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CHAPTER 8

Human Energetics

J. JOSH SNODGRASS

INTRODUCTION

What Are the Big Questions?

- How does an energetics perspective provide a better understanding of key adaptive shifts in human evolution such as the development of bipedalism and enlarged brain size?
- How do environmental stressors such as extreme cold and a low-energy ecosystem shape trade-offs in the energy allocated to different physiological functions?
- What cultural and behavioral strategies do human populations use to extract energy from the environment, and what contributes to population differences in energy expenditure and physical activity?
- How does the process of Westernization lead to shifts in energy dynamics, and what are the consequences for health?

Energetics—the study of the use and transfer of energy—provides a powerful tool with which to examine an array of issues central to human evolutionary biology. Energy is a fundamental limiting resource, occupying a central position between an organism and its environment. How energy is extracted from limited environmental resources and allocated to various somatic functions has consequences for health, survival, and reproduction (McNab 2002; Ellison 2003). Energy used for basic survival costs, such as **basal metabolic rate** (BMR), physical activity, or **thermoregulation**, cannot be used for productive costs such as growth, reproduction, or storage of calories as fat (see Fig. 8.1). The study of energy dynamics provides a means by which to operationalize **life history** theory, the branch of evolutionary biology that focuses on **trade-offs** in the allocation of finite resources in order to maximize **fitness** under different ecological circumstances (Stearns 1992; Hill and Hurtado 1996; Chapter 11 of this book). In turn, life history theory, with its emphasis on variables

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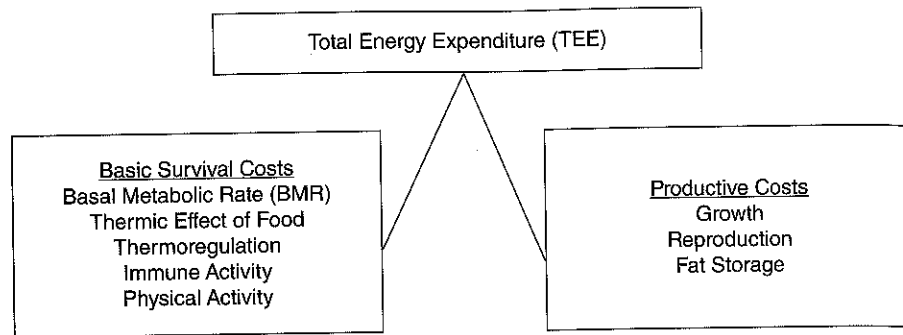


Figure 8.1 Components of total energy expenditure (TEE), showing metabolic costs associated with basic survival (basal metabolic rate [BMR], thermic effect of food, thermoregulation, immune activity, and physical activity) and production (growth, reproduction, and fat storage). Reproduced from Snodgrass and Leonard (2009).

such as age at **maturity**, growth rate, **fecundity**, and **life span**, provides an explanatory framework for human demographic patterns (Bogin 2001).

Human energetics is today a growing area of biological anthropology, and is rapidly expanding in its application as it increases in theoretical and methodological sophistication. Issues in human evolutionary biology that are currently being addressed using an energetics approach include the ecology and evolution of ancestral humans, including topics such as the origin of bipedalism and **encephalization** in the genus *Homo*; the increasing global **prevalence** of obesity and associated **chronic degenerative diseases**; life history trade-offs and the evolution of human growth patterns; human adaptation to climatic conditions, such as cold stress and **hypoxia**; and the influence of diet and physical activity on reproductive function.

In the present chapter, I use an evolutionary biocultural perspective to review the state of the science in human energetics. I begin with an introduction to human energetics, describing the basic principles of energy transfer within an ecosystem. I then describe the components of the human energy budget, and discuss the laboratory and field techniques used to measure different energetic parameters. I then turn to focus attention on two key topics in human energetics research: (1) human evolutionary history and (2) human adaptation, concentrating on adaptation to environmental **stressors** and biocultural dimensions of human adaptive strategies. I conclude with a discussion of energetics and health, paying particular attention to how contemporary lifestyle transitions, such as urbanization and economic development, lead to fundamental shifts in energy dynamics that shape contemporary patterns of human health and disease.

ANTHROPOLOGY AND ENERGETICS

A hallmark of anthropology is its integrated, holistic approach, which combines a comparative, evolutionary perspective with recognition of the extent to which human biology is shaped by social and ecological factors. The evolutionary approach allows us the ability to interpret contemporary human biology through an understanding of the biology of closely related species and, additionally, provides perspec-

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tive by framing the biology of humans in contemporary industrialized societies with an understanding of the extent of variation seen in human populations worldwide. Furthermore, when addressing contemporary health issues, an evolutionary approach is essential for establishing “normal” parameters in clinical practice, as has been recognized by the growing field of evolutionary medicine (Gluckman et al. 2009). For example, recent studies of reproductive ecology among non-Western populations supply data on the typical range of variation in human populations, and provide information with which to interpret female reproductive physiology in Western clinical settings (Ellison 2008; Ellison and Jasienska 2009; Chapter 15 in this book). Instead of a simplistic view of “normal” versus “pathological,” a more sophisticated understanding comes from the recognition that human ovarian function is highly sensitive to energetic conditions and that relatively small changes in energy expenditure, energy intake, or energy stores can impact ovarian **hormone** levels, which in turn can affect fecundity (the biological ability to reproduce). Thus, in response to current energy dynamics, there is a facultative modulation of ovarian hormones, which affects the likelihood of conception, and is consistent with an evolutionary life history approach that predicts that energy allocation will be adaptively tuned to optimize reproduction within particular environmental conditions.

The anthropological approach also uses a biocultural framework, which considers the dynamic interactions between social and ecological factors in shaping human biology. The merits of this biocultural approach are evident in the studies of human energetics, since cultural factors shape how populations extract energy from the environment and allocate it to various functions at the level of the individual and the group. This focus on social components of energetics provides us with insights into how cultural practices can have implications for health, survival, and reproduction. Examples include the cultural strategies that allow horse, reindeer, and cattle herders to extract food resources from the low-energy ecosystem of the Siberian *taiga* (boreal forest) (Leonard et al. 2002a; Crate 2006) (see Fig. 8.2), and the social



Figure 8.2 Evenki reindeer herders from the central Siberian *taiga* of Russia. Photo by W.R. Leonard.



Figure 8.3 After transporting the roots from their garden, *Ribeirinha* women sit together to peel manioc roots, the first major step in processing the staple crop. Photo by B.A. Piperata.

support system that allows lactating *Ribeirinha* (a term for rural Amazonian women of mixed Portuguese, Native Amazonian, and African ancestry) women from Brazil to minimize subsistence work and **physical activity levels** (PALs) during the time of intense energy stress immediately following childbirth (Piperata 2009) (see Fig. 8.3).

The explanatory power inherent in an integrated approach that combines evolutionary and biocultural elements is well illustrated by studies of the evolution of **lactase persistence** (the ability to digest the milk sugar **lactose** into adulthood) in northern Europeans and African pastoralist populations. This **genetic adaptation**, which evolved independently on multiple occasions, can only be fully understood as a **gene-culture coevolution**, with a cultural change to subsistence cattle-herding selecting for individuals able to digest milk and other dairy products into adulthood (Bersaglieri et al. 2004; Tishkoff et al. 2007; Chapter 7 of this book).

BASIC PRINCIPLES OF ENERGETICS

The foundation of the energetics approach is **energy transfer**—namely how chemical energy is extracted from foods and transformed into energy that is usable for muscular work and other somatic functions. According to the **law of the conservation of energy** (first law of thermodynamics), energy cannot be created or destroyed but instead can be converted from one form to another. The ultimate source of energy in nearly all environments on Earth is **photon** energy from the sun, which is captured by plants during **photosynthesis**. Plants serve as the **primary producers** in virtually all ecosystems, as they convert the sun's energy into chemical energy (see Fig. 8.4). Plants are then consumed by herbivorous animals (**primary consumers**),

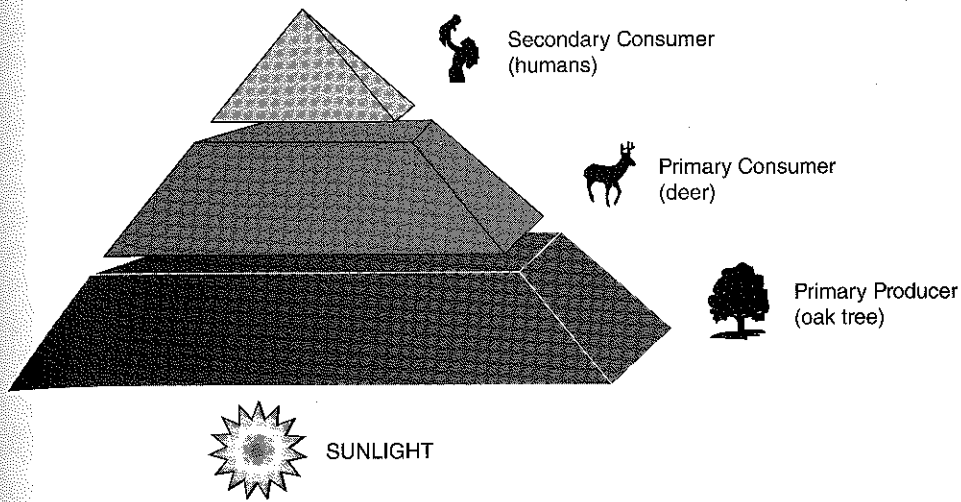


Figure 8.4 Simplified ecological pyramid, showing a terrestrial food chain with a deer consuming oak tree acorns, and humans, in turn, consuming the deer. Note that like all ecological pyramids, energy is lost with each step up the food chain as a result of trophic inefficiency.

and these animals are, in turn, consumed by other animals that eat herbivores (**secondary consumers**); in some environments, this continues with **tertiary consumers**—carnivores that primarily consume other carnivores (Campbell and Reece 2005; McElroy and Townsend 2009). The field of **ecology** focuses on interactions among organisms, and between organisms and their physical environments. Each species occupies a particular **trophic level** (or feeding level), which is connected to other trophic levels in an ecosystem by a food chain. Most organisms participate in multiple food chains, which interconnect in complex food webs. Energy is lost rapidly with increasing trophic position since 80–95% of the available energy at each trophic level is lost at the next step up the food chain (Campbell and Reece 2005). Consequently, very little (approximately 0.1%) of the chemical energy of photosynthesis is available to tertiary consumers. This limits the length of food chains, and contributes to relatively low population numbers and low overall biomass among top-level predators.

Energy obtained from food is used for three main purposes: (1) the synthesis of cells, tissues, and other organic materials (**biosynthesis**) (e.g., **proteins** and lipids); (2) somatic maintenance (sometimes referred to as “internal work”), such as is necessary for respiratory, circulatory, and nervous system activity; and (3) muscular work to allow physical activity (sometimes referred to as “external work”) (Hill et al. 2008) (see Fig. 8.5). Heat is generated as a by-product of the metabolic conversion of food into energy during each step of energy transfer because energy transformation is always incomplete (i.e., inefficient), with the consequence that high levels of heat are produced in mammals and other homeotherms. Animals are thus required to eat regularly in order to provide a continuous source of chemical energy because of the constant use of energy for cellular growth and repair, maintenance, muscular work, and the inevitable loss of heat during energy transfer.

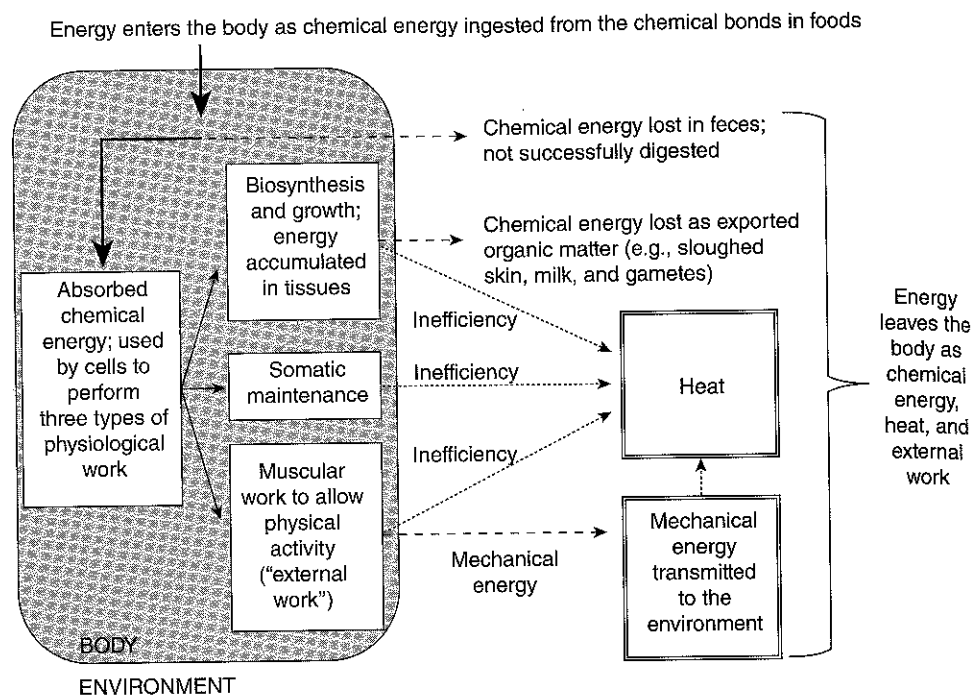


Figure 8.5 Simplified illustration showing energy flow in humans, depicting the pathways from energy ingested as chemical energy from foods to physiological work to energy lost as heat from the body. Note that heat is generated in all types of physiological work. Adapted from Hill et al. (2008).

Metabolism

The rate of energy turnover (i.e., the rate of conversion of chemical energy in foods to energy for biosynthesis, somatic maintenance, muscular work, and heat) is known as the **metabolic rate**, and is expressed as calories or joules per unit time. The **calorie**, technically a measure of heat (1 cal being the amount of heat necessary to raise 1 g of water 1°C), is the traditional measure, with **kilocalorie** (or Calorie; 1000 cal) being the commonly used unit in the United States. The international system of units (SI) uses joules (a measure of energy) and watts (a measure of rates of energy use over time; 1 W = 1 J/s). The conversion of calories to joules is

$$1 \text{ kcal} = 4.186 \text{ kJ.}$$

An animal's metabolic rate is shaped by a variety of factors, including body size, age, sex, activity level, and environmental temperature. As discussed in more detail in Chapter 7, the close relationship between body size and metabolic rate has been recognized since the pioneering work of Kleiber (1932) and Brody and colleagues (Brody et al. 1934), who documented a strong association between body mass and **resting metabolic rate** (RMR) among small to large mammals (i.e., the "mouse-to-elephant curve") (see Fig. 7.3). More recently, studies of wild populations have

demonstrated that body size is less than expected for low metabolic rates. This has implications for understanding the evolution of primates and other mammals (1994; Ai...

Dietary

Oxidative metabolism of molecules from food (digested) to produce ATP is a primary source of energy for cellular work. Carbohydrates (sugar) are primarily used during periods of sunlight for storing energy...

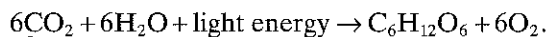
After ingesting food, energy is placed in the body to energy and water...

This process is available to be used by energy bonds of approximately 1000 kcal per day. This is a significant amount of energy for cellular work (Guyton et al. 2002). The energy of transport is supplied by...

demonstrated that **total daily energy expenditure** (TDEE) is also closely related to body size (Nagy 2005). Importantly, metabolic rates among mammals scale at a rate less than proportional with body mass, meaning that large mammals have relatively low metabolic rates and small mammals have relatively high metabolic rates. This has implications for physiology and ecology, and a large body of research has documented links between body size, intensity of living, and diet (Gaulin 1979; McNab 2002; Snodgrass et al. 2007a). The comparative perspective on metabolic rates has shown that humans have maintenance costs that are broadly similar to nonhuman primates and other mammals, which has formed the basis for research on key dietary and body composition changes during human evolution (Leonard and Robertson 1994; Aiello and Wheeler 1995).

Dietary Sources of Energy

Oxidation by **aerobic** respiration is the process by which energy-rich organic molecules found in dietary sources are combusted in the presence of oxygen (i.e., oxidized) to convert energy to a more stable and usable form. **Adenosine triphosphate** (ATP) is a molecule composed of adenine (a nitrogenous **base**), ribose (a sugar), and three phosphate radicals (connected by high-energy phosphate bonds). It is primarily formed by the oxidation of **glucose** during **cellular respiration** and used for cellular storage and transfer of energy and, ultimately, to perform physiological work (Campbell and Reece 2005; Guyton and Hall 2006; Freeman 2010). The simple sugar glucose ($C_6H_{12}O_6$) is a key intermediary molecule, being produced by plants during photosynthesis from carbon dioxide (CO_2), water (H_2O), and light energy (sunlight), and used as a building block for carbohydrates, fats, and other energy-storing compounds. The basic formula is



After ingestion and digestion by human consumers, cellular respiration, which takes place in the mitochondria, transforms organic compounds in foods such as glucose to energy through chemical reactions with oxygen; this process also produces CO_2 and water. The equation for the breakdown of glucose is



This process releases chemical energy found in foods (here, glucose) and makes it available for the formation of ATP. For glucose, 686,000 cal of free energy is liberated by the oxidation of 1 mol (180 g) of glucose (Guyton and Hall 2006). The energy from the oxidation of foods is then stored in the high-energy phosphate bonds of ATP, each of which under standard physiological conditions contains approximately 12,000 cal of energy per mole of ATP. ATP serves as the most important energy currency in the body, is present in all cells, and provides energy for cellular processes such as biosynthesis, membrane transport, and muscle contraction (Guyton and Hall 2006).

There is an interchangeability of **macronutrients** as energy sources, as this process of transformation can utilize carbohydrates, proteins, and fats, as well as alcohol, to supply energy for ATP. This is the ultimate basis for dietary flexibility in humans.

Energy leaves the body as chemical energy, heat, and external work

Fats are the most calorically dense of the macronutrients, providing approximately 9 kcal/g (37 kJ/g), while protein and carbohydrates each provide approximately 4 kcal/g (17 kJ/g) of energy. Alcohol provides energy at approximately 7 kcal/g (29 kJ/g), but it is not a useful source of energy or nutrition due to its toxic properties and lack of vitamins and minerals. The single largest energy source among economically developed populations today is carbohydrates, with recent data from the United States (National Health and Nutrition Examination Survey [NHANES] 1999–2000) showing that over 50% of calories come from carbohydrates, 33% from fat, and only 15% from protein (Wright et al. 2003). Subsistence populations show extensive variation in dietary macronutrient composition, with some agricultural groups consuming very low protein (<10%), high carbohydrate (>80%) diets, and many high-latitude hunter-gatherer groups consuming very low-carbohydrate (<10%), high-protein (>40%), high-fat (>40%) diets (Ulijaszek 1995; Cordain et al. 2000). There are important consequences of these dietary patterns for health, which are discussed later in this chapter.

Energy Balance

The **energy balance** equation (energy balance = energy intake – energy expenditure) describes the interrelationship of energy input and energy output. When energy intake and expenditure are equal, the body is said to be in a steady state. When energy expenditure exceeds energy consumption, the body is in negative energy balance, and body mass in the form of body fat and/or lean tissue is reduced by conversion of tissue to energy. Conversely, when excess dietary energy is ingested above and beyond energy requirements, the body is in positive energy balance, and storage in the form of glycogen and/or fat results. Since fat is the primary energy storage deposit in humans, long-term positive energy balance results in increased adiposity, which increases risk for overweight and obesity.

The extent of energy storage as fat in humans is unusual for tropically adapted terrestrial mammals, such as nonhuman primates who tend to be of low body fat. In non-Western populations, who may be representative of the ancestral human condition, average body fat is 25% in women and 13% in men (Wells 2010). In Western populations with high levels of obesity, such as the United States, these body fat percentages can reach more than 50% in many individuals. It is, however, challenging to interpret the adaptive dimensions of human body fatness since surprisingly little published data are available on body fat in free-ranging (i.e., noncaptive) nonhuman primates. Based on the limited available data, humans are considerably fatter than other primates, although some species (e.g., orangutans) show seasonal increases of body fat (Pond 1998; Wells 2010). The human condition of relatively high levels of body fat begins during fetal and early postnatal life, and appears to be an adaptation to provide nutritional buffering within the context of an unpredictable environment (Kuzawa 1998; Wells 2010). This propensity to deposit fat in good times is highly adaptive, especially in buffering the extremely high energetic costs of the human brain during lean times (Leonard et al. 2003; Snodgrass et al. 2009; Wells 2010). However, the human capacity to quickly store fat can be maladaptive within the context of some novel environments, such as in much of the industrialized world with plentiful calories and sedentary occupations. This issue will be discussed in detail below.

ENERGY EXPENDITURE

Total energy expenditure (TEE), sometimes referred to as TDEE, represents the total metabolic costs incurred over a 24-hour period. It includes energy costs associated with processes necessary for survival such as cellular maintenance, thermoregulation, digestion, immune function, and physical activity, as well as, in certain segments of the population, growth, and reproduction.

Maintenance

BMR is one of the primary contributors to the human energy budget. BMR is an estimate of the amount of energy used while a person is in an awake, relaxed state. BMR is the single largest component of energy expenditure in most contemporary human populations, occupying approximately 45–70% of TEE (FAO/WHO/UNU 2004). Because of the major contribution of maintenance costs to the overall human energy budget, and the relative ease and standardization of measurement, maintenance costs occupy a central role in estimates of population-level energy requirements. Body mass is highly correlated with maintenance energy costs, with its lean component (fat-free mass [FFM]) explaining approximately 60–90% of variation (Cunningham 1991). There are modest sex differences in BMR, but most of this can be explained by differences in body size (i.e., men on average are larger than women) and body composition (i.e., men on average have relatively greater amounts of metabolically active lean tissue and women have larger stores of body fat); however, most studies have shown that when controlling for body size and composition, nonpregnant, nonlactating women have a slightly lower BMR than men (Elia 1992a; Arciero et al. 1993). It is not fully understood why this sex difference exists. Also, there is typically a modest age-related decline in BMR that primarily reflects body composition shifts that often occur with age (i.e., increased body fat and reduced lean tissue) (Henry 2000). Finally, genetic factors are also important contributors to variation in maintenance costs both at the individual level and between populations.

Thermic Effect of Food (TEF)

The TEF represents the energy costs above maintenance level that are associated with the digestion, absorption, and oxidation of foods. Studies of Western populations have shown that TEF averages less than 10% of total energy costs (Westerterp 2004). However, composition of the diet has a major effect on TEF, with the most important variable being protein consumption. While carbohydrates and fats induce small and transient metabolic effects, with increases of less than 5% that last for only several hours after a meal, protein has a larger effect with a more protracted duration and consequently makes a greater contribution to the total energy budget. Protein induces metabolic elevations of up to 30% that may not return to baseline for 12 hours. Therefore, although TEF is relatively minimal in Western populations (virtually all of which consume diets with carbohydrates as the largest source of energy), many traditionally living populations consume diets with higher protein content and likely have considerably higher energy costs associated with TEF (Cordain et al. 2000). This is particularly true for northern populations, including

traditionally living Alaskan Inuit, who in the 1950s consumed large quantities of protein on the order of 130–200 g/day (Rodahl 1952; Draper 1977; Schaefer 1981).

Thermoregulation

Thermoregulatory costs are typically divided into two components: obligatory thermogenesis and facultative (or adaptive) thermogenesis. **Obligatory thermogenesis** represents the heat produced as a by-product of energetic processes from maintenance metabolism. When obligatory thermogenesis is sufficient to maintain body temperature, the body temperature is said to be in the **thermoneutral range**, which for unclothed adult humans is 25–27°C (77–81°F). Outside of this range, **facultative thermogenesis** is initiated, which allows the body to maintain **homeostasis**. At cold temperatures, heat-conserving mechanisms such as peripheral **vasoconstriction** are initiated and, if cold continues, metabolic responses follow. Increased heat production is accomplished through short-term metabolic elevation (e.g., voluntary physical activity, **shivering** thermogenesis, and short-term increases in **nonshivering thermogenesis** [NST]) or long-term metabolic upregulation (Hanna et al. 1989; Frisanco 1993). However, while shivering can substantially increase metabolic rate—by two to three times maintenance level—it also increases heat loss due to increased airflow over the body; furthermore, the involuntary nature of shivering limits the ability to perform many tasks essential to daily life. NST can raise metabolic rate substantially in human infants, while in adult humans, the ability to increase metabolic rate through NST appears to be modest (~10–15%). However, the recent confirmation that adult humans can retain functional brown adipose tissue (Schoeller 2001; van Marken Lichtenbelt et al. 2009), a highly thermogenically active tissue involved with NST in many mammals and human infants, is suggestive that greater NST in human adults may be possible under certain circumstances (Snodgrass et al. 2007b).

Research has also documented long-term upregulation of maintenance energy expenditure among indigenous circumpolar populations in Siberia and North America, which appear to reflect a physiological adaptation to chronic and severe cold stress experienced in the harsh northern environment (Roberts 1978; Leonard et al. 2005; Snodgrass et al. 2007b). This is supported by additional studies that have documented seasonally altered BMRs among Northern European and Japanese populations (i.e., higher during the winter months than during the summer) that negatively track environmental temperature (Kashiwazaki 1990; Plasqui et al. 2003). At the other end of the temperature spectrum, high environmental temperatures lead to a variety of physiological changes such as peripheral **vasodilation** and evaporative cooling that increase heat dissipation and help maintain body temperature within tolerable limits (see Chapter 6).

Immune Function

The immune system provides protection against a variety of external (e.g., **infectious disease**) and internal threats (e.g., cancers), but has sizable costs associated with maintenance and activation (McDade 2003). Furthermore, there are consequences when immune processes are misdirected and contribute to allergy, asthma, and **autoimmune disease**. There is surprisingly little information on the energetic costs

of immune function in humans, but several lines of evidence suggest that these costs are sizable. First, the energy costs associated with fever in humans are considerable: for every 1°C increase in **core temperature**, metabolic rate increases approximately 10–15% (Elia 1992b). Furthermore, recent research indicates that even mild respiratory infections without fever can lead to substantial elevations of metabolic rate on the order of approximately 8% (Muehlenbein et al. 2010). Second, several studies are suggestive of high costs of protein synthesis during response to infection in humans, which are related to increased production of inflammatory proteins, leukocytes, and other biomolecules (McDade 2003). Third, research among nonhuman organisms has documented high costs of immune maintenance and activation, including those associated with mounting an **antibody** response (Demas et al. 1997; Martin et al. 2003; Eraud et al. 2005). Finally, human studies indicate that immune function is closely related to nutritional factors, and that shortages of energy and various nutrients, as well as reductions in body fat, can compromise **immunocompetence** (McDade 2003; Demas 2004).

Physical Activity

Physical activity describes the energetic costs associated with voluntary movement and is one of the larger components of the human energy budget. Energy costs of physical activity are typically described over a 24-hour period in energy terms (e.g., kilocalories or kilojoule) as “**activity energy expenditure**” (AEE; commonly estimated as $TEE - BMR$, but sometimes calculated as $0.9 \times TEE - BMR$ to reflect the costs of TEF), or in multiples of BMR. The latter measure, the PAL (estimated as TEE/BMR), is particularly useful in that it minimizes the effects of size and facilitates comparisons between individuals and populations. Physical activity costs vary considerably, but at a population level, the lowest sustained PALs are approximately 1.4, which represents the minimal amount of energy among healthy but essentially sedentary subjects. However, lower PALs (~1.2) are sometimes seen among hospitalized individuals. The upper bounds of sustainable population-level energy expenditure is a PAL of approximately 2.4–2.5, which has been documented in several subsistence groups during peak seasonal energy demands (FAO/WHO/UNU 2004; Shetty 2005). Higher PALs are attainable over a more limited period of time (days or weeks), such as seen among certain competitive athletes in training or competition (~3.5; Black et al. 1996) and in individuals involved in heavy physical labor (>3.0; Diaz et al. 1991). The 3-week Tour de France bicycle race, with PALs of approximately 4.5–5 among elite male cyclists (Westertorp et al. 1986), probably represents the energetic ceiling of short-term sustained human performance. However, these levels, and the energy consumption they require, do not appear to be sustainable as a permanent lifestyle over the course of months or years (Shetty 2005). As discussed in Chapter 7, the most recent FAO/WHO/UNU (2004) assigned PAL ranges to different lifestyle categories: sedentary/light activity (1.4–1.69); active/moderate activity (1.7–1.99); and vigorous/vigorous activity (2.0–2.4), (see Table 7.2).

Individual activities are often described in terms of their metabolic costs above basal levels, with the **physical activity ratio** (PAR) describing the energetic costs of individual activities. These range from sedentary (e.g., sitting quietly or standing, with PARs of 1.2 and 1.4, respectively) to vigorous (e.g., shoveling snow or pulling

a cart with a load, with PARs of 7.9 and 8.3, respectively) (Ulijaszek 1995; FAO/WHO/UNU 2004) (see Table 8.1). Summing the costs of these individual activities and the amount of time spent in each over a 24-hour period allows the calculation of PAL using the following formula:

$$PAL = \left[\sum PAR_i(T_i) \right] / 24,$$

where

PAR_i = physical activity ratio of each activity "i" and

T_i = time spent (hours) in each activity "i."

An alternative to PAR for expressing the intensity of physical activities is the **metabolic equivalent** (MET), which describes the **ratio** of exercising metabolism to RMR for specific activities (Ainsworth et al. 2000). This measure has been gaining in popularity in recent decades as a public health tool (Haskell et al. 2007). METs for various activities are roughly equivalent to PARs, with activities classified by intensity as light (<3.0 METs), moderate (3.0–6.0 METs), or vigorous (>6.0 METs) (Haskell et al. 2007).

One component of physical activity that has attracted considerable attention in recent years is **nonexercise activity thermogenesis** (NEAT) and refers to a variety of postural and nonexercise activities (e.g., fidgeting, talking, or gesturing) that can make up a sizable amount of total daily physical activity (Levine et al. 2005). Since activities such as fidgeting can elevate metabolic rate 20–40% above resting levels, postural differences and other nonexercise activities have the potential to contribute to the risk of overweight and obesity (Levine 2004; Levine et al. 2005). In practice, however, NEAT is difficult to measure as a separate variable from other forms of physical activity, which limits its utility in human population biology.

Growth

Energetic demands change radically during the life cycle as a result of shifts in body size and composition, amount of energy devoted to growth, and the energetic demands of reproduction. The energetic costs of growth in humans, which include the energy costs of synthesizing tissue as well as the energy (in the form of protein and fat) deposited in those tissues, are actually fairly minimal during most of **development** (further discussion is found in Chapter 11). Thus, they occupy a relatively small proportion of total energy requirements except during the earliest stages of life (Norgan 2002; FAO/WHO/UNU 2004). During the first month of life, growth accounts for approximately 40% of daily energy requirements, but drops to less than 2% by year two (FAO/WHO/UNU 2004). The cost of growth is high in early development (especially late fetal life and early infancy), when the rapid deposition of muscle and fat, and the rapid growth of energetically expensive tissues such as the brain, lead to high costs overall. For example, brain metabolism comprises approximately 20–25% of resting energy demands in adult humans, and upward of 60% in infants (Leonard et al. 2003). The relatively small energetic costs of growth per unit

TABLE 8.1 Energy Costs of Various Activities for Males and Females Expressed as Physical Activity Ratios (PARs) with Ranges (When Available)

Activity	Males	Females
	PAR Average (Range)	PAR Average (Range)
Sleeping	1.0	1.0
Lying	1.2	1.2
Sitting quietly	1.2	1.2
Standing	1.4	1.5
Eating and drinking	1.4	1.6
Writing	1.4	1.4
Sewing/knitting	1.6	1.5 (1.3-1.8)
Typing	1.8	1.8
Fishing with a line	1.9	
Peeling vegetables	1.9 (1.3-2.4)	1.5
Driving a car	2.0	
Riding a motorcycle	2.7 (2.4-3.0)	
Walking slowly	2.8 (2.6-2.8)	3.0
Hunting (bats, birds, pigs)	3.2	
Weeding garden	3.3 (2.4-5.1)	2.9 (2.7-3.6)
Carrying 20- to 30-kg load on head	3.5 (2.4-4.2)	
Harvesting rice	3.5 (2.4-4.2)	3.8 (3.5-4.4)
Milking by hand	3.6 (3.1-4.1)	
Cleaning/sweeping yard	3.7 (2.9-4.5)	3.6
Walking quickly	3.8	
Planting maize	4.1	
Chopping wood (for fuel)	4.2 (2.3-6.5)	
Grinding grain with a mill stone		4.6
Hoeing	4.2 (3.6-4.6)	5.3 (4.7-6.5)
Harvesting tubers	4.4 (3.5-5.7)	3.0 (2.8-3.4)
Tending animals (feeding, watering, etc.)	4.6	
Ploughing with horse	4.8	
Climbing stairs	5.0	
Carrying 27-kg load with shoulder straps	5.0 (2.3-7.7)	
Harvesting maize	5.1	
Cycling (moderate speed)	5.6 (3.8-8.6)	3.6
Digging	5.6	5.7
Long-distance running	6.3	6.6
Cutting trees	6.9 (5.4-8.0)	
Walking uphill	7.1 (5.5-8.6)	5.5 (4.8-6.1)
Pulling a rickshaw (two-person load)	7.2 (6.7-7.8)	
Shoveling snow	7.9	
Sprinting	8.2	8.3
Pulling handcart with 185- to 370-kg load	8.3 (7.0-9.6)	

Source: FAO/WHO/UNU (2004).

tissue can be contrasted with the high costs of the continuous cellular metabolism of existing cells and tissues. The high costs of cellular maintenance—and the costs associated with disruption—helps explain why growth is so sensitive to energetic disruptions (see Chapter 12) and why body fat stores in humans are already so well developed at birth. An example is the rapid growth that occurs during the **adolescent growth spurt**. At this time, the relative costs of growth are fairly small (well below 10%) compared with the overall energy expenditure required to maintain the relatively large **adolescent** body. Chronic or acute **undernutrition** at the time of adolescence can, however, delay the onset of the growth spurt and/or decrease its intensity or duration (Bogin 1999).

Despite the relatively low energetic costs of growth during most stages of ontogeny, human growth is extremely sensitive to positive and negative environmental conditions, including social factors that affect energetic conditions (see Chapter 12). This **plasticity** appears to optimize growth under particular environmental conditions, but there are limits and pathological growth (e.g., stunting or obesity) is also a risk. Sensitivity to environmental conditions begins in early life, where a variety of studies have indicated developmental programming that permanently changes structure, physiology, and metabolism under conditions where energy and nutrient demands exceeds maternoplacental supply (Gluckman and Hanson 2004; Chapter 11 of this book).

Human plasticity in growth can be viewed through a life history framework that considers the high costs of immune defenses within a high disease environment, coupled with decreased energy availability, leading to less energy and fewer nutritional resources available for growth. In fact, recent research has indicated that early exposure to helminths (**parasitic** worms) alter energy dynamics in profound and lasting ways, shifting energy toward humoral (antibody) helminth defense and away from other demands such as growth and other types of immune function (e.g., inflammatory responses) (Blackwell et al. 2010). In response to more favorable environmental conditions, such as lower infectious disease burden and better nutritional resources, generational or **secular trends** can be seen with better growth (e.g., as measured in adult height) and a shifting of resources to reproduction (with earlier sexual maturation, as measured by age at **menarche**) (Bogin 1999; Johnston 2002; Norgan 2002; Chapter 12 of this book).

Reproduction

The energetic costs of pregnancy and lactation are relatively high in humans, with human females bearing the primary metabolic burden of conception and gestation. During pregnancy, energy requirements above maintenance costs are needed for growing the fetus and placenta, growth in size of various maternal tissues (e.g., the breasts and uterus), and deposition of body fat (FAO/WHO/UNU 2004). Optimal weight gain during pregnancy is defined based on healthy birth outcomes; typical weight gain associated with healthy birth weight babies varies by individual and population but is typically 10–14 kg. Energy costs are not equal throughout pregnancy, and recent estimates of average energy costs from the FAO/WHO/UNU (2004) reflect the increasing costs of advancing pregnancy: 85 kcal/day (356 kJ/day) during the first **trimester**, 285 kcal/day (1193 kJ/day) during the second trimester,

and 475 kcal/day (1988 kJ/day) during the third trimester. During lactation, energy costs are also high and include the costs associated with milk production and the energy content of the secreted milk. Recent estimations of average energy costs of lactation (FAO/WHO/UNU 2004) consider shifts in energetic costs over time: 675 kcal/day (2826 kJ/day) with exclusive breast-feeding during the first 6 months of life, and 460 kcal/day (1926 kJ/day) after 6 months (when milk is supplemented with other foods). While these costs are high, energy from fat stores that are accumulated during early pregnancy typically contribute to lactation costs during the first several months.

Multiple energetic variables, not just the extent of energy stored as body fat, influence female reproductive physiology and shape reproductive capacity (Ellison 2003, 2008). As discussed in greater detail in Chapter 15, research among athletes and subsistence populations have demonstrated that in addition to fat stores, both energy balance (i.e., whether gaining or losing weight, and how fast) and **energy flux** (i.e., the rate of energy turnover) influence ovarian function and affect fecundity. This continuum of ovarian function, with facultative modulation of ovarian hormones and fecundity in response to energetic parameters, serves to optimize the energy allocated to reproduction. Energy dynamics can also help explain the duration of lactational **amenorrhea** and the return to fecundity after birth. Recent research has also identified a developmental component of this functional modulation, in which conditions in early ontogeny (e.g., fetal life) shape responses to energetic conditions in adulthood (Jasienska et al. 2006). Finally, changing environmental conditions can influence energy dynamics and have rapid effects on life history patterns. For example, research by Gibson and Mace (2006) has demonstrated that a water development initiative in rural Ethiopia, which reduced the amount of energy spent by women carrying water, precipitated a shift of energy from physical activity to reproduction, led to a higher birth rate, and had the unintended consequence of increasing childhood **malnutrition**.

The relationship between energetics and reproduction is profoundly different among human males who, like most other mammalian males, contribute little direct metabolic effort toward offspring production (Bribiescas 2001, 2006; Ellison 2008; Chapter 15 of this book). Unsurprisingly, men are far less sensitive to energetic stress than women, with measures of male fecundity (e.g., sperm quantity and quality) not closely related to energetic conditions. However, other dimensions of male reproductive effort are closely related to energy dynamics, including somatic investments such as body size and muscularity, which may serve to increase fitness by maximizing mate access. It appears that **testosterone** plays a critical role in modulating life history trade-offs between investment in somatic reproductive effort (e.g., muscularity and various behaviors) and survival and maintenance (e.g., fat deposition and immune function) in response to energetic conditions (Bribiescas 2001; Muehlenbein and Bribiescas 2005; Ellison 2008). Furthermore, males in most human societies contribute substantially to parental care and provisioning, and studies among several subsistence populations suggest that adult males may increase levels of energy expenditure as an indirect contribution to reproduction. For example, research among the Hadza hunter-gatherers (Marlowe 2003) and Shuar forager-horticulturalists (Madimenos et al. 2011) indicates that male partners increase activity levels and food returns to compensate for the increased energetic needs of pregnant or lactating females.

MEASUREMENT OF ENERGY PARAMETERS

Techniques for the measurement of energy expenditure can be divided into direct and indirect approaches. **Direct calorimetry** uses a specialized insulated laboratory to measure heat loss from the body through changes in air temperature (Frisancho 1993; Leonard 2004). While this approach allows extremely accurate measurement of metabolic rate, it requires expensive equipment and, more importantly, it confines the subject to a laboratory chamber that severely constrains their typical daily behaviors. Therefore, while this technique provides an excellent measure of metabolic rate at rest, it cannot provide a long-term measure of typical (i.e., “free-living”) behavior.

In contrast to direct measurement, **indirect calorimetry** measures a proxy of heat loss; most commonly, a metabolic analyzer is used to measure oxygen (O_2) consumption and/or carbon dioxide (CO_2) production as proxies for metabolic rate. This is possible given the known relationship between O_2 consumption and calories—1 L of O_2 is equal to approximately 5 kcal (or 21 kJ). Simultaneous measurement of O_2 consumption and CO_2 production increases the accuracy of metabolic rate estimation because the **respiratory quotient** ($RQ = CO_2/O_2$) provides an estimate of the contribution of different dietary components (i.e., carbohydrates, lipids, and proteins) to metabolism (see Table 8.2), each of which produce slightly different quantities of energy per unit oxygen (see Table 8.3).

TABLE 8.2 Respiratory Quotients (RQs) during Aerobic Metabolism of Different Macronutrients in Humans

Macronutrient	RQ
Carbohydrates	1.0
Fats	0.71
Proteins	0.83

Adapted from Hill et al. (2008).

Source: Kleiber (1975).

TABLE 8.3 Energetic Equivalents (kcal) for Oxygen (O_2 ; Liters) Consumption at Various Respiratory Quotients (RQs)

RQ	kcal/L O_2
0.71	4.690
0.75	4.739
0.80	4.801
0.85	4.862
0.90	4.924
0.95	4.985
1.00	5.057

Adapted from Leonard (2010).

Source: McArdle et al. (2001).

Measuring Maintenance Costs

Maintenance energy costs are typically measured in humans as BMR (kilocalories per day). BMR is measured under standardized conditions: with the participant lying still, awake but relaxed, not under emotional stress, in a postabsorptive condition (after a 10- to 12-hour fast), and in a thermoneutral environment (Blaxter 1989; FAO/WHO/UNU 2004). Variants of this measure are RMR and sleeping metabolic rate (SMR); the former is typically measured after only a 4-hour fast, while the latter measures the participant during sleep when subjects do not have to maintain energy costs associated with arousal. Although these measures are sometimes used interchangeably, they have distinct meanings. For example, RMR is typically 5–10% higher than BMR because of additional energy costs related to the TEF and residual metabolic costs from earlier physical activity. Furthermore, RMR is generally more variable than BMR and is more difficult to compare across populations (Ulijaszek 1995). SMR usually differs from BMR because metabolic rate drops below “basal” levels during sleep, on average by approximately 5% (Goldberg et al. 1988).

Maintenance energy costs can be measured using direct or indirect calorimetry. The traditional technique for gas exchange, which is still used in some current research, is the Douglas bag technique. This technique uses a specialized valve and collection container to allow the subject to breathe room air, which is then exhaled into the Douglas bag (a plastic bag of approximately 200-L volume); the respired air sample is later analyzed in a laboratory for measurement of total volume as well as O_2 and CO_2 content. Because this bag is cumbersome to use and move about, most studies today are conducted using open-circuit metabolic analyzers that continuously measure respiratory gases (O_2 and CO_2) and ventilation (breathing) rates while the subject breathes ambient air (see Fig. 8.6). Laboratory-based studies are

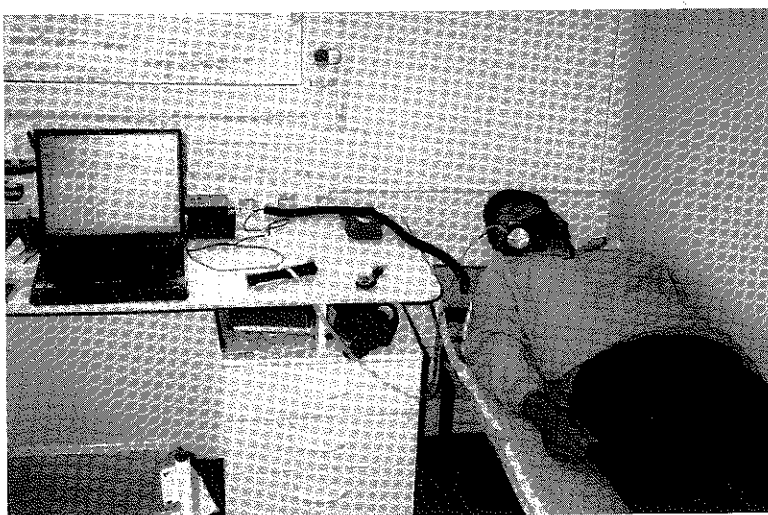


Figure 8.6 Measurement of basal metabolic rate (BMR) using a MedGraphics VO2000 metabolic analyzer, which continuously measures respiratory gases (oxygen and carbon dioxide) and ventilation rates. Photo by W.R. Leonard.

TABLE 8.4 Comparison of Schofield and Oxford Prediction Equations for Estimating BMR (kcal/day) from Body Weight (Wt, in Kilograms)

Age and Sex	Schofield	Oxford
Group	BMR (kcal/day)	BMR (kcal/day)
Males		
0-3 years old	59.5(Wt) - 30	61.0(Wt) - 33.7
3-10 years old	22.7(Wt) + 504	23.3(Wt) + 514
10-18 years old	17.7(Wt) + 658	18.4(Wt) + 581
18-30 years old	15.1(Wt) + 692	16.0(Wt) + 545
30-60 years old	11.5(Wt) + 873	14.2(Wt) + 593
≥60 years old	11.7(Wt) + 588	13.5(Wt) + 514
Females		
0-3 years old	58.3(Wt) - 31	58.9(Wt) - 23.1
3-10 years old	20.3(Wt) + 486	20.1(Wt) + 507
10-18 years old	13.4(Wt) + 693	11.1(Wt) + 761
18-30 years old	14.8(Wt) + 487	13.1(Wt) + 558
30-60 years old	8.1(Wt) + 846	9.74(Wt) + 694
≥60 years old	9.1(Wt) + 659	10.1(Wt) + 569

Source: Schofield equations (Schofield 1985; FAO/WHO/UNU 2004); Oxford equations (Henry 2005).

typically performed using metabolic cart systems, which are highly accurate and reliable; however, this class of metabolic instruments is generally expensive and their size and power needs prohibit use in some field settings. Other metabolic analyzers, including the MedGraphics VO2000 (St. Paul, MN) and the Cosmed K4b² (Rome, Italy), sacrifice some of the accuracy and reliability of metabolic carts but are portable and can be used to measure maintenance costs as well as energy costs associated with individual physical activities.

Most population-level studies, including those designed to estimate nutritional requirements, do not measure maintenance costs directly but instead estimate these costs using published equations that consider variables such as body size (body mass or FFM), age, and sex (e.g., Cunningham 1991; FAO/WHO/UNU 2004; Henry 2005). Predictive equations typically estimate BMR within approximately 10% of measured values. The Schofield (1985) norms (see Table 8.4) were endorsed by FAO/WHO/UNU (1985) and again by the latest expert commission (FAO/WHO/UNU 2004). These equations have been criticized because of sampling issues and their overestimation of BMR in certain populations (Henry 2005). Despite this, the Schofield norms remain the primary prediction equations used today.

Based on a recent meta-analysis of a large number of published BMR measurements (>10,500 participants from 166 studies), a new set of equations (the Oxford equations; Henry 2005) are available for BMR estimation (see Table 8.4). These equations exclude some of the measurements deemed particularly problematic from the Schofield data set, and also include a considerable sample of individuals from the tropics, a group underrepresented in the Schofield data set. Overall, the Oxford equations produce lower BMR values for most adult age groups than those of Schofield.

In addition to prediction equations based on body weight, highly accurate published prediction equations for maintenance costs based on FFM are also available, such as the general predictive equation of Cunningham (1991):

$$\text{RMR (kcal/day)} = 370 + 21.6 (\text{FFM})$$

BMR equations based on FFM, although they require the assessment of fat mass in order to calculate FFM, have two main advantages over those that use body mass. First, they ease comparisons between different populations with diverse body shapes and sizes. Second, a large number of studies have documented that FFM is highly correlated with BMR, explaining approximately 60–90% of BMR variation, and is the best single predictor of BMR (Cunningham 1991; Nelson et al. 1992; Weinsier et al. 1992; Sparti et al. 1997).

Measuring Physical Activity

There are a number of methods currently available for estimating physical activity and TEE in humans outside of a laboratory setting. These include **doubly labeled water (DLW)**, heart rate (HR) monitoring, accelerometry, and time allocation techniques. All have advantages and disadvantages (see Table 8.5), and the choice of the method or methods should be carefully chosen based on the goals of the study, time frame, budget, sample size, and subject population. Studies of physical activity patterns are most useful when assessment covers a long enough period (at least 2–3 days) to obtain information on activity patterns that are typical or representative of daily life.

TABLE 8.5 Advantages and Disadvantages of Different Methods for Estimating Physical Activity

Technique	Data Quality	Activity Structure	Contextual Information	Participant Effort	Participant Interference	Observer Time/Cost
Doubly labeled water (DLW)	1	5	5	2	1	4
Heart rate monitoring (HRM)	3	3	4	4	3	3
Accelerometers	2	1	3	3	2	1
Time allocation (interviews/questionnaire/diaries)	5	4	2	5	4	2
Time allocation (behavioral observation)	4	2	1	1	5	5

Methods are ranked from best (1) to worst (5) according to quality of activity data, information it provides on activity structure, information it provides on the context of activity, extent of participant effort required, interference with participant behavior, and time and cost. Adapted from Westerterp (2009).

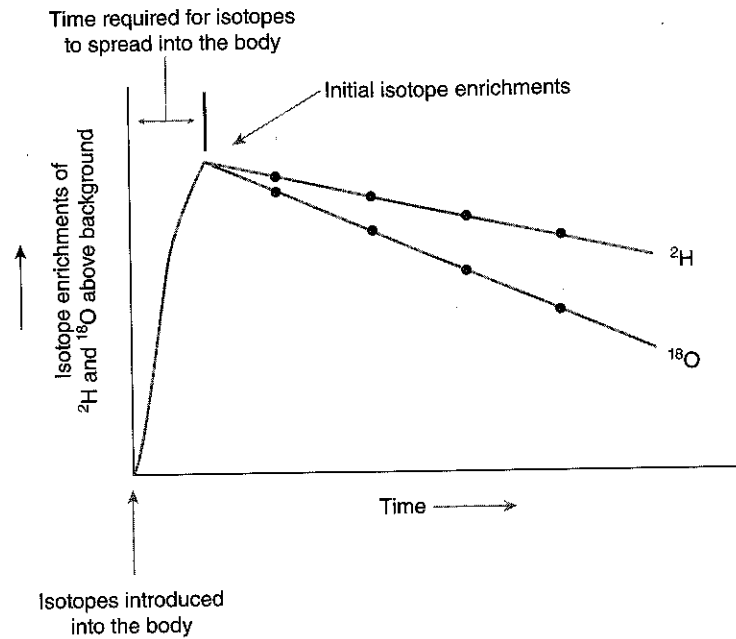


Figure 8.7 Basic principles of the doubly labeled water method, which introduces two stable isotopes (^{18}O and ^2H) orally and uses washout rates of these isotopes to calculate energy expenditure.

DLW The DLW technique uses two labeled stable (i.e., nonradioactive) isotopes of water (^{18}O and ^2H) to calculate TEE based on the differences in elimination rates of these isotopes from the body (see Fig. 8.7). The technique introduces the isotopes orally and monitors the changes in concentration of each of these isotopes over time (typically 7–14 days in adults); in human studies, isotopic concentrations are typically assessed from urine samples. Oxygen-18 declines in the blood through water exchange and CO_2 production, while deuterium declines through water exchange only. Carbon dioxide production is then calculated based on the difference in the rates of disappearance of these isotopes, which allows TEE to be estimated based on the known relationship between CO_2 production and energy expenditure. DLW has been used extensively in human nutrition research in industrialized nations to explore aspects of energy dynamics, and is generally accepted as the most accurate technique for measuring free-living energy costs in both humans and other vertebrates (Speakman 1997). However, the high cost of obtaining enriched ^{18}O and problems with its availability, coupled with the need for specialized equipment and training for isotopic analysis, contributes to its limited use in energetic studies in populations in the developing world.

HR Monitoring HR monitoring makes use of the relationship between HR and energy expenditure in order to calculate TEE. Participants wear a HR monitor (see Fig. 8.8), such as one of the Polar models (Polar Electro, Kempele, Finland), at all times during waking hours; the instrument automatically records HR at a set inter-

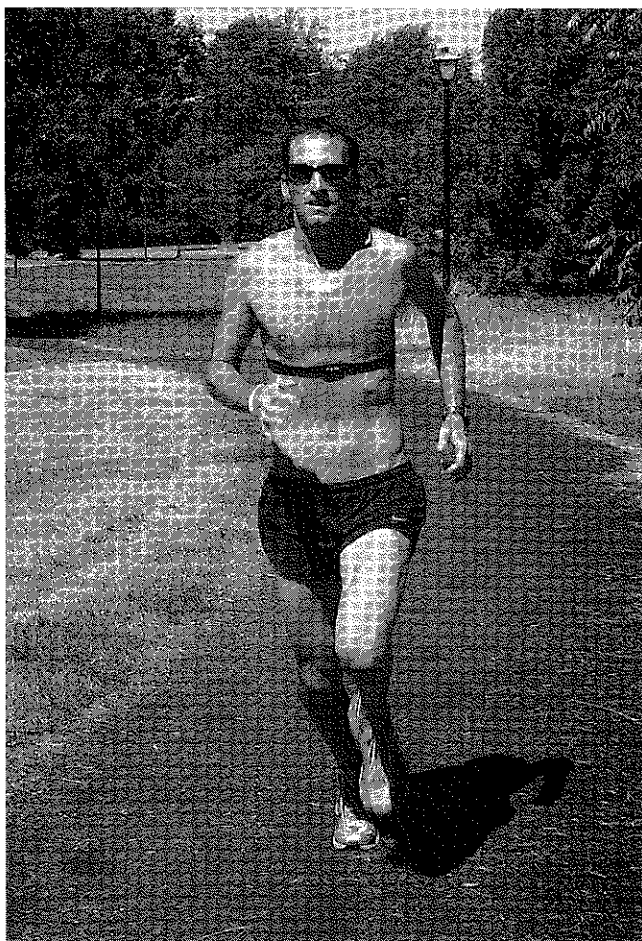


Figure 8.8 Subject wearing a Polar S610 heart rate monitor; the unit includes a chest strap transmitter and wrist-worn receiver watch.

val (e.g., every 1 minute). In order for HR to be accurately converted into energy expenditure and TEE to be estimated, the relationship of HR to energy expenditure must be established for each individual both at rest (while lying, sitting, and standing) and during graded submaximal exercise, typically by simultaneously measuring O_2 consumption using a metabolic analyzer (Leonard 2003). The most commonly used HR monitoring technique is the flex-HR method (see Fig. 8.9), which establishes a flex point for each subject based on the mean value of the highest resting and the lowest exercising HR (Spurr et al. 1988; Katzmarzyk et al. 1994). For HRs above the flex point, energy expenditure is calculated based on an individually established regression equation (i.e., a best fit line for HR and energy expenditure during exercise), and for HRs below the flex point, energy expenditure is calculated based on the mean energy expenditure for the three resting positions. Sleeping energy expenditure is estimated as BMR. At the end of the measurement period

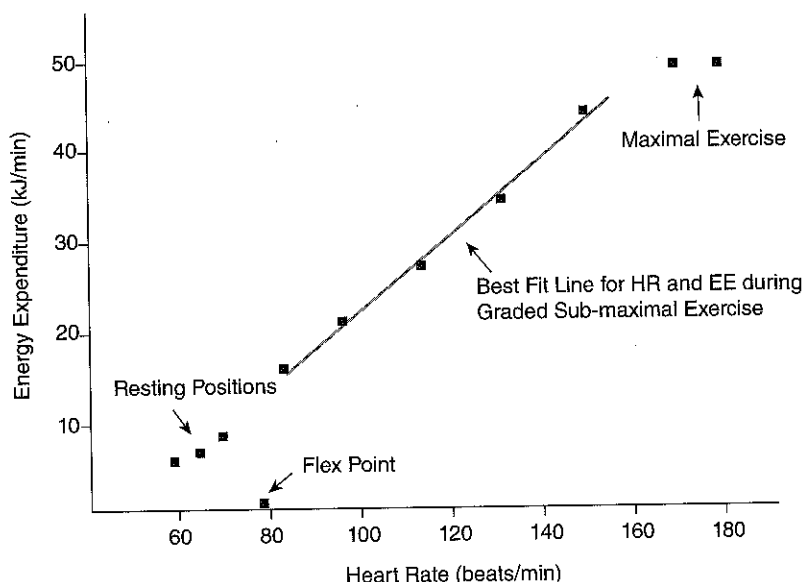


Figure 8.9 Basic principles of the flex heart rate (flex-HR) method. The method establishes the relationship of heart rate (HR) to energy expenditure (EE) for each participant in three resting positions (lying, sitting, and standing) and during graded submaximal exercise; the flex point is determined based on the mean value of the highest resting and the lowest exercising HR. Adapted from Katzmarzyk et al. (1994) and Ulijaszek (1995).

(typically 1–3 days), activity files are downloaded from the HR monitor and data are analyzed. HR monitoring is highly accurate at the population level, showing only minor differences compared with DLW; however, the method is less accurate for measuring individual energy expenditure (Kashiwazaki 1999). This method is also useful in that it provides information on the intensity and duration of physical activity during the day. However, one of the major limitations is the need to individually calibrate HR–energy expenditure relationships, which is both time-consuming and adds additional measurement burden for the participant. Furthermore, data cleaning can be a complex and time-consuming procedure, such as when dealing with temporary data gaps that occur when the monitor loses contact and does not record a HR signal.

Accelerometry Accelerometers are motion sensors that are typically worn at the waist, and objectively measure movement of the body by detecting and recording acceleration in one or multiple planes (see Fig. 8.10). Participants wear an accelerometer such as the Actigraph GT3X (Pensacola, FL) or the Respironics/MiniMitter Actical (Bend, OR) for 1–7 days and then the unit is returned and data are downloaded (see Fig. 8.11). Accelerometers record activity at a specified interval or “epoch” (typically every 1 minute) and report raw data in “counts” (Chen and Bassett 2005). Most early accelerometers measured only one axis of motion and were severely limited in the amount of time that could be continuously measured. Many of the newer generation accelerometers are highly sensitive, can measure acceleration in multiple planes, and allow for a longer duration of continuous data

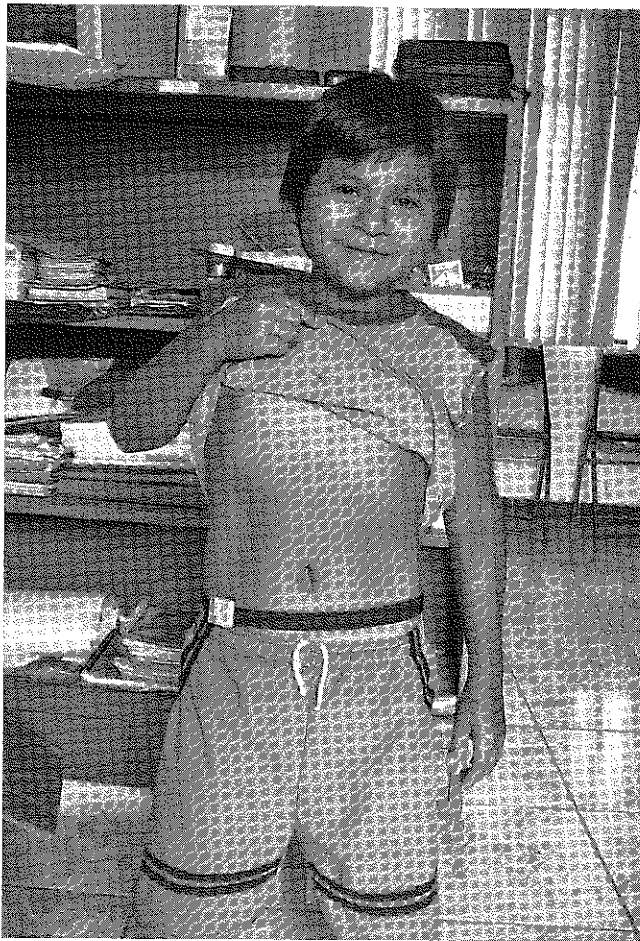


Figure 8.10 Shuar participant from a study of physical activity in lowland Ecuador showing the placement of the Mini-Mitter/Respironics Actical accelerometer. Photo by F.C. Madimemos.

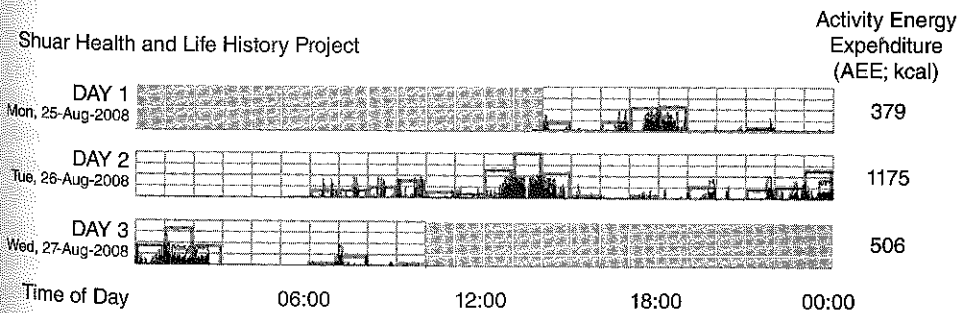


Figure 8.11 Graphical representation of activity data collected on a 20-year-old male participant from Ecuador using a Mini-Mitter Actical accelerometer. The Actical 2.1 software displays activity intensity and duration over the days that the participant wore the monitor. The display shows activity and number of steps taken, as well as the hourly sum of activity energy expenditure (calculated using Actical software).

collection (e.g., the Actigraph GT3X accelerometer is triaxial and can collect data continuously for over 20 days). Accelerometers are small, durable, minimally intrusive, and can provide accurate and detailed information on physical activity patterns, including the duration and intensity of activity. Several models of accelerometers have been validated and show a high **correlation** with DLW, though there is substantial variation between different models (Hoos et al. 2003; Plasqui and Westerterp 2007). In addition to the extensive use with adults, accelerometers have also been used successfully to measure physical activity in children (Rowlands 2007; McClain and Tudor-Locke 2009) and older adults (Copeland and Eslinger 2009).

One of the limitations of accelerometry is that when worn at the waist, accelerometers do not detect many upper body movements and also cannot estimate effort associated with load carrying. The rapidly increasing use of accelerometers is beginning to establish a substantial published literature (Troiano et al. 2008); however, to date, very little data have been generated using the same unit and protocol, which makes comparative studies challenging. In addition to advancements in accelerometer technology, there has also been an increasing sophistication of the algorithms used to estimate physical activity and energy expenditure from accelerometer counts. For example, Crouter et al. (2006) pioneered a two-regression model, which uses accelerometer count variability to parse activity type (i.e., walking/running vs. leisure-time physical activity) in order to apply the appropriate regression for energy expenditure calculation. Another approach, used in the SenseWear armband devices (BodyMedia, Pittsburgh, PA), is based on pattern recognition and incorporates the measurement of several additional physiological parameters (heat flux, skin temperature, and skin response) to contextualize accelerometry data and better estimate energy expenditure in different types of physical activity (Jakicic et al. 2004; Johannsen et al. 2010). Furthermore, some researchers have simultaneously used multiple accelerometers, with one unit worn at the waist and the other at the wrist; however, this approach has not been extensively utilized and is not well validated.

A recent advance in the measurement of the energy costs of physical activity has been achieved by integrating accelerometry with HR monitoring, using instruments such as the Actiheart (CamNtech Ltd., Cambridge, UK) and ActiTrainer (Actigraph, Pensacola, FL). The Actiheart, in particular, has been well-validated and provides highly accurate measures of energy expenditure across a wide variety of activities (Crouter et al. 2008; Assah et al. 2011). This unit, which is lightweight and water resistant and is attached to the chest through standard electrocardiogram (ECG) electrodes, simultaneously records HR along with the intensity and frequency of torso movements. HR and activity data are then downloaded and a branched-equation model is used to calculate activity parameters and energy expenditure (Brage et al. 2004, 2005).

Finally, pedometers, which record movement through step counts, can be used to measure walking distance (based on stride length) and provide an approximation of physical activity. These instruments typically record steps based on adequate vertical acceleration of the hip necessary to move a horizontally mounted, spring-suspended lever arm (McClain and Tudor-Locke 2009). While pedometers are inexpensive and widely available, their utility for measurement of energy expenditure is limited since they do not measure intensity, duration, or frequency of activities

TABLE 8.6 Categories of Physical Activity for Adults According to Pedometer-Based Step Counts

Activity Category	Steps/Day
Sedentary	<5000
Low activity	5000–7499
Somewhat active	7500–9999
Active	10,000–12,499
Highly active	≥12,500

Source: Tudor-Locke et al. (2008).

(Plasqui and Westerterp 2007; Kumahara et al. 2009). Measurement inaccuracies can be compounded by the use of pedometers that are inexpensive and untested (Clemes et al. 2010). Despite their ability to provide only a crude estimate of energy expenditure, pedometers have proven to be an effective public health tool for motivating physical activity increases (Bravata et al. 2007), with 10,000 steps per day being the most widely used target. Those who achieve this goal are more likely to reach daily physical activity recommendations and to show improvements in body composition and cardiovascular health (Tudor-Locke and Bassett 2004; Bravata et al. 2007; Tudor-Locke et al. 2008). Furthermore, a recent review by Tudor-Locke et al. (2008) defined categories of adult physical activity according to pedometer-based step counts (see Table 8.6).

Time Allocation The time allocation technique estimates physical activity and TEE by obtaining information on the amount of time an individual spends performing different activities during the course of a day and combining it with information on energy costs of each activity. A sample 24-hour activity recall form is available at the following website, which is maintained by the author: <http://www.bonesandbehavior.org/activityrecall.pdf>. Energy costs of different activities are based on direct measurement (using a portable metabolic analyzer or a calorimetry chamber) or published values (e.g., Ulijaszek 1995; FAO/WHO/UNU 2004) and are expressed in multiples of BMR (i.e., PARs). BMR is itself either measured directly or estimated from published equations. Total time spent in activities of each category (based on activity diaries, participant recall, or behavioral observation) are summed and multiplied by BMR to calculate TEE, as described above.

Time allocation studies can be accomplished using one of two methods: (1) behavioral observation, where a researcher records the behaviors of a study participant; and (2) the use of interviews, questionnaires, or activity diaries to obtain information from the study participants about the type and duration of activities that they engaged in over the course of the study period. Time allocation studies are sometimes referred to as the factorial method; however, there is confusion in the literature and some refer to the factorial method only for diary-based studies, while others use this term for all time allocation studies.

Like all activity studies, those that are conducted over multiple days are better able to capture average activity level. Behavioral observation can provide valuable information on the types of activity throughout the day and the context of energy expenditure; however, this method is itself time-consuming, suffers from subjectivity

in how activities are classified by the observer, and may cause participants to alter their behavior in response to being observed. Use of interviews, questionnaires, or activity diaries are the most common approaches for the measurement of activity at a population level, having been used extensively in a variety of populations around the world. These methods are inexpensive and there is an increasing availability of validated questionnaires, such as the recent physical activity questionnaire (RPAQ; Besson et al. 2010).

Time allocation studies substantially underestimate TEE compared with values obtained from DLW and HR monitoring because time allocation does not consider spontaneous physical activities, such as fidgeting, and may miss any number of the myriad activities that occur during normal daily life. The time allocation method is most inaccurate at moderate to high activity levels, often underestimating TEE by 15% or more (Leonard et al. 1997; Kashiwazaki et al. 2009); this can have important consequences for estimating population-level energy requirements. Despite limitations in the accuracy of energy estimates, time allocation studies allow accurate ranking between participants of activity levels and time spent in different types of activities (Westerterp 2009; Besson et al. 2010). Finally, activity diaries are generally more accurate than recall interviews or questionnaires for assessing activity patterns.

Measuring Energy Intake and Energy Balance

Energy Intake Accurate measurement of energy intake is notoriously difficult outside of the laboratory, and no method is without limitations (Huss-Ashmore 1996; Rutishauser and Black 2002). An indirect measure of energy intake can be made by collecting data on the amount of energy available in the food supply, either at the level of the population, country, or household (Rutishauser and Black 2002). While this supply-focused approach is limited in that it does not provide individual-level intake information, it nonetheless provides valuable data that can be used to consider various questions, including the role of energy intake in the recent secular increase in obesity in the United States (Swinburn et al. 2009).

Direct measures of energy intake can be accomplished using several different techniques, each with its advantages and disadvantages. Two of the most commonly used are dietary records and dietary recalls. In the dietary record method, the participants record the types of foods (either in the form it is consumed or as individual ingredients) and their quantities (either as weight or volume) in a diary (or on printed forms) at the time they are consumed. The record method requires each participant to record food and drink consumption information over the course of the measurement period, which typically lasts 3–7 consecutive days; this is preferable to attempting to accurately recall dietary information at the end of the study (Rutishauser and Black 2002). In some cases, the investigator rather than the participant weighs or measures the food items; this method has been used extensively in work with nonliterate populations. While direct food measurement of ingredients and individual portions is the most accurate method for measuring dietary intake, it is extremely labor intensive and, therefore, not feasible in most population-level studies (Buzzard 1998; Nelson et al. 2004). Potentially more problematic is the fact that food weighing is disruptive to research participants and may alter patterns of food consumption (Gibson 1990).

Dietary recall techniques ask participants to recall their intake in terms of type and quantity of foods they have eaten over a given time period, typically over the

past 24 hours or on the previous day (Rutishauser and Black 2002). These dietary recalls can be performed in an interview, by telephone, or as a self-completed questionnaire. The 24-hour daily recall is the most common method for quantifying nutritional consumption in population-based research, and has been used extensively in national health surveys and anthropological studies (Rutishauser and Black 2002); this method has the added benefit of not requiring participants to be literate. Dietary recalls are most accurate when conducted by an experienced observer and when repeated over multiple days (at least 2 days, preferably nonconsecutive), since this approach allows better capturing of information on the typical or average diet. Despite their many advantages, 24-hour dietary recalls tend to underestimate consumption of both energy and nutrients (Dwyer 1999; Rutishauser and Black 2002).

After using dietary records or recall to compile information on dietary food items and quantities, daily energy intake and dietary (macronutrient and **micronutrient**) composition are then estimated according to regional food composition tables or using computer databases with dietary composition information (see Box 8.1). Many studies also obtain additional dietary data using food frequency questionnaires, such as the Harvard food frequency questionnaire (Rimm et al. 1992), which provide semiquantitative information on recent food consumption patterns for a subset of foods and beverages (Rutishauser and Black 2002). Food frequency questionnaires typically ask about frequency of consumption based on several choices (e.g., daily, three to four times per week, one to two times per week, one to two times per month, or never), and can be fairly exhaustive (including up to several hundred food items) or more focused on a small subset of dietary items. In order to be used with non-Western populations, food frequency questionnaires must be adapted to include regionally specific foods, which typically require preliminary research on local dietary patterns.

BOX 8.1 ESTIMATING ENERGY INTAKE

Dietary recalls, which can be administered through interviews or completed individually by participants, are the most common method of quantifying energy intake in population-level research. A common protocol is the use of a standard 24-hour dietary recall form, which is administered on at least 2 days. While the 24-hour recall has its limitations, most seriously its consistent underestimation of energy intake, it can be used as a highly effective tool for the study of population-level energy dynamics. Furthermore, it is often used in conjunction with other dietary instruments, such as a food frequency questionnaire, to provide a nuanced picture of human dietary patterns.

The 24-hour recall method requires participants to record the type and quantity of all foods eaten over the course of a full day. Interview-based methods can also incorporate examples of food quantities (e.g., plastic models of commonly eaten foods), which increase the accuracy of recalling the portion size of consumed foods. A sample 24-hour recall form is available at the following website, which is maintained by the author: <http://www.bonesandbehavior.org/dietrecall.pdf>.

(Continued)

Energy intake and dietary (macronutrient and micronutrient) composition of these individual foods are calculated according to standard food values available in the United States or using regional food composition values for other regions (e.g., FAO 1982; LATINFOODS 2002). Several computer programs (e.g., Nutritionist Pro, Axxya Systems, Stafford, TX) and online resources (e.g., USDA National Nutrient Database; <http://www.nal.usda.gov/fnic/foodcomp/search/>) are available that allow calculation of energy and nutrient content of foods based on a database of raw and processed foods.

When collecting dietary data, it is generally easier and more accurate to have participants record food consumption information throughout the course of the day rather than waiting until the next day to recall what foods were eaten. Also, it is a good idea to have participants make as many specific notes as possible about food items (e.g., recording the exact quantity of a food and whether it was eaten raw or as a processed product) to improve matching food items to published tables or energy/nutrient databases. Recording this information greatly improves the accuracy of energy estimation.

In order to quantify daily intake of food energy (calories) and other nutrients, the individual food items and quantities from the 24-hour dietary form are entered into an online dietary analysis program or manually calculated from published tables.

An example of a completed 24-hour dietary form is included in Figure 8.12. For the purposes of this exercise, the Nutrient Analysis Tools and System (NATS) version 2.0 was used, which is a commonly used tool available from the following website: <http://www.nat.uiuc.edu/mainnat.html>.

The results of the nutritional analysis for this example day indicate that the total energy consumed during the 24-hour period was 2648 kcal (11,085 kJ). In addition to energy consumption, the NATS software, like many other dietary analysis tools, also provides information on consumption of protein, fat, and carbohydrates, as well as several other nutrients (e.g., vitamins A and C).

To consider whether the energy consumed on this example day was adequate and whether the participant would have balanced energy intake with expenditure, we need to know some basic information about the individual (age, sex, and body weight) and their activity level over the course of the day (or their average for their lifestyle). Using the example from Box 7.1 in Chapter 7, which compares two adults with similar office jobs (a 32-year-old man who weighs 72.5 kg [160 lb] and a 28-year-old woman who weighs 54.4 kg [120 lb]), we can calculate energy expenditure, with which we can compare to our energy intake estimate. By estimating BMR from the table provided in Chapter 7 (Table 7.1) and the estimation of activity using PAL information from Table 7.2, the man's TDEE was calculated as 2646 kcal (11,076 kJ), while the woman's energy expenditure was calculated as 2002 kcal (8380 kJ). In our example day, energy expenditure for the man matched nearly identical energy intake (2646 vs. 2648 kcal), demonstrating a balancing of energy intake and expenditure (at least on this one hypothetical day). However, for the woman, energy intake greatly exceeded energy expenditure (2648 vs. 2002 kcal), which puts the woman in a positive energy balance, and, if this pattern continued, she would rapidly gain weight through increases in body fat.

24-Hour Dietary Recall

Name: EXAMPLE Sex: _____ Age: _____ Date: _____

Record the foods and amounts (as precisely as possible) consumed in 1 day.

BREAKFAST		LUNCH	
Food Items	Quantity	Food Items	Quantity
<u>Bagel with cream cheese</u>		<u>Tuna sandwich</u>	
Cinnamon raisin bagel	1 medium	Bread (whole wheat)	2 slices
Cream cheese (low fat)	1 oz.	Tuna (canned; in water)	1/2 can
Grapefruit juice (fresh)	8 oz.	Low-fat mayonnaise	1 oz.
<u>Coffee</u>		Apple (raw with skin)	1 fruit
Coffee (freshly brewed)	16 oz.	Plain corn tortilla chips	5 oz.
Cream (half and half)	2 oz.		
DINNER		SNACKS/OTHER FOODS	
Food Items	Quantity	Food Items	Quantity
<u>Cheesburger</u>		<u>Tea</u>	
Hamburger roll (wheat)	1 roll	Black tea (freshly brewed)	12 oz.
Ground beef burger	1 large patty	Low-fat milk (2% fat)	3 oz.
Cheddar cheese	1 oz.		
Lettuce (romaine, raw)	1 leaf		
Tomato (raw)	1 oz.		
Mustard	1 oz.		
<u>Salad</u>			
Lettuce (loose-leaf, raw)	8 oz.		
Tomato (raw)	1 fruit		
Avocado	1/2 fruit		
Beer (alcoholic, lager)	16 oz.		

Notes:

Figure 8.12 Example of a completed 24-hour recall form, showing types and quantities of all foods consumed over a 24-hour period.

Nutritional Status Nutritional status is typically used to refer to body size and the amount of body fat as long-term measures of energy balance. The primary indicators of nutritional status in most studies are based on height and weight, which are simple and inexpensive to measure. A variety of techniques are available for the assessment of body fat, many of which require sophisticated measurement devices and specialized training; a discussion of the basis of each technique and their

advantages and disadvantages is beyond the scope of this chapter (see review in Heymsfield et al. 2005). Most anthropological and **epidemiological** studies use one or more of the following techniques to assess the extent of body fatness: (1) estimation of body fat from standardized **anthropometric** measures of **subcutaneous fat** at multiple **skinfold** sites (e.g., sum of four skinfolds); (2) calculation of body fat percentage using **bioelectrical impedance** analysis (e.g., using a Tanita [Tokyo, Japan] scale or the RJL Systems [Clinton Township, MI] instrument); and (3) calculation of **body mass index** (BMI; body weight (kg)/[height (m)]²) as a proxy measure of body fat percentage. Additional information on anthropometric techniques used in human biology can be found in the *Anthropometric Standardization Reference Manual* (Lohman et al. 1988) and in an integrative measurement protocol (Antón and Snodgrass 2009) made available by the author at the following website: <http://www.bonesandbehavior.org/protocol.pdf>.

ENERGETICS AND HUMAN EVOLUTIONARY HISTORY

An energetics approach can provide insights into trends and patterns in human evolution, and has been increasingly utilized in recent years to investigate key adaptive shifts among **hominins** (members of the evolutionary group that includes modern humans and closely related extinct species). This approach is particularly powerful since many of the adaptive shifts that have occurred during human evolution, including habitual bipedalism, encephalization, and increased body size, led to profound shifts in energy dynamics. Furthermore, a hallmark of human evolutionary history is the increasing ability and efficiency in extracting energy from the environment. In this section, I use an energetics perspective to consider three key transitions in human evolution history: (1) the evolution of bipedalism, (2) encephalization in the genus *Homo*, and (3) the evolution of the human diet.

Bipedalism

The defining adaptive shift among hominins was the evolution of habitual bipedalism, which current evidence suggests emerged by 6–7 million years ago (Zollikofer et al. 2005; Richmond and Jungers 2008). While the origins and adaptive significance of bipedalism continue to be hotly debated, energetic studies of living humans, nonhuman primates, and other mammals, as well as energetics modeling studies of fossil hominins, provide data with which to consider competing hypotheses related to this evolutionary transition. Comparative studies have demonstrated that bipedal locomotion at walking speeds (but not at running speeds) is significantly less energetically expensive compared with that of most mammalian quadrupeds (Rodman and McHenry 1980; Leonard et al. 2007). According to calculations by Leonard and Robertson (1997), over the range of walking speeds males expend 13% less energy than quadrupeds, and females expend 25% less energy. Furthermore, studies of great apes show that their locomotion on the ground is extremely energetically inefficient. The adoption and refinement of bipedal locomotion in hominins from a quadrupedal ape ancestor would have reduced energy costs of travel, which likely became increasingly important with changing environmental conditions during the late Miocene and early Pliocene that would likely have increased range sizes and distance between resource patches (Leonard and Robertson 1997; Leonard et al. 2007).

Encephalization in the Genus *Homo*

Another key transition in human evolutionary history was the massive increase in brain size that occurred in the genus *Homo*. While a number of paleoanthropological studies have focused on identifying the causal selective factors associated with encephalization (the increase in the relative size of the brain), energetic studies have largely concentrated on the factors associated with the ability to grow and maintain large brains among these taxa. Much attention has focused on explaining the seeming paradox that despite relatively large brains with their high associated metabolic costs (the human adult brain accounts for 20–25% of the resting energy budget compared with 8–10% in nonhuman primates and 3–5% in other mammals), humans have overall metabolic maintenance costs similar to other mammals and primates (Leonard and Robertson 1994; Aiello and Wheeler 1995). As discussed in more detail in Chapter 7, these studies suggest three key changes that were necessary for overcoming the energetic constraints on encephalization: (1) a shift to a higher-quality diet, with a substantial quantity of animal foods; (2) an increase in body size, particularly among females, that would have allowed greater transfer of energy to offspring; and (3) changes in body composition, including reduced gut size and muscularity, and increased levels of body fat early in life (Leonard et al. 2003; Snodgrass et al. 2009).

Evolution of the Human Diet

Studies focused on the evolution of the human diet have increased exponentially over the past several decades following the watershed event of the publication of Eaton and Konner's (1985) influential article on Paleolithic nutrition. Since then, there has been attention to elucidating the key dietary transitions in hominin evolutionary history, and using multiple lines of evidence (e.g., comparative primate studies, stable isotopes, dental microwear, and cross-cultural human studies; Ungar 2007) to consider the evolutionary context of contemporary human diets. From this research, there has been a recognition that the evolutionary history of hominins can be characterized by an increasing ability and efficiency of extracting energy and nutrients from the environment (Leonard 2008). There have been at least four key shifts that characterize human dietary evolution. First, **diet quality** (i.e., the energy and nutrient density of food) increased markedly in early members of the genus *Homo*, including *Homo habilis* and *Homo erectus*, and this transition likely involved a substantial increase in the use of animal source foods and high value plant foods (Plummer 2004; Antón 2008). Second, the emergence of fully modern humans is linked to increased dietary flexibility and diversity, with a heightened ability to specialize (e.g., on medium- and large-bodied terrestrial herbivores) or to broaden diets by incorporating fish and small game depending on environmental circumstances (Stiner et al. 1999; Richards et al. 2001). Third, food production (agriculture and animal domestication), which emerged multiple times independently and began initially at approximately 10,000 years ago, led to selection for higher productivity in several food species and an overall increased caloric availability; however, there was also a dramatic narrowing of primary food items in the diet (Barker 2006; Larsen 2006). While this gain in energy extraction ability increased the ability to feed larger populations, this dietary transition also led to overall declines in

population-level health, as a result of nutritional deficiencies, a higher burden of infectious disease, and increased social stratification (Larsen 2006; Cohen and Crane-Kramer 2007). Finally, global changes in industrialization and urbanization that began in the 18th century with technology-based changes in food production (e.g., increased use of fertilizers, processing, and long-distance transport), have accelerated post World War II and have led to global changes in the diet with increased dietary diversity, increased consumption of saturated fats and simple carbohydrates (including added sugars and refined grains), and overall energy intake increases (Popkin 2002; WHO/FAO 2003). I will return to the topic of this recent dietary transition later in this chapter.

ENERGETICS AND ADAPTATION AMONG CONTEMPORARY HUMAN POPULATIONS

Human adaptation and adaptability to environmental stressors can be examined through the lens of energetics. Life history trade-offs, which shift energy allocation to different somatic functions and structure patterns of growth and reproduction, may be adaptive in that they can optimize fitness under different environmental circumstances by contributing to differential survival and **mortality**. Life history trade-offs can operate at multiple levels, including through genetic, developmental, and facultative (i.e., short-term responses to environmental conditions) pathways (Hill and Hurtado 1996; McDade 2003). Given that energy is a fundamental limiting resource in humans and that humans inhabit a diversity of environments, we should expect to see extensive evidence for life history trade-offs at different life stages and through multiple mechanisms, and this is borne out by research. In particular, biocultural adaptation provides a perspective on how cultural strategies, such as subsistence economy and division of labor, allow humans to adapt and survive in different environments, and how social, political, and economic forces shape energetic patterns within the context of a changing world.

Energetics and Adaptation to Environmental Stressors

Thermal Stress While much of the interindividual variation in maintenance costs is structured by differences in size, sex, and age, there is also evidence for population-level variation, with relatively depressed values in tropical populations and elevated values among indigenous northern groups (Roberts 1978; Henry and Rees 1991; Leonard et al. 2005; Snodgrass et al. 2007b). Population-level differences in BMR as a result of climatic factors were recognized by the FAO (1957) nutritional guidelines, which incorporated climate into its calculation of energy needs by recommending a 3% addition for every 10°C decrease in annual temperature below the baseline of 10°C. This position was reversed by more recent expert panels (e.g., FAO/WHO/UNU 1985), which have not included a climate adjustment and remain identical for all populations. There is, however, a growing recognition of the presence and importance of population variation in BMR, and the latest expert panel (FAO/WHO/UNU 2004) has recommended conducting additional studies aimed at clarifying the extent of population-level variation. Furthermore, despite years of controversy that has attributed population-level variation in BMR to anxiety, body size/

composition, and dietary factors, a number of recent studies with controlled measurement conditions support the conclusion that population-level variation in BMR exists and that it is related to climatic factors (Henry and Rees 1991; Leonard et al. 2005; Snodgrass et al. 2005; Froehle 2008).

Some studies have focused on the potential adaptive dimensions of reduced BMR in hot environments but most attention has focused on relatively high metabolic rates among indigenous northern populations as a physiological adaptation to chronic cold stress. Research among indigenous circumpolar populations in Alaska, Canada, and Russia has documented BMRs that are systematically elevated relative to international standards for body mass, FFM, and **surface area** (Leonard et al. 2002b, 2005; Snodgrass et al. 2007b). In the pooled Siberian sample, BMR measurements among males are 15% above and females 18% above predicted values using FFM standards (Snodgrass et al. 2008) (see Fig. 8.13); furthermore, these BMRs are

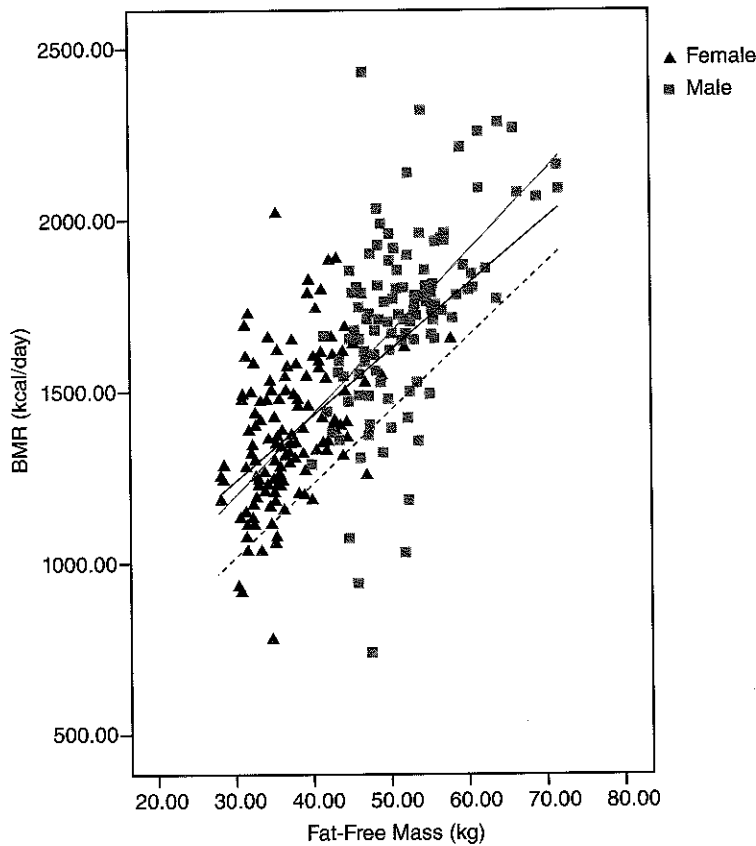


Figure 8.13 Relationship between basal metabolic rate (BMR; kcal/day) and fat-free mass (kg) among indigenous Siberian men and women compared with estimated values from the Cunningham (1991) reference norm for lower-latitude populations (dashed line). Indigenous Siberian men average 1720 kcal/day, 15.2% higher than predicted, while Siberian women average 1378 kcal/day, 17.7% higher than predicted values. Reproduced from Snodgrass and Leonard (2009).

substantially higher than nonindigenous individuals (i.e., Russians) living in the same communities (Leonard et al. 2002b). Metabolic elevation in these populations has been interpreted as a physiological adaptation to chronic and severe cold stress experienced in the circumpolar environment (Roberts 1978; Leonard et al. 2005; Snodgrass et al. 2007b); this relationship with climate is supported by geographic studies that demonstrate a strong negative association between BMR and mean annual temperature, which remains when controlled for differences in body size (Roberts 1978; Leonard et al. 2005). Additional evidence comes from shorter-term studies that demonstrate that in response to acute thermal stress, cold-living groups such as the North American Inuit, the Alacaluf of Tierra del Fuego, and Peruvian Quechua are able to (1) upregulate their metabolic heat production, (2) maintain high peripheral temperatures, and (3) preserve core temperatures better than those of nonindigenous "control samples" (Frisancho 1993). Among the most extreme seasonal changes in metabolic rate documented for cold-living groups is that of traditional Ama divers of Korea, whose metabolic rates increased by ~30% between summer and winter (Frisancho 1993).

Recent studies of the global distribution of **mitochondrial DNA (mtDNA) haplogroups** may also help us interpret the elevated BMRs documented among native northern inhabitants (Mishmar et al. 2003; Ruiz-Pesini et al. 2004; Wallace 2005). This research has shown that mtDNA lineages common to Siberia are associated with greater uncoupling of **oxidative phosphorylation** (the metabolic process that forms ATP), which increases metabolic heat production (at the expense of storage of chemical energy as ATP) and may have helped human populations to successfully settle extreme northern environments. While provocative, this research is highly speculative as it has to date not linked mtDNA haplogroup variation (or any specific **mitochondrial** genes involved in heat production) with variation in BMR or functioning in the cold.

In addition to possible evidence for genetic differences, present research suggests that thyroid hormones play an important role in structuring metabolic adaptation among indigenous northern populations, and that they likely mediate short-term upregulation of metabolic rate during winter months (Leonard et al. 1999, 2005). Exposure to cold temperatures and shifts in photoperiod lead to hormonal changes that involve increased circulating concentration of T_3 (triiodothyronine) and T_4 (thyroxine); this boosts thermogenesis and ATP turnover (Tkachev et al. 1991; Levine et al. 1995; Silva 2003). Thyroid hormone levels are closely associated with BMR through their direct effects on rates of oxidative metabolism; this metabolic effect is mediated by changes in mitochondrial function and Na⁺/K⁺ ATPase (a sodium pump **enzyme** found in the cell membrane) activity (Danzi and Klein 2003; Guyton and Hall 2006). Indigenous northern populations appear to have a greater propensity for seasonal thyroid elevation than nonindigenous residents of northern latitudes, which likely structures functional BMR upregulation in response to acute cold stress (Tkachev et al. 1991). Research among the Evenki of central Siberia, for example, has documented a link between free T_4 levels and BMR, as well as overall elevated levels of free T_4 compared with nonindigenous Russian residents living in the same communities (Leonard et al. 1999).

The elevated metabolic rates documented among northern populations have obvious implications for caloric requirements but may also have consequences for life history trade-offs and chronic disease patterns. Relatively high BMRs generally

mean that less energy is available for other somatic functions, such as growth and reproduction, and the slow somatic growth and delayed menarche documented among northern populations has been hypothesized to have been shaped by relatively high maintenance costs (Roberts 1978; Leonard et al. 1994). Furthermore, research among native Siberians has suggested a link between metabolic elevation and chronic disease patterns. BMR is positively associated with **systolic blood pressure** and pulse pressure, even after adjusting for body size and composition, and a variety of potential confounders such as age, smoking status, and extent of urbanization (Snodgrass et al. 2008). The systematically elevated BMRs of indigenous Siberians may help explain the relatively high blood pressures and **hypertension rates** documented among native Siberians in the post-Soviet period.

Seasonal Energy Stress A large body of literature has addressed the issue of physiological and **behavioral adaptations** to seasonal energy stress (e.g., Ulijaszek and Strickland 1993). Most studies have examined seasonality in tropical populations and, in particular, the differences between energy availability in the wet and dry seasons. In the absence of adequate cultural strategies such as storage or redistribution networks, humans faced with severe energy shortages use physiological means to reduce energy costs. These include (1) reductions in body mass, which may include both body fat and lean tissue; (2) reduction in the amount of physical activity; and (3) downregulation of BMR (Ulijaszek 1995; Shetty 1999). Furthermore, seasonal shifts in energy dynamics in subsistence populations can also affect the timing of conception to synchronize it with times of increased energy availability (Ellison 2008; Chapter 15 of this book). Energetics thus helps explain the reproductive seasonality among subsistence populations, with improved energetic conditions increasing ovarian function and conception likelihood, as well as allowing weight gain and the accumulation of fat reserves that help buffer women and their developing offspring during pregnancy and lactation.

Energy Stress and Genetic Adaptation Several energetic arguments have been advanced to consider whether the distinct life history pattern of reduced amount of growth and small adult body size among “pygmy” populations—defined by some as an average male height <150 cm and by others as <160 cm—is the result of **natural selection** (Shea and Bailey 1996). Some researchers hypothesize that small body size in these groups is primarily determined by genetic factors rather than poor growth during childhood as a result of malnutrition. Other researchers have found evidence for malnutrition in some of these groups, especially the lack of one or more essential nutrients (Bogin 1999). One example is the Maya of Guatemala, who have been described as a “pygmy” population due to their short stature. The lack of iodine in the traditional Maya diet accounts for much of the small stature of Maya adults (Bogin and Rios 2003). In addition, Maya children and juveniles who grow up in the United States are 10–11 cm taller than Maya of the same age in Guatemala. Increases in body size and improved nutrition have also been noted in another pygmy population, the Mountain Ok of Papua New Guinea (Schwartz et al. 1987). It is well known that certain pygmy populations have variations in the hormonal regulation of growth (Bozzola et al. 2009). This variation is a key element of life history evolution and is likely due to a history of genomic–nutritional interactions (Finch and Rose 1995).

Whatever the cause of pygmy short stature, it is clear that there has been convergence to a similar pygmy-like **phenotype** in different populations in Africa, Southeast Asia, and South America. This may be due to the shared environmental conditions of a hot, humid, low-energy, and highly seasonal environment of tropical rainforests, in which small adult body size minimizes caloric requirements (Shea and Bailey 1996; Perry and Dominy 2008). This hypothesis is consistent with extensive evidence for an adaptive shift in body size in various vertebrate species on resource poor island environments and in several island-like environments that result from ecological fragmentation (Lomolino 2005). Small body size is also beneficial for coping with heat stress that occurs in hot and humid environments, where the effectiveness of evaporative cooling by sweating is reduced. In these conditions, small body size has the dual effect of decreasing absolute heat production and maximizing heat dissipation as a result of a high surface-area-to-mass ratio (Ruff 1993).

Energetics and Biocultural Adaptation

Energy patterns are affected not only by environmental factors, including physical and biological environments, but also by cultural factors that shape food preferences, subsistence strategies, and distribution networks (Leonard 2004). Even subsistence groups living in broadly comparable environments and with similar subsistence economies may have distinct energy patterns. For example, research among the Amazonian Tukanoan Indians of Colombia and the *Ribeirinhas* of Brazil documented significantly higher activity levels among Tukanoan women (PAL = 1.77) compared with the *Ribeirinha* women (PAL = 1.55) (Dufour and Piperata 2008). These differences were attributed to household-level division of labor (i.e., whether men participated in the harvesting and processing of agricultural crops), settlement pattern (i.e., proximity to gardens, which shaped the amount of time spent walking), and minor dietary differences (i.e., amount of processing required of the cassava staple).

An energetics approach has been utilized in human biology research to study the various dimensions of human biocultural adaptation, including strategies and responses at individual and group levels. This approach is well illustrated by biocultural studies of native high-altitude groups and their ability to cope with the myriad stressors (e.g., hypoxia, cold, seasonality, and low overall energy availability) that these environments present to residents. For example, indigenous groups in these areas use a variety of cultural and behavioral strategies to maintain adequate energy intake and minimize seasonal disruptions, including through food-processing techniques such as freeze-drying potatoes and meats, resource exchange networks between highland and lowland areas, and household-level seasonal adjustments in energy expenditure and food consumption (Thomas 1976; Leonard 1991; Moore et al. 1998). Several of these biocultural studies, such as by Thomas (1976) among residents of the Peruvian *altiplano*, have used a comprehensive energy flow approach to track energy extraction, consumption, and expenditure in order to identify adaptive strategies that enable the Nuñoa population to efficiently procure and utilize energy within this harsh environment (Thomas et al. 1989). Furthermore, this energy flow approach can be used to interpret or model the effects of social changes, such as shifts in health care availability, economic inequality, or population size.

Biocultural Adaptations among Circumpolar Populations The extent to which cultural factors shape human energy patterns can be appreciated through an examination of subsistence-level circumpolar groups, such as the Inuit of North America and the Yakut (Sakha) of Siberia. The circumpolar environment exposes humans to a unique suite of ecological stressors including chronic and severe cold stress (mean monthly temperatures can drop to below -40°C [-40°F] in places and isolated temperatures can drop to below -60°C [-76°F]), marked seasonality with extreme photoperiod variation, and sparse vegetation (Krebs 1972; Cox and Moore 1993; Folk et al. 1998; Snodgrass et al. 2007b). Also, the low biological productivity of circumpolar environments means that these ecosystems have a low overall energy available to human populations. A biocultural approach to energetics in northern populations focuses on how cultural factors shape the different dimensions of energy intake and expenditure, such as energy extraction and storage, patterns of physical activity, and thermoregulation (McElroy and Townsend 2009). In turn, this provides a window onto the adaptive dimensions of human settlement of high-latitude environments.

The harsh circumpolar environment presents an intense energetic challenge to human populations, given the low biological productivity of northern ecosystems and their extreme seasonal shifts in energy availability. Additional challenges are presented directly through cold exposure as well as indirectly through human adaptations to cold stress. For example, northern groups have relatively large body sizes and elevated BMRs as adaptations to cold stress, but these adaptations have energetic consequences as they increase caloric needs. Furthermore, many of the dietary strategies that allow life in this extreme environment, such as marine mammal hunting and reindeer herding, require intense inputs of physical activity, which lead to increased energy expenditure and the caloric intakes necessary to sustain them. Three important points follow from this focus on energy dynamics in circumpolar residents. First, as discussed earlier in this chapter, the energetically intense lifeways of northern populations appear to have important life history consequences, such that energy trade-offs help explain delayed menarche and the slow somatic growth schedule seen in circumpolar populations (Roberts 1978; Leonard et al. 1994). Second, cultural and behavioral adaptations to the cold (e.g., sophisticated fur clothing and thermally efficient shelters) can have important energetic consequences since buffering from cold stress reduces the need for functional metabolic responses. Thus, by minimizing functional metabolic responses, there is an overall decrease in energy expenditure (as a result of lowered thermoregulatory costs) and a concomitant reduction in caloric needs. Finally, circumpolar environments require complex subsistence strategies in order to effectively extract calories from the environment and meet the high energy demands of these populations. In the following section, I provide two examples of biocultural adaptation to the circumpolar environment, concentrating on the hunting-focused economy of traditional Inuit of North America and Greenland, and the dairying economy of the Yakut of northeastern Siberia.

The subsistence economy of traditionally living Inuit populations was well-documented through research by human biologists, cultural anthropologists, and nutritionists during the 20th century. Much of this research, such as the multidecade study among an Inuit group from Igloodik in the Northwest Territories of Canada, has addressed the health consequences of the massive changes in lifeways experienced in the late 20th century as a result of increasing market integration (Shephard

and Rode 1996). Although only a limited amount of direct information on energy intake and expenditure exist for traditionally living Inuit, a large body of literature on dietary patterns and subsistence strategies enables us to reconstruct energy patterns for this group. Traditional Inuit groups typically practiced a flexible hunting-focused subsistence strategy that involved a high degree of seasonal mobility, which allowed for the use of both marine and terrestrial resources. The traditional economy in tundra and coastal ecosystems focused on hunted and fished foods, with fish, seals, whales, and caribou being the most important foods (McElroy and Townsend 2009). With little availability of carbohydrates except seasonally available resources such as berries, diets contained approximately 85–95% of calories coming from meat and other animal tissues (Cordain et al. 2000; McElroy and Townsend 2009). Protein levels in these populations were generally extremely high, with consumption averaging approximately 200 g/day and in some groups exceeding 300 g/day (Rodahl 1952; Draper 1977; Schaefer 1981). Given the inability of humans to habitually consume quantities of protein over approximately 35–50% of calories without detrimental health effects that result from physiological limitations in the ability to metabolize **amino acids** (Cordain et al. 2000), consumption of fat was key to survival and provided the most important source of calories. Finally, food preparation strategies, including eating fresh meat raw or consuming the lichen in caribou stomachs, also contributed to survival in this environment and allowed groups to maximize consumption of key nutrients such as vitamin C (McElroy and Townsend 2009).

Few studies of energy expenditure and physical activity were conducted among traditionally living Inuit groups, in large part, because of limited technological options available at the time and the immense challenges of working in this extreme environment among a highly mobile population. A number of early studies, as well as a recent and well-controlled study by Rode and Shephard (1995), documented elevated BMRs among Inuit from Igloolik, consistent with the metabolic upregulation described earlier for Siberian populations. Information on activity patterns among the Inuit come from time allocation methods, which were used to assess energy expenditure and physical activity among the Igloolik Inuit during the early 1970s, when this region was in its initial stages of economic development (Godin and Shephard 1973). Inuit males had PALs of 1.8–2.2, with the highest values among individuals most involved in the traditional hunting economy. Inuit women at the time of the study were already less involved in the subsistence economy and had PALs that averaged 1.8. The study may have underestimated activity costs, especially among men, since it relied on the time allocation method, which often significantly underestimates TEE, especially at high levels of physical activity. Furthermore, activity levels may have already experienced reductions since there was already substantial economic development and the population was less dependent on the subsistence economy than in earlier times. Recent environmental, economic, and social changes have led to altered patterns of diet and physical activity, which help explain the increased prevalence of obesity, declines in fitness and muscular strength, and elevated occurrence of cardiovascular disease and type 2 diabetes that has been documented in this population (Shephard and Rode 1996; Bjerregaard et al. 2004).

An alternate dietary strategy for coping with a low-energy environment is demonstrated by the Yakut horse and cattle herders of the northeastern Siberian *taiga*. Many early ethnographic accounts (e.g., Wrangell 1842; Seroshevski 1896) emphasized the role of dietary fat, which was considered a delicacy among the Yakut.

Traditionally, the Yakut consumed vast quantities of *kumyss*, a fermented drink made from mare's milk; this beverage, while having a somewhat lower fat content than cow's milk, has a much greater quantity of milk sugar. During the Russian colonial period, the Yakut subsistence economy was transformed from one reliant on horses to one centered on cattle (Tokarev and Gurvich 1964). As a result of this shift, the use of high-fat products made from cow's milk, such as butter, cream, sour milk, and sour cream, increased, while the consumption of *kumyss* declined. Butter appears to have been of prime importance to the Yakut in the late Russian colonial period, and many authors emphasized the huge quantities consumed by the Yakut (Seroshevski 1896; Tokarev and Gurvich 1964); as proof of this importance, butter was used as currency in parts of Siberia. Seroshevski (1896), who conducted 12 years of ethnographic research in Siberia in the late 19th century, documented routine consumption of large quantities of warm butter, which was used to replenish energy and elevate body temperature. According to Seroshevski (1896), in cold conditions, it was not unusual for individuals to consume 1 kg of butter at a time, while some individuals consumed up to 4 kg in one sitting.

In the aftermath of the collapse of the Soviet Union in 1991, the Yakut (and many other indigenous Siberian groups) were forced to return to traditional subsistence strategies to meet needs no longer met by the government (Vinokurova 1995; Jordan and Jordan-Bychkov 2001; Crate 2006). In the post-Soviet economy, cows returned to prime importance among rural residents for food as well as cultural identity, with cattle and horse herding occupying a central role in the subsistence economy. Herding was supplemented by foods from other subsistence activities (e.g., fishing, hunting, gathering, and horticulture), as well as some market foods (Crate 2006, 2008). The reliance on cattle—either directly from household-level food production or indirectly via redistribution networks with kin—is well illustrated in a study by Crate (2006), who documented that while 55% of households owned cows, an additional 35% of households consumed cow products they had received from kin. The dairying economy structures the Yakut calendar and shapes energy patterns because of the year-round input of energy needed to maintain cows (Crate 2006). Cow tending in this environment necessitates a sizable daily input of labor as the cows require nearly year-round milking and milk processing, and cattle must also be transferred between the home and pastures on a daily basis during summer months. Because of the harsh northern environment, cows are penned for approximately 8 months per year and during this time must be foddered; in addition, animals must be taken to water daily and manure must be removed from barns (Tokarev and Gurvich 1964; Jordan and Jordan-Bychkov 2001; Crate 2006). Though tending activities are at their nadir during the summer months, hay must be cut manually from distant meadows in order to provide winter cow feed, and this requires a vast input of physical labor. Each cow requires approximately 1.2 t of hay for the winter, and the entirety of this hay must be cut from distant meadows and transported to the home community. Finally, within the past several years, increasing economic development in rural Siberia has led many to abandon the subsistence economy. Cardiovascular and metabolic health are rapidly deteriorating among the population in part as a result of shifting energy dynamics that have occurred as people reduce participation in labor-intensive subsistence tasks and consume market foods high in refined carbohydrates (Snodgrass et al. 2006, 2007b, 2010).

These two examples illustrate several important points about human biocultural adaptation. First, humans display extreme flexibility in their ability to inhabit diverse environments. This flexibility is made possible by a plethora of cultural and biological adaptations working in concert that increase the extent with which humans can buffer themselves from environmental stressors. Second, cultural strategies such as the development of thermally efficient clothing can affect energy dynamics. Third, humans are able to obtain energy from an enormous variety of food sources, including the consumption of diets with extreme quantities of protein and fat. Most surprisingly, these diets did not lead to high levels of cardiovascular disease among traditionally living northern populations such as the Inuit. Finally, small shifts in energy dynamics, such as changes in the diet and physical activity, can have dramatic effects on energy balance and health. I will return to this final point in a later section of this chapter.

Energetic studies of contemporary high-latitude populations can also be used to interpret paleoanthropological data on the settlement of northern environments by other hominin species. Recent research has modeled energy dynamics among Neanderthals and early modern humans in Europe in order to evaluate key behavioral and biological differences that may have contributed to the extinction of Neanderthals (Sorensen and Leonard 2001; Steegmann et al. 2002; Aiello and Wheeler 2003; Snodgrass and Leonard 2009). These studies indicate that Neanderthals occupied an ecologically precarious position in the European glacial environment, adhering to a high-risk, energy-intensive subsistence strategy that was highly sensitive to environmental change (Snodgrass and Leonard 2009). The high turnover of metabolic energy reconstructed for Neanderthals, combined with severe limitations on energy availability, would have almost certainly shaped Neanderthal life history traits, including growth rate, reproductive patterns, and life span. This research further suggests that several behavioral and biological features of modern humans would have led to more favorable energetic profiles and may have contributed to higher **fertility** and served as a competitive advantage (Snodgrass and Leonard 2009). Key cultural developments in modern humans included increased cold weather protection (e.g., tailored clothing) and refinements in tools that increased hunting efficiency through increased capture and processing ability. These would have lowered energy expenditure by reducing thermoregulatory and physical activity costs, respectively. Furthermore, the development of sex-based division of labor in modern humans (Soffer 1994; Kuhn and Stiner 2006) would have reduced female energetic costs by transferring more of the energetic burden to males. The results of this energetic modeling demonstrates that modern humans would likely have had advantages in both mortality and fertility compared with Neanderthals, and that this may have led to rapid extinction of Neanderthals and replacement by modern humans.

Worldwide Variation in Energy Dynamics Limited data are available on activity patterns and TEE among subsistence populations, and very few studies have measured activity patterns among hunter-gatherer groups. The limited number of DLW studies among subsistence populations show variation by type of subsistence economy, season, and location (see Table 8.7). Very high activity levels were documented among Bolivian Aymara agropastoralists (Kashiwazaki et al. 1995, 2009) and Gambian agriculturalists (Singh et al. 1989; Heini et al. 1991, 1996). Among the

TABLE 8.7 Energy Expenditure Data from Doubly Labeled Water Studies of Energy Expenditure in Selected Populations

Group	Weight (kg)	TEE (kcal/day)	BMR (kcal/day)	PAL (TEE/BMR)	AEE (kcal/day)	Source(s)
Males						
Aymara (preharvest)	54.8	2654	1354	1.96	1300	Kashiwazaki et al. (1995)
Aymara (harvest)	55.7		1373	2.18		Kashiwazaki et al. (2009)
Chinese	73.4	2891	1648	1.75	1243	Yao et al. (2002)
Gambian	61.2	3880	1604	2.42	2276	Heini et al. (1996)
Nigerian	60.8	2482	1464	1.70	1018	Luke et al. (2002)
Pima Indian	88.0	2985	1902	1.58	1083	Tataranni et al. (2003)
Yakut	72.2	3102	1848	1.68	1254	Snodgrass et al. (2006)
Developed nations	70.1	2873	1659	1.73	1214	FNB/IOM (2002); Leonard (2008)
Females						
Aymara (preharvest)	48.6	2329	1145	2.03	1184	Kashiwazaki et al. (1995)
Aymara (harvest)	45.8		1146	2.26		Kashiwazaki et al. (2009)
Chinese	65.5	2269	1362	1.67	907	Yao et al. (2002)
Gambian	49.7	2366	1220	1.94	1145	Singh et al. (1989); Heini et al. (1991)
Guatemalan	54.1	2070	1296	1.60	774	Stein et al. (1988)
Nigerian	53.1	2114	1192	1.77	922	Luke et al. (2002)
Pima Indian	95.0	2684	1714	1.57	970	Tataranni et al. (2003)
Polynesian	85.8	3043	1703	1.79	1340	Rush et al. (1999)
Swazi	54.2	1717	1293	1.33	424	Huss-Ashmore et al. (1989)
Yakut	65.2	2298	1533	1.50	765	Snodgrass et al. (2006)
Developed nations	58.6	2234	1300	1.72	934	FNB/IOM (2002); Leonard (2008)

TEE, total energy expenditure; BMR, basal metabolic rate; PAL, physical activity level; AEE, activity energy expenditure.

Gambians, men had PALs of 2.4, which reflects intense physical activity associated with harvesting activities, while women had somewhat lower PALs (1.9). The Aymara study compared activity levels in the harvest and preharvest seasons and documented relatively high activity levels across seasons and sexes, with very high PALs in both sexes (men 2.2, women 2.3) during the peak season of agricultural and herding activities. Other studies have documented low-to-moderate activity levels in other subsistence populations (e.g., the Yakut [Snodgrass et al. 2006]) and rural populations in developing nations (e.g., Nigerians [Luke et al. 2002]); however, many of these groups are undergoing rapid changes in lifestyle as a result of economic development and none are fully dependent on subsistence activities. Unsurprisingly, among the Yakut, higher activity levels were found among individuals most involved in the subsistence herding economy (Snodgrass et al. 2006).

As discussed in Chapter 7, a meta-analysis by Leonard (2008) shows broadly similar TEEs between subsistence populations (3015 kcal/day [12,623 kJ/day] in males and 2294 kcal/day [9605 kJ/day] in females) and industrialized societies (2873 kcal/day [12,029 kJ/day] in males and 2234 kcal/day [9353 kJ/day] in females). However, this overall similarity masks pronounced differences in components of TEE, with subsistence populations having higher physical activity costs and overall lower maintenance costs. Western populations, with larger body sizes (by 7 kg in females and 12 kg in males) and more sedentary lifestyles, have higher maintenance costs and lower levels of physical activity. Activity levels of 1.98 in males and 1.82 among females in subsistence populations were considerably higher than the average for healthy, normal-weight adults in the United States and other developed nations which have PALs that average 1.73 for males and 1.72 for females. These conclusions are similar to other analyses (e.g., Schulz and Schoeller 1994; Dufour and Piperata 2008) but the findings are surprising in that activity differences between subsistence populations and industrialized nations are not as large as anticipated, with higher than expected values among industrialized populations and lower than expected values among subsistence populations. In fact, most of the subsistence groups surveyed in these studies had activity levels classified as moderate (PAL = 1.7–1.99) by the current FAO/WHO/UNU (2004) definition. Furthermore, activity levels among subsistence groups were in many instances highly seasonal with very low activity levels (especially among males) during certain times of the year (Dufour and Piperata 2008).

An area of intense investigation has been the existence of sex differences in activity patterns. Activity data from three hunter-gatherer groups (!Kung, Ache, and Inuit), as well as several other subsistence populations (e.g., Evenki reindeer herders), and farmers in the developing world, have demonstrated that men on average are moderately more physically active than women (Panter-Brick 2002; Dufour and Piperata 2008; Leonard 2008). However, the average differences are small and the pattern is not universal. Sex-based division of labor appears to increase resource extraction ability and increase environmental buffering through the use of a broader diet (Kuhn and Stiner 2006). In fact, sexual division of labor appears to be a hallmark of our species (as discussed earlier) and energetics modeling has been used to suggest that small energetic differences related to division of labor in modern humans may have reduced female energetic costs by transferring more of the energetic burden to males, with consequences for increased fertility compared with other hominins (Snodgrass and Leonard 2009). Importantly,

subsistence participation by men, children, juveniles, adolescents, and postreproductive women relatives are critical for supplementing a woman's energetic needs during pregnancy and lactation, and enabling relatively rapid reproductive rates (Kaplan et al. 2000; Marlowe 2003; Bogin 2009; Reiches et al. 2009; Madimenos et al. 2011).

ENERGETICS AND HEALTH

Many of the global health challenges being faced today are closely related to energy dynamics, from obesity and cardiovascular problems associated with positive energy balance, to reduced immunocompetence, poor childhood growth, and increased infectious disease burden associated with negative energy balance. In addition, an energetics approach can provide valuable insights into dietary shifts associated with changing cultural and economic conditions because lifestyle transitions often involve shifts in energy intake and expenditure. Research over the past several decades by human biologists indicates that even minor shifts in energy patterns can lead to energy imbalance and result in changes in body composition, nutritional status, and health. In this section, I review the links between energetics and health, concentrating both on the effects of under- and overnutrition on health. In this section, I also discuss recent research that suggests that long-term caloric restriction in adults leads to a lower risk for chronic degenerative diseases and a healthier pattern of aging. I conclude by discussing the health effects of economic development and lifestyle change that is occurring today in much of the world.

Undernutrition

Undernutrition refers generally to nutritional deficiency, of which energy intake is one of the most important deficiencies. Other important aspects of undernutrition, as discussed in Chapter 7, are protein inadequacy (often with simultaneous deficiency in energy) and micronutrient deficiencies, such as vitamin A and zinc (Vaz 2003). Undernutrition is generally divided into either **acute energy deficiency** or **chronic energy deficiency**, the former characterized by negative energy balance and declining body weight, while the latter is defined by a low but stable body weight (James et al. 1988). Measurement of undernutrition is typically accomplished in adults using BMI, where underweight is defined as a BMI of less than 18.5. Additional categories are used to indicate extent of underweight: mild thinness (17.0–18.49), moderate thinness (16.0–16.99), and severe thinness (<16.0) (WHO 2000). In children, BMI has many problems of interpretation due to changes in body size, body composition, and body proportions during the years of growth. BMI references for children do exist but are not extensively used. Most human biologists and nutritionists prefer to use growth references or standards to define undernutrition based on whether children are **stunted** (low height for age), **wasted** (low weight for height), or underweight (low weight for age) (Hamill et al. 1977; Kuczmarski et al. 2002; WHO 2006). Chapter 12 explains these methods in more detail.

In acute energy deficiency, the body is in negative energy balance and there is both a decrease in body mass as well as a shift in body composition (with loss of

body fat and lean tissue); however, in overweight and obese individuals, more of this weight loss is typically the result of loss of body fat (Vaz 2003). BMR is typically reduced in response to acute energy stress as a result of the reduction in metabolically active tissues and the downregulation of BMR. Furthermore, individuals in acute energy deficiency typically show reduced physical activity, decreased work capacity, reduced ability to respond to cold stress, negative impacts on cognition, and diminished immune function (Vaz 2003; Kurpad 2005). In chronic energy deficiency, body weight is relatively low and body composition has been altered by low levels of body fat and lean tissue. BMR is generally low as a result of small body size and reduced lean tissue mass, but in most cases, there is no permanent downregulation of BMR. As with acute energy deficiency, metabolic responses to cold are less effective and there is often an impaired ability to thermoregulate. In chronic energy deficiency, there is a general reduction in costs of physical activity because of body size, but also reductions in muscular strength and physiological work capacity.

Undernutrition is widespread globally, with 800 million people worldwide estimated to be undernourished (Vaz 2003). Undernutrition is most severe in sub-Saharan Africa and Asia. According to recent World Health Organization (WHO) data, approximately 40% of children under the age of 5 in South Asia and Africa are stunted (indicating long-term energy stress), while over 20% of children in these same regions are underweight (indicating more recent energy stress) (Black et al. 2008). Undernutrition, as a result of its close relationship with immune function, is responsible for a huge amount of **morbidity** and mortality related to infectious diseases such as gastrointestinal illnesses, pneumonia, malaria, and measles (Caulfield et al. 2003). Adding to the problem is that many countries are dealing with a dual burden of energy-related disease, with a simultaneous increase in obesity and its associated diseases and continued problems of undernutrition, particularly childhood malnutrition (Prentice 2006; Varela-Silva et al. 2007, 2009).

Caloric Restriction and Health

An interesting window onto energetics, health, and aging comes from studies of caloric restriction, which call into question our notion of energy requirements. Caloric restriction studies, where energy intake in adults is reduced substantially for long periods of time (e.g., 30% below "requirements") but without nutrient deficiencies, demonstrate that across a variety of animals, including various mammals (e.g., mice and monkeys), there is generally a delay in the pace of life history, with later onset of chronic degenerative diseases, an overall reduction in morbidity, and an increased life span (Masoro 2005; Colman et al. 2009; Chapter 13 of this book). There is suggestive evidence that the same pattern is seen in humans, with recent studies showing better cardiovascular and metabolic health, including reduced inflammatory markers and reduced evidence for **atherosclerotic** changes (Holloszy and Fontana 2007). The mechanism or mechanisms remain to be fully elucidated but many have pointed to decreased **free radical** (a by-product of oxidative metabolism that can damage DNA and compromise cellular function) production, altered **insulin** sensitivity, and increased investment in cellular repair mechanisms as potential mechanisms (Masoro 2005; Redman et al. 2008).

Overnutrition and Obesity: Human Energy Dynamics in a Changing World

Overnutrition refers to the type of malnutrition when consumption of energy or nutrients exceeds requirements; excess energy intake is the primary form of overnutrition. Long-term positive energy balance leads to increased adiposity and risk for overweight and obesity. Obesity is generally defined as excess accumulation of adipose tissue necessary to cause negative health effects; this "condition" is recognized to be a heterogeneous collection of disorders with varied causes (WHO 2000). The WHO has recognized obesity as a global **epidemic**, reflecting the widespread distribution of the condition, its status as a disease with metabolic and endocrine abnormalities, and its well-established association with a variety of negative health outcomes (WHO 2000).

Excess adiposity is associated with decreased life expectancy, an increase in all-cause mortality, and is a major **risk factor** for cardiovascular disease, type 2 diabetes, musculoskeletal disorders (e.g., **osteoarthritis**), certain cancers, respiratory disease, sleep apnea, gout, and polycystic ovary syndrome. Fat distribution affects the risk of negative health outcomes, with abdominal obesity (especially **visceral adipose tissue [VAT]**; adipose tissue found within the abdominal cavity) most closely related to risk for a variety of health conditions (Kannel et al. 1991; Fox et al. 2007; Ibrahim 2010; Wells 2010). At one level, obesity is a simple phenomenon, as it reflects an imbalance between energy intake and energy expenditure, with the result that excess dietary energy is deposited as stores of fat. At another level, obesity is a staggeringly complex and multifactorial disease, with genetic, environmental, and developmental components (Frühbeck 2005; Wells 2010). While most researchers recognize some role for both energy intake and energy expenditure in the development of obesity, no general consensus exists on the specific factors that are most important, and how much intra- and interpopulation variation exists in the etiology of obesity.

As discussed in Chapter 7, obesity is typically diagnosed in population research using proxy measures that are based on relationships with morbidity and mortality. The most common classification system for adults is based on BMI, with overweight being defined as 25.0–29.9 and obesity at 30.0 or above (WHO 2000). According to recent figures, there are over 900 million adults worldwide who are considered overweight, and another 400 million classified as obese (Kelly et al. 2008). Identification of overweight and obesity is more complicated in children than among adults because of age-related shifts in body size and composition. In general, BMI values are compared with age- and sex-specific growth norms, and overweight and obesity are defined based on specific **percentile** cutoffs. Recent research has also identified a rapid increase in childhood obesity on a global scale, with nearly all countries showing increasing overweight and obesity, and approximately 10% of school-age children globally recognized as being overweight or obese (Lobstein et al. 2004; Wang and Lobstein 2006).

Once considered a disease of affluence and confined to industrialized nations, obesity is emerging as a major health concern in nearly every country in the world; in many nations, obesity was virtually absent only a generation ago (WHO 2000). Available data suggest that the prevalence rate of obesity has reached unprecedented levels in most developing countries; in much of Asia, North Africa, and Latin America, obesity is continuing to increase at a rate that

far outpaces that of developed nations (Popkin 2003; WHO/FAO 2003; Hossain et al. 2007; Kelly et al. 2008). Furthermore, cardiovascular disease and diabetes are rapidly increasing in developing nations, and chronic degenerative diseases are fast becoming among the top causes of morbidity and mortality in all human populations.

The growing challenge of obesity and other chronic diseases in the developing world is closely related to lifestyle changes that occur with economic development, a topic that has attracted considerable attention from human biologists (Baker et al. 1986; Friedlaender et al. 1987; Huss-Ashmore et al. 1992; Snodgrass et al. 2007b). The mechanisms responsible for this health transition remain incompletely understood, although dietary changes, physical inactivity, alcohol consumption, tobacco use, and chronic psychosocial stress have all been implicated. Energetics provides a key to understanding the health changes associated with economic development, as lifestyle transitions are often related to shifts in energy intake and expenditure. Decreased energy expenditure is generally considered to be an important factor in the increase in chronic degenerative diseases seen with economic development, since traditional economies are characterized by intensive reliance on human physical labor and relatively simple technology, while modernized economies are industrialized, mechanized, and rely less on human physical labor (WHO/FAO 2003). As discussed above, physical activity data are fairly limited for non-Western populations, but the available evidence demonstrates that subsistence populations have only marginally higher PALs than those documented among Western populations (Schulz and Schoeller 1994; Dufour and Piperata 2008; Leonard 2008). However, even relatively small reductions in activity can lead to positive energy balance which, over time, can lead to the development of overweight and obesity. At present, almost no data are available that measure activity patterns repeatedly over the course of economic development and assess their role in the development of obesity and other chronic diseases.

Dietary studies have generally indicated that economic development involves shifts in overall energy intake and dietary composition (Popkin 2003; WHO/FAO 2003). Total energy intake often increases with economic development, with an overall rise in the contribution of market foods and a decrease in reliance on local food resources, such as polyunsaturated omega-3 **fatty acids**. For example, Leonard (2004) estimated that individuals in developed nations consume, on average, over 50% more energy per day compared with individuals in developing countries. Additionally, with greater reliance on imported products, there is often an increased consumption of nutrient-dense foods, including fats (especially saturated fats) and refined sugars; these increases are typically offset by decreases in unrefined carbohydrates and protein (Cordain et al. 2000; WHO/FAO 2003).

The increasing global prevalence of obesity and associated chronic degenerative diseases is in many ways the product of a long-term trend in human evolution that has increased our ability to extract energy from the environment. This combined with our propensity to minimize physical activity and the decreased metabolic costs associated with thermoregulation, digestion, and immune function has fundamentally shifted human energy dynamics and puts all of us at risk for long-term energy imbalance and obesity. As a consequence, today's urbanized, cosmopolitan condi-

tions seen increasingly on the planet present vastly different energetic challenges than those encountered during much of human evolutionary history. An appreciation for our evolved biology and for changing energy patterns is essential for a complete understanding of the causes of and the best strategies for dealing with obesity and related chronic degenerative diseases.

CHAPTER SUMMARY

Energetics provides a valuable tool for examining the ecology and evolution of human populations. Energetics is today a growing area of biological anthropology that is rapidly expanding in its application as it increases in theoretical and methodological sophistication. Returning to the questions outlined at the beginning of the chapter, we can see the utility of an energetics approach for providing insights into the ecology and evolution of early hominins, since many of the key adaptive transitions in human evolutionary history such as bipedalism and enlarged brain size had energetic consequences. Furthermore, we have seen that a hallmark of human evolutionary history is the increasing ability and efficiency in extracting energy from the environment.

An energetics perspective can also provide insights into adaptive strategies used by contemporary human populations for coping with the myriad environmental stressors encountered in the diverse ecosystems in which humans inhabit. This is evident in circumpolar environments, which present adaptive challenges to human populations as they struggle to cope with extreme cold stress within the context of a low-energy, highly seasonal ecosystem. Certain physiological adaptations, such as the elevated BMRs seen among indigenous northern groups in response to chronic and severe cold stress, require trade-offs in energy allocation and structure human life history patterns. Furthermore, by using a biocultural perspective, we can see how social factors shape energy patterns, such as how household-level division of labor, and how settlement pattern affects PAL and energy expenditure.

Finally, energetics provides a key to understanding the health changes associated with Westernization, as lifestyle transitions are often related to shifts in energy intake and expenditure. Research among populations undergoing economic development has documented rapidly deteriorating cardiovascular and metabolic health, which results from shifts in diet and physical activity patterns. The increasing global prevalence of obesity and associated chronic degenerative diseases can be seen as the product of a long-term trend in human evolution that has increased our ability to efficiently extract energy from the environment. Reversing that trend will require a sophisticated understanding of human energy dynamics and an appreciation for our evolved biology.

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