• 1 •

What Did Humans Evolve to Eat?

Metabolic Implications of Major Trends in Hominid Evolution

W. R. Leonard, M. L. Robertson, and J. J. Snodgrass

Introduction

Over the last twenty years, the evolution of human nutritional requirements has received ever-greater attention among both anthropologists and nutritional scientists (Crawford 1992; Eaton and Konner 1985; Garn and Leonard 1989; Leonard and Robertson 1992, 1994; Aiello and Wheeler 1995; Cordain et al. 2005; Ungar 2007). Research in nutritional anthropology has demonstrated that many of the key features that distinguish humans from other primates have important implications for our distinctive nutritional needs (Leonard 2002; Leonard and Robertson 1997b; Aiello and Wheeler 1995). In addition, our colleagues in the nutritional sciences are coming to realize that an evolutionary perspective is useful for understanding the origins of and potential solutions to the growing problems of obesity and associated metabolic disorders (e.g., Cordain et al. 2005; Eaton 2006; O'Dea 1991).

Yet, despite this growing consensus that an evolutionary approach has an important place in the study of human nutrition, we find that many constructions of the "natural" human diet are remarkably narrow (e.g., Audette and Gilchrist. 2000; Crawford and Marsh 1995; Cunanne 2005; Eaton, Shostack, and Konner 1988). We believe that many of these "paleodiets" are based on a misreading of both human evolutionary history and comparative human biology. Humans did not evolve to subsist

on a single Paleolithic diet. To the contrary, one of the hallmarks of our evolutionary success has been our ability to find or create a meal in any environment. Compared to other primates, humans have diets of much higher quality—that is, more dense in calories and nutrients. Indeed, many of the major changes in human evolutionary history have been about increasing the quality of our diets or increasing the efficiency with which we extract energy and nutrients from our environments.

This chapter specifically considers the nutritional implications of one of the most profound transition periods in human evolution—the emergence of the first members of the genus *Homo*. This phase of human evolution—between ~2.0 and 1.5 million years ago—was associated with major changes in brain size, body size, and foraging and ranging behavior.

To establish the context for interpreting the fossil evidence, we begin by considering the energetic and nutritional correlates of variation in brain and body size among living primates. We then turn to an examination of the human fossil record to consider when and under what conditions in our evolutionary past key changes in brain size, body size, diet, and foraging behavior likely took place. Finally, we explore the implications of our distinctive metabolic requirements for understanding and confronting the nutritional problems of our modern world. We will specifically consider (1) the problem of early childhood growth stunting among populations of the developing world, and (2) the growing problem of obesity in the United States and other industrialized nations.

Comparative Nutrition and Metabolism

From a nutritional perspective, what is extraordinary about our large human brains is their high metabolic costs. Brain tissue has very high energy demands per unit weight, roughly 16 times greater than those of muscle tissue (12 kcal/kg/min versus 0.75 kcal/kg/min; Holliday 1986; Kety 1957). On average about 400 kcal/day are spent on brain metabolism by an adult human. Yet, despite the fact that humans have much larger brains per body weight than other primates or terrestrial mammals, the resting energy demands for the human body are no more than for any other mammal of the same size (Leonard and Robertson 1994).

Figure 1.1a shows the relationship between Resting Metabolic Rate (RMR; kcal/ day) and body mass in kilograms (kg) for humans and nonhuman primates, and other mammals. It is clear that humans, as well as other primate species, conform to the general mammalian scaling relationship between RMR and body weight, the "Kleiber Relationship" (Kleiber 1961). The Kleiber Relationship shows that metabolic rates in mammals of vastly different sizes increase as a function of body weight raised to the 3/4th power. Thus for a mammal of a given body mass, we can predict their resting energy needs as:
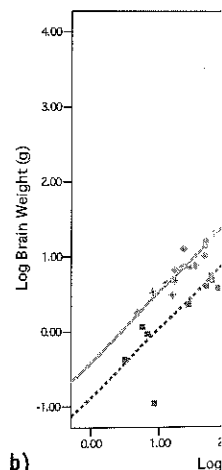
$$\text{RMR (kcal/day)} = 70(Wt^{0.75})$$

On average, adult hu dicted for other prim allocate a much larg other species.

The disproportic scaling relationship l other primate specie The solid line denote dashed line denotes point for humans is
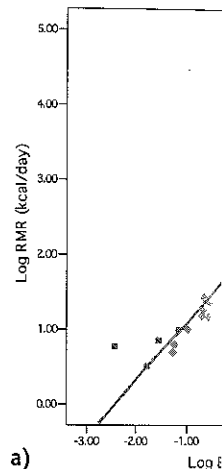
a)

b)

On average, adult humans have RMRs that fall within 3–4 percent of the value predicted for other primates and other mammals. The implication of this is that humans allocate a much larger share of our daily energy budget for brain metabolism than other species.

The disproportionately higher energy costs of our large brains are evident in the scaling relationship between brain weight (grams) and RMR for humans, thirty-five other primate species, and twenty-two nonprimate mammalian species (Fig. 1.1b). The solid line denotes the best-fit regression for nonhuman primate species, and the dashed line denotes the best-fit regression for the nonprimate mammals. The data point for humans is denoted with a star.
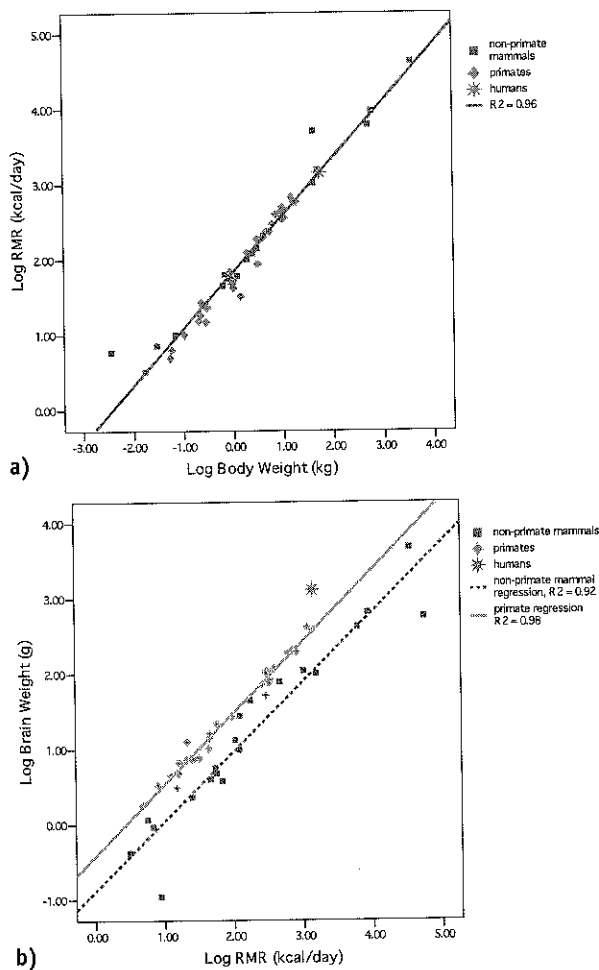

Figure 1.1. a) Log-Log plot of resting metabolic rate (RMR; kcal/day) versus body weight (kg) for 51 species of terrestrial mammals (20 non-primate mammals, 30 primates, and humans). Humans conform to the general mammalian scaling relationship, as described by Kleiber (1961); b) Log-Log plot of brain weight (BW;g) versus RMR (kcal/day) for humans, 35 other primate species, and 22 non-primate mammalian species. The primate regression line is systematically and significantly elevated above the non-primate mammal regression. For a given RMR, primates have brain sizes that are three times those of other mammals, and humans have brains that are three times those of other primates.

As a group, primates have brains that are approximately 3 times the size of other mammals (relative to body size). Human brain sizes, in turn, are some 2.5 to 3 times those of other primates (Martin 1989). In caloric terms, this means that brain metabolism accounts for ~20–25 percent of RMR in an adult human body, as compared to about 8–10 percent in other primate species, and roughly 3–5 percent for nonprimate mammals (Leonard et al. 2003).

The large allocation of our energy budget to brain metabolism raises the question of how humans are nutritionally able to accommodate the metabolic demands of our large brains. It appears that humans consume diets that are more dense in energy and nutrients than other primates of similar size.

Across all primates, diet quality is inversely related to body size. That is, small primates (e.g., the pygmy marmoset) consume diets that are rich in energy and nutrients, whereas large-bodied primates (e.g., the gorilla) consume large amounts of low-quality foods (Richard 1985). These feeding strategies are shaped by between-species variation in metabolic rates, specifically the Kleiber Relationship, mentioned previously.

Small-bodied primates have low total energy needs but very high energy demands per unit mass (i.e., kcal/kg/day). Consequently, they meet their dietary needs by consuming foods that are limited in abundance but high in quality (insects, saps, gums). Large primates have high total energy need, but low mass-specific costs. Hence they are large-volume feeders, eating foods that are widely available, but of low nutritional density (leaves, bark, and low-quality plant foods).

Humans, however, have substantially higher-quality diets than expected for a primate of our size. Figure 1.2 shows the association between dietary quality and body weight in living primates, including modern human foragers. The diet quality (DQ) index is derived from the work of Sailer et al. (1985) and reflects the relative proportions (percentage by volume) of (1) structural plant parts (*s;* e.g., leaves, stems, bark), (2) reproductive plant parts (*r;* e.g., fruits, flowers), and (3) animal foods (*a;* including invertebrates):
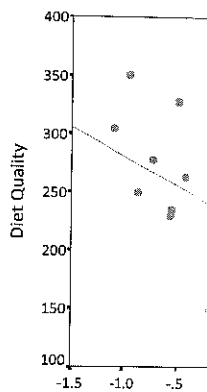
DQ index = s + 2(r) + 3.5 (a)

The index ranges from a minimum of 100 (a diet of all leaves and/or structural plant parts) to 350 (a diet of all animal material).
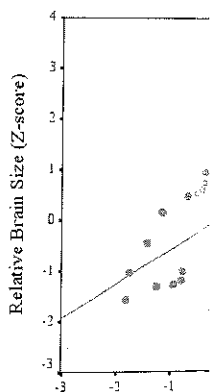
There is a strong inverse relationship between DQ and body mass across primates; however, note that the diets of modern human foragers fall substantially above the regression line in Figure 1.2a. Indeed, the staple foods for all human societies are much more nutritionally dense than those of other large-bodied primates. Although there is considerable variation in the diets of modern human foraging groups, recent studies have shown that modern human foragers typically derive over half of their dietary energy intake from animal foods (Cordain et al. 2000). In comparison, modern great apes obtain much of their diet from low-quality plant foods. Gorillas derive over 80 percent of their diet from fibrous foods such as leaves and bark (Richard

1985). Even amon
cent of their caloric
1996). This "highe
to get the energy a

The link betwe
shows relative brai
primate species for
brain size for each
the primate brain
residual from the D
ship (r = 0.63; P <
the caloric and nut
higher-quality diets
the largest relative

a) Log B

b) Relative D

...mes the size of other
...some 2.5 to 3 times
...means that brain me-
...body, as compared
...percent for nonpri-

...raises the question
...olic demands of our
...dense in energy and

...y size. That is, small
...ch in energy and nu-
...me large amounts of
...shaped by between-
...tionship, mentioned

...high energy demands
...dietary needs by con-
...(insects, saps, gums).
...fic costs. Hence they
...ut of low nutritional

...than expected for a
...dietary quality and
...gers. The diet quality
...d reflects the relative
...(s; e.g., leaves, stems,
...(3) animal foods (a;

...nd/or structural plant

...ody mass across pri-
...all substantially above
...ll human societies are
...d primates. Although
...raging groups, recent
...ive over half of their
...In comparison, mod-
...foods. Gorillas derive
...es and bark (Richard

1985). Even among common chimpanzees (*Pan troglodytes*), only about 5–10 percent of their calories are derived from vertebrate animal foods (Teleki 1981; Stanford 1996). This "higher-quality" diet means that we need to eat a lower volume of food to get the energy and nutrients we require.

The link between brain size and dietary quality is evident in Figure 1.2b, which shows relative brain size versus relative dietary quality for the thirty-three different primate species for which we have metabolic, brain size, and dietary data. Relative brain size for each species is measured as the standardized residual (z-score) from the primate brain versus body mass regression, and relative DQ is measured as the residual from the DQ versus body mass regression. There is a strong 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, larger brains require higher-quality diets. Humans fall at the positive extremes for both parameters, having the largest relative brain size and the highest quality diet.
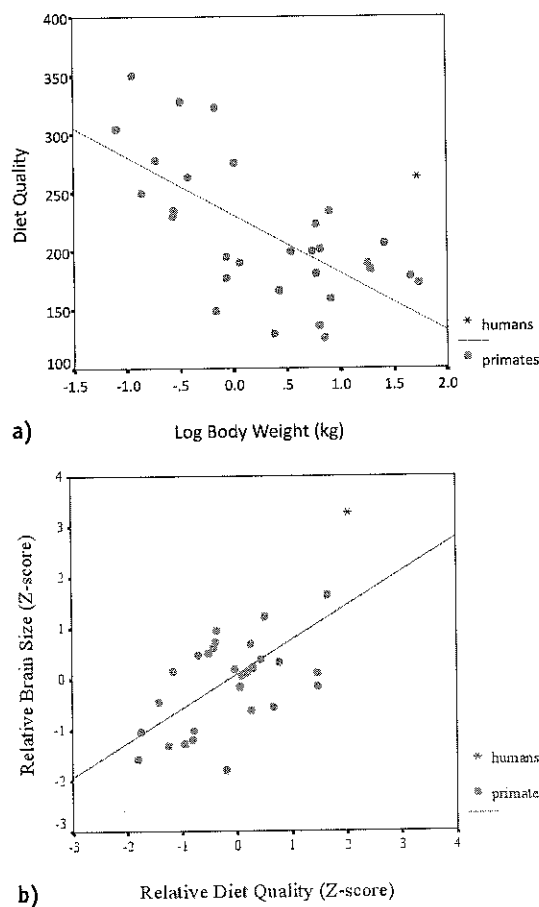

Figure 1.2. a) Plot of diet quality (DQ) versus log-body mass for 33 primate species. DQ is inversely related to body mass ($r = -0.59$ [total sample]; -0.68 [non-human primates only]; $P < 0.001$), indicating that smaller primates consume relatively higher quality diets. Humans have systematically higher quality diets than predicted for their size; b) Plot of relative brain size versus relative diet quality for 31 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 large brain:body size and a substantially higher quality diet than expected for their size.

Thus, the high cost of the large, metabolically expensive human brain is partially offset by the consumption of an energy- and nutrient-rich diet. This relationship implies that the evolution of larger hominid brains would have necessitated the adoption of a sufficiently high-quality diet (including meat and energy-rich fruits) to support the increased metabolic demands of greater encephalization.

Evolutionary Trends in Diet, Brain Size, and Body Size

When we look at the human fossil record, we find that the first major burst of evolutionary change in hominid brain size occurs at about 2.0 to 1.7 million years ago, associated with the emergence and evolution of early members of the genus *Homo* (see Table 1.1). Prior to this, our earlier hominid ancestors, the australopithecines, showed only modest brain size evolution from an average of 400 to 510 cm³ over a 2-million-year span from 4 to 2 million years ago. With the evolution of the genus *Homo* there is rapid change, with brain sizes of, on average, ~600 cm³ in *Homo habilis* (at 2.4–1.6 mya) and 800–900 cm³ in early members of *Homo erectus* (at 1.8–1.5 mya). Furthermore, while the relative brain size of *Homo erectus* did not reach the size of modern humans, it is outside of the range seen among other living primate species.

Table 1.1. Geological ages (millions of years ago), brain size (cm³), estimated male and female body weights (kg), and estimated home range sizes (hectares) for selected fossil hominid species.

Species	Geological age (mya)	Brain size (cm³)	Body Weight Male (kg)	Body Weight Female (kg)	Home Range (ha)
A. afarensis	3.9–3.0	438	45	29	40
A. africanus	3.0–2.4	452	41	30	38
A. boisei	2.3–1.4	521	49	34	47
A. robustus	1.9–1.4	530	40	32	38
Homo habilis (sensu strictu)	1.9–1.6	612	37	32	226
H. erectus (early)	1.8–1.5	863	66	54	480
H. erectus (late)	0.5–0.3	980	60	55	452
H. sapiens	0.4–0.0	1350	58	49	410

Data for brain size and body weights are from McHenry and Coffing (2000), except for *Homo erectus*. Early *H. erectus* brain size is the average of African specimens as presented in McHenry (1994b), Indonesian specimens from Antón and Swisher (2001) and Georgian specimens from Gabunia et al. (2000, 2001). Brain size and body weight data for late *H. erectus* are from McHenry (1994a). Estimates of home range size are from Antón, Leonard and Robertson (2002).

human brain is par-
h diet. This relation-
have necessitated the
energy-rich fruits) to
tion.

t major burst of evo-
.7 million years ago,
the genus *Homo* (see
lopithecines, showed
cm^3 over a 2-million-
he genus *Homo* there
no habilis (at 2.4–1.6
3–1.5 mya). Further-
h the size of modern
te species.

, estimated male and
s) for selected fossil

Weight Female (kg)	Home Range (ha)
29	40
30	38
34	47
32	38
32	226
54	480
55	452
49	410

000), except for
ens as presented in
01) and Georgian
t data for late *H.*
m Antón, Leonard

The evolution of *H. erectus* in Africa is widely viewed as a major adaptive shift in human evolution (Antón 2003; Antón, Leonard, and Robertson 2002; Wolpoff 1999). Indeed, what is remarkable about the emergence of *H. erectus* in East Africa at 1.8 million years is that we find (a) marked increases in both brain and body size, and (b) the evolution of human-like body proportions at the same time that we see (c) major reductions of posterior tooth size and craniofacial robusticity (McHenry 1992, 1994a, 1994b; McHenry and Coffing 2000; Ruff, Trinkaus, and Holliday 1997). These trends clearly suggest major energetic and dietary shifts: (a) the large body sizes necessitating greater daily energy needs; (b) bigger brains suggesting the need for a higher-quality diet; and (c) the craniofacial changes suggesting that they were consuming a different mix of foods than their australopithecine ancestors.

The ultimate driving factors responsible for the rapid evolution of brain size, body size and craniodental anatomy at this stage of human evolution appear to have been major environmental changes that promoted shifts in diet and foraging behavior. The environment in East Africa at the Plio-Pleistocene boundary (2.0–1.8 mya) was becoming much drier, resulting in declines in forested areas and an expansion of open woodlands and grasslands (Bobe and Behrensmeyer 2002; deMenocal 2004; Reed 1997; Vrba 1995; Wynn 2004). Such changes in the African landscape likely made animal foods an increasingly attractive resource for our hominid ancestors (Behrensmeyer et al. 1997; Harris and Capaldo 1993; Plummer 2004).

This can be seen by looking at the differences in ecological productivity between modern-day woodland and savanna ecosystems of the tropics. Despite the fact that tropical savanna environments produce only about half as much plant energy per year as tropical woodlands (4050 vs. 7200 kcal/m^2/year), the abundance of herbivores (secondary productivity) is almost three times greater than in the savanna (10.1 vs. 3.6 kcal/m^2/year) (Leonard and Robertson 1997a). Consequently, the expansion of the savanna in Plio-Pleistocene Africa would have limited the amount and variety of edible plant foods (to things like tubers, etc.) for hominids, but also resulted in an increase in the relative abundance of grazing mammals such as antelope and gazelle. These changes in the relative abundance of different food resources offered an opportunity for hominids with sufficient capability to exploit the animal resources. The archeological record suggests that this is what occurred with *Homo erectus*—the development of the first rudimentary hunting and gathering economy in which (1) game animals became a significant part of the diet and (2) food resources were shared within foraging groups.

The other major evolutionary event seen with early *Homo erectus*—the rapid initial spread of hominids from Africa to other parts of the Old World—appears to be linked to changes in ecology and the associated changes in brain size, body size, and foraging behavior. In living species, we know that an important correlate of dispersal distance is territorial needs—day range (the distance [km] that an animal travels on a typical day) and home range sizes (the total area [hectares] utilized by an animal population). Species with relatively larger territories for their size have greater poten-

tial for more rapid dispersion. Additionally, we know that human foragers are distinct from other primate species in having very large territorial needs for their size (Antón, Leonard, and Robertson 2002; Leonard and Robertson 1997b).

Comparative studies on territorial needs and ranging behavior have shown that strongest predictors of variation in home range (HR) size are: (a) body mass (kg), (b) diet (with carnivores having much larger HR sizes than herbivores), and (c) ecosystem structure, with species living in more-open, less-productive habitats having larger territorial needs (Harestad and Bunnell 1979). With the emergence of *H. erectus* we see changes in all three of these parameters that would have promoted increased territorial requirements.

To model how changes in body size and diet may have influenced HR sizes in our hominid ancestors, we compiled data on body size, HR area, and DQ for forty-seven nonhuman primate species and six human hunting and gathering groups (data presented in Antón, Leonard, and Robertson 2002). HR size is strongly associated with body mass; however, human foragers have substantially larger HRs than other primates of their size.

Using a multiple regression approach, we explored the joint influences of weight and DQ on variation HR size. When diet was included along with body mass in the prediction, the model explained 77 percent of the variation in HR size (see Antón, Leonard, and Robertson 2002). In light of the high predictive power of the model, it is useful for exploring changes in the evolutionary past, since the model effectively applies to both human foragers and nonhuman primates.

Using the model derived from living species, we estimated evolutionary changes in HR size among prehistoric hominid species by: (a) using mid-sex estimates of body weight derived from McHenry and Coffing (2000), and (b) assuming a modest increase in dietary quality between the australopithecines and early *Homo*. Specifically, we assumed australopithecines to have DQ equal to the average for modern ape species, whereas early members of the genus *Homo* had DQ equal to the minimum value for contemporary foragers.

With the above-noted changes in body size and modest improvement in DQ with the evolution of the genus *Homo*, we find dramatic increases in HR sizes with the evolution of *H. erectus*. Estimated HR size for *H. erectus* is ~450 hectares, about 8 to 10 times that of their australopithecine ancestors. Thus the changes in body mass and dietary quality with origins of *H. erectus* would have dramatically influenced territorial needs and dispersal capability (see Table 1.1 for estimated home range sizes for selected fossil hominid species).

Thus we find several major, interrelated changes with the emergence of *Homo erectus*. With the expansion of the African grassland, there were declining levels of primary productivity and changes in resource distribution (i.e., more grazing animals and calories "on the hoof"). These changes appear to have promoted shifts in foraging behavior and dietary quality that helped to provide the energetic/nutrition fuel to

support the ra
ecological proc
tributed to gre

This adapt
nutritional cha
requiring a hig
the adoption c
required high l

Modern Huma

Since the eme
Africa, human
planet. Our an
dependent upo
from subsisten
During the co
all of the follo
opment of agr
novel food pro
of maize in the
bitter manioc,
cussion). Toda
diversity of die
of animal mate
exclusively on

In the face
these human g
port the dema
energy to supp
ary history, we
tritional needs.
challenges that
will explore two
its associated r

Linear Growth .

The problem o
of brain metabo
20–25 percent
percent (Hollic

support the rapid evolution of both brain size and body size. In addition, the lower ecological productivity, dietary change, and increased body size all would have contributed to greater HR needs and dispersal potential.

This adaptive package that we see with *H. erectus* highlights the evolution of key nutritional characteristics that are distinctly human: (a) evolution of our large brains, requiring a higher-quality, nutritionally dense diet, and (b) increased body size and the adoption of a foraging strategy that necessitated movement of large ranges that required high levels of daily energy expenditure.

Modern Human Nutritional Problems

Since the emergence of the genus *Homo* and the initial spread of hominids out of Africa, humans have successfully colonized almost every major ecosystem on the planet. Our ancestors' ability to exploit diverse environments was, in large measure, dependent upon developing strategies and technologies for increasing energy returns from subsistence activities, and raising the nutritional quality of staple food items. During the course of more recent human evolution, these strategies have included all of the following: (a) technological and foraging changes, (b) cooking, (c) development of agricultural and pastoral subsistence regimes, and (d) development of novel food processing/preparation techniques still seen today (e.g., alkali processing of maize in the Americas, potato processing/preservation in the Andes, processing of bitter manioc, processing of soy beans in Asia) (see Leonard 2000 for additional discussion). Today, we find that humans are able to subsist and thrive on a remarkable diversity of diets, ranging from those of arctic populations consisting almost entirely of animal material to those of many small-scale farming societies, subsisting almost exclusively on plant foods.

In the face of this enormous diversity, the features that are common across all these human groups are: (a) the ability to produce a nutritionally dense diet to support the demands of our large brains, and (b) the ability to obtain sufficient total energy to support our relatively large bodies and activity levels. Over our evolutionary history, we have been quite successful developing strategies for meeting our nutritional needs. However, even today many important health problems reflect the challenges that exist in accommodating our distinctive nutritional biology. Here we will explore two of these problems: early childhood growth stunting, and obesity and its associated metabolic disorders.

Linear Growth Stunting

The problem of growth stunting is, in part, driven by the extraordinarily high costs of brain metabolism in very young children. Whereas brain metabolism accounts for 20–25 percent of resting needs in adults, in an infant of < 10 kg, it is upwards of 60 percent (Holliday 1986)! Table 1.2 shows changes in the percent of RMR allocated

Table 1.2. Body weight (kg), brain weight (g), percent body fat (%), resting metabolic rate (RMR; kcal/day), and percent of RMR allocated to brain metabolism (BrMet, %) 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	1045	25	590	53
5 years	19.0	1235	15	830	44
10 years	31.0	1350	15	1160	34
Adult male	70.0	1400	11	1800	23
Adult female	50.0	1360	20	1480	27

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).

to the brain over the course of human growth and development. These enormously high energy demands for infants reflect both their high brain to body weight ratios and their rapid rates of brain growth.
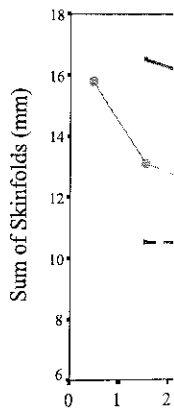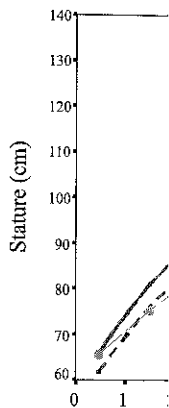
To accommodate the extraordinary energy demands of the developing infant brain, human infants are born with an ample supply of body fat (Kuzawa 1998; Leonard et al. 2003). At ~15–16 percent body fat, human infants have the highest body fat levels of any mammalian species (Dewey et al. 1993). Further, human infants continue to gain body fat during their early postnatal life. During the first year, healthy infants typically increase in fatness from about 16 percent to about 26 percent (see Table 1.2).

Research on children of the developing world suggests that chronic, mild to moderate undernutrition has a relatively small impact on a child's fatness—that is, it appears to be preserved in the face of nutritional stress. Instead of taking away the fat reserves, nutritional needs appear to be down-regulated by substantially reducing rates of growth in height/length—producing the common problem of infant/child-hood growth stunting or growth failure that is ubiquitous among impoverished populations of the developing world.

Figure 1.3 shows an example of this process based on growth data collected from the Tsimane' farmers and foragers of lowland Bolivia (from Foster et al. 2005). Note that stature early in life closely approximates the US median, but by age three to four years it has dropped below the 5th centile, where it will track for the rest of life. In contrast, body fatness (as measured by the sum of the triceps and subscapular skin-folds) compares more favorably to US norms, tracking between the 15th and 50th

US centiles. The problem of early childhood growth failure is the product of both increased infectious-disease loads and reduced dietary quality.

International health research has consistently shown that higher dietary quality is the strongest nutritional predictor of improved growth in young children of the developing world. For example, work with agricultural populations of highland and coastal Ecuador (Leonard et al. 2000; Berti, Leonard, and Berti 1998) and long-term studies carried out in Mexico (Allen 1994; Allen et al. 1992) and Guatemala (Martorell and Habitch 1986; Habitch, Martorell, and Rivera 1995) have all found that percent of dietary energy derived from animal sources was the single strongest predictor of growth velocities for children under the age of three years. In our research in Ecuador, we specifically found that home production and consumption of eggs
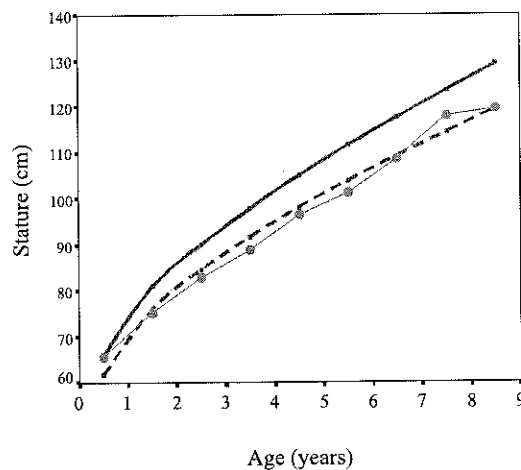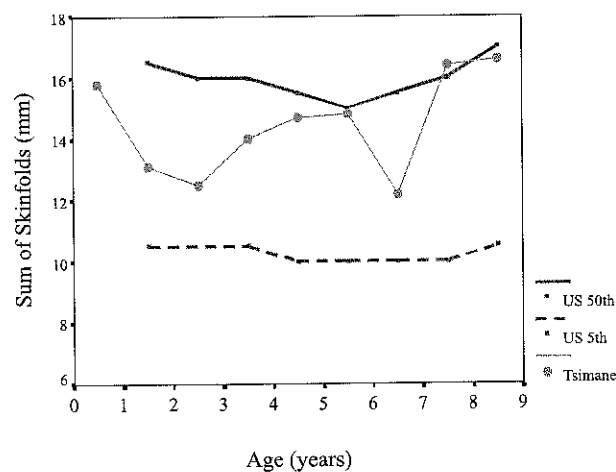

Figure 1.3. Patterns of physical growth in stature (cm) and body fatness (as sum of triceps and subscapular skinfolds, mm) in girls of Tsimane' of lowland Bolivia. Growth of Tsimane' girls is characterized by marked linear growth stunting, whereas body fatness compares more favorably to US norms. Data from Foster et al. (2005)

was strongly correlated with improved DQ and growth in young children (Leonard et al. 2000).

These findings highlight the distinctive nutritional constraints faced by human infants and toddlers—very high nutritional demands (driven by brain metabolism and the energy needs for rapid body growth) with a stomach of limited volume, placing a premium on foods of high nutritional density and digestibility.

Obesity and Chronic Metabolic Disorders

In contrast to the problems of undernutrition that continue to plague young children of the developing world, the United States and other industrialized nations are now experiencing unprecedented increases in obesity rates. In the United States, rates of obesity have increased dramatically over the last forty years. As shown in Table 1.3, US national data (NHANES data) show that since the early 1960s the prevalence of obesity (BMI ≥ 30.0 kg/m^2) has almost tripled in men and more than doubled in women. As of 2004, approximately a third of all Americans were classified as obese (31.1% of men; 33.2% of women). The most recent data suggest that obesity rates are continuing to climb in men, but may be leveling off in women (Flegal et al. 2002; Ogden et al. 2006). (See Katzmarzyk in this volume for a North American overview).

Two of the factors most often cited for the dramatic increases in obesity rates in the United States are the ever-greater availability of inexpensive high calorie/high fat food items, and expansion of "portion sizes" (i.e., the "Supersize Me" phenomenon).

Yet, while these changes in consumption patterns are certainly contributing to the problem, they are not nearly the entire story. In fact, national data show that there have been only modest increases in energy consumption over the last thirty years. This point is evident in Table 1.4, which shows mean daily calorie intakes for adult men and women between 1971 and 2000, derived from the US NHANES data (Briefel and Johnson 2004). Over this period—when body weights and obesity rates were dramatically increasing—daily energy intakes increased by ~200 kcal in men (8 percent increase) and ~300 kcal in women (20 percent increase). In addition, the percent of calories from fat actually declined during this span from 36 percent to 33 percent.

Table 1.3. Percentage of US Adults (20 years and older) who are obese (BMI ≥ 30 kg/m^2), 1960 to 2004.

Sample	Percent Obese (BMI > 30)					
	1960–1962	1971–1974	1976–1980	1988–1994	1999–2000	2003–2004
Men	10.7	12.1	12.7	20.6	27.5	31.1
Women	15.8	16.6	17.0	25.9	33.4	33.2

Sources: Flegal et al. (2002), Ogden et al. (2006)

(partial text from right column, cut off at page edge)

Table 1.4. Dietar[
intakes among US[

Dietary Paramet[
Energy (kcal/d)
Males
Females
Macronutrients
Fat
Protein
Carbohydrate

Source: Briefel an[

These data [
by looking at th[
ity patterns. Un[
penditure, we d[
levels. However, [
lations with diff[
influences daily [

The most c[
abolic intensity[
Daily Energy E[
to RMR is kno[
tive research co[
established a ran[
adults (FAO/W[
with minimal d[
men and wome[
men and 1.56 f[
greater. Modera[
women, wherea[
farmers during [
respectively.

Human po[
diture. Several r[
human groups [
et al. 1996; Inst[
of 1.20 to 1.25[

Table 1.4. Dietary energy (kcal/day) and macronutrient (percent of dietary energy) intakes among US adults (20 years and older), 1971 to 2000.

Dietary Parameter	1971–1974	1976–1980	1988–1994	1999–2000
Energy (kcal/d)				
Males	2450	2439	2666	2618
Females	1542	1522	1798	1877
Macronutrients (% energy)				
Fat	36	36	34	33
Protein	15	15	14	14
Carbohydrates	49	49	52	53

Source: Briefel and Johnson (2004)

These data clearly suggest that the obesity epidemic cannot be understood solely by looking at the intakes; rather we must also consider energy expenditure and activity patterns. Unfortunately, because of the difficulty in measuring daily energy expenditure, we do not have national-level data on changes in expenditure and activity levels. However, a look at some comparative data on energy expenditure across populations with different lifestyles can give us a handle on how urbanization of lifestyles influences daily energy demands.

The most common approach to quantifying differences in "activity level" (metabolic intensity) associated with different lifestyles is simply by expressing Total Daily Energy Expenditure (TDEE) as a ratio relative to RMR. This ratio of TDEE to RMR is known as the Physical Activity Level (PAL) index. Based on comparative research conducted on human populations around the world, the WHO has established a range of PALs associated with different occupational workloads among adults (FAO/WHO/UNU 1985; FAO/WHO/UNU 2004). The PAL associated with minimal daily activities (simply dressing, washing, and eating) is 1.40 for both men and women. Sedentary lifestyles (e.g., office work) require PALs of 1.55 for men and 1.56 for women. At high workloads, the sex differences in PALs tend to be greater. Moderate workloads commensurate with PALs of 1.78 for men and 1.64 for women, whereas heavy occupational workloads (e.g., manual laborers, subsistence farmers during harvest periods) require PALs of 2.10 and 1.82 for men and women, respectively.

Human populations show considerable variation in levels of daily energy expenditure. Several recent comparative analyses indicate that daily energy expenditure in human groups typically ranges from 1.2 to 5.0 × RMR (i.e., PAL = 1.2–5.0) (Black et al. 1996; Institute of Medicine 2002). The lowest levels of physical activity, PALs of 1.20 to 1.25, are observed among hospitalized and nonambulatory populations.

The highest levels of physical activity (PALs of 2.5 to 5.0) have been observed among elite athletes and soldiers in combat training.

Table 1.5 presents data on body weight (kg), TDEE (kcal/day), RMR (kcal/day), and PALs of adult men and women from selected human groups. Values for individuals of the industrialized world are based on a sample of 258 men and 259 women aged twenty years or older compiled by the Institute of Medicine for their most recent references on dietary energy intakes (Institute of Medicine 2002). These data were derived from twelve studies of human energy expenditure using the doubly labeled water method, generally accepted as the most accurate technique for assessing TDEE in free living humans. The data for human subsistence-level populations (i.e., foragers, pastoralist animal herders, and agriculturalists) were derived from anthropological studies conducted over the last forty years.

Among subsistence-level populations, the average daily energy expenditure is about 3000 kcal/day for men and about 2300 kcal/day for women. The energy demands of life in the industrialized world are more modest. Men of the Western world sample are, on average, 12 kg (26.5 pounds) heavier than their counterparts from the subsistence populations, and yet have daily caloric needs that are 150 to 200 kcal less. The pattern is similar, although somewhat less dramatic, for women. Those of the industrialized world are 7 kg (15.5 pounds) heavier and have daily energy demands that are about 60 kcal less than those from food-producing societies.

This means that adults living a "modern" lifestyle in the industrialized world have lower physical activity levels than those living more "traditional" lives. Among men, PALs in the industrialized societies average 1.73, significantly less than the average of 1.98 among the subsistence-level groups (P < 0.01). Thus, the difference in the predicted TDEEs at a body weight of 70.1 kg (the average for the industrialized sample) is over 900 kcal (3784 vs. 2874 kcal/day) (see Figure 1.4). Similarly, PAL values among women average 1.72 in the industrialized world and 1.82 among the subsistence-level societies. The difference in predicted energy demands at the average body weight of the industrialized world sample (58.6 kg) is about 330 kcal (2565 vs. 2234 kcal/day). These large differences in daily energy demands underscore how the substantial reductions in intense physical activities have dramatically lowered the metabolic costs of survival in the modern world. The more modest declines in TDEE observed in women is partly a product of their smaller body size and partly a consequence of the large average sex-differences in TDEE and PAL that characterize traditional, subsistence-level societies. In subsistence-level societies, the most metabolically demanding activities (e.g., hunting, plowing fields) are generally performed by men. Consequently, the transition from a "traditional" to a more "modern" way of life is often associated with greater reductions in physical energy demands in men.

In sum, the daily energy demands in modern subsistence-level societies are considerably greater than those observed in the industrialized world. These comparisons suggest that the transition from a subsistence to a sedentary, modern lifestyle is associated with a 15–30 percent reduction in one's maintenance energy needs.

Table 1.5. Com[...] kcal/day), restin[...] subsistence-leve[...]

Group
Hunter-gatherers:
!Kung (Botswan[...]
Ache (Paraguay)
Inuit (Canada)
Pastoralists:
Evenki (Russia)
Agriculturalists:
Aymara (Bolivia[...]
Quichua (Ecuad[...]
Coastal Ecuador
Gambia
Huli (PNG)
Thailand
Subsistence Popul[...] (Average):
Industrial Societie[...]

Table 1.5. Comparison of body weight (kg), total daily energy expenditure (TDEE; kcal/day), resting metabolic rate (RMR; kcal/day), and Physical Activity Level (PAL) of subsistence-level and industrial societies.

| Group	Sex	Weight (kg)	TDEE (kcal/day)	RMR (kcal/day)	PAL	References
Hunter-gatherers:						
!Kung (Botswana)	M	46.0	2319	1383	1.68	Lee (1979);
	F	41.0	1712	1099	1.56	Leonard and Robertson (1992)
Ache (Paraguay)	M	59.6	3327	1531	2.17	Hill et al. (1984)
	F	51.8	2626	1394	1.88	Leonard and Robertson (1992)
Inuit (Canada)	M	65.0	3010	1673	1.80	Godin and
	F	55.0	2350	1305	1.80	Shephard (1973)
Pastoralists:						
Evenki (Russia)	M	58.4	2681	1558	1.75	Leonard
	F	52.7	2067	1288	1.63	(2002)
Agriculturalists:						
Aymara (Bolivia)	M	54.6	2713	1355	2.00	Kashiwazaki
	F	50.5	2376	1166	2.03	(1999)
Quichua (Ecuador)	M	61.3	3810	1601	2.38	Leonard et
	F	55.7	2460	1252	1.96	al. (1995
Coastal Ecuador	M	55.6	2416	1529	1.58	Leonard et
	F	47.8	1993	1226	1.63	al. (1995)
Gambia	M	61.2	3848	1604	2.40	Heini et al. (1996)
	F	50.3	2500	1236	2.03	Heini et al. (1991)
Huli (PNG)	M	63.6	3138	1704	1.84	Yamauchi et
	F	53.3	2639	1391	1.88	al. (2001)
Thailand	M	55.1	2892	1322	2.20	Murayama and
	F	57.7	2218	1217	1.83	Ohtsuka (1999)
Subsistence Populations (Average):	M	58.0	3015	1525	1.98	
	F	51.6	2294	1257	1.82	
Industrial Societies:	M	70.1	2873	1659	1.73	Institute of
	F	58.6	2234	1300	1.72	Medicine (2002)
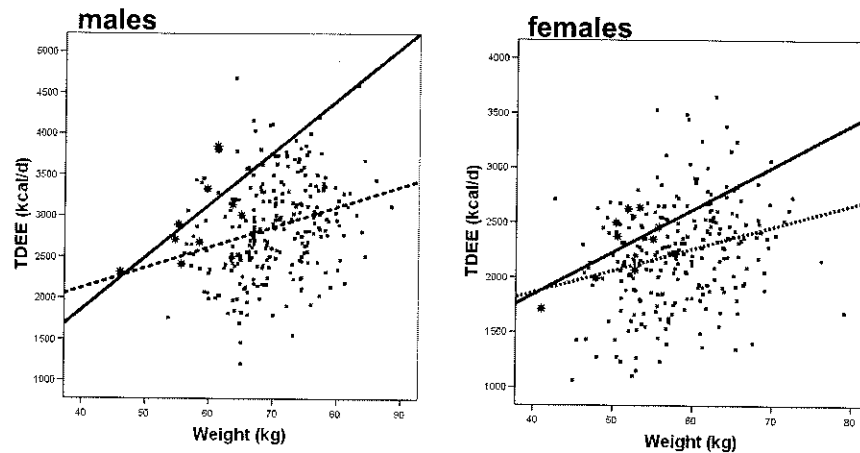
Figure 1.4. Total daily energy expenditure (TDEE; kcal/day) versus body weight (kg) for adult men and women of industrial and subsistence-level populations. Individuals from subsistence-level groups have systematically higher levels of energy expenditure at a given body weight.

Such reductions in daily energy expenditure associated with our "modern" life-styles are a main contributor to the growing problem of obesity throughout the world. In some sense obesity and other chronic diseases of the modern world (diabetes and cardiovascular disease, for example) represent a continuation of trends that were started early in our evolutionary history. We have developed a diet that is extremely rich in calories while at the same time minimizing the amount of energy necessary for physical work and activity.

Thus, it is not simply the consumption of "bad" or "unhealthy" foods that has produced the obesity epidemic. Rather, it is changes in both diet and activity patterns that have produced ever greater surpluses of energy. The ongoing processes of change are in reality an extension of adaptive trends seen throughout human evolution—increasing the nutritional density of our diets, while reducing the time and energy associated with obtaining food. The difference now is that the changes are occurring at a much more rapid rate—producing large imbalances between "energy in" and "energy out."

Consequently, we suggest that in addressing the obesity problem and promoting better nutritional health, additional attention needs to be given to energy expenditure and activity levels. We see movement in this direction—the most recent Institute of Medicine's dietary and nutritional guidelines (2002) include recommendations on physical activity. At this point, however, there remains considerable debate about how much physical activity is necessary to promote a healthy lifestyle. This is an issue that we can and should address from a comparative, ecological, and evolutionary perspec-
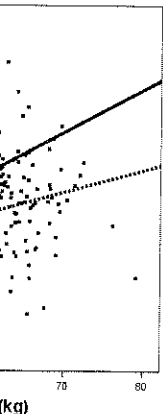
tive—looking at the range of energy needs and activity levels of more traditionally living societies to give us a better sense of the level of exertion and metabolic demands for much of our evolutionary history.

Conclusion

Like other primates, we are omnivores, who can subsist on a diverse and eclectic mix of foods (e.g., Harding and Teleki 1981; Stanford 1996). However, the evolution of our disproportionately large human brains has had important and unique implications for the nutritional biology of our species. Our large brains are energetically expensive, yet, paradoxically, our overall metabolic requirements are similar to those of any comparably sized mammal. As a consequence, humans expend a relatively larger proportion of their resting energy budget on brain metabolism than other primates or nonprimate mammals.

Comparative analyses of primate dietary patterns indicate that the high costs of large human brains are supported, in part, by diets that are relatively rich in energy and other nutrients. Among living primates, the relative proportion of metabolic energy allocated to the brain is positively correlated with dietary quality. Humans fall at the positive end of this relationship, having both a very high-quality diet and a large brain.

The metabolic demands of the brain are particularly extreme during infancy and early childhood, when rapid brain growth is occurring and brain to body mass ratios are higher than in adulthood. To accommodate the very high energy demands of brain during early life, human infants are born with relatively high levels of adiposity, and continue to gain fat during the first twelve to eighteen months of life. These greater levels of body fatness and reduced levels of muscle mass allow human infants to accommodate the growth of their large brains in two important ways: (1) by having a ready supply of stored energy to "feed the brain," and (2) by reducing the total energy costs of the rest of the body.

The difficulties associated with fueling brain metabolism in infants are evident among impoverished populations of the world today. Under conditions where disease load and poor diet quality limit the availability of energy and nutrients to young children, we find that growth in length/height is severely compromised while levels of body fatness are preserved. This response allows for brain metabolism to be relatively protected by down-regulating the energy costs of body growth and preserving sufficient stores of energy as fat.

In addition to the nutritional demands of our large brains, throughout most of our evolutionary history, the acquisition of our high-quality diets required substantial expenditure of energy and movement over much larger areas than other primates. Over time, however, we have become ever-more efficient at extracting energy and nutrients from our environments. Today, daily energy demands in populations of the industrialized world are considerably less than those of subsistence-level (e.g.,

foraging, farming) societies. When matched for body weight, the differences in daily energy expenditure between Western and subsistence-level adults is between 300 and 900 kcal/day. This suggests that the transition from a subsistence to a sedentary, modern lifestyle is associated with a 15–30 percent reduction in one's maintenance energy needs.

In contrast to changes in energy expenditure, absolute daily energy intakes for adults of the industrialized world do not appear to differ markedly from those of subsistence-level societies. Thus, contrary to conventional wisdom, the dramatic rise of obesity in the United States and others parts of the industrialized world cannot be attributed simply to marked increases in absolute caloric consumption. Rather, it is the "imbalance" between energy intake and energy expenditure that is the root cause.

In this context, the problems of "overnutrition" currently seen worldwide are the extension of deep trends from our past. Addressing these problems will thus require attention to both the intake and expenditure sides of the energy balance equation.

References

Aiello, L. C., and P. Wheeler. 1995. The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology* 36: 199–221.

Allen, L. H. 1994. Nutritional influences on linear growth: A general review. *European Journal of Clinical Nutrition* 48: S75–S89.

Allen, L. H., J. R. Backstrand, E. J. Stanek, G. H. Pelto, et al. 1992. Interactive effects of dietary quality on the growth and attained size of young Mexican children. *American Journal of Clinical Nutrition* 56: 353–64.

Antón, S. C. 2003. A natural history of *Homo erectus. Yearbook of Physical Anthropology* 46: 126–70.

Antón, S. C., and C. C. Swisher III. 2001. Evolution of cranial capacity in Asian *Homo erectus.* In *A Scientific Life: Papers in Honor of Dr. T. Jacob,* ed. E. Indriati, 25–39. Yogyakarta, Indonesia: Bigraf.

Antón, S. C., W. R. Leonard, and M. L. Robertson. 2002. An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution* 43: 773–85.

Audette, R.V., and T. Gilchrist. 2000. *Neanderthin: Eat Like a Caveman and Achieve a Lean, Strong, Healthy Body.* New York: St. Martins.

Behrensmeyer, K., N. E. Todd, R. Potts, and G. E. McBrinn. 1997. Late Pliocene faunal turnover in the Turkana basin, Kenya and Ethiopia. *Science* 278: 1589–94.

Berti, P. R., W. R. Leonard, and W. J. Berti. 1998. Stunting in an Andean community: Prevalence and etiology. *American Journal of Human Biology* 10: 229–40.

Black, A. E., W. A. Coward, T. J. Cole, and A. M. Prentice. 1996. Human energy expenditure in affluent societies: An analysis of 574 doubly-labeled water measurements. *European Journal of Clinical Nutrition* 50: 72–92.

e differences in daily
s is between 300 and
ence to a sedentary,
n one's maintenance

y energy intakes for
kedly from those of
m, the dramatic rise
alized world cannot
nsumption. Rather,
ture that is the root

n worldwide are the
ms will thus require
balance equation.

e brain and the diges-
36: 199–221.
iew. *European Journal*

teractive effects of di-
ildren. *American Jour-*

sical Anthropology 46:

n Asian *Homo erectus.*
i, 25–39. Yogyakarta,

ological model of the
3: 773–85.
i and Achieve a Lean,

Pliocene faunal turn-
94.
n community: Preva-

n energy expenditure
surements. *European*

Bobe, R., and A. K. Behrensmeyer. 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution* 42: 475–97.

Briefel, R. R., and C. L. Johnson. 2004. Secular trends in dietary intake in the United States. *Annual Review of Nutrition* 24: 401–31.

Cordain, L., J. Brand-Miller, S. B. Eaton, N. Mann, et al. 2000. Plant to animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *American Journal of Clinical Nutrition* 71: 682–92.

Cordain, L., S. B. Eaton, A. Sebastian, N. Mann, et al. 2005. Origins and evolution of the Western diet: Health implications for the 21st century. *American Journal of Clinical Nutrition* 81: 341–54.

Crawford, M. A. 1992. The role of dietary fatty acids in biology: Their place in the evolution of the human brain. *Nutrition Reviews* 50: 3–11.

Crawford, M. A., and D. Marsh. 1995. *Nutrition and Evolution.* London: Keats.

Cunnane, S. C. 2005. *Survival of the Fattest: The Key to Human Brain Evolution.* Singapore: World Scientific Publishing Co.

DeMenocal, P. B. 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* 220: 3–24.

Dewey, K. G., M. J. Heinig, L. A. Nommsen, J. M. Peerson et al. 1993. Breast-fed infants are leaner than formula-fed infants at 1 y of age: The Darling Study. *American Journal of Clinical Nutrition* 52: 140–45.

Eaton, S. B. 2006. The ancestral human diet: What was it and should it be a paradigm for contemporary nutrition? *Proceedings of the Nutrition Society* 65: 1–6.

Eaton, S. B., and M. J. Konner. 1985. Paleolithic nutrition: A consideration of its nature and current implications. *New England Journal of Medicine* 312: 283–89.

Eaton, S. B., M. Shostack, and M. J. Konner. 1988. *The Paleolithic Prescription.* New York: Harper-Collins.

Flegal, K. M., M. D. Carroll, C. L. Ogden, and C. L. Johnson. 2002. Prevalence and trends in obesity among US adults, 1999–2000. *Journal of the American Medical Association* 288: 1723–27.

Food and Agriculture Organization, World Health Organization, and United Nations University (FAO/WHO/UNU) 1985. *Energy and Protein Requirements. Report of Joint FAO/WHO/UNU Expert Consultation.* WHO Technical Report Series No. 724. Geneva: World Health Organization.

———. 2004. *Human Energy Requirements. Report of a Joint FAO/WHO/UNU Expert Consultation.* Geneva: World Health Organization.

Foster, Z., E. Byron, V. Reyes-García, T. Huanca et al. 2005. Physical growth and nutritional status of Tsimane' Amerindian children of lowland Bolivia. *American Journal of Physical Anthropology* 126: 343–51.

Gabunia, L., A. Vekua, D. Lordkipanidze, C. C. Swisher III et al. 2000. Earliest Pleistocene cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting, and age. *Science* 288: 1019–25.

Gabunia, L., S. C. Antón, D. Lordkipanidze, A. Vekua et al. 2001. Dmanisi and dispersal. *Evolutionary Anthropology* 10: 158–70.

Garn, S. M., and W. R. Leonard. 1989. What did our ancestors eat? *Nutrition Reviews* 47: 337–45.

Godin, G., and R. J. Shephard. 1973. Activity patterns of the Canadian Eskimo. In *Polar Human Biology,* ed. O. G. Edholm and E. K. E. Gunderson, 193–215. Chichester, UK: Heinemann Books.

Habitch J. P., R. Martorell, and J. A. Rivera. 1995. Nutritional impact of supplementation in the INCAP longitudinal study: Analytic strategies and inferences. *Journal of Nutrition* 125: 1042S–1050S.

Harding, R. S. O., and G. Teleki. 1981. *Omnivorous Primates.* New York: Columbia University Press

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight: A re-evaluation. *Ecology* 60: 389–402.

Harris, J. W. K., and S. Capaldo. 1993. The earliest stone tools: Their implications for an understanding of the activities and behavior of late Pliocene hominids. In *The Use of Tools by Human and Nonhuman Primates,* ed. A. Berthelet and J. Chavaillon, 196–220. Oxford: Oxford Science Publications.

Heini, A., Y. Schutz, E. Diaz, A. M. Prentice et al. 1991. Free living energy expenditure measured by two independent techniques in pregnant and non-pregnant Gambian women. *American Journal of Physiology* 261: E9–E17.

Heini, A. F., G. Minghelli, E. Diaz, A. M. Prentice et al. 1996. Free-living energy expenditure assessed by two different methods in rural Gambian men. *European Journal of Clinical Nutrition* 50: 284–89.

Hill, K. R., K. Hawkes, M. Hurtado, and H. Kaplan. 1984. Seasonal variance in the diet of Ache hunter-gatherers in Eastern Paraguay. *Human Ecology* 12: 101–35.

Holliday, M. A. 1986. Body composition and energy needs during growth. In *Human Growth: A Comprehensive Treatise,* volume 2. 2nd ed., ed. F. Falkner and J. M. Tanner, 101–17. New York: Plenum Press.

Institute of Medicine of the National Academies 2002. *Dietary Reference Intakes: Energy, Carbohydrate, Fiber, Fat, Fatty Acids, Cholesterol, Protein, and Amino Acids.* Washington, DC: National Academies Press, http://www.iom.edu/?id=15075.

Kashiwazaki, H. 1999. Heart rate monitoring as a field method for estimating energy expenditure as evaluated by the doubly labeled water method. *Journal of Nutritional Science and Vitaminology* 45: 79–94.

Kety, S. S. 1957. The general metabolism of the brain *in vivo.* In *Metabolism of the Central Nervous System,* ed. D. Richter, 221–37. New York: Pergamon.

Kleiber, M. 1961. *The Fire of Life.* New York: Wiley.

Kuzawa, C. W. 1998. Adipose tissue in human infancy and childhood: An evolutionary perspective. *Yearbook of Physical Anthropology* 41: 177–209.

Lee, R. B. 1979. *The !Kung San: Men, Women, and Work in a Foraging Society.* Cambridge: Cambridge University Press.

Omanisi and dispersal.

Nutrition Reviews 47:

dian Eskimo. In *Polar*
–215. Chichester, UK:

ct of supplementation
es. *Journal of Nutrition*

rk: Columbia Univer-

: A re-evaluation. *Ecol-*

mplications for an un-
. In *The Use of Tools by*
on, 196–220. Oxford:

ergy expenditure mea-
ant Gambian women.

ng energy expenditure
ean Journal of Clinical

variance in the diet of
–35.

th. In *Human Growth:*
. M. Tanner, 101–17.

e Intakes: Energy, Car-
ids. Washington, DC:

imating energy expen-
Nutritional Science and

abolism of the Central

An evolutionary per-

g Society. Cambridge:

Leonard, W. R. 2000. Human nutritional evolution. In *Human Biology: An Evolutionary and Biocultural Approach,* ed. S. Stinson, B. Bogin, R. Huss-Ashmore, and D. O'Rourke, 295–344. New York: Wiley-Liss.

———. 2002. Food for thought: Dietary change was a driving force in human evolution. *Scientific American* 287 (6): 106–15.

Leonard, W. R., and M. L. Robertson. 1992. Nutritional requirements and human evolution: A bioenergetics model. *American Journal of Human Biology* 4: 179–95.

———. 1994. Evolutionary perspectives on human nutrition: The influence of brain and body size on diet and metabolism. *American Journal of Human Biology* 6: 77–88.

———. 1997a. Comparative primate energetics and hominid evolution. *American Journal of Physical Anthropology* 102: 265–81.

———. 1997b. Rethinking the energetics of bipedality. *Current Anthropology* 38: 304–9.

Leonard, W. R., K. M. DeWalt, J. S. Stansbury, and M. K. McCaston. 2000. The influence of dietary quality on the growth of highland and coastal Ecuadorian children. *American Journal of Human Biology* 12: 825–37.

Leonard, W. R., P. T. Katzmarzyk, M. A. Stephen, and A. G. P. Ross. 1995. Comparison of the heart rate-monitoring and factorial methods: Assessment of energy expenditure in highland and coastal Ecuador. *American Journal of Clinical Nutrition* 61: 1146–52.

Leonard, W. R., M. L. Robertson, J. J. Snodgrass, and C. W. Kuzawa. 2003. Metabolic correlates of hominid brain evolution. *Comparative Biochemistry and Physiology, Part A* 135: 5–15.

Martin, R. D. 1989. *Primate Origins and Evolution: A Phylogenetic Reconstruction.* Princeton, NJ: Princeton University Press.

Martorell, R., and J-P. Habicht. 1986. Growth in early childhood in developing countries. In *Human Growth: A Comprehensive Treatise,* volume 3. 2nd ed., ed. F. Falkner and J. M. Tanner, 241–62. New York: Plenum.

McHenry, H. M. 1992. Body size and proportions in early hominids. *American Journal of Physical Anthropology* 87: 407–31.

———. 1994a. Tempo and mode in human evolution. *Proceedings of the National Academy of Sciences (USA)* 91: 6780–86.

———. 1994b. Behavioral ecological implications of early hominid body size. *Journal of Human Evolution* 27: 77–87.

McHenry, H. M., and K. Coffing. 2000. *Australopithecus* to *Homo:* Transformations in body and mind. *Annual Reviews of Anthropology* 29: 125–46.

Murayama, N., and R. Ohtsuka. 1999. Heart rate indicators for assessing physical activity level in the field. *American Journal of Human Biology* 11: 647–57.

O'Dea, K. 1991. Traditional diet and food preferences of Australian aboriginal hunter-gatherers. *Philosophical Transactions of the Royal Society of London Biological Sciences* 334: 233–40.

Ogden, C. L., M. D. Carroll, L. R. Curtin, M. A. McDowell et al. 2006. Prevalence of overweight and obesity in the United States, 1999–2004. *Journal of the American Medical Association* 295: 1549–55.

Plummer, T. 2004. Flaked stones and old bones: Biological and cultural evolution at the dawn of technology. *Yearbook of Physical Anthropology* 47: 118–64.

Reed, K. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* 32: 289–322.

Richard, A. F. 1985. *Primates in Nature.* New York: W. H. Freeman.

Ruff, C. B., E. Trinkaus, and T. W. Holliday. 1997. Body mass and encephalization in Pleistocene *Homo. Nature* 387: 173–76.

Sailer, L. D., S. J. C. Gaulin, J. S. Boster, and J. A. Kurland. 1985. Measuring the relationship between dietary quality and body size in primates. *Primates* 26: 14–27.

Stanford, C. B. 1996. The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist* 98: 96–113.

Teleki, G. 1981. The omnivorous diet and eclectic feeding habits of the chimpanzees of Gombe National Park. In *Omnivorous Primates,* ed. R. S. O Harding and G. Teleki, 303–43. New York: Columbia University Press.

Ungar, P. S. 2007. *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable.* New York: Oxford University Press.

Vrba, E. S. 1995. The fossil record of African antelopes relative to human evolution. In *Paleoclimate and Evolution, with Emphasis on Human Origins,* ed. E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burkle, 385–424. New Haven, CT: Yale University Press.

Wolpoff, M. H. 1999. *Paleoanthropology.* 2nd ed. Boston: McGraw-Hill.

Wynn, J. G. 2004. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols from the Turkana Basin, Kenya. *American Journal of Physical Anthropology* 123: 106–18.

Yamauchi, T., M. Umezaki, and R. Ohtsuka. 2001. Physical activity and subsistence pattern of the Huli, a Papua New Guinea highland population. *American Journal of Physical Anthropology* 114: 258–68.

C
Sout

Introduction

The survival of a
of the next gener
For many millen
hunter-gatherers;
to here as forager
merous. This sug
specific about its

Characterist
population densi
storage. Taken to
security, combine
hazards. The latt
and animals, an
from gestation o
available can lea
manent stunting

On the oth
within their hab

Human Diet and Nutrition in Biocultural Perspective

Past Meets Present

● ● ●

Edited by Tina Moffat and Tracy Prowse