

ENERGETICS AND THE EVOLUTION OF THE GENUS *HOMO*

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■ **Abstract** The genus *Homo* as represented by *Homo ergaster* (=early African *Homo erectus*) is characterized by a pattern of features that is more similar to modern humans than to the earlier and contemporaneous australopithecines and paranthropines. These features include larger relative brain sizes, larger bodies, slower rates of growth and maturation, dedicated bipedal locomotion, and smaller teeth and jaws. These features are phenotypic expressions of a very different lifestyle for the earliest members of the genus *Homo*. This paper considers the energetic correlates of the emergence of the genus *Homo* and suggests that there were three major changes in maintenance energy requirements. First, there was an absolute increase in energy requirements due to greater body size. Second, there was a shift in the relative requirements of the different organs, with increased energy diverted to brain metabolism at the expense of gut tissue, possibly mediated by changes in the proportion of weight comprised of fat. And third, there was a slower rate of childhood growth, offset by higher growth costs during infancy and adolescence. These changes, as well as energetic requirements of reproduction and bipedal locomotion, are considered in a discussion of one of the major transitions in adaptation in human evolution, the appearance of our own genus.

INTRODUCTION

Modern humans are very different than our closest living relatives, the African apes. Among other traits, we have larger brains, walk on two legs, have slower rates of growth and maturation, longer lifespans, a long period of post reproductive life for females, differently shaped bodies, different foraging behaviors, and higher quality diets. These features are all phenotypic expressions of the human life history pattern and reflect the pace and energetic requirements of human life. Humans, as well as all other organisms, are confronted by constraining relationships, or trade-offs, in terms of how energy is invested in either growth, maintenance, activity, or reproduction (Stearns 1992). Natural selection operates very strongly on these

trade-offs because of their overall influence on lifetime reproductive success (Wells 2002).

This paper reviews the energetic consequences of the evolution of *Homo*. It identifies the features of the modern human life history pattern that were present at the first appearance of our genus and considers their costs and benefits in relation to adaptive fitness. The assumption underlying this is that features should only be selected for when the cost/benefit ratio is optimal (Ulijazek 1995). Physical and behavioral adaptations seen in our early *Homo* ancestors should minimize their use of energy and optimally balance expenditure to achieve optimal reproductive success.

When the genus *Homo* first appeared is a matter of debate that depends largely on how the genus is defined. Wood & Collard (1999) convincingly argue that *Homo ergaster* (= early African *Homo erectus*), as defined by Wood (1992) and best known from the Turkana basin in Kenya between 1.9 and 1.5 Ma, is the first known species in the genus *Homo*. *Homo ergaster* is distinguished from earlier possible members of the genus *Homo* such as *H. habilis* (2.3–1.6 Ma) or *H. rudolfensis* (2.4–1.8 Ma) by a complex of skeletal and dental features reflecting a lifestyle that was more similar to that of modern humans than that inferred for earlier and contemporaneous hominins. These skeletal and dental features include a larger body mass, more human-like body proportions, relatively long legs, obligate bipedalism coupled with a limited facility for climbing, relatively small teeth and jaws suggesting major dietary change, and a tendency towards an extended period of growth and development. Although not all anthropologists agree that *Homo ergaster* is the first member of the genus *Homo* (e.g., McHenry & Coffing 2000), this review follows Wood & Collard (1999) and focuses on the energetic consequences of the human-like complex of features that distinguishes *Homo ergaster*.

INCREASED BODY MASS

One of the most obvious and energetically important features of *Homo ergaster* is its significantly larger body mass in comparison to earlier and contemporaneous hominins. The body mass estimates (Table 1) that are commonly accepted in the literature are derived largely from the work of McHenry (1992a,b; 1994) and are determined on the basis of hindlimb joint size (but see Aiello & Wood 1994 and Kappelman 1996 for cranially determined body mass estimates). It is clear from these estimates that *Homo ergaster* is considerably heavier than any of the australopithecines or paranthropines and that females have increased in mass more than males. This means that *Homo ergaster* is not only characterized by a significant size increase but also by a marked reduction in sexual dimorphism (Leonard & Robertson 1997, Aiello & Key 2002).

There is increasing evidence that *Homo ergaster* was occupying a more open (xeric) environment than were the australopithecines and paranthropines (de Menocal 1995, Reed 1997, Sikes 1999). Large body size has a number of advantages in a more open environment including the capacity to exploit broader dietary niches in larger foraging areas, greater mobility and prey size, and increased sociality (Foley 1987). Large body size also permits females to efficiently

TABLE 1 Inferred body mass and daily energy requirements for the hominins

	Sex	Body mass ^a	RMR ^b	DEE ^c	DEE ^c + gestation ^d	DEE ^c + lactation ^e	DEE ^f	DEE ^f + gestation ^d	DEE ^f + lactation ^e
<i>A. afarensis</i>	f	29.3	881.6	1175.3	1469.1	1633.7	1248.1	1560.2	1734.9
	m	44.6	1208.1	1610.6			1740.9		
<i>A. africanus</i>	f	30.2	901.8	1202.3	1502.8	1671.2	1278.4	1598.0	1777.0
	m	40.8	1130.0	1506.6			1622.3		
<i>A. robustus</i>	f	31.9	939.6	1252.7	1565.9	1741.2	1335.1	1668.8	1855.7
	m	40.2	1117.6	1489.9			1603.4		
<i>A. boisei</i>	f	34.0	985.6	1314.0	1642.6	1826.5	1404.2	1755.3	1951.8
	m	48.6	1288.5	1717.8			1863.4		
<i>H. ergaster</i>	f	52.0	1355.5	1807.2	2259.0	2475.8	1966.0	2457.4	2732.7
	m	63.0	1565.3	2086.9			2288.6		
<i>H. sapiens</i>	f	56.8	1448.3	1930.9	2413.6	2664.7	2108.3	2635.4	2930.6
	m	70.0	1694.0	2258.5			2487.8		

^aBody mass (kg) after McHenry (1992).

^bRMR (resting metabolic rate) is computed according to the Kleiber equation (Kleiber 1932, 1961) $RMR = 70 W^{0.75}$, where W = body mass (kg).

^cDaily energy requirements (kcal d^{-1}) = $93.3 W^{0.75}$ (Key & Ross 1999).

^dDaily energy requirements during gestation = $DEE * 1.25$ (Aiello & Key 2002).

^eDaily energy requirements during lactation = $DEE * 1.39$ for the australopithecines and paranthropines, = $DEE * 1.37$ for *Homo ergaster*, and = $DEE * 1.38$ for *Homo sapiens* (Aiello & Key 2002).

^fDaily energy requirements (DEE) = $86.0 W^{0.792}$ (Leonard & Robertson 1997). Note that this equation produces daily energy requirements that are between 6%–10% higher than those produced by the Aiello & Key (2002) equation (DEE^3). The daily energy requirements during gestation and lactation are correspondingly elevated. See text for explanation.

carry their children to an older age and increased mass (Kramer 1998). Coupled with the taller and more linear physique of *Homo ergaster*, there are also physiological advantages in relation to thermoregulation and water budgets (Ruff 1991; Wheeler 1992, 1993). These physiological advantages may have been particularly important to pregnant females because of their increased susceptibility to heat stress as the result of their increased weight for height as the pregnancy developed (J. C. K. Wells, submitted). A recent analysis found that 10% of the between population variability in modern human birth weight could be attributed to thermal load, after taking confounding factors into account (Wells & Cole 2002). It would benefit both mothers and their unborn children to maximize their thermoregulatory advantage. In modern humans, hot weather mothers are smaller, gain less weight, and are less fat than cold weather mothers. Further modeling is needed to demonstrate the net thermoregulatory advantage of the larger body mass coupled with the more linear physique of *Homo ergaster* in comparison to the lighter but squatter australopithecines. It is, however, highly probable that the *Homo ergaster* body form provided a net thermoregulatory advantage in the relatively xeric conditions of the African Plio-Pleistocene.

One major disadvantage of larger body size in *Homo ergaster* is the increased energetic burden it represents and the correspondingly increased dietary requirements necessary to fuel the increased energy demands. The extra maintenance metabolic requirements of this weight gain can be calculated using Kleiber's

standard formula for the relationship between body mass and resting metabolic rate (RMR). RMR is the amount of energy utilized by an inactive organism under thermal neutral conditions (Durnin & Passmore 1967), and in the following formula $W = \text{body mass (kg)}$ and $\text{RMR} = \text{kcal/d}^{-1}$ (Kleiber 1932, 1961):

$$\text{RMR} = 70 W^{0.75}.$$

The resting metabolic requirements of *Homo ergaster* would have been 39% higher than for *Australopithecus afarensis* (30% higher for males and 54% higher for females) (Table 1).

DIETARY IMPLICATIONS OF INCREASED ENERGY EXPENDITURE

The larger body size in *Homo* implies a corresponding increase in either the daily amount of food or the quality of the food eaten in order to satisfy the increased energy needs. If *Homo ergaster* ate the same type of diet as the smaller bodied australopithecines, this would imply a significant alteration in the activity budget where feeding time would have to be increased in proportion to the extra calories required by the larger body mass. Even if this had been possible and *Homo ergaster* could have balanced time needed for traveling, socializing, and resting against the necessarily increased feeding time, it is unlikely that they adopted this strategy. *Homo ergaster* jaws and teeth are reduced in size, which suggests a major dietary shift away from more fibrous and more difficult to masticate foods (Walker & Leakey 1993, Wood & Aiello 1998). Equally, the trunk proportions in *Homo ergaster* suggest a relatively small gut that is compatible with a higher quality and more easily digested diet (Aiello & Wheeler 1995). The more open xeric habitat occupied by *Homo ergaster* would also offer different dietary opportunities.

It is probable that meat comprised a greater proportion of the *Homo ergaster* diet than it did for the earlier and contemporaneous australopithecines and paranthropines (Aiello & Wheeler 1995). However, it is unlikely that meat by itself would have met the increased energy requirements of *Homo ergaster*. It is clear from analyses of modern people that humans are incapable of metabolizing sufficient protein to meet more than 50% of their energy needs (Speth & Spielmann 1983, Speth 1989). Those modern people who rely more heavily on animal-based resources also rely heavily on fat for the remainder of their energy requirements.

For a number of reasons such a diet would have been unlikely for *Homo ergaster*. The specific dynamic action, the rise in metabolism or heat production resulting from ingestion of food, is very high for protein. If modern people such as the Eskimos for whom 90% of caloric needs are met by meat and fat are anything to go by, such a diet would elevate RMR by 13%–33%, with significant implications for thermoregulation in a hot open country environment. This also means that they would have had to eat correspondingly more meat to satisfy their basic energy requirements. A high meat diet also demands increased water intake, and this is an

unlikely strategy to adopt in a hot open environment (Speth & Spielmann 1983). Furthermore, wild African ungulates have a relatively low fat content (Speth & Spielmann 1983, Speth 1989), and modern African hunters and gatherers such as the San or Hadza who rely heavily on meat during the dry season also rely on cultural means to recover maximum fat from the carcasses—a strategy that would not have been available to the early hominins.

Meat protein is easier to digest than plant protein and even with a limited amount of fat would still have been a valuable source of essential amino and fatty acids, fat soluble vitamins, and minerals (Milton 1999). It would satisfy nutritional requirements with a lower dietary bulk. This would allow increased reliance on plants of lower overall nutritive quality but high carbohydrate content, such as underground storage organs, to provide the majority of the energy to fuel their larger bodies. Carbohydrates also have a protein sparing advantage over dietary supplementation with fat. In situations of calorie restriction such as might be expected during the dry season on the African savanna, a diet supplemented with carbohydrates is more efficient than one supplemented by fat in sparing limited protein from being metabolized for energy and thereby restricts the availability of the limited essential nutrients and amino acids derived from that protein (Speth & Spielmann 1983).

An added advantage of including meat in the diet is the high methionine content of animal protein (Milton 1999). This would provide an adequate supply of sulfur-containing amino acids that are necessary for the detoxification of toxic (cyanogenetic) plant foods. Milton (1999) also points out that infants need dietary protein consisting of 37% of its weight in essential amino acids (compared to 15% in adults) and that animal protein would have been a valuable component of weaning foods.

Homo ergaster would undoubtedly have made use of a variety of other food resources such as invertebrates (e.g., termites) or nuts, seeds, honey, etc. However, increased reliance on mammalian meat and fat would have altered the basic balance between dietary quality and dietary bulk and would be consistent with the assumptions of the expensive tissue hypothesis (ETH) (Aiello & Wheeler 1995) and also the work of Barton (1992), which suggests that for our body sizes, humans eat less bulk than nonhuman primates. The diet of *Homo ergaster* was therefore not an australopithecine diet with added meat, but involved a change in the proportions and type of both animal and vegetable foods (Leonard & Robertson 1992, 1994).

WHAT RMR IS ACTUALLY MEASURING—THE ROLE OF EXPENSIVE TISSUES AND ADIPOSE TISSUE

Overall RMR is the sum total of the RMR of the tissues that compose the body. Organ tissues tend to be of high metabolic rate per unit mass whereas muscle and adipose tissue is of substantially lower metabolic cost. There is considerable

variation across species and during ontogeny. For example, in adult humans the brain takes up approximately 20% of the total RMR of the individual, whereas in other primates it takes up 8%–9% (Holliday 1986, Mink et al. 1981). There is also considerable variation in the size of other organ masses across species (Stahl 1965).

The differential contribution of tissues to total body RMR is the basis of the ETH for the co-evolution of brain size, gut size, and diet in human evolution (Aiello & Wheeler 1995, Aiello 1997, Aiello et al. 2001). Prior to the publication of the ETH, there was considerable puzzlement over the apparent lack of correlation between relative brain size and relative RMR across mammals (e.g., Leonard & Robertson 1994). Humans have a RMR predicted by the Kleiber equation, but have a significantly larger brain size that would be expected to considerably elevate human RMR (Leonard & Robertson 1994, Aiello & Wheeler 1995). Aiello & Wheeler (1995) demonstrated that the metabolic costs of the relatively large and energy-expensive human brain were balanced by a corresponding reduction of the size of the equally expensive human gut. Diet quality in primates is significantly correlated with relative brain size (Leonard & Robertson 1994) but also determines the relative size of the gut. The higher the quality of the diet the smaller and simpler is the gut. It is probable that the well-known relationship between diet quality and relative brain size is explained, at least in part, by the energy sparing consequences of the relatively smaller gut. Aiello & Wheeler (1995) also suggest that the change in the size and shape of the thorax and pelvis between australopithecines and *Homo ergaster* reflects a reduction in the size of the gut in *Homo ergaster*.

It is important to remember that this does not negate other possible relationships between diet quality and brain size such as the importance of essential fatty and amino acids, vitamins, and minerals (Broadhurst et al. 1998, Horrobin 1998, Milton 1999) or the role of a high quality diet in supporting maternal nutrition during gestation and especially lactation (Martin 1996, Leonard & Robertson 1994). It is also important to remember that the hypothesis is not necessarily weakened by the fact that there is no universal correlation between relative brain size and relative gut size across mammals. Brain size does not make up a significant component of total body RMR in many other animals as it does in humans and therefore is not a limiting factor. The emerging field of ecophysiology also clearly demonstrates that animals as varied as snakes, birds, and mammals manipulate their RMRs through differential size of other expensive tissues to meet varying environmental or lifehistory challenges (Aiello et al. 2001).

Changes in the expensive tissues are also not the only potential source of changes in the constituents of the human RMR. A further hypothesis, to our knowledge not considered previously, is that the increased adiposity of later *Homo* species has partially concealed an increase in RMR of *Homo sapiens*. Reconstruction of hominin energy stores is well nigh impossible due to the poor preservation of soft tissue in the fossil record. Data on body fatness of nonhuman apes is sparse, and body composition is rarely considered when addressing the relationship between

body size and metabolic rate. Although orangutans, like humans, appear to have the capacity to store fat in the abdomen (Zihlman & McFarland 2000), wild-living individuals from most contemporary primate species have percentage body fat lower than the 26%–28% of a well nourished woman or than the 14% of a man (Forbes 1987, Rutenberg et al. 1987, McFarland 1997). Even in populations inhabiting harsh environments, body fatness in women is around 20% (Lawrence et al. 1987).

In modern humans, both fat mass and fat-free mass contribute to total RMR. Based on 104 normal women, the relative contribution of fat mass (FM) and fat-free mass (FFM) is:

$$\text{RMR} = k_1 \text{ FM} + k_2 \text{ FFM},$$

where values for k_1 and k_2 are 0.31 and 1.35 Joules $\text{s}^{-1} \text{ kg}^{-1}$, respectively (Garby et al. 1988). These values increase to 0.96 and 2.14 Joules $\text{s}^{-1} \text{ kg}^{-1}$ at moderate activity levels, indicating that the relative metabolic cost of fat stores rises with the level of activity. The contribution of FM to RMR is attributed to the energy requirements of adipose tissue (Simonsen et al. 1994).

A change in the relative contributions of fat mass and fat-free mass to body mass confounds between-species energetic comparisons on a per kg body weight basis. In this instance, the greater fatness of humans suggests that, relative to nonhuman primates, RMR per unit fat-free mass of *Homo sapiens* has increased. Such an increase would suggest that rather than increased brain costs being fully offset by reduced gut costs, they may in part remain, concealed by the low-cost requirements of increased adipose tissue.

A higher maintenance expenditure of energy than expected on the basis of body size implies that humans must either compensate on expenditure energy on non-basal functions such as physical activity or obtain increased food resources. In general, higher resting energy requirements are predicted to be favored when food supply is abundant (Mueller & Diamond 2001). This may not be the case in hominin evolution; however, an alternative strategy for supporting high maintenance expenditure is the preservation of energy as fat in order to overcome fluctuations in food availability.

We do not know when hominins began to become fat, although Pond (1997) demonstrates that the distribution of fat deposits is similar in many mammals, including humans. In her opinion, bipedal posture is important in the distribution of human fat and, for example, the groin deposits in other mammals are extended in humans to form a continuous layer from pelvis to knee. Because the details of the anatomy and distribution of adipose tissue in living apes remain largely unknown, it is not possible to say when the unique features of human adipose tissue evolved (Pond 1991, 1997).

The ability to accumulate fat would be of enormous value in the more seasonal open environments occupied by *Homo ergaster*. Horrobin (2001) notes a kilogram of fat provides around 9000 calories, enough to survive reasonably well

for 4–6 days (assuming consumption of 1500–2500 kcal d⁻¹). Although famine conditions may have been relatively rare in hominin evolution, less extreme fluctuations in food availability may have been relatively common. Contemporary Gambian farmers experience successive hunger and harvest seasons in which the highest energy expenditure on subsistence is required in the season of lowest food availability (Lawrence et al. 1987). Gambian women accommodate these seasonal stresses through highly flexible fat stores, and may gain or lose up to 4 kg of fat depending on the ability of energy intake to satisfy requirements (Lawrence et al. 1987). The ability to accommodate seasonal variation in food supply through physiological adaptation contrasts with the alterations of group size and structure that characterize closely related species such as chimpanzees, although orangutans also store fat to buffer against seasonal food supply fluctuations (Knott 1997).

Accumulation of fat to buffer seasonal stresses may therefore have been a crucial factor in the survival of *Homo ergaster* as compared to other hominin lines, and may have influenced group structure and sociality as well as energy balance per se. This hypothesis is particularly interesting given the faster reproductive turnover of human versus ape females and the proposed role of grandmothers in feeding older dependent offspring, implying a greater need to preserve group structure over time (see below).

The significance of energy stores for female reproductive fitness is also supported by observations of a reduced ability to conceive (Frisch & MacArthur 1974) and a higher rate of miscarriage in thin women, consistent with the life history theory prediction that unpredictable environments should favor maintaining parental survival probability at the expense of reproductive investment (Hirschfield & Tinkle 1975).

MORE ON THE ENERGETIC COSTS OF THE BRAIN

There is more in relation to the energetic costs of the brain than the relationship between relatively large brain and the energy balance of the adult individual. The increased brain costs of later hominin species are particularly significant in early life, when brain weight is a higher proportion of total body mass and takes up to 60%–70% of total energy requirements in the individual (Holliday 1986). Modern human infants and children have an elevated RMR throughout ontogeny that undoubtedly supports the higher energy demands of the proportionally large brain as well as the costs of growth (see below). Foley & Lee (1991) have calculated the human brain to increase energy requirements by 8.7% relative to *Pan* during the first 18 months postpartum.

Aiello and colleagues (2001) have suggested that the payoff between the size of the brain and gut may be particularly important to the child's energy balance after it is weaned and before it has acquired the necessary skills to acquire food for itself. However, increased energy intake is not the only strategy for meeting the costs of a larger brain, and during childhood the alternative strategy of reduced growth is observed.

A comparison of modern humans and *Pan* indicates that whereas growth in weight up to 2 years is relatively similar, for the ensuing 10 years *Pan* grows at a significantly faster rate (Ulijaszek 1995). Subsequently, this pattern is reversed, with growth in *Pan* slowing and mature size attained by about 12 years, whereas humans maintain and even increase their childhood growth rate during an adolescent growth spurt that continues to about 18 years.

The total energy cost of tissue growth is relatively constant between primate species, regardless of whether the weight gain comprises fat or lean tissue (Roberts & Young 1988). Further, given that much of the weight gain represents water, it is possible to ascribe a final cost of 4.5 kcal g⁻¹ of tissue gain (FAO/WHO/UNU 1985). Growth costs, averaged over the first 10 years can therefore be calculated as 57 kcal d⁻¹ and 44 kcal d⁻¹ in male and female *Pan*, but only 27 kcal d⁻¹ in both sexes in modern humans. In the following 8 years, the contrast is reversed, with *Pan* costs averaging 11 kcal d⁻¹ in both sexes, and human costs being 42 kcal d⁻¹ in both sexes.

This comparison indicates that the energy costs of growth are divided into three periods, with the most vulnerable childhood period protected by a slower growth rate. The initial growth period is funded directly through maternal metabolism (see also Martin 1996), whereas the final period is funded by the independent offspring when the ability to compete against adult conspecifics is improved (Jansen & van Schaik 1993).

Foley & Lee (1991) use the increased costs of brain growth to infer the likely evolution of slowed growth rate across hominin taxa. They suggest that with the evolution of *Homo* the burden becomes sufficiently severe to benefit from slower growth. Consistent with this prediction of the importance of brain size for growth rate, growth in *Homo ergaster*, with a brain size two-thirds of that of average modern humans, appears not to be slowed to the degree present in *Homo sapiens* (Dean et al. 2001).

Furthermore, slowed growth is a general feature of highly social species such as primates and carnivores (Bogin & Smith 1996). However, the association between slowed growth and sociality need not necessarily be attributed only to increased costs of brain growth. In social species, weaned offspring may remain partially dependent on the mother for food during the juvenile period, and selection may have favored slowed childhood growth in humans in order to protect maternal total fitness at the expense of fitness of individual offspring (Wells 2002). Thus parent-offspring conflict as well as increased energy requirements for brain growth may have favored slower growth during human childhood.

THE ENERGETIC COSTS OF LOCOMOTION

Homo ergaster was not only significantly larger than the australopithecines and paranthropines, but also had significantly longer legs in relation to its body mass. This has further ramifications for energy turnover. The majority of the literature on bipedalism and energetics has been concerned with the energetic advantage of

human bipedalism over primate quadrupedalism. It has been well established that, at maximum running speed, human bipedalism is twice as expensive energetically than estimated for a quadrupedal mammal of the same body mass (Taylor et al. 1970, Fedak & Seeherman 1979) and that human walking is energetically much more efficient than human running (Fedak et al. 1974). At an average walking speed of 4.5 km h^{-1} , human bipedalism is slightly more efficient than is quadrupedalism in the average mammal (Rodman & McHenry 1980). Both bipedalism and quadrupedalism are equally as expensive in chimpanzees (Taylor & Rowntree 1973), and at average walking speeds the chimpanzee consumes 150% more energy ($\text{g}^{-1} \text{ km}^{-1}$) than does a similarly sized quadruped (Rodman & McHenry 1980).

This means that if the proto-hominin was energetically equivalent to a modern chimpanzee there would have been considerable energy savings through adoption of bipedalism, particularly if a large proportion of time was spent moving on the ground (Foley & Elton 1998). Foley (1992) calculated that at the same body mass a bipedal hominin would have been able to travel up to 11 km for the same level of energy expenditure as a chimpanzee would use over a 4-km distance. At a larger body size, bipedal hominins were likely to have been more energy efficient than chimpanzees, to the extent that a 53-kg hominin would have been able to travel 14 km, while a 57-kg hominin would have been able to travel 13 km. This would have allowed a greater foraging area. Similarly, using data on the energetics of modern human locomotion, Leonard & Robertson (1995) calculate that the energy savings for females would have been considerably greater than that for males, an important conclusion in relation to the high-energy demand of gestation and lactation (see below).

These estimates assume that bipedalism in hominins was as efficient as that in modern humans. However, it has generally been assumed that the relatively long legs in *Homo ergaster* gave it an advantage over the shorter-legged australopithecines and paranthropines (e.g., Jungers 1982, 1991; McHenry 1991; Webb 1996). Kramer (1999) and Kramer & Eck (2000) convincingly demonstrates that although long legs allow an individual to take fewer steps to cover a given distance and thereby reduce energy, long legs also are heavier and require more energy to move. The mass-specific mechanical power (W kg^{-1}) required to move australopithecine lower limbs (specifically AL 288-1, *Australopithecus afarensis*) is considerably less than in modern humans, whereas the cost of transport ($\text{J kg}^{-1} \text{ m}^{-1}$) is virtually identical (Kramer 1999). The main disadvantage of australopithecine short legs would be a reduced walking speed, and on this basis Kramer & Eck (2000) calculate that the daily range of AL 288-1 would have been between 20%–40% smaller than for a modern human.

The advantage of bipedalism appears to be energy savings at walking speeds, whereas the advantage of relatively long *Homo* legs would have been the potential for a significantly increased daily range. Put simply, *Homo* could have moved faster at an energetically advantageous walking speed than would have been possible for the australopithecines. The cost of locomotion, however, is still proportional to

body mass and distance covered. This brings up the issue of the daily energy expenditure (DEE) of the hominins.

DAILY ENERGY EXPENDITURE (DEE)

In spite of the fact that bipedalism is more efficient than primate quadrupedalism, Leonard & Robertson (1997) have established that human hunter-gatherers have substantially higher daily energy requirements than would be expected for a primate of our body mass. Their analysis is based on time-budget data from the literature, and DEE was computed by summing the caloric needs for maintenance (i.e., sleeping) and daily activities. Data for nonhuman primates were converted to caloric costs using the energetic models derived from Coelho (Coelho 1974, Coelho et al. 1979) and those for humans (!Kung and Ache) using models from the World Health Organization (FAO/WHO/UNU 1985). Their analysis results in a positive relationship between DEE and body mass ($DEE = 86.0 W^{0.793}$, where W = body mass in kilograms), although the relationship is isometric when humans are excluded from the analysis (Key & Ross 1999, Aiello & Key 2002). Based on the inferred body mass of *Homo ergaster*, Leonard & Robertson suggest that its DEE would be between 40% and 85% greater than that of the australopithecines (see also Table 1). The higher percentage increase (80%–85%) is based on the assumption that *Homo ergaster* had human-like and not chimpanzee-like ranging behavior.

Leonard & Robertson (1997) also demonstrate that relative energy expenditure and day ranges are positively correlated with diet quality across primates, including humans. The relationship between diet quality and increased energy levels is also consistent with the observation that primates with higher diet quality have higher levels of social activity (Milton 1999).

SPECULATIONS ON THE RELATIONSHIP BETWEEN ENERGETICS AND THE EVOLUTION OF HUMAN SOCIAL ORGANIZATION

A further effect of the increased size of *Homo ergaster* mothers and hence offspring would have been the greater energy requirements during gestation and lactation. Gestation increases DEE by 20%–30% in mammals (Gittleman & Thompson 1988) and lactation by at least 37%–39% in primates (Ofstedal 1984, Aiello & Key 2002). Aiello & Key (2002) demonstrate that the DEE for a lactating *Homo ergaster* female is about 45% higher than for a lactating australopithecine or paranthropine and almost 100% higher than for a nonlactating and nongestating smaller-bodied hominin (Table 1). They argue that the resulting high per offspring energy costs could have been considerably reduced by decreasing the interbirth interval, with the additional benefit of increasing the number of offspring per mother. A faster

reproductive schedule reduces the most expensive part of reproduction, lactation, although the benefit would be countered by a smaller increase in the energy required to support dependent offspring. Interbirth intervals have been estimated at around 4 years in gorillas, 5.5 years in wild chimpanzees, and 8 years in orangutans (Galdikas & Wood 1990), considerably longer than in most contemporary hunter-gatherer societies (Sear et al. 2000, Aiello & Key 2002).

Even taking into account this improved efficiency of reproduction in *Homo*, Aiello & Key (2002) argue that the increased requirements could only have been attained through a radical shift in foraging strategy involving the dietary changes highlighted earlier in this paper including increased exploitation of both animal products and underground storage organs (O'Connell et al. 1999, Wrangham et al. 1999).

An important aspect of this is that the energetic costs of feeding dependent offspring need not be met only by the mother. Hawkes and colleagues (1997a,b; 1998) have proposed the grandmother hypothesis, whereby postmenopausal women contribute to the parenting of their daughter's offspring. An increased level of paternal care, possibly mediated by changes in the stability of the parental pair bond, represents another potential source of energy for parental investment (Key 1998, 1999; Key & Aiello 1999, 2000; Kaplan et al. 2000). A recent analysis of data from the Gambia provided support for the grandmother hypothesis, showing that maternal grandmothers had a significant effect on offspring height (Sear et al. 2000). In contrast, the effect of paternal grandfathers and male kin on child height was negligible. An alternative and simpler hypothesis is that the cost of supporting offspring is reduced when there are several dependent offspring simultaneously (Peccei 2001), although the principal energetic costs of growth and maintenance are predicted to be minimally affected by such a strategy (Aiello & Key 2002).

SUMMARY

In summary, the emergence of *Homo* is characterized by three changes in maintenance energy requirements: (a) an absolute increase, due to greater body size; (b) a shift in the relative requirements of different organs, with increased energy diverted to brain metabolism at the expense of gut tissue, possibly mediated by changes in the proportion of weight comprised of fat; and (c) a slower rate of childhood growth, offset by higher growth costs during infancy and adolescence when faster growth rates are more viable. These direct changes then impose significant knock-on costs, including increased costs of reproduction, and also must be viewed in the context of the inferred changes in foraging strategy for *Homo ergaster*, which would have involved larger daily ranges and correspondingly elevated locomotor costs. Collectively, these increased costs are predicted to have been met by adaptations in energy stores, reproductive schedule, social interaction, changes in body form and leg length, and in foraging strategies that were modified by some form of economic division of labor. Of particular interest, given the contemporary increase

in obesity, is the increased tendency to store fat as a buffer between high energy turnover and variable food supply.

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