

Energetic Models of Human Nutritional Evolution

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Over the past decade, biological anthropologists have increasingly begun to rely on energetic models for understanding patterns and trends in hominin evolution (e.g., Leonard and Robertson, 1994, 1997a; Aiello and Wheeler, 1995; Leonard, 2002). The study of energetics is important to evolutionary research for several reasons. First, food energy represents a critical interface between organisms and their environment. The search for food energy, its consumption, and ultimately its allocation for biological processes are all critical aspects of an organism's ecology (McNab, 2002). In addition, the energy dynamic between organisms and their environments—energy expenditure in relation to energy consumed—has important adaptive consequences for both survival and reproduction. Energy thus provides a useful currency for measuring fitness. Indeed, the two components of Darwinian fitness—survival and reproduction—are reflected in the way that total energy budgets for animals are typically divided (see fig. 18.1). “Maintenance” energy expenditure represents the costs of keeping an animal alive on a day-to-day basis. This includes resting (or basal) energy expenditure and energy expenditure associated with normal daily activities of work, play, and recreation. “Productive” energy costs, on the other hand, are those associated with growth from infancy into adulthood and the production of offspring for the next generation. For mammals like ourselves, productive energy costs include the increased energy costs of a mother during pregnancy and lactation.

Clearly, the type of environment that an organism lives in will strongly shape the relative allocation of energy to these different components. However, from an evolutionary perspective, the goal for all organisms is the same: to allocate sufficient energy to “production” to ensure their genes are passed on to future generations. Consequently, by looking at the ways that animals go about acquiring and then allo-

Components of Energy Expenditure

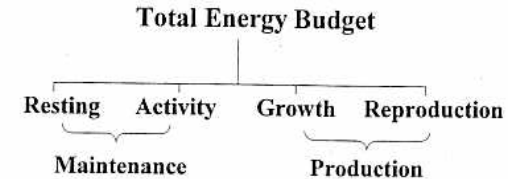


Figure 18.1 Components of an animal's total energy budget. Maintenance energy costs are those associated with keeping the animal alive on a daily basis. Productive energy costs are those required for growth and reproduction.

cating food energy, we can better understand how natural selection produces important patterns of evolutionary change. This approach is particularly useful in studying human evolution because it appears that key transitions in our evolutionary past likely had important implications for energy allocation. In this chapter, we examine the use of energetic models to help understand two of these “turning points” in human evolution: (1) the evolution of bipedal (upright) movement and (2) the rapid evolution of brain size with the emergence of the genus *Homo*.

Energetics and Bipedality

The Known

The potential energetic benefits of hominin bipedal locomotion have been long debated among biological anthropologists and other evolutionary biologists (Taylor and Rowntree, 1973; Rodman and McHenry, 1980; Steudel, 1994, 1996; Leonard and Robertson, 1995, 1997b, 2001; Steudel-Numbers, 2001). To address whether bipedality was a more “economical” form of movement, scholars have examined the energy costs of human locomotion relative to those of other mammalian species. Locomotor energy costs are measured using standard methods of indirect calorimetry in which respiratory gases (oxygen and carbon dioxide) and ventilation (breathing) rates are measured while the subject is moving at a known speed (see McLean and Tobin, 1987; McArdle et al., 2001). Energy costs of human movement have been well studied in the fields of nutrition and exercise science (e.g., Consolazio, Johnson, and Pecora, 1963; Margaria et al., 1963; Morgan and Craib, 1992), whereas those of other animal species have been examined by comparative and evolutionary physiologists (e.g., Taylor, Schmidt-Nielsen, and Raab, 1970; Taylor, Heglund, and Maloiy, 1982; Tucker, 1970).

Both within and between species, the strongest predictors of locomotor energy costs are body weight (mass) and speed. For most species, weight-specific energy costs increase as a simple linear function of speed (Taylor, Heglund, and Maloiy, 1982). However, for humans, this linear relationship is evident only at running

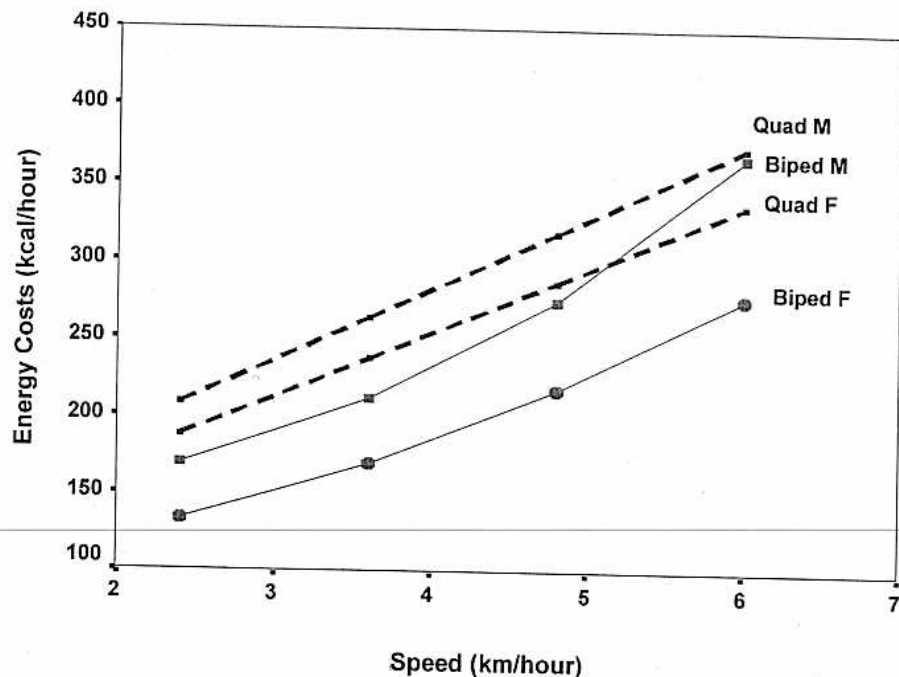


Figure 18.2 Energy costs (kcal/hour) of bipedal versus generalized quadrupedal locomotion for males and females moving at speeds between 2.4 and 6.0 km/hour. Values are average costs for females of 60 kg and males of 70 kg. For both males and females, bipedal energy costs are less than quadrupedal costs over the entire range of speeds. Modified from Leonard and Robertson (1997b).

speeds (of about 6 to 8 km/hour or more); at walking speeds, the relationship is curvilinear (Margaria et al., 1963; Menier and Pugh, 1968). Comparative analyses indicate that at walking speeds (between 2.4 and 6.0 km/hour), humans expend significantly less energy than most quadrupeds (Rodman and McHenry, 1980; Leonard and Robertson, 1995, 1997b). At running speeds, however, bipedality is less economical, as humans expend significantly more energy than quadrupeds (Taylor, Heglund, and Maloiy, 1982).

The relative economy of human bipedal walking is evident in figure 18.2, which shows the energy costs of locomotion (in kcal/hour) for adult men and women compared with those of typical (average) mammalian quadrupeds of the same weight over a range of typical walking speeds. Note that the human energy costs are lower than those of the typical quadrupeds over all these speeds, with the relative energy savings of walking bipedally being greatest at slower rates. Over the entire range of walking speeds, human males expend 13% less energy than their quadrupedal counterparts, whereas human females expend 25% less (Leonard and Robertson, 1997b).

In contrast to humans, the available data on modern apes indicates that they have relatively high energy costs for locomotion. Taylor and Rowntree (1973) and Taylor, Heglund, and Maloiy (1982) found that chimpanzees expend 35% to 40% more

energy for quadrupedal locomotion than an "average" mammalian quadruped of the same size. The differences in relative energy costs of movement for humans and apes appear to reflect differences in the environment in which they evolved and adapted. The great apes evolved and continue to exist in forested environments. Conversely, much of early hominin evolution involved living in more open mixed woodland and grassland environments (Reed, 1997). As a consequence, hominin forms living in more open environments would have moved over much greater areas in pursuit of food, whereas apes typically do not have to move over large distances during a course of the day.

These differences in typical movement patterns between humans and apes are evident when we compare the day ranges of modern apes to those of human hunter-gatherers. Modern apes move only about 1.8 km/day, whereas human foragers move an average of 13.1 km/day (Leonard and Robertson, 1997b). Differences in day range have important implications for the total energy costs of locomotion. Because apes move only short distances each day, the potential energetic differences between moving "efficiently" or "inefficiently" are very small. However, for animals that must move over longer distances, moving more efficiently has the potential to save substantial energy from maintenance.

This point is evident in table 18.1, which shows the results of a model estimating the energy costs of moving bipedally and quadrupedally for an animal the size of an early australopithecine (*Australopithecus afarensis*) with day ranges of 2.0, 5.0, and 13.0 km/day. With movement over larger day ranges, the net energetic benefit of moving bipedally increases from 20–25 kcal/day up to 120–150 kcal/day. For the smaller day ranges, the energetic savings accounts for about 1% to 3% of estimated resting metabolic rate (RMR, kcal/day); however, for day ranges similar to those of modern human foragers, the savings is 12% to 16% of RMR, a substantial portion of the daily energy budget. Thus, for movement over larger areas, the greater economy of bipedal movement offers the potential for substantial reductions in maintenance energy demands, allowing for the energy savings to be allocated to reproduction. Selection for energetically efficient locomotion is therefore likely to be more intense

Table 18.1 Estimated Weight, Resting Metabolic Rate, and Energy Costs of Bipedal and Quadrupedal Movement for *Australopithecus afarensis* Moving Over Day Ranges of 2, 5, and 13 Kilometers

Sex	Weight (kg)	RMR (kcal/day)	Range (km)	Energy Costs of Movement			RMR (%)
				Biped (kcal)	Quad. (kcal)	Difference (kcal)	
Male	45	1,216	2	86	109	23	1.8
Female	29	874	2	59	81	22	2.4
Male	45	1,216	5	216	272	56	4.6
Female	29	874	5	148	201	53	6.1
Male	45	1,216	13	565	712	147	12.1
Female	29	874	13	389	528	139	15.9

Sources: Body weight estimates are from McHenry and Coffing (2000); RMR and energy costs for bipedal movement estimated from FAO/WHO/UNU (1985); quadrupedal energy costs are estimated from Taylor et al. (1982).

among animals that must move over larger areas because they have the most to gain by being more efficient.

The Unknown

What remains unclear about the energetics of human bipedal locomotion is whether our earliest hominin ancestors had a sufficiently humanlike gait to reap the full benefits of this locomotor strategy. This uncertainty is reflected in the ongoing debate over the effectiveness of early australopithecine bipedality. Lovejoy (1988, 2005) and Latimer and Lovejoy (1989, 1990a, 1990b), for example, have argued that the skeletal anatomy of Lucy and other members of *A. afarensis* is consistent with a fully functional biped that was committed to terrestrial movement. In contrast, Stern and Susman (1983); Susman, Stern, and Junger (1984); and Jungers (1982, 1988) have argued that *A. afarensis* remained partially arboreal and did not walk as effectively as modern humans. Steudel (1994, 1996) has further suggested that the ape-like body proportions of the earliest australopithecines (i.e., long arms and short legs) likely would have reduced their locomotor efficiency relative to modern human bipedality. Stuedel-Numbers and Tilkens (2004) have shown that among humans, relatively longer legs are associated with greater locomotor economy.

Recent paleoenvironmental analyses have also suggested that the first hominins may have emerged in environments that were more heavily forested than previously thought (Woldegabriel et al., 1994; Potts, 1998). This raises the question about how widely our earliest hominin ancestors moved. If day ranges for the earliest australopithecines were similar to those of modern chimpanzees, then the initial benefits of upright movement would have been more modest. If true, this would suggest that the full energetic benefits of human bipedal locomotion were not gained during a limited period of time but were accrued over a larger span of evolutionary time. The archaeological evidence suggests that with the drying of the African landscape between 4 and 1.5 million years ago, hominins were moving over larger areas and adapting to more open grassland environments (Reed, 1997; Potts, 1998). It is over this time that we also see the evolution of humanlike body size and proportions that become fully realized with the advent of *Homo erectus* at 1.8 million years ago (McHenry and Coffing, 2000).

Further understanding of the energetics of hominin locomotion will also depend on the collection of more data from living apes and other large-bodied primates. The available information on locomotor energetics in modern apes is limited to data collected on two small chimpanzees by Taylor and Rowntree (1973). Additional information on a broader sample of apes is necessary to better understand how variation in body size, proportions, and movement patterns may shape differences in energy demands.

Energetics and Hominin Brain Evolution

The Known

Energetic models have also provided important insights into hominin brain evolution. What is remarkable about the large human brain is its high metabolic cost. The

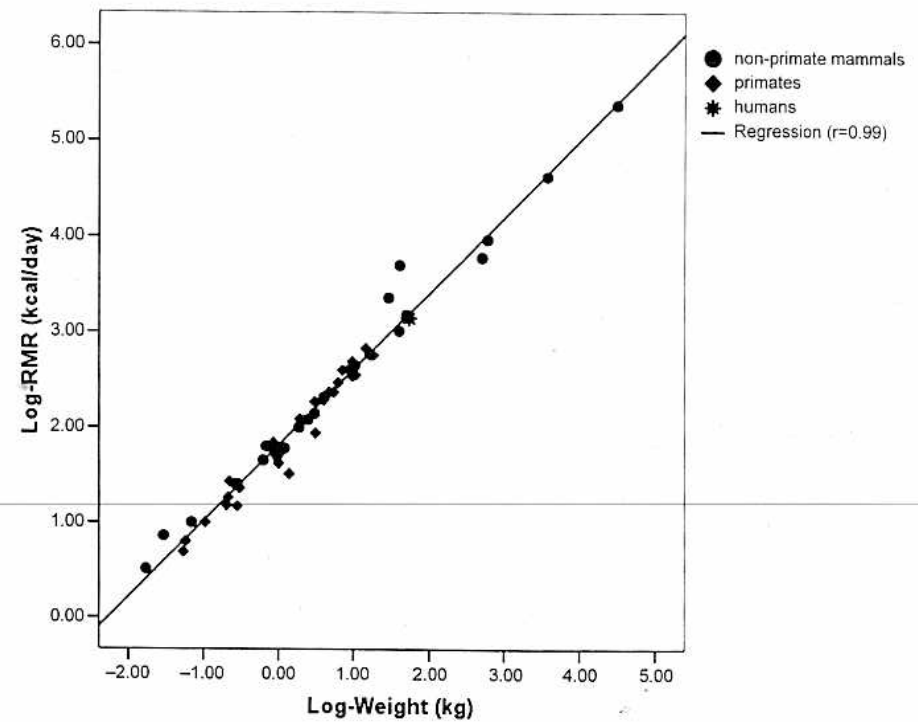


Figure 18.3 Log-log plot of resting metabolic rate (RMR; kcal/day) versus body weight (kg) for fifty-two mammalian species (twenty-one nonprimate mammals, thirty primates, and humans). Humans conform to the general mammalian scaling relationship, as described by Kleiber (1961). Data are from Leonard et al. (2003) and Snodgrass et al. (1999).

energy requirements of brain tissue are about 29 kcal/100grams/day, roughly sixteen times that of skeletal muscle tissue (Kety, 1957; Holliday, 1986). This means that for a 70-kg adult human (with a brain weight of about 1,400 grams), approximately 400 kcal per day are allocated to brain metabolism. Although humans have much larger brains than most other mammals, the total energy demands for our body—our resting energy requirements—are no greater than those of a comparably sized mammal (Kleiber, 1961; Leonard and Robertson, 1992). This point is evident in figure 18.3, which shows the relationship between RMR (kcal/day) and body weight (kg) in nonprimate mammals, primates, and humans. Humans conform to the general mammalian scaling relationship between RMR and body weight (the “Kleiber relationship”), and as a consequence, we allocate a much larger share of our daily energy budget for brain metabolism. In humans, brain metabolism accounts for 20% to 25% of RMR, as compared to 8% to 10% in other primate species, and 3% to 5% in nonprimate mammals (Leonard and Robertson, 1994).

Key aspects of human nutritional biology appear to be associated with the high-energy demands of our large brains. In particular, humans consume diets that are more energy and nutrient dense than other primates of similar size. Recent analyses

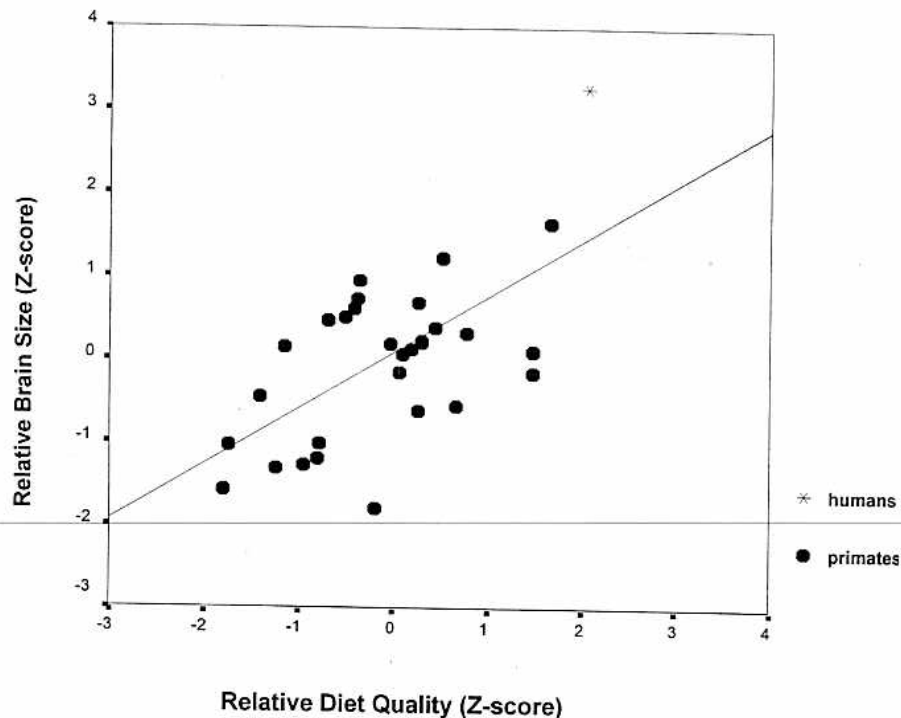


Figure 18.4 Plot of relative brain size versus relative diet quality for thirty-one primate species (including humans). Primates with higher quality diets for their size have relatively larger brain size ($r = 0.63$; $P < 0.001$). Humans represent the positive extremes for both measures, having relatively large brains and a substantially higher quality diet than expected for their size. Adapted from Leonard et al. (2003).

by Cordain et al. (2000) have shown that modern human foraging populations typically derive 45% to 65% of their dietary energy intake from animal foods. In contrast, modern great apes obtain much of their diet from low-quality plant foods. Gorillas derive more than 80% of their diet from fibrous foods such as leaves and bark (Richard, 1985). Even among chimpanzees, the most predatory of the great apes, only about 5% of their calories are derived from animal foods, including insects (Teleki, 1981; Stanford, 1996). Meat and other animal foods are much more dense in calories and nutrients than most of the plant foods typically eaten by large-bodied primates. This higher-quality diet means that humans need to eat less volume of food to get the energy and nutrients we require.

Comparative analyses support the link between brain size and dietary quality. Figure 18.4 shows relative brain size versus dietary quality (an index based on the relative proportions of leaves, fruit, and animal foods in the diet) for 31 different primate species (from Leonard et al., 2003). There is a significant positive relationship ($r = 0.63$; $P < 0.001$) between the amount of energy allocated to the brain and

the caloric and nutrient density of the diet. Across all primates, bigger brains require better-quality diets, and humans are the extreme example of this, having the largest relative brain size and the highest-quality diet. This relationship implies that the evolution of larger hominin brains would have necessitated the adoption of a sufficiently high-quality diet to support the elevated energy demands.

The morphology of the human gut also appears to reflect our high-quality diet. Most large-bodied primates have expanded large intestines (colons), an adaptation to fibrous, low-quality diets (Milton, 1987). Fermentation of plant fiber in these enlarged colons allows for extraction of additional energy in the form of volatile fatty acids (Milton and Demment, 1988; Milton, 1993). Humans, however, have relatively enlarged small intestines and a reduced colon. This morphology is more similar to a carnivore and reflects an adaptation to an easily digested, nutrient-rich diet (Sussman, 1987; Martin, 1989).

The comparative dietary and energetic data thus suggest that the dramatic expansion of brain size over the course of human evolution likely would have required the consumption of a diet that was more dense in energy and nutrients than is typically the case for most large primates. This *does not* imply that dietary change was the driving force behind major brain expansion during human evolution. Rather, the available evidence indicates that a sufficiently high-quality diet was probably a necessary condition for supporting the metabolic demands associated with evolving larger hominin brains.

Evidence from the human fossil record shows that the first major burst of evolutionary change in hominin brain size occurs about 2.0 to 1.7 million years ago, associated with the emergence and evolution of early members of the genus *Homo*. Data on evolutionary changes in hominin brain size (cm^3), estimated body weight (kg), and posterior tooth area (mm^2) are presented in table 18.2. The australopithecines showed only modest brain size evolution from about 430 to 530 cm^3 over more than 2 million years (from about 4 to 1.5 million years ago). However, with the evolution

Table 18.2 Geological Ages, Brain Size, Estimated Male and Female Body Weights, and Postcanine Tooth Surface Areas for Selected Hominin Species

Species	Geological Age (Mya)	Brain Size (cm^3)	Body Weight		Postcanine Tooth Surface Area (mm^2)
			Male (kg)	Female (kg)	
<i>Australopithecus afarensis</i>	3.9–3.0	438	45	29	460
<i>A. africanus</i>	3.0–2.4	452	41	30	516
<i>A. boisei</i>	2.3–1.4	521	49	34	756
<i>A. robustus</i>	1.9–1.4	530	40	32	588
<i>Homo habilis (sensu strictu)</i>	1.9–1.6	612	37	32	478
<i>H. erectus (early)</i>	1.8–1.5	863	66	54	377
<i>H. erectus (late)</i>	0.5–0.3	980	60	55	390
<i>H. sapiens</i>	0.4–0.0	1,350	58	49	334

Sources: All data from McHenry and Coffing (2000), except for *Homo erectus*. Early *H. erectus* brain size is the average of African specimens as presented in McHenry (1994a), Indonesian specimens from Antón and Swisher (2001) and Georgian specimens from Gabunia et al. (2000, 2001). Data for late *H. erectus* are from McHenry (1994a).

of the genus *Homo* there is rapid change, with brain sizes of over 600 cm³ in *Homo habilis* (at 1.9–1.6 Mya) and 800–900 cm³ in early members of *H. erectus* (at 1.8–1.5 Mya). Although the relative brain size of *H. erectus* is smaller than the average for modern humans, it is outside of the range seen among other living primate species (Leonard and Robertson, 1994).

Additionally, changes in the skeletal and dental anatomy of *H. erectus* relative to the australopithecines indicate that these forms were consuming different foods. As shown in table 18.2, with the evolution of the australopithecines the surface area of the postcanine teeth increased dramatically from 460 mm² in *A. afarensis* to 756 mm² in *Australopithecus boisei*. However, with the emergence of early *Homo* at approximately 2 million years ago, we find rapid reductions in the size of the posterior teeth. Postcanine tooth surface area is 478 in *H. habilis* and 377 mm² in early *H. erectus*. *H. erectus* also shows substantial reductions in craniofacial and mandibular robusticity relative to the australopithecines (Wolpoff, 1999). Yet, despite having smaller teeth and jaws, *H. erectus* was a much bigger animal than the australopithecines, being humanlike in its stature, body mass, and body proportions (McHenry, 1992, 1994b; Ruff and Walker, 1993; Ruff, Trinkaus, and Holliday, 1997; McHenry and Coffing, 2000). Together these features indicate that early *H. erectus* was consuming a richer, more calorically dense diet with less low-quality fibrous plant material.

The Unknown

The comparative evidence clearly indicates that humans allocate more energy to brain metabolism than other primate species. Moreover, it appears that a higher-quality, more nutritionally dense diet is critical for “fueling” our large brains. However, a number of issues remain unresolved with regard to our understanding of the energetics of hominin brain evolution. Two of the most important unresolved issues are (1) how energy metabolism was altered during the course of human evolution to support the costs of larger brain size and (2) what kinds of dietary/nutritional changes likely occurred to promote the initial increases in brain size that we find with the evolution of early *Homo*.

Analyses of human and primate body composition have suggested possible answers to the first question. Aiello (1997) and Aiello and Wheeler (1995) have argued that the increased energy demands of the human brain were accommodated by the reduction in size of the gastrointestinal tract. Since the intestines are similar to the brain in having very high energy demands (so-called expensive tissues), the reduction in size of the large intestines of humans, relative to other primates, is thought to provide the necessary energy savings required to support elevated brain metabolism. Aiello and Wheeler (1995) have shown that among a sample of eighteen primate species (including humans), increased brain size was associated with reduced gut size. However, recent analyses by Snodgrass, Leonard, and Roberson (1999) have failed to demonstrate significant differences in gastrointestinal size between primates and non-primate mammals that are predicted from the “expensive tissue hypothesis.”

Leonard and colleagues (2003) and Kuzawa (1998) have suggested that differences in muscle and fat mass between humans and other primates may also account

Table 18.3 Body Weight, Brain Weight, Percent Body Fat, Resting Metabolic Rate, and Percent of RMR Allocated to Brain Metabolism for Humans from Birth to Adulthood

Age	Body Weight (kg)	Brain Weight (g)	Body Fat (%)	RMR (kcal/day)	BrMet (%)
Newborn	3.5	475	16	161	87
3 months	5.5	650	22	300	64
18 months	11.0	1,045	25	590	53
5 years	19.0	1,235	15	830	44
10 years	31.0	1,350	15	1,160	34
Adult male	70.0	1,400	11	1,800	23
Adult female	50.0	1,360	20	1,480	27

Sources: All data are from Holliday (1986), except for percent body fat data for children 18 months and younger, which are from Dewey et al. (1993).

for variation in the budgeting of metabolic energy. Relative to other primates and other mammals, humans have lower levels of muscle mass and higher levels of body fatness (Leonard et al., 2003). The relatively high levels of body fatness (adiposity) in humans have two important metabolic implications for brain metabolism. First, because fat has lower-energy requirements than muscle tissue, replacing muscle mass with fat mass results in energy “savings” that can be allocated to the brain. Additionally, fat provides a ready source of stored energy that can be drawn on during periods of limited food availability. Consequently, the higher levels of body fat in humans may also help to support larger brain size by providing stored energy to buffer against environmental fluctuations in nutritional resources.

The importance of body fat is particularly notable in human infants, which have both high brain-to-body weight ratios and high levels of body fatness. Table 18.3 shows age-related changes in body weight (kg), brain weight (g), fatness, RMR (kcal/day), and percent of RMR allocated to the brain for humans from birth to adulthood. We see that in infants, brain metabolism accounts for upward of 60% of RMR. Human infants are also considerably fatter than those of other mammalian species (Kuzawa, 1998). Body fatness in human infants is about 15% to 16% at birth and continues to increase to 25%–26% during the first 12 to 18 months of postnatal growth. Fatness then declines to about 15% by early childhood (Dewey et al., 1993). Thus, during early human growth and development, it appears that body fatness is highest during the periods of the greatest metabolic demand of the brain.

It is likely that fundamental changes in body composition (i.e., the relative sizes of different organ systems) during the course of hominin evolution allowed for the expansion of brain size without substantial increases in the total energy demands for the body. At present, we do not know which alterations were the most critical for accommodating brain expansion. Variation in body composition both within and between primates species is still not well understood. Among humans, our knowledge of variation in body composition is based largely on data from populations of industrialized world. Consequently, more and better data on interspecific and ontogenetic variation in primate and human body composition are necessary to further resolve these issues. In addition, new imaging techniques such as positron emission tomography

(PET scans) offer the potential to directly explore variation in organ-specific blood flow and energy demands in humans and other primates.

An additional unanswered question is what types of dietary changes allowed for the evolution of brain size in early *Homo*. The skeletal evidence (larger body size, reduced postcanine tooth size, and reduced craniofacial robusticity) indicates that these hominins were eating foods that were more nutritionally dense and required less chewing than those consumed by the australopithecines. The most widely held view is that the diet of early *Homo* included more animal foods. The environment at the Plio-Pleistocene boundary (2.0–1.8 Mya) was continuing to become drier, creating more arid grasslands (Vrba, 1995; Reed, 1997; Owen-Smith, 1999). These changes in the African landscape made animal foods more abundant and thus, an increasingly attractive food resource (Behrensmeyer et al., 1997). Greater relative abundance of animal resources would have offered an opportunity for hominins with sufficient capability to exploit those resources. The archaeological record provides evidence that this occurred with *H. erectus* the development of the first rudimentary hunting and gathering economy in which game animals became a significant part of the diet and resources were shared within foraging groups (Potts, 1988; Harris and Capaldo, 1993; Roche et al., 1999). These changes in diet and foraging behavior would not have turned our hominin ancestors into carnivores; however, the addition of even modest amounts of meat to the diet combined with the sharing of resources that is typical of hunter-gatherer groups would have significantly increased the quality and stability of hominin diets.

Greater consumption of animal foods also may have promoted brain evolution in early *Homo* by providing higher amounts of two polyunsaturated fatty acids that are critically important to brain growth, docosahexaenoic acid (DHA) and arachidonic acid (AA); Crawford et al., 1999; Cordain et al., 2001). The composition of all mammalian brain tissue is similar with respect to these two fatty acids (Crawford et al., 1999). Consequently, higher levels of encephalization are associated with greater requirements of DHA and AA. Because mammals also appear to have limited capacity to synthesize these fatty acids from dietary precursors, it has been suggested that dietary sources of DHA and AA may have been limiting nutrients that constrained the evolution of larger brain size in many mammalian lineages (Crawford, 1992; Crawford et al., 1999).

Cordain and colleagues (2001) have shown that wild-plant foods available on the African savanna (e.g., tubers, nuts) contain, at most, only trace amounts of AA and DHA, whereas muscle tissue and organ meat of wild African ruminants provide moderate to high levels of these key fatty acids. Brain tissue is a rich source of both AA and DHA, whereas liver and muscle tissues are good sources of AA and moderate sources of DHA. Other good sources of AA and DHA are freshwater fish and shellfish (Broadhurst, Cunnane, and Crawford, 1998; Crawford et al., 1999; Cordain et al., 2001); however, there is little archaeological evidence for the systematic use of aquatic resources until later in human evolution (Klein, 1999).

Wrangham and colleagues (1999) and Wrangham and Conklin-Brittain (2003) have suggested an alternative strategy for increasing diet quality in early *Homo*—cooking. They note that cooking not only makes plant foods softer, it also increases the energy content of those foods, particularly starchy tubers such as potatoes and manioc. In their raw form, the starch in tubers is not absorbed in the small intestine

and is passed through the body (Tagliabue et al., 1995; Englyst and Englyst, 2005). However, when heated, the starch granules swell and are disrupted from the cell walls. This process, known as gelatinization, makes the starch much more accessible to breakdown by digestive enzymes (García-Alonso and Goñi, 2000). Thus, cooking increases the nutritional quality of tubers by making more of the carbohydrate energy available for biological processes.

Although cooking is clearly an important innovation that would have improved diet quality, there is considerable debate about when hominins began to use fire systematically for cooking (Pennisi, 1999). At present, there is limited evidence for early (>1.5 million years ago) controlled use of fire by hominins (Brain and Sillen, 1988; Bellomo, 1994). The more widely held view is that the use of fire and cooking did not occur until later in human evolution, at 200,000–250,000 years ago (Straus, 1989; Weiner et al., 1998).

In addition, Cordain and colleagues (2001) have noted that even after being cooked, wild tubers still have lower-energy content than most animal foods and lack both DHA and AA. Consequently, there remain major questions about whether cooking was an important force for promoting rapid brain evolution with the emergence of early *Homo*.

The Unknowable

Biological anthropologists have long relied on the study of anatomical and morphological variation in modern species to provide a comparative context for understanding patterns and trends in the human fossil record. The more recent development of energetic models employs a similar approach in drawing on the study of physiological variation in contemporary species to shed light on ecological and behavioral trends in our hominin ancestors. By exploring the ecological correlates of variation in energy metabolism among living primates and other mammals, we are able to gain insights into the nutritional and metabolic implications of important changes in brain size, body size, and locomotor strategies during the course of human evolution. Because variation in energy allocation has direct adaptive consequences, energy represents a particularly useful currency for studying human evolutionary processes.

Nonetheless, in developing and applying energetic models, we must recognize the limits in what these models can tell us. Although we can create a model that will estimate the locomotor energy costs for a 29 kg australopithecine, we will never know how many calories “Lucy” or her contemporaries spent to move around or how far they moved on a typical day. Likewise, while we can estimate the increased energy costs associated with the larger brain and body sizes of *H. erectus* relative to the australopithecines, we will never know with accuracy how much energy our hominin ancestors were consuming or where those calories were derived from.

Critics of energetic modeling have noted the potential for “false quantification” and for drawing inferences with inappropriate levels of precision (e.g., Smith, 1996). However, this critique largely misinterprets the principal objectives of energetic models and ecological models in general. The goal of these approaches is not to quantify precisely some energetic or physiological parameter (e.g., calories

consumed or expended) but rather to use the information on ecological variation in extant species to explore the energetic consequences of key changes in hominin evolution (e.g., changes in body size, proportions, day ranges, diet). For example, rather than measuring how many calories Lucy spent on a foraging trip, we seek to explore how changes in body size, foraging range, and locomotor efficiency may interact to produce meaningful variation in daily energy demands.

Obviously, the predictions of any model are only as good as the data and assumptions that go into that model. The fossil and archaeological records have limitations that will continue to constrain our insights. However, there are many insights still to be gained by more broadly studying the ecological correlates of nutritional and metabolic variation in modern humans, primates, and other mammals. A richer understanding of these patterns of modern physiological variation will provide us with a stronger and more rigorous framework for interpreting the fossil record and refining our understanding of the evolution of our species and its distinctive nutritional needs.

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