This paper examines the evolutionary origins of human dietary and activity patterns, and their implications for understanding modern health problems. Humans have evolved distinctive nutritional characteristics associated with the high metabolic costs of our large brains. The evolution of larger hominid brain size necessitated the adoption of foraging strategies that both provided high quality foods, and required larger ranges and activity budgets. Over time, human subsistence strategies have become ever more efficient in obtaining energy with minimal time and effort. Today, populations of the industrialized world live in environments characterized by low levels of energy expenditure and abundant food supplies contributing to growing rates of obesity. Analyses of trends in dietary intake and body weight in the US over the last 50 years indicate that the dramatic rise in obesity cannot be explained solely by increased energy consumption. Rather, declines in activity are also important. Further, we find that recent recommendations on physical activity have the potential to bring daily energy expenditure levels of industrialized societies surprisingly close to those observed among subsistence-level populations. These findings highlight the importance of physical activity in promoting nutritional health and show the utility of evolutionary approaches for developing public health recommendations.

**Keywords:** human evolution, energy expenditure, diet quality, obesity, NHANES

Over the last 25 years, evolutionary approaches to study of human health and nutrition have received ever-greater attention among scholars in a number of fields, including anthropology, nutritional science, and exercise science. Increasingly, we have come to understand that many of the key features that distinguish humans from other primates (eg, our bipedal form of locomotion and large brain sizes) have important implications for our distinctive nutritional needs. In addition, we 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.

A hallmark of human evolution has been our ability to increase the efficiency with which we extract food from our environments. Humans show remarkable diversity in their dietary regimes; in reality, what makes us human is our ability to find a meal in virtually any environment. Throughout most of our past, human lifestyles were characterized by high levels of physical activity and energy expenditure, seasonal fluctuations in food availability, and frequent periods of marginal or negative energy balance. These conditions selected for improvements in the energetic efficiency of human foraging strategies. Today, we are in many respects victims of our own evolutionary success. Human populations of the industrialized world live in what have been characterized as “obesogenic” environments with low levels of energy expenditure and abundant food supplies contributing to strongly positive energy balances and growing rates of obesity and chronic, metabolic disorders.

When we consider the evolutionary history of the hominid lineage, we find many of the key distinguishing features of human nutritional ecology arise with the emergence of *Homo erectus* at ~1.8 million years ago (mya) in Africa. This phase of human evolution—the emergence of the first ‘human form’—was associated with major changes in brain size, body size, diet composition, and foraging behavior that have had profound influences on shaping the nutritional and energy demands of our species. Indeed, the changes that occurred with *H. erectus* established 2 of the prime drivers of human energy and nutritional needs that persist through time. The first is the need for a high quality (energy and nutrient dense) diet to fuel the energy costs of our large brains. The second is the development of foraging regimes that required movement over wide areas to procure those nutritionally dense diets. These expanded foraging ranges were associated with large activity budgets and high levels of daily energy expenditure.

In this paper, I trace the evolutionary origins of these distinctive human nutritional and energy needs, and consider their implications for current health problems of our modern world. I start by considering the energetic and nutritional correlates of variation in brain and body size among living primates (including humans) to provide a context for interpreting the fossil evidence for human
Evolutionary Perspectives on Physical Activity

I then examine data from 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, I explore the implications of our distinctive metabolic requirements for understanding and confronting the growing problem of obesity and physical inactivity in modern societies of the industrialized world.

Comparative Nutrition and Metabolism

Energetic Correlates of Variation in Body and Brain Size

From a nutritional perspective, what is extraordinary about our large human brains is their high energy costs. Brain tissue has very high energy demands per unit weight, roughly 16 times greater than those of muscle tissue (12 kcal/kg/min vs. 0.75 kcal/kg/min). Over the span of a day, the brain accounts for about 400 kcal in an adult human. Yet, despite the fact that humans have much larger brains per body weight than other primates or terrestrial mammals, the total resting metabolic rates (RMR; kcal/day) for the human body are no more than for any other mammal of the same size.4

Figure 1 shows the log-log plot of RMR (kcal/day) versus body weight (kg) for humans, 36 nonhuman primate species, and 22 nonprimate mammalian species. Humans conform to the general mammalian scaling relationship between RMR and body weight (the “Kleiber Relationship”). The Kleiber scaling relationship shows that metabolic rates of mammals of different sizes increases as a function of mass such that RMR can be predicted by the following equation:

$$RMR = 70(Mass^{0.75})$$

On average, adult humans have RMRs that fall within 3 to 4% of the values predicted by the Kleiber relationship. 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 seen in Figure 2, which shows the log-log scaling relationship between brain weight (grams) and RMR for the species shown in Figure 1. The y-intercept of the primate regression is significantly greater ($P < .01$) than that of the nonprimate mammalian regression, whereas the slopes are comparable. This indicates that for a given RMR, primates have brains that are approximately 3 times the size of other mammals. Human brain sizes, in turn, are some 2.5 to 3 times those of other primates.

In energetic terms, this means that brain metabolism accounts for 20 to 25% of RMR in an adult human body; as compared with about 8 to 10% in other primate species, and roughly 3 to 5% for nonprimate mammals.4 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 (eg, pygmy marmoset) consume diets that are rich in energy and nutrients, whereas large bodied primates (eg, the gorilla) consume large amounts of low quality foods. These feeding strategies are shaped by the interspecific scaling relationship of RMR to mass (the above-noted Kleiber Relationship). Because metabolic rates scale to the 3/4th power of body weight, mass-specific energy costs (eg, kcal/kg) decrease with increasing body size. This implies that small primates have low total energy needs but very high energy demands per unit mass. 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 very low mass-specific costs. Hence they are large volume feeders, eating foods that are widely available, but low nutritional density (eg, leaves, bark, other foliage).

Humans, however, have substantially higher quality diets than expected for a primate of our size. Figure 3 shows the association between dietary quality (DQ) and body weight in living primates. The DQ index is derived from the work of Sailer and colleagues, and reflects the relative proportions of (1) structural plant parts, (2) reproductive plant parts (eg, fruits, flowers), and (3) animal foods (including invertebrates). The index ranges from a minimum of 100 (a diet of all leaves and/or structural plant parts) to a maximum of 350 (a diet of all animal material).

Note that the diets of modern human hunter-gatherers fall substantially above the best-fit regression line for other primates. Indeed, the staple foods for all human societies are much more nutritionally dense than those of other large-bodied primates. In comparison, modern great apes obtain most of their diet from low quality plant foods. This “higher quality” diet means that we need to eat less volume of food to get the energy and nutrients we require.

The link between brain size and dietary quality is evident in Figure 4, which shows relative brain size versus relative dietary quality for the 31 different primate species (including humans) 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 vs. body weight regression, and relative DQ is measured as the residual from the DQ vs. body mass regression. There is a strong positive relationship ($r = .63; P < .001$) 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.

The relative size and morphology of the human gastrointestinal (GI) tract also reflect adaptation to our
Figure 3 — Plot of diet quality (DQ) vs. log-body weight for 72 primate species and 5 human hunter-gatherer groups. DQ is inversely related to body weight \( r = -0.66; \text{ for non human primates; } P < .001 \), indicating that smaller primates consume relatively higher quality diets. Humans have systematically higher quality diets than predicted for their size.

Figure 4 — Plot of relative brain size vs. relative diet quality for 31 primate species (including humans). Primates with higher quality diets for their size have relatively larger brain sizes \( r = .63; P < .001 \). Humans represent the positive extremes for both measures, having the largest brain:body weight ratio and the highest relative diet quality.
high-quality diet. Most large-bodied primates have expanded large intestines (colon), an adaptation to fibrous, low quality diets. Humans, on the other hand, have small total gut volumes for our size with relatively enlarged small intestines and a reduced colon.

The enlarged colons of apes and other large primates permit fermentation of low quality plant fibers, allowing for extraction of additional energy in the form of volatile fatty acids. In contrast, the GI morphology of humans (small colon and relatively enlarged small intestine) is more similar to a carnivore and reflects an adaptation to an easily digested, nutrient-rich diet.

These comparative analyses suggest that the high costs of the large, metabolically expensive human brain are partially offset by the consumption of an energy and nutrient-rich diet. They imply 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.

Correlates of Variation in Movement and Activity Budgets

Another important difference between subsistence-level humans and other primate species is our territorial needs. Compared with other primates, human foragers have relatively large day and home ranges. Day ranges, the typical distance moved over the course of day, average 13 km/day in human hunter-gatherers, as compared with less than 2 km/day among great apes (chimps and gorillas).

Similarly, Home Range (HR) size, the total area exploited by an animal group, is much greater in humans than in other primates. Figure 5 shows the log-log plot of HR size (in hectares) versus body weight for 47 nonhuman primate species and 6 tropical human hunter-gatherer groups. Note that HR size is strongly associated with weight; however, human foragers have substantially larger HRs than other primates of their size.

The reasons for this difference appear to stem in large part from dietary differences. Comparative studies on territorial needs of mammalian species have shown that 3 of the strongest predictors of between species variation in HR size are (1) body weight (larger animals need more territory); (2) dietary patterns (carnivore HRs >> herbivore HRs); and (3) ecosystem productivity, the more open and less productive the habitat, the larger the HR size. Table 1 presents results of a multiple regression analysis testing whether differences in DQ could explain deviations from the HR vs. mass relationship in primates. Note that after adjusting for differences in body mass, DQ remains a significant predictor of variation in HR size ($P < .001$). Moreover, these analyses show that that together body mass and DQ model explain almost 80% of variation in HR size ($R^2 = .77$).

Thus, from a comparative perspective it appears that 2 of the key distinguishing features of human nutritional biology are (1) a high quality, energetically dense diet to support our large brains, and (2) a foraging strategy that necessitated large ranges and high activity budgets. The first evidence of these trends in human evolution appear with the emergence of the genus Homo.

![Figure 5](image-url) — Log-log plot of Home Range Size (ha) vs. body weight (kg) for a sample of 47 nonhuman primate species and 6 tropical human foraging groups. The scaling relationship between home range size and body weight is $HR = 0.61(Wt^{1.21})$; $r^2 = .58$. Human foragers have relatively large HRs for their body size. Adapted from ref. 19.
From Africa to other parts of the Old World.\textsuperscript{14}

Over larger areas.\textsuperscript{30}

Comparable to modern humans, facilitating movement

Human-like body proportions, suggesting a striding gate

Shortened legs. In contrast, with

Proportions—having relatively elongated arms and

Were clearly bipeds, they retained their ape-like body

From that we have body sizes comparable to modern humans.

Small in both mass and stature. It is not until

Dietary shifts: (1) the large body sizes necessitating

Note. $R^2 = .77; P < .0001$. Adapted from ref. 5.

**Table 1 Multiple Regression Analysis of the Predictors of Variation in Log-HR Size Among Extant Primates**

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Regression coefficient ($b \pm SE$)</th>
<th>Beta weight</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log-weight</td>
<td>1.36 ± 0.11</td>
<td>0.854</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Diet quality</td>
<td>0.009 ± 0.001</td>
<td>0.446</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Constant</td>
<td>−2.01 ± 0.29</td>
<td>—</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

**Evolutionary Trends in Diet, Brain Size, and Body Size**

When we look at the human fossil record, the emergence of *Homo erectus* in Africa at ~1.8 mya is widely viewed as a major adaptive shift in human evolution. What is remarkable about this period of human evolution is that we find (1) marked increases in both brain and body size,\textsuperscript{29,30} (2) the evolution of human-like body proportions, with shortened arms and longer legs,\textsuperscript{30} (3) archeological and skeletal evidence for increased hunting and meat eating,\textsuperscript{31,32} and (4) the rapid expansion of hominids from Africa to other parts of the Old World.\textsuperscript{15}

Table 2 shows trends in brain size and body weight among hominin species over the last 4 million years.\textsuperscript{33} 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*. Before this, our earlier hominid ancestors, the australopithecines, showed only modest brain size evolution from 438 to 530 cm$^3$ over a 2-million year span, with all the australopithecines having brain sizes comparable to modern apes. With the evolution of the genus *Homo* there is rapid change, with brains sizes of about 600 cm$^3$ in *Homo habilis* (at 2.4 to 1.6 mya) and 800 to 900 cm$^3$ in early members of *Homo erectus* (at 1.8 to 1.5 mya). Furthermore, while the relative brain size of *H. erectus* has not yet reached the size of modern humans, it is outside of the range seen among other living primate species.

Trends in body weight also show a major shift with *H. erectus*. Sex-specific estimates of body weight presented in Table 2 are based on measurements of joint surface areas using predictive equations developed for modern humans and apes from McHenry and colleagues.\textsuperscript{30,34} All of the australopithecine species were small in both mass and stature. It is not until *H. erectus* that we have body sizes comparable to modern humans.

Similarly, despite that fact that australopithecines were clearly bipeds, they retained their ape-like body proportions—having relatively elongated arms and shortened legs. In contrast, with *H. erectus* we have human-like body proportions, suggesting a striding gate comparable to modern humans, facilitating movement over larger areas.\textsuperscript{30}

These trends clearly suggest major energetic and dietary shifts: (1) the large body sizes necessitating greater daily energy needs; (2) bigger brains suggesting the need for a higher quality diet; and (3) changes in the face, teeth, and tools, 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 facial/dental 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 E. Africa between 2.0 and 1.8 mya was continuing to become drier, creating more arid grasslands.\textsuperscript{35–37} Such changes in the African landscape likely made animal foods an increasingly attractive resource for our hominin ancestors.\textsuperscript{32,38}

This can be seen by looking at the differences in energetic productivity between modern-day woodland and savanna ecosystems of the tropics. Table 3 shows the levels of primary (plant), secondary (herbivore), and tertiary (carnivore) productivity in the 2 ecosystems.\textsuperscript{39} Note that while the overall level of primary productivity in the savanna is only ~56% that of the woodland (4050 vs. 7200 kcal/m$^2$/year), secondary productivity (ie, the abundance of herbivores) is almost 3 times that of the savanna (10.1 versus 3.6 kcal/m$^2$/year). 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, seeds, and grasses) 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 and fossil records suggest that this is what occurred with *H. 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 groups.\textsuperscript{31,32}

The other major evolutionary event seen with early *H. 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.\textsuperscript{40} In living species, a central determinant of dispersal distance is territorial needs, or home range sizes.\textsuperscript{41} As noted previously, the strongest correlates of species variation in HR size are body weight, diet, and ecological productivity. With *H. erectus*, all of these parameters changed in direction that would predict larger HR sizes. Using the relationship
between body mass, DQ, and HR size described in Table 1, we have estimated changes in HR size among early hominids. If we assume changes in hominid body mass as shown in Table 2, and a modest shift in DQ with early Homo (i.e., animals foods contributing an additional 5 to 10% of dietary energy), estimated HR sizes of *H. erectus* are 8 to 10 times the size of the earlier australopithecines (~450 hectares in *H. erectus* vs. 40 to 50 hectares in the later australopithecines).14

The ecological changes associated with the expansion of the African grasslands appear to have produced changes in foraging behavior and dietary quality that helped to provide the energetic fuel to support the rapid evolution of both brain size and body size. In addition, the changes in body size, diet, and ecological productivity all would have contributed to greater HR needs and dispersal potential.

This adaptive package seen with *H. erectus* highlights the evolution of key nutritional characteristics that are distinctly human relative to other primates: (1) the evolution of our large brains, requiring a higher quality, nutritionally dense diet, and (2) increased body size, and the adoption of foraging strategy that necessitated movement of large ranges requiring high levels of daily energy expenditure.

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 and colonize the globe was, in large measure, dependent upon developing strategies and technologies for further 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: (1) technological and foraging changes;31 (2) the development of cooking;42 (3) the origins of agriculture;43 and (4) the development of novel food processing/preparation techniques, such as the alkali processing of maize in the Americas and potato processing/preservation in the Andes.44

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

### Table 2  Geological Ages (Millions of Years Ago), Brain Size (cm³), and Estimated Male and Female Body Weights (kg) for Selected Fossil Hominid Species

<table>
<thead>
<tr>
<th>Species</th>
<th>Geological age (mya)</th>
<th>Brain size (cm³)</th>
<th>Male (kg)</th>
<th>Female (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. afarensis</em></td>
<td>3.9–3.0</td>
<td>438</td>
<td>45</td>
<td>29</td>
</tr>
<tr>
<td><em>A. africanus</em></td>
<td>3.0–2.4</td>
<td>452</td>
<td>41</td>
<td>30</td>
</tr>
<tr>
<td><em>A. boisei</em></td>
<td>2.3–1.4</td>
<td>521</td>
<td>49</td>
<td>34</td>
</tr>
<tr>
<td><em>A. robustus</em></td>
<td>1.9–1.4</td>
<td>530</td>
<td>40</td>
<td>32</td>
</tr>
<tr>
<td><em>Homo habilis</em></td>
<td>1.9–1.6</td>
<td>612</td>
<td>37</td>
<td>32</td>
</tr>
<tr>
<td><em>H. erectus</em> (early)</td>
<td>1.8–1.5</td>
<td>863</td>
<td>66</td>
<td>54</td>
</tr>
<tr>
<td><em>H. erectus</em> (late)</td>
<td>0.5–0.3</td>
<td>980</td>
<td>60</td>
<td>55</td>
</tr>
<tr>
<td><em>H. sapiens</em></td>
<td>0.4–0.0</td>
<td>1350</td>
<td>58</td>
<td>49</td>
</tr>
</tbody>
</table>

*Note.* Adapted from ref. 33.

### Table 3  Productivity of Modern Tropical Forest/Woodland and Savanna Ecosystems

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Primary productivity (kcal/m²/yr)</th>
<th>Herbivore (2°) productivity (kcal/m²/yr)</th>
<th>Carnivore (3°) productivity (kcal/m²/yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest/woodland</td>
<td>7200</td>
<td>3.6</td>
<td>0.03</td>
</tr>
<tr>
<td>Savanna</td>
<td>4050</td>
<td>10.1</td>
<td>0.08</td>
</tr>
</tbody>
</table>

*Note.* From ref. 19.
Figure 6 — Mean BMIs (kg/m²) of adult men from selected subsistence-level populations and industrialized nations. The average for the subsistence-level groups is significantly less than that of the industrialized world sample (21.7 ± 1.8 vs. 26.1 ± 1.8 kg/m²; $P < .001$). Adapted from ref. 45.

Figure 7 — Mean BMIs (kg/m²) of adult women from selected subsistence-level populations and industrialized nations. The average for the subsistence-level groups is significantly less than those of the industrialized world sample (21.9 ± 2.0 vs. 25.7 ± 2.1 kg/m²; $P < .001$). Adapted from ref. 45.
societies, subsisting on a mix of plant and animal foods. Over our evolutionary history, we have been quite successful in developing strategies for meeting our nutritional needs; however, when we look at our modern industrialized societies, it appears that our nutritional strategies have been a bit too successful. That is, we have become so efficient in obtaining energy with minimal time and effort that we have created ever-larger positive energy balances.

Figures 6 and 7 show patterns of variation in mean BMI among men and women of several subsistence-level populations (foragers, pastoralists, and agriculturalists) and industrialized nations. Among males, the BMIs of all but one of the subsistence-level groups cluster in the ‘healthy range’ (span = 18.2 to 24.2 kg/m²), and the average for the subsistence societies is significantly less that the average for the 7 industrialized nations (21.7 vs. 26.1 kg/m²; P < .001). The patterns are similar for women. For those of the subsistence-level populations, BMIs span from 18.1 to 24.6 kg/m² and are, on average, significantly lower than those in the industrialized world (mean = 21.9 vs. 25.7 kg/m²; P < .001).

In the United States, the trends in BMI are particularly troubling, as evidenced by the dramatic increases in the prevalence of obesity over the last 50 years, based on the NHANES data. Table 4 shows changes in the prevalence of obesity (BMI ≥ 30.0 kg/m²) in the US between 1960 and 2008. During this span, rates of obesity have tripled in US men and more than doubled in women. As of 2008, approximately a third of all Americans were classified as obese: 32.2% of men and 35.5% of women.

Currently there is great debate over which forces are most responsible for promoting the growing rates of obesity in the US. For example, increasing use of air conditioning, greater urban sprawl, and decline rates of cigarette smoking have all been suggested as contributing factors; however, the 2 factors most often cited for the dramatic increases in obesity rates in the US are (1) the ever-greater availability of inexpensive high calorie/high fat food items, and (2) expansion of portion sizes. 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 relatively modest increases in energy consumption over the last 40 years. Table 5 presents mean daily energy intakes, body weights, and the ratios of energy intake to estimated RMR (EI:RMR) for adult men and women between 1971 and 2006, derived for the US NHANES data. Over this period, when body weights and obesity rates were dramatically increasing, daily energy intakes increased by 188 kcal in men and larger ~243 kcal in women.

In addition, from these data it appears that all of the increase took place between the NHANES II (1976–80)
and NHANES III (1988–94) surveys. This is notable because there was a change in the methods used to assess dietary intake with NHANES III. All of the NHANES surveys rely on single 24-hr dietary recalls to estimate daily energy and nutrient intakes; however, for NHANES I and II, no weekend days were surveyed, whereas, weekends were included in all of the subsequent NHANES surveys.66 Consequently, at least some of the apparent increase in dietary energy intakes between 1980 and 1988 may be attributable to methodological changes that allowed for weekend dietary patterns to be captured.

If we consider only the data collected since 1988, for which we have comparable methods, we find that dietary energy intakes have not kept pace with changes in body weight. As shown in Table 5, mean energy intakes for both men and women are unchanged since 1988, while average body weights have increased by 5.2 kg in men and 4.7 kg in women. When energy intakes are expressed as a ratio of estimated RMRs (from the WHO 2004 predictive equations63), we find that these values have declined over this period. In other words, over the last 20 years, when adult obesity rates have increased by 40 to 50% (see Table 4), the level of physical activity that can be sustained by average daily energy intakes has decreased.

It should be noted that one of the limitations of the dietary recalls used in national surveys such as the NHANES is their systematic underreporting of energy intakes.64 Previous research has shown that levels of underreporting tend to be greater among women, the elderly, and the overweight.64–67 However, Briefel and colleagues have also noted that improvements in the 24-hour recall methodology used in the NHANES surveys since 1988 (ie, improved probes and better visual aides for estimating portion sizes) appear to have reduced levels of underreporting.56,66 Consequently, it appears unlikely that increased levels of underreporting in the NHANES dietary surveys are responsible for explaining the small changes in energy intakes since the early 1970s.

Thus, contrary to what has been argued in the recent nutrition literature,68–70 these data suggest that the obesity epidemic cannot be understood solely by looking at intakes; rather we must also consider energy expenditure levels. Unfortunately, we don’t have good national data on changes in activity and energy expenditure. Because of the difficulty in accurately measuring daily energy expenditure in ‘free-living’ conditions until recently it has been difficult to effectively assess how lifestyle changes influence activity levels and energy expenditure.

However, with the use of techniques, such as doubly labeled water and HR monitoring over the last 20 years, we now have a much better picture of what daily activity and energy expenditure levels look like in both modern urban societies and traditional subsistence-level populations.71–73 In our work on both subsistence and urbanizing indigenous populations, we have found that changes in lifestyle often have a much larger impact on energy expenditure levels than they do on absolute intake levels.72,74–76

We can explore how energy expenditure and activity levels change with modern life by systematically comparing information from modern industrial populations to those collected among traditional food producing societies today. Data on individuals of the industrialized world are drawn on 12 DLW studies recently compiled by the Institute of Medicine for their most recent references on dietary energy intakes.71 The data for human subsistence-level societies are based on the studies of 12 populations that we have recently compiled from the literature.45

Table 6 compares body weight, RMR, total energy expenditure (TEE), and physical activity levels (PAL; TEE/RMR) for men and women of subsistence-level and industrialized world populations. Men of the subsistence-level populations are, on average, 12 kg lighter than their counterparts from the industrialized world (P < .001), and yet have TEEs that are ~140 kcal greater. Thus, we find that men of subsistence sample have physical activity levels that significantly higher than those of the industrialized world (PALs of 1.98 vs. 1.73; P < .05).

The pattern is similar, although somewhat less dramatic for women. Those of the subsistence-level group are 8 kg lighter (P < .001) and yet have TEEs that are ~90 kcal more than those of their industrialized world peers. PAL values among women average 1.88 among

### Table 6 Comparison of Body Weight (kg) Resting Metabolic Rate (RMR; kcal/day), Total Energy Expenditure (TEE; kcal/day), and Physical Activity Level (PAL) of Adult Males and Females of Subsistence-Level and Industrial Societies

<table>
<thead>
<tr>
<th>Measure</th>
<th>Subsistence</th>
<th>Industrial</th>
<th>Subsistence</th>
<th>Industrial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight (kg)</td>
<td>58.0 ± 5.5</td>
<td>70.0 ± 6.3***</td>
<td>50.2 ± 6.4</td>
<td>58.6 ± 6.2***</td>
</tr>
<tr>
<td>RMR (kcal/day)</td>
<td>1526 ± 132</td>
<td>1659 ± 201*</td>
<td>1242 ± 103</td>
<td>1300 ± 161</td>
</tr>
<tr>
<td>TEE (kcal/day)</td>
<td>3015 ± 527</td>
<td>2874 ± 601</td>
<td>2325 ± 279</td>
<td>2234 ± 464</td>
</tr>
<tr>
<td>PAL</td>
<td>1.98 ± 0.30</td>
<td>1.73 ± 0.30*</td>
<td>1.88 ± 0.22</td>
<td>1.72 ± 0.33*</td>
</tr>
</tbody>
</table>

Note. All values are Mean ± SD. Differences between the subsistence and industrialized world samples are different at *P < .05; **P < .01; ***P < .001.
Leonard

the subsistence-level societies, significantly more than
the 1.72 level for the industrialized world sample \((P < .05)\). For both sexes, the PALs of the subsistence groups
suggest intense/vigorous lifestyles, whereas those of the
industrialized world fall at the low end of the 'moderate' lifestyle category.\(^63\)

Table 7 presents the energetic implications of
industrialized world adults shifting to an activity
budget comparable to that of a subsistence farmer or
forager; that is the additional energy costs if they were
to “match” the PAL level for a subsistence level popu-
lation. For a man of 70 kg, this shift would correspond
to an increase in daily energy expenditure of 411 kcal.
For women of 58.6 kg, this would involve an additional
210 kcal/day. These differences in daily energy demands
underscore how the reductions in physical activities have
dramatically lowered the metabolic costs of survival in
the modern world.

In this context, we can ask the question of how much
discretionary activity would have to be added to our daily
lives to more closely approximate the PALs of more tra-
ditionally living societies? Table 8 presents the energetic
implications of 3 different activity regimes for adult men
and women, compared with the differences estimated
between industrialized and subsistence lifestyles. The
first activity regimen is based on the American College
of Sports Medicine (ACSM) and the American Heart
Association (AHA) recommendations of 150 minutes of
moderate intensity exercise per week (ie, 30 minutes, 5
times/week).\(^77\) The second is the US Institute of Medi-
cine’s recent recommendations of an hour/day of mod-
erately intense exercise, as derived their recent Dietary
Reference Intakes.\(^71\) Finally, the third column presents
the energetic implications of adding a full hour per day
of intense aerobic exercise to one’s activity budget. The
differences between the ASCM/AHA and IOM recom-
mendations reflect the differences in their goals. The
ACSM/AHA guidelines are geared toward promoting
fitness and reducing chronic disease risks, whereas the
IOM’s recommendations are concerned with maintenance
of energy balance and prevention of weight gain.

We find that replacing an hour of sitting with moder-
ate intensity aerobic exercise results in a corresponding
energy increase of 190 kcal/day for men and 152 kcal/day
for women. A full hour intense exercise raises a man’s
energy budget by 330 kcal/day and a women’s by 260
kcal. At this level, the women’s energy budget exceeds
that of her subsistence-world counterparts.

The comparisons are explored in greater detail in
Figure 8, which presents the additional daily energy costs
(kcal/day) associated with the 4 activity regimes in Table
8 for men and women of different body weights. For
men, the shift to a subsistence lifestyle would require the
most additional energy, approximately 350 to 510 kcal/
day, depending on weight. Adding 1 hour/day of intense
exercise to their activity budgets would produce slightly
lower increases of 290 to 410 kcal/day. The IOM’s rec-
mendations would produce increases of 170 to 240
kcal/day, whereas those of the ACSM/AHA would require
+60 to +85 kcal/day.

For women, adding 1 hour of intense exercise to
their daily activity budgets produces the largest increases
in energy demands (+235 to +322 kcal/day), ~50 to 65
kcal more than what the shift to a subsistence lifestyle
would require (185 to 260 kcal/day). The IOM’s rec-
mendations would require increases of 140 to 190 kcal/
day, while those of the ACSM/AHA would imply an
additional 50 to 70 kcal/day.

These findings help to frame current recommenda-
tions on daily physical activity in a broader, comparative

Table 7  Changes in Total Energy Expenditure (TEE; kcal/day) Associated With Shifting From
the Physical Activity Levels of Industrialized World Populations to Those of Subsistence Level
Populations\(^a\)

<table>
<thead>
<tr>
<th>Sex</th>
<th>Weight (kg)</th>
<th>TEE-Industrial (kcal/day)</th>
<th>TEE-Subsistence (kcal/day)</th>
<th>Difference (kcal/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>70.0</td>
<td>2874</td>
<td>3285</td>
<td>+411</td>
</tr>
<tr>
<td>Female</td>
<td>58.6</td>
<td>2234</td>
<td>2444</td>
<td>+210</td>
</tr>
</tbody>
</table>

\(^a\) PALs of Industrialized populations are 1.73 for males and 1.72 for females. Those of subsistence-level populations are 1.98 and 1.88 for males
and females, respectively.

Table 8  Energetic Consequences (Extra kcal/day) of Adding Various Amounts of Exercise to the
Daily Activity Budgets of Typical Adult Men and Women of the Industrialized World\(^a\)

<table>
<thead>
<tr>
<th>Alternative activity recommendations</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACSM/AHA [150 min Mod/wk] (kcal/day)</td>
</tr>
<tr>
<td>-------------------------------------</td>
</tr>
<tr>
<td>Male</td>
</tr>
<tr>
<td>Female</td>
</tr>
</tbody>
</table>

\(^a\) Baseline PALs of Industrialized populations are 1.73 for males and 1.72 for females. Physical activity ratios (PARs) of moderate exercise = 4.0;
intense exercise = 6.0; sitting = 1.2 (see ref. 63).
and evolutionary perspective. Although it is not realistic to recommend that all Western world adults match the activity budgets of their subsistence world peers, the analyses presented here show that targeted lifestyle modifications have the potential to bring typical energy expenditure levels of industrialized world populations surprisingly close to those seen among more traditionally-living rural populations. We often view the lives and work habits of ‘traditional’ populations as being vastly (qualitatively) different from our own. The analyses presented in Table 8 show that this is not the case.

These results also underscore an important feature of physical work among most traditional societies—that much of the daily work is done at a slow-to-moderate pace. Consequently, the high levels of physical activity found in traditional societies generally reflect the sustained modest increases in metabolic intensity over large portions of the waking day, rather than very high intensity work outputs in short bouts.

This observation has direct implications for our urban societies, because it supports a “slow and steady” approach to promoting healthier lifestyles with greater activity. That is, you don’t have to be exercising at near maximal capacity to gain the benefits of greater daily activity.

Summary and Conclusions

From the perspective of evolution, it appears that many of today’s ongoing processes of change in diet and activity are not new, but an extension of adaptive trends witnessed throughout human evolution. These include (1) increasing the nutritional density of our diets, while (2) 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.”

In addressing the growing obesity problem around the world, too much attention is often paid only to the consumption side of the energy balance equation. In this light, it is encouraging to see the recent Institute of Medicine’s dietary and nutritional guidelines include recommendations on physical activity. Yet, there remains considerable debate about how much physical activity is necessary to promote a healthy lifestyle. As suggested from the analyses presented here, I believe that this is an issue that we can and should address from a comparative, ecological, and evolutionary perspective, looking at the range of energy needs and activity levels of more-traditionally living societies to give us better sense of the level of exertion and metabolic demands for much of our evolutionary history.
In conclusion, an evolutionary approach offers to provide important insights into the origin and nature of human chronic health problems. It provides a framework for both evaluating the ways in which our distinctive energy and nutritional demands are “at odds” with dimensions of our modern world, and formulating changes that specifically address those “imbalances.”

Like other primates we are omnivores who can subsist on a diverse and eclectic mix of foods. However, our disproportionately large brains necessitate that the quality and nutritional density of our foods be higher than those of our primate kin. In addition, 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. In this context, the problems of “over-nutrition” currently seen the US and around world 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.

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