy input (i.e., dietary quantity or quality) and/or shifts in allocation to somatic functions. Total daily energy expenditure (TDEE), or an individual's total metabolic cost per day, encompasses the energy required for basic bodily survival and maintenance (thermoregulation, immune function, physical activity, etc.) and that required for growth and reproduction. If basal metabolic rate (BMR) and physical activity level (PAL) are known, TDEE can be estimated ($TDEE = PAL \times BMR$). BMR has a strong correlation to body weight, and average PALs have been measured for subsistence populations of humans and some great apes (Pontzer et al. 2010; Schroepfer, Hare, and Pontzer 2012; Snodgrass 2012). Thus, we can calculate a range of TDEEs for each fossil hominin species by using alternately an ape (1.7) or human (1.9) subsistence average for PAL and human equations for BMR (tables 1, 2).

When data from contemporary humans and other primates are used to estimate key energy parameters for fossil species, TDEE increases in all early *Homo* over the condition in *Australopithecus* because of body size increases. If we assume that different species and genera shared similar PALs (i.e., are either all apelike or all humanlike), then *H. habilis* TDEE increases only modestly (5%) over the condition in *A. afarensis*. *Homo erectus* increases by 15% over *A. afarensis*. African *H. erectus* TDEE estimates are 10% greater than those for Georgian *H. erectus*. Alternatively, if suggestions of increased ranging in *H. erectus* (or early *Homo*) are considered to indicate that *Homo* species can be attributed more humanlike PALs compared with *A. afarensis*, then the differences between the genera would be greater. In either case, *Homo* appears to have required more energy input than *Australopithecus* or perhaps a shift to a higher throughput system (i.e., more calories consumed and expended per day) than *Australopithecus* such as is seen in humans versus great apes (see Pontzer 2012).

Summary of Fossil Changes in Early *Homo*

The suite of morphological and behavioral traits that characterize modern humans does not first appear with the origin of *H. erectus*, at least not to the extent previously believed. Some critical changes such as hind-limb elongation occur at the base of the hominin lineage (i.e., well before the origin of genus *Homo*). Other traits, including modest brain and

body size increases and dietary differences, occur with the origin of *Homo*. Still other changes, such as pelvic narrowing and marked encephalization, occur considerably later in time than previously believed, with several of these traits not appearing until the origin of modern humans.

While the nature of the fossil record makes any interpretation preliminary, current evidence is consistent with the view that there was not a radical shift in the biology and behavior of *H. erectus* but instead that the full suite of morphological and life history traits that characterize our own species first emerged in modern humans. The shift from *Australopithecus* to *Homo* was marked by body and brain size increase, dental and other indicators of a dietary shift, and changes in ranging behavior that imply increased TDEE. These shifts became more pronounced in *H. erectus*, but substantial intraspecific variation exists. It also appears that the developmental shift to the modern human condition occurred piecemeal. *Homo erectus* development (based on the timing of M1 eruption) was later relative to *Australopithecus* but was quicker than that seen in later *Homo*. This delay may have been present in non-*erectus* early *Homo* as well. An important point that has emerged especially from Schwartz's (2012) work is that there were diverse life history patterns among fossil hominins, and an approach to human life history evolution that considers only "ape" versus "human" or "slow" versus "fast" is overly simplistic (see also Leigh and Blomquist 2007, 2011; Robson and Wood 2008).

The increasing variability of climate over time suggests that both developmental and behavioral flexibility may have been prized and that the apparent variation seen in the past needs to be carefully compared and parsed against extant variation. These data imply that the extant record should be plumbed in new ways for evidence of how the skeletons of living humans and nonhuman primates reflect their environments, life histories, and behaviors. These analyses require the development of data sets in which the extant and fossil records can be more fully integrated.

Human Biology and the Origins of *Homo*: Implications for Understanding the Fossil Record

Here we integrate recent advances in the study of contemporary human and primate biology with the fossil record to better interpret the evidence discussed above (tables 3, 4). We concentrate on inferences regarding (1) the emergence of genus *Homo*, (2) the transition between non-*erectus* early *Homo* and *Homo erectus*, and (3) the appearance of regional morphological variation in *H. erectus*. We outline predictions that we hope will help guide future research and suggest areas in which additional data from extant taxa would be particularly useful.

Table 3. Inferences regarding behavioral/cultural differences between *Australopithecus* and *Homo*

	<i>Australopithecus</i> vs. early <i>Homo</i>	<i>Australopithecus</i> vs. <i>Homo erectus</i> / <i>Homo ergaster</i>	<i>H. erectus</i> vs <i>Homo habilis</i> / <i>Homo rudolfensis</i>
Energetic requirements:			
Brains	<i>Homo</i> larger on average	<i>H. erectus</i> / <i>H. ergaster</i> larger	<i>H. erectus</i> larger on average
Bodies	<i>Homo</i> larger on average	<i>H. erectus</i> / <i>H. ergaster</i> larger	<i>H. erectus</i> larger on average
Developmental rate:			
Brains	?	?	?
Teeth (Schwartz 2012)	?	<i>H. erectus</i> / <i>H. ergaster</i> slower than <i>Australopithecus</i> but still fast compared with <i>Homo sapiens</i> ?	?
Bodies (Dean et al. 2001; Graves et al. 2010)	?	<i>H. erectus</i> / <i>H. ergaster</i> body relatively faster than teeth intermediate between <i>Pan</i> and <i>H. sapiens</i>	?
Diet (from teeth; Ungar 2012; Ungar et al. 2012)	Tougher, less brittle food items in <i>Homo</i> ; more incisal preparation in <i>Homo</i> ?	Tougher, less brittle food items in <i>H. erectus</i> / <i>H. ergaster</i> ; greater diet breadth in <i>H. erectus</i> / <i>H. ergaster</i> than <i>Australopithecus</i>	Tougher, less brittle food items in <i>H. erectus</i> ; greater diet breadth in <i>H. erectus</i> than <i>H. habilis</i> / <i>H. rudolfensis</i>
Nutritional environment/diet:			
From brains/bodies	<i>Homo</i> somewhat higher-quality diet	<i>H. erectus</i> / <i>H. ergaster</i> higher-quality diet	<i>H. erectus</i> probably higher-quality diet
From archaeology	<i>Homo</i> greater use of animal products?	<i>H. erectus</i> / <i>H. ergaster</i> more significant use of animal products	<i>H. erectus</i> likely greater use of animal than <i>H. habilis</i> / <i>H. rudolfensis</i>
Locomotor repertoire	Both have significant arboreal component	<i>H. erectus</i> / <i>H. ergaster</i> strongly terrestrial	<i>H. erectus</i> more terrestrial
Home range (HR):			
Bodies	Somewhat larger because of larger body size?	<i>H. erectus</i> / <i>H. ergaster</i> larger because of body size	<i>H. erectus</i> larger because of body size
Site distribution	Similar?	<i>H. erectus</i> / <i>H. ergaster</i> larger HR	<i>H. erectus</i> larger HR
Stone transport	?	<i>H. erectus</i> / <i>H. ergaster</i> larger HR	<i>H. erectus</i> larger HR

Note. Based on hard-evidence differences in table 1.

The Emergence of Early Homo

The fossil record for earliest *Homo* is especially sparse, and inferences from it must be made cautiously. Nonetheless, available fossil evidence suggests that non-*erectus* early *Homo* species were somewhat larger in average brain and body size and had slower developmental patterns than *Australopithecus* (Antón 2012; Holliday 2012; Pontzer 2012; Schwartz 2012). If confirmed, the extant record indicates that this brain and body size increase was most likely to result from an increase in food availability and dietary quality and a reduction in extrinsic mortality risk.

Considerable evidence exists that improved diet quality and nutrient availability during growth influences adult body size (Kuzawa and Bragg 2012). In contemporary human populations, secular trends to larger body size and earlier reproductive maturation occur quickly via developmental shifts that alter energy allocation during improved environmental conditions such as higher-quality and more stable food resources and reduced infectious disease exposure (Boas 1912; Bogin 1999; Kaplan 1954; Shapiro 1939; Stinson 2012). For example, in a single generation, Mayan children growing up in the United States experienced a 10-cm population-level increase in stature compared with those in Guatemala (Bogin and Rios 2003). Conversely, under stable yet extremely poor environmental conditions, there is evidence for a reduced

plasticity that leads to early maturation and small adult body size (see Migliano and Guillon 2012). While we focus mainly on body size, we note that cranial characteristics and brain size are subject to similar developmental plasticity (e.g., Boas 1912), and we note that nondietary variables also contribute to growth and adult outcomes.

Recent work has provided extensive evidence that extrinsic mortality risk is a primary contributor to life history variation both within and between species, with faster growth and earlier reproduction in environments of high (especially juvenile) mortality (Charnov 1993; Kuzawa and Bragg 2012; Stearns 1992; Walker et al. 2006). For example, arboreal nonhuman primates tend to have relatively protracted life histories that appear to result from the relatively low predation risk and mortality they experience (Borries et al. 2011). And in humans, extremely high mortality environments with pronounced juvenile and adult risk may help explain the fast developmental life history pattern and small adult body size of “pygmy” populations such as the Aeta and Batak of the Philippines (Migliano 2005; Migliano and Guillon 2012; Migliano, Vinicius, and Lahr 2007).

Thus, proximate environment-related shifts in life history can influence morphology and are potentially identifiable in the fossil record. Further, these developmental shifts may provide a foundation for longer-term population-level adaptation

Table 4. Regional behavioral/cultural differences inferred between early *Homo erectus* samples

	African <i>Homo erectus</i> / <i>Homo ergaster</i> (1.8–1.5 Ma)	Georgian <i>H. erectus</i> / <i>H. ergaster</i> (1.8–1.7 Ma)	Asian <i>H. erectus</i> (>1.5 Ma)
Inferred energetic requirements:			
Brains (TDEE)	Increased contribution of brain size to metabolism	Increased contribution of brain size to metabolism over condition in <i>H. habilis</i>	Increased contribution of brain size to metabolism
TDEE	Higher in Africa because of body size differences	Lower in Georgia, with seasonal upregulation of metabolic expenditures?	?
Inferred developmental rate	Same as Asia	?	Same as Africa
Inferred diet (teeth)	Tougher, less brittle food items in <i>H. erectus</i> / <i>H. ergaster</i> Greater diet breadth than <i>Homo habilis</i> / <i>Homo rudolfensis</i>	Tougher, less brittle food items in <i>H. erectus</i> / <i>H. ergaster</i> Greater diet breadth than <i>Homo habilis</i> / <i>Homo rudolfensis</i>	?
Inferred nutritional environment:			
Anatomy	High quality	Nutritionally less sufficient during growth given small size	High quality given brain size
Archaeology	High quality	Perhaps more seasonal?	?
Transit distances?	12–13 km	?	?
Extrinsic mortality?	Lower than <i>Australopithecus</i> based on body and brain size	Lower than <i>Australopithecus</i> but possibly higher than other <i>H. erectus</i>	Lower than <i>Australopithecus</i> based on brain size

Note. Inferred from primary data in table 2. TDEE = total daily energy expenditure.

through natural selection (Kuzawa and Bragg 2012). The complicated web of interactions means that shifts in body size, for example, may result from a variety of different inputs working together or at cross-purposes (Kuzawa and Bragg 2012; Migliano and Guillon 2012). It is nonetheless possible to begin to make some predictions regarding the expected outcomes that various kinds of changes to extrinsic mortality and other proximate factors might have on skeletal size and shape. In particular, increases in overall body size might result from several different decreases in, for example, extrinsic mortality. These could include reduced susceptibility to predation or decreased infectious disease or parasite burden, for example. Future research should develop means of assessing from separate records (i.e., archaeological, paleontological, geological, and contemporary biological) the presence and rate of these various sources of mortality.

If decreases in extrinsic mortality and increases in energy availability and dietary quality are driving factors in the origin of *Homo*, then we can predict that if further evidence of multiple early non-*erectus* *Homo* taxa is found, each will be larger in average body size than *Australopithecus*. However, these multiple *Homo* species, while showing anatomical evidence of niche partitioning, may or may not differ from one another in body size.

The fossil record also suggests that non-*erectus* early *Homo* was smaller and developed more quickly than *H. erectus*, although again the early *Homo* record is quite sparse. When additional fossils of early *Homo* are available, we predict that non-*erectus* early *Homo* will be found to have had a life history pattern intermediate between *Australopithecus* and *H. erectus* with a modestly extended growth period, including the presence of short childhood and adolescent periods. We base our

prediction on archaeological and paleontological evidence for dietary change in earliest *Homo* as well as modest body size increase over the condition in *Australopithecus*. Additional studies of dental macro- and microstructure will help lay a foundation in extant taxa for understanding the relationship of tooth form (especially molars) to diet. While we acknowledge that proxies for life history patterns are more complicated to reconstruct than proxies for other types of shifts, studies that consider how dental developmental profiles and their variation are correlated with life history attributes within populations of living human and nonhuman primates will be an important means of contextualizing fossil data.

Another hypothesized contributor to the emergence of early *Homo* is related to the influence of increasing climatic variability on biology. The geological record indicates increased climatic variability during the rise of early *Homo*, which, based on extant human and primate biology, hints at the possibility that greater developmental plasticity than in *Australopithecus* may have facilitated adjustments to short-term environmental change and initiated a cascade of events leading to greater capacity for phenotypic plasticity as well as increased dispersal capability. Given the paucity of the *Homo* record from 2.5 to 1.5 Ma, part of the primary research agenda should be an emphasis on exploring sediments from this time period with a particular focus on differentiating between early non-*erectus* and early *H. erectus* lifeways. However, additional work on the substantial fossil record of *Australopithecus afarensis*, which shows distinct temporal changes in morphology (Lockwood, Kimbel, and Johanson 2000), might be useful in providing a comparative hominin data set for testing the idea of increased developmental plasticity in *Homo*. Studies that focus on comparing variation potentially related to developmental

Table 5. Tertiary inferences regarding life history and behavior between *Australopithecus* and *Homo*

	<i>Australopithecus</i> vs. early <i>Homo</i>	<i>Australopithecus</i> vs. <i>Homo erectus</i> / <i>Homo ergaster</i>	<i>H. erectus</i> vs. <i>Homo habilis</i> / <i>Homo rudolfensis</i>
Extrinsic mortality	Possibly lower in <i>Homo</i> given body size	Lower in <i>H. erectus</i>	Lower in <i>H. erectus</i>
Developmental plasticity	?	Greater in <i>H. erectus</i>	Greater in <i>H. erectus</i>
Body composition	Larger brains in <i>Homo</i> but similar adiposity	Larger brains in <i>H. erectus</i> / <i>H. ergaster</i> and greater adiposity	Larger brains in <i>H. erectus</i> / <i>H. ergaster</i> and greater adiposity
Cooperative breeding (alloparenting; Isler and van Schaik 2012)	Possibly more cooperative breeding in <i>Homo</i>	<i>H. erectus</i> / <i>H. ergaster</i> more cooperative breeding necessitated by larger average brain size	<i>H. erectus</i> / <i>H. ergaster</i> more cooperative breeding necessitated by larger average brain size
Cooperative hunting	Possibly greater in <i>Homo</i>	Likely greater cooperative hunting based on diet shift in <i>H. erectus</i> / <i>H. ergaster</i>	Likely greater cooperative hunting based on diet shift in <i>H. erectus</i> / <i>H. ergaster</i>

Note. Based on hard-evidence differences in table 1.

plasticity (e.g., variation in body size or dimorphism at a given time) among time packets of this taxon and with early *Homo* would facilitate the identification of genus-level differences in biology. If increased developmental plasticity is present in *Homo*, one should find greater variation in the genus at any given time than in other well-represented genera. While non-*erectus* *Homo* samples are currently insufficient for such comparisons, *H. erectus* provides more opportunities for such investigations.

The Transition between Non-erectus Early Homo and Homo erectus

Even though recent fossil and archaeological discoveries challenge the idea that the origin of *H. erectus* involved a punctuated transformation of biology and behavior, present evidence suggests that this species did diverge from other hominins in several important ways. The life history pattern of *H. erectus* appears to have been more protracted than that of *Australopithecus* and *Paranthropus* and possibly non-*erectus* early *Homo*. Despite this, when compared with modern humans and later *Homo* (e.g., Neanderthals), *H. erectus* appears to have had a more rapid life history, with less pronounced secondary altriciality, an earlier maturation, and a less pronounced adolescent growth spurt (Dean and Smith 2009; Graves et al. 2010; Guatelli-Steinberg 2009; Thompson and Nelson 2011).

Present evidence suggests that a childhood phase of development (i.e., "early childhood"), with offspring being weaned yet still dependent for food and experiencing rapid brain growth but slow somatic growth, was in place by the time of *H. erectus* (Bogin 2006; Thompson and Nelson 2011). Contemporary human biology suggests that this life history shift in *H. erectus* most likely would have involved a shortening of infancy with earlier weaning and probably also shorter IBIs. Importantly, this pattern would have resulted in higher fertility and greater potential for population increase. Extending childhood by even a year would allow more time for cognitive development, including the development of eco-

logical skills such as in foraging as well as the refinement of social behaviors (Bogin 1999).

In order to assess, interpret, and characterize a species' life history pattern, we need to study multiple somatic systems simultaneously (Leigh and Blomquist 2007, 2011; Šešelj 2011). While multisystem studies have only begun to be applied to the fossil record, in large part because of a dearth of associated skeletal remains, they point to the need for extensive research on extant taxa for which somatic and physiological data are knowable. So far, these integrative studies have focussed on the hard tissues of the extant and fossil record (Clegg and Aiello 1999; Guatelli-Steinberg 2009; Šešelj 2011), and many more such studies are needed. Further, there is a critical need for studies that reach across both living and skeletal populations to combine hard-tissue parameters (e.g., age, sex, and size proxies), soft-tissue measures, and physiological data in living humans, nonhuman primates, and other mammals (see <http://bonesandbehavior.org>; Smith et al. 2012). Work that links conditions of nutritional stress to variation in both skeletal maturation (e.g., Frischno, Garn, and Ascoli 1970) and dental emergence patterns (e.g., Gaur and Kumar 2012) suggests that multiple modalities are influenced by this developmental process. A key step forward will be to define data sets in extant taxa that are explicitly designed to be collected and/or closely proxied in the fossil record in order that physical or archaeological clues can be identified as signals for development of behavioral or physiological shifts in deep time (see <http://bonesandbehavior.org>).

The other significant life history shift that arguably emerged in early *H. erectus* is the extended time to maturity through an elongated adolescence coupled with the development of a pronounced late adolescent growth spurt (Bogin and Smith 1996). The extant record indicates that this most likely would have involved a reduction in extrinsic mortality risk and greater nutritional access and stability than in early hominin species (e.g., Robson and Wood 2008). Fossil and archaeological evidence is consistent with increased access to higher-quality foods (i.e., those with relatively high energy and nu-

trient density; Potts 2012; Ungar 2012), resulting in potentially fewer periods of nutritional inadequacy that would have reduced associated declines in immune function.

Beyond diet, the extant record strongly implicates reduced extrinsic mortality as a means of increasing size and delaying development; however, it remains unclear just how mortality risk might have been lowered for *H. erectus*. An important clue may come from the extensive system of cooperative behavior and breeding seen in modern humans. Cooperative behavior, defined here as behaviors that provide a benefit to another individual and may or may not have a cost to the actor, occurs widely in the natural world, yet the degree of cooperation between unrelated individuals is unique to humans (Clutton-Brock 2009; Melis and Semmann 2010). In cooperative breeders, allocare (including paternal care) allows the mother to channel resources to her own somatic maintenance and reproduction; thus, allocare should generally be favored evolutionarily when the risk to the offspring is not too high (Lappan 2009; Ross and MacLarnon 2000). Among mammalian species, those with greater allocare exhibit relatively rapid infant growth with earlier weaning and faster reproductive (birth) rates, although these infants are not larger at birth (Borries et al. 2011; Isler and van Schaik 2009; Mitani and Watts 1997; Ross and MacLarnon 2000; Smith et al. 2012). The well-developed system of cooperation in humans plays a critical role in supporting the high costs of encephalization that must be paid during pregnancy and lactation (Ellison 2008; Kramer 2010; Wells 2012) and is a major factor in enabling early weaning, relatively low extrinsic mortality, extended subadult dependence, and high fertility (Gurven and Hill 2009; Hill and Hurtado 2009; Kaplan et al. 2000; Lancaster and Lancaster 1983). Thus, cooperative breeding was almost certainly a critical contributor to brain size increase in the *Homo* lineage, although the timing of this occurrence is elusive.

An important observation related to the likely presence of cooperative breeding in *H. erectus* is the link between demographic viability and encephalization. Isler and van Schaik (2012) suggest that demographic viability in primates is untenable at average cranial capacities over 700 cm³ (i.e., a “gray ceiling”) because of low fertility related to a protracted subadult period characterized by rapid brain growth but slow somatic growth. Smith (2012) and colleagues also found support from the carnivores for the idea of the co-occurrence of brain size expansion and cooperative breeding. Cooperative breeding in the form of direct care and the provisioning of juveniles with high-quality resources (e.g., animal fat and protein) would have enabled early *H. erectus* to circumvent this demographic constraint and evolve a relatively large brain while also having a life history pattern with early weaning and short IBI that led to greater fertility and facilitated population growth. Thus, a system of cooperative breeding, although not as well developed as in modern humans, seems likely to have been in place by the time of *H. erectus* if not

in non-*erectus Homo* (Bribiescas, Ellison, and Gray 2012; Gettler 2010; Key and Aiello 2000; Swedell and Plummer 2012).

Additionally, once cooperative breeding is present, we expect a fundamental shift in social organization that may be visible in the archaeological record (Potts 2012; Smith et al. 2012; Swedell and Plummer 2012). This may be reflected in evidence for greater or more complicated extractive foraging (Swedell and Plummer 2012) or in the aggregation of multiple individuals (Potts 2012; Smith et al. 2012). Future archaeological endeavors should aim to identify material cultural signatures reflecting these shifts. This research could potentially be coupled with stable isotope studies, which have shown great potential for identifying signatures of population movement during the lifetime of an individual (e.g., Copeland et al. 2011). Finally, we suggest that future studies focus on other aspects of extrinsic mortality relevant to shaping body size and shape, including predation rates as well as contributors to intrinsic mortality rates such as dietary breadth, quality, and availability.

Regional Variation, Climatic Adaptation, and Dispersal in Homo erectus

By the time of *H. erectus*, the trend toward greater ranging that may have started at the base of the genus had blossomed into long-range dispersals into a variety of different climatic contexts (e.g., the Republic of Georgia and tropical southeast Asia; Antón and Swisher 2004). Widely dispersed living mammals face a number of similar challenges and tend to share a number of attributes including behavioral plasticity, sociality, and relatively high rates of reproduction (i.e., high intrinsic rates of natural increase; Antón, Leonard, and Robertson 2002). In addition, contemporary humans add greater adiposity that buffers individuals in shifting environments and also allows maintenance of brain metabolic requirements, both of which are critical to successful dispersal (Kuzawa 1998; Leonard et al. 2003; Wells 2010). And humans exhibit great developmental plasticity that preserves flexibility in the face of short-term environmental changes (Walker et al. 2006). As such, it seems likely, based on what we know of the extant record, that *H. erectus* (1) had a different body composition than earlier hominins, with higher levels of adiposity; (2) possessed a level of developmental plasticity similar to that seen in modern humans, which may help explain the long existence of this species; and (3) may have had greater behavioral plasticity, which would have favored their success over less versatile members of genus *Homo* (see Smith et al. 2012).

To see how body composition might have changed, we look to humans who differ from other mammals (including non-human primates) by having particularly high levels of fat, large brains, small guts, and low muscularity (Aiello and Wheeler 1995; Leonard et al. 2003; Wells 2010). These differences in body composition structure variation in energy demands because of marked differences in organ-specific met-

abolic rates. While most internal organs—such as the heart, lungs, kidneys, liver, and spleen—appear to be tightly scaled with body mass (Calder 1984; Stahl 1965), the brain, gut, skeletal muscle, and adipose tissue vary according to functional demands (Aiello and Wheeler 1995; Calder 1984; Muchlinski, Snodgrass, and Terranova 2012; Schmidt-Nielsen 1984; Wells 2010). Nonhuman primates are “undermusclcd” when compared with other mammals, which likely reflects the arboreal heritage of the order. Humans, and especially human females, appear to be even less muscular (Muchlinski, Snodgrass, and Terranova 2012; Snodgrass, Leonard, and Robertson 2009). Although this could be an adaptation to reduce energetic costs associated with bipedal locomotion, it is more likely a reflection of our high levels of adipose tissue for a primate of our size.

Thus, besides the brain, the single most important component of body composition for understanding human evolution is arguably adipose tissue (Wells 2010, 2012). This tissue is closely linked to brain development and immune function, likely underpins the exceptional dispersal abilities of our genus, and helps explain our ability to withstand seasonal and periodic fluctuations in food availability (Kuzawa 1998; Wells 2010, 2012). Humans are exceptional in having fat stores considerably larger than most free-living primates and terrestrial tropically living mammals, and this is true for non-Western human populations as well (body fat levels average 25% for adult females and 13% for adult males; Pond 1998; Wells 2006, 2010). Humans are extremely fat at birth (~15% fat) and during infancy (peaking at ~25%–30% fat), which contrasts markedly with wild primates (baboons, 3%), domesticated species (pigs, 1.3%), and even seals (harp seals, 10.4%; Kuzawa 1998). Adipose tissue in humans serves primarily as a nutritional buffer against long-term (e.g., seasonal or periodic) decreases in energy availability, and fat is an important adaptation for preserving cerebral metabolism in the face of the high and obligate metabolic demands of the large human brain (Kuzawa 1998; Leonard et al. 2003). Further, human sex differences in adiposity are shaped by differences in reproductive strategies—in particular, the enormous energetic costs of pregnancy and lactation borne by females (Snodgrass 2012; Vallengia and Ellison 2001). This shift in body composition and concomitant increased energetic buffering (i.e., “somatic capital” of Kaplan et al. 2000) may have played a central role in the ability of *H. erectus* to successfully disperse into new environments, especially those with seasonal and periodic variation in climate and food availability.

Our ability to identify shifts in body composition in the fossil record is, of course, limited, and we are further constrained by the surprisingly little body composition data available for living primates and other mammals. Refining our understanding of body composition in extant species will help to identify which aspects of body composition in humans are derived and to outline adaptive scenarios related to their divergence (Wells 2012). It may also allow more nuanced pre-

dictions of body composition in fossil hominins as well as tests as to when in our lineage adiposity and sex-specific patterns of adiposity arose.

Plavcan (2012) notes that because of the difference between total body mass and lean body mass in humans and the differential distribution of fat in human females, degrees of cranial and postcranial skeletal variation differ in humans but not other apes. As in all other primates, postcranial variation (as reflected in CVs of linear dimensions) is similar to that of lean body mass variation (excluding adipose tissue) in humans. But unlike other primates, these CVs are greater than cranial CVs. Cranial variation in humans is similar to that of total body mass variation (including adipose tissue, which may indicate the importance of adipose tissue to brain maintenance). Presumably this reflects increased adiposity in humans and differential fat distribution in human females versus males. Thus, finding the point at which measures of cranial and postcranial skeletal dimorphism diverge may provide a preliminary clue as to when greater (or at least differential) adiposity arose in the lineage. At present, endocranial and femoral length CVs are similar to one another within early non-*erectus* *Homo*, early *H. erectus*, and *A. afarensis*. Thus, at least the differential fat distribution seen in human males and females had yet to develop by the time of early *H. erectus*, although we currently have no window on to whether increased adiposity was present in both sexes (table 1; and see table 5 in Antón 2012).

Our inference of greater developmental plasticity in *H. erectus* is supported by the variation seen in size across regional samples but is also an insight that requires that we use caution in interpreting the meaning of morphological differences among samples in body proportions, size, and sexual dimorphism. Caution is required for several reasons. First, some of the size variation shows a temporal trend in *H. erectus* (see Plavcan 2012). Second, total variation in *H. erectus* is not particularly remarkable relative to extant primates (Plavcan 2012). Third, it is well established that developmental plasticity can shift these signals rapidly in extant human and nonhuman primates (e.g., Bogin and Rios 2003) and for a variety of different reasons (Kuzawa and Bragg 2012).

To test the extent to which developmental plasticity was present in *H. erectus* and how similar it was to the human form, we need to understand how such plasticity is reflected in the skeletons of humans and nonhuman primates. Surprisingly, the extent of variation in developmental plasticity among primates is not well studied, and the lack of these data is a barrier to interpreting variation in the human fossil record. One study of baboons demonstrates the potential for dramatic shifts in growth, reproduction, and body size with altered environmental conditions (Altmann and Alberts 2005). Garbage-foraging baboons *Papio cynocephalus* show faster maturation and larger body size than other savannah baboons as a result of better food availability during ontogeny. Given their generalized ecologies and broad geographic distributions, papionin monkeys (baboons, mandrills, and ma-

caques) and modern humans are arguably the best analogues for early *Homo*, especially *H. erectus* (Jolly 2001; Swedell and Plummer 2012), and should prove a fruitful area of focus for future studies.

A related issue with importance for interpreting the hominin fossil record is the influence of developmental plasticity on sexual dimorphism (see Bribiescas, Ellison, and Gray 2012). Although both sexes experience developmental plasticity, males are disproportionately able to capitalize on high-quality environments, whereas females are more environmentally buffered and less negatively influenced by poor environments (Altmann and Alberts 2005; Kuzawa 2007; Stinson 1985). Thus, sexual dimorphism can shift rapidly over time with reduced sexual dimorphism in bad times and accentuated sexual dimorphism under more optimal environmental conditions (Stini 1972, 1975). This may hint at the cause of the apparent reduction in dimorphism in Georgian *H. erectus* (see table 2). Additionally, environmental conditions experienced during development influence testosterone and thus shape sexually dimorphic traits, including stature, bone growth, and muscle mass (Bribiescas, Ellison, and Gray 2012; Kuzawa et al. 2010). This topic has not been systematically studied across primates, but we believe it should form the basis for future investigations as it has important implications for making inferences from morphological variation.

Although we recognize that other, longer-term forces such as mate competition are critical to shaping differences in sexual dimorphism across taxa (see Plavcan 2012), a more systematic understanding of intraspecific variation across geographic, environmental, and nutritional contexts in primates is critical to contextualizing variation in the fossil record. Evaluations of specific skeletal responses (e.g., brow development) to environmental signals in extant taxa may help elucidate the meaning of sexual dimorphism in the fossil record (Bribiescas, Ellison, and Gray 2012). More systematic studies of geographic variation in nonhuman primate samples, both skeletal and living, that pay particular attention to how the adult form of skeletal traits (including overall size but also secondary sex characteristics such as robusticity) is affected by developmental plasticity and how the sexes are differentially affected in different environments will greatly improve our ability to differentiate adaptation from epiphenomenal variation in the fossil record (Plavcan 2012; see Fernandez-Duque 2011 for an example of the use of skeletal proxies from living animals).

Another means of differentiating among hypotheses for intraspecific variation in body size and shape considers differences in proportions due to the timing of growth disruptions. Poor growth related to environmental conditions typically occurs during infancy when growth rate is rapid and the body is uniquely vulnerable to insult. In humans, this heightened vulnerability is associated with the introduction of supplemental, often low-quality foods, which usually begins at ~4–6 months of age. These foods may also inadvertently introduce pathogens (Sellen 2001; Snodgrass, Leonard, and

Robertson 2009). For this reason, poor growth resulting from environmental conditions disproportionately affects limbs and their distal segments, which grow at a more rapid rate than the trunk during infancy. At ~2–3 years of age, declining growth rates and more developed immune and digestive systems reduce the risks of permanent growth disruptions (Bogin 1999; Kuzawa 1998). As a result, the secular increase in height experienced by most human populations in the twentieth century was associated with disproportionate gains in limb length, particularly distal segments (Stinson 2012). In fact, relatively short legs are interpreted as reflecting an adverse early developmental environment (Bogin and Varela-Silva 2010). Although genetic factors related to ultimate causes such as climatic adaptation (Katzmarzyk and Leonard 1998; Roberts 1978) are important contributors to body proportions, proximate factors such as nutrition during development clearly play an important role in humans (Bogin and Rios 2003; Eveleth and Tanner 1990; Stinson 2012). Studies of how the skeleton is affected by nutritional insufficiency during the longer weaning period of great apes will be important to considering the applications to the fossil record.

Further, exposure to persistent and ubiquitous stressors that are not effectively buffered by cultural/behavioral mechanisms will lead to adjustments initially through developmental plasticity and later, if experienced at a population level over multiple generations, by genetic changes resulting from polygenic adaptation (Kuzawa and Bragg 2012). Thus, studies that combine dental, cranial, and postcranial analysis can potentially expand our ability to interpret variation in body size and proportions seen among regional samples of *H. erectus*. While the state of the fossil record is currently quite far from adequate for such purposes, regional samples of *H. erectus* may begin to be probed using integrative studies, and additional research on extant taxa will help provide the comparative foundation for this work.

We could hypothesize, for example, that the smaller overall size of Georgian *H. erectus* is due to decreased nutritional sufficiency during development or increased extrinsic mortality (due to predation or disease; Antón 2012; Migliano and Guillon 2012). Or, we might predict it results from small-packet resources that are widely dispersed in a topographically challenging area with little selective pressure for large body size—an explanation offered for the small adult body size of Late Stone Age humans of southern Africa (Pfeiffer 2012). Or, the apparently shortened arms of the Dmanisi group may perhaps reflect climatic adaptation (Pontzer 2012).

We could test these hypotheses by considering the specific anatomical and archaeological signatures each implies. For example, nutritional stress-related small adult body size likely would be accompanied by shortened distal limb segments and marked enamel hypoplasias, the latter of which provide a permanent record of systemic physiological stress, whereas climatic adaptation might result in shortened arms but not necessarily differentially short distal limb segments in both arms and legs. Alternatively, increased extrinsic mortality such

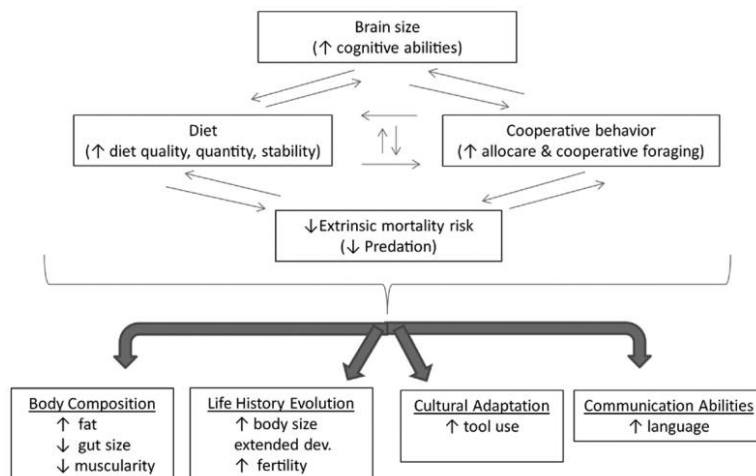


Figure 1. A positive feedback loop between cooperative behavior (initially in breeding), diet quality and stability, cognitive abilities (brain size), and extrinsic mortality risk drove life history evolution and contributed to cultural change in genus *Homo*. Gradual, self-reinforcing shifts in these central elements had consequences for life history traits including extending the developmental period, increased fertility, and larger body size; body composition including increased adiposity, reduced gut size, and reduced muscularity; communication including eventually the development of language; and cultural change including more complex extractive foraging. Early *Homo* showed only modest increases in the central elements. The fully modern package of life history and other consequences may not have emerged until recent humans.

as predation and parasites should lead to differences in neonatal size (Kuzawa and Bragg 2012) relative to nonstressed groups but not necessarily to indicators of nutritional stress and may also yield archaeological signals. Evidence of packet size may come from archaeological evidence. Surprisingly, research of this nature in contemporary humans and non-human primates is fairly limited. However, a study among Aboriginal Australians—which found that permanent stunting was seen only in individuals with enamel defects that were early (within the first 18 months of life), severe (enough to produce paired enamel defects), and repeated (during infancy and childhood; Floyd and Littleton 2006)—shows the potential of multisystem studies. Such an integrative approach may help us interpret body size and proportion variation in *Homo* and to differentiate adaptive variation from responses to proximate environmental factors such as diet and disease.

Finally, we suggest that from other records, local environmental signals should also be plumbed and developed to understand the specific as well as the regional and global context of fossil groups. If extrinsic mortality has such important consequences for size and shape variation, then additional means of assessing extrinsic mortality must be pursued. As mentioned earlier, these include archaeological means for assessing predation and diet as well as geochemical means for reconstructing plausible climates and diets. Thus, we advocate a multipronged approach to future research agendas that (obviously) includes collection of new fossil hominins and a focus in extant mammals on skeletal end results of environmental and physiological parameters, especially in widely dispersed taxa.

A Model for the Origins and Evolution of Genus *Homo*

The integration of paleoanthropological data with information from primatology and human biology leads us to the conclusion that the origin and evolution of early *Homo* was characterized by a positive feedback loop that drove life history evolution and contributed to cultural change. The central elements of this model are cooperative behavior, diet, cognitive abilities, and extrinsic mortality risk (fig. 1). The model postulates gradual self-reinforcing shifts in these central elements with consequences for life history traits (e.g., extended developmental period, increased fertility, and larger body size), body composition (e.g., adiposity, gut size, and muscularity), communication abilities (the development of language), and cultural change (tool use). The model expands on Hrdy's (2009) cooperative breeding hypothesis, which postulates that beginning with the rise of the genus *Homo*, allo-maternal care and provisioning drove life history evolution, and it recognizes, as does Kaplan et al. (2000), that reducing mortality rates, investing in embodied capital (fat), and increasing cooperation are in a positive feedback loop with brain size. However, it does not rest on a particular kind of food resource or social structure but recognizes that increasing diet quality and/or throughput and cooperation remain critical to growing big brains and large bodies.

At present, it is impossible to identify the initial evolutionary change or changes, but it seems most likely that behavioral changes related to diet and perhaps cooperation were early additions. In contrast, encephalization would likely have

been a secondary change, because comparative studies suggest that alterations in diet quality and body composition were necessary preconditions of hominin brain expansion. Further, reductions in mortality risk (both intrinsic and extrinsic) most likely would have been substantially influenced by dietary shifts and increased cooperative behavior and thus would likely have been downstream changes.

Present fossil and archaeological evidence suggests substantial changes in diet occurred initially with non-*erectus* early *Homo* and were followed by marked dietary change in *Homo erectus*. In particular, earliest *Homo* likely consumed a substantially higher-quality diet than *Australopithecus* and *Paranthropus*, as the result of the consumption of high-quality plant foods (e.g., underground storage organs) as well as animal source foods. *Homo erectus* appears to have occupied a new ecological position for hominins that almost certainly involved a considerable increase in access to animal foods. This dietary shift to more energy- and nutrient-dense foods would potentially have allowed for an increase in brain size by removing constraints on brain growth; in addition, this dietary change may have selected for increased brain size and cognitive capacity related to increased foraging, extraction, and processing abilities associated with higher-quality diets. The reliance on high-quality foods may have also selected for cooperative social systems that would have increased the ability to hunt and process foods. A variable and flexible system of cooperative breeding would have reduced extrinsic mortality risk even further, especially for juveniles, through direct care and provisioning, and it would have contributed energetically to reproductive-aged females. Cooperative breeding would have contributed to the ability of hominins to support the growth and high maintenance costs of large brains among juveniles through care and provisioning and would also have selected for enhanced social cognitive processes that may have led to further increases in brain size.

While we do not suggest that a fully human pattern of life history traits (e.g., extended developmental period, increased fertility, and larger body size), body composition, communication abilities, and cultural change was present in early *Homo* or *H. erectus*, by the time of *H. erectus* the archaeological record of dispersal provides evidence of sufficient plasticity and perhaps adiposity to colonize various environments. The best evidence for developmental plasticity in *H. erectus* comes from the degree of morphological variation in size in the species both within and outside of Africa, which provides not only evidence of long-term trends but also short-term variability at all times and in all places. Our expectation is that regional morphs of *H. erectus* were established fairly quickly but that significant population divergence was mitigated by these same short-term developmental parameters.

The greatest advances in understanding the evolution of the early genus *Homo* will be guided by multipronged research agendas that pay careful attention to determining the local environmental conditions (broadly understood) of fossil groups and coordinate this work with multisystem evaluations

of the behavior, physiology, and anatomy of extant groups. These data sets must be explicitly designed to be measurable or closely proxied in the fossil record.

Acknowledgments

We benefited greatly from the lively discussions at the Wenner-Gren Foundation workshop “Human Biology and the Origins of *Homo*” held in Sintra, Portugal, in March 2011. We thank Leslie Aiello, who co-organized the workshop with S. C. Antón, our fellow participants, and Laurie Obbink for making the Sintra meeting such a productive, stimulating, and convivial week. Following Sintra, Chloe, Bill Leonard, and Herman Pontzer engaged in critical discussions of energetics and organ-specific metabolism, Leslie Aiello and Tom Schoenemann provided important input on the early conception of this paper, Chris Kuzawa provided critical feedback on a later iteration, and Leslie Aiello and the reviewers greatly improved the final paper. Emily Middleton and the *Current Anthropology* staff provided expert editorial advice.

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