AMERICAN JOURNAL OF HUMAN BIOLOGY 24:372–384 (2012)

Toolkit: Methods in Human Biology

Laboratory and Field Methods for Measuring Human Energy Expenditure

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Energetics research is central to the field of human biology. Energy is an important currency for measuring adaptation, because both its acquisition and allocation for biological processes have important implications for survival and reproduction. Recent technological and methodological advances are now allowing human biologists to study variation in energy dynamics with much greater accuracy in a wide variety of ecological contexts. This article provides an overview of the methods used for measuring human energy expenditure (EE) and considers some of the important ecological and evolutionary questions that can be explored from an energetics perspective. Basic principles of calorimetry are first presented, followed by an overview of the equipment used for measuring human EE and work capacity. Methods for measuring three important dimensions of human EE—resting metabolic rate, working/exercising EE, and total EE—are then presented, highlighting key areas of ongoing research. Am. J. Hum. Biol. 24:372–384, 2012. © 2012 Wiley Periodicals, Inc.

The study of energy dynamics has long held a central place in human biology research. Pioneering work during the 1960s and 70s examined patterns of variation in energy expenditure (EE) among subsistence-level populations living in diverse environments ranging from the arctic to the tropics (Norgan et al., 1974; Rode and Shephard, 1971; Spurr et al., 1975; Thomas, 1976). This work focused on how human populations responded to different ecological constraints on energy availability, and what the implications were for human health and well being.

Today, energetics remains a major focus of human biology research, in part, because energy is an important currency for measuring adaptation (Leonard and Ulijaszek, 2002; Snodgrass, 2012; Ulijaszek, 1995). Both the acquisition of energy and its allocation for biological processes have important implications for survival and reproduction. An individual's daily energy budget reflects this—being divided into "maintenance costs," those associated with keeping one alive on a day-to-day basis (i.e., resting and activity costs), and "productive costs," those associated with investments in the future (i.e., growth/maturation and reproduction). In applying life history theory to human biology, we explicitly consider the adaptive consequences of variation in the allocation of energy to maintenance versus production in different ecological circumstances. Comparative analyses have shown that the amount of energy allocated to these different components varies greatly across human populations living in different environments (see Kramer et al., 2009; McDade et al., 2008; Tracer, 2002). Additionally, over the course of an individual's lifespan, the relative allocations will also change (Holliday, 1986).

Over the last 20 years, both technological and methodological advances have facilitated the measurement of human EE in both laboratory and field settings. These advances are now allowing human biologists to study variation in energy dynamics with much greater accuracy. In this article, I first discuss the basic principles of calorimetry, particularly as they apply to the study of human EE and activity. Next, I present a brief overview of the equipment used for measuring human EE and work capacity. Finally, I outline the methods used for measuring three important dimensions of human EE—resting metabolic rate (RMR), exercising/working EE, and total EE (TEE)—and discuss how the assessment of these three dimensions can provide insights into human biological variation and health.

PRINCIPLES OF CALORIMETRY

The study of energetics relies on the principle of calorimetry, the measurement of heat transfer. In human biology research, energy is most often measured in kilocalories (kcal). One kilocalorie is the amount of heat required to raise the temperature of 1 kg (or 1 l) of water, 1°C. Another common unit for measuring energy is the joule or the kilojoule [1 kilojoule (kJ) = 1,000 J], with the conversion between calories and joules being 1 kcal = 4.184 kJ. Less frequently, human EE is expressed as watts, a measure of power. One watt is equal to the rate of energy output of 1 J/s. Thus, the conversion of watts into kcal/min is as follows: 1 watt = 0.01433 kcal/min.

Of the food energy that a person consumes, a portion of it is nondigestible and is passed from the body in the feces. The remaining portion, assimilated energy, is available for metabolic processes and may be allocated to maintenance or production. Maintenance costs include the energy expended for somatic repair and upkeep (e.g., cell repair, immune activity, and thermoregulation), digestion of food, and muscular work or physical activity. Productive costs, on the other hand, are those associated with tissue growth, fat storage, and reproduction (Karasov and Martinez del Rio, 2007; McArdle et al., 2001).

Techniques for measuring EE involve either measuring heat loss directly (direct calorimetry) or measuring a proxy of heat loss (indirect calorimetry) such as oxygen (O_2) consumption or carbon dioxide (CO_2) production. Direct calorimetry is done under controlled laboratory conditions in insulated chambers that measure changes in air temperature associated with the heat being released by a subject (Consolazio et al., 1963; McLean and Tobin, 1987). Although quite accurate, direct calorimetry is not

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Received 9 January 2012; Revision received 1 February 2012; Accepted 5 February 2012

DOI 10.1002/ajhb.22260

Published online 15 March 2012 in Wiley Online Library (wileyonlinelibrary.com).

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TABLE 1. Estimated energetic equivalents (kcal) per 1 l of O_2 consumed for selected RQ values[a]

RQ	Energetic equivalent (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

[a]Adapted from McArdle et al. (2001).

widely used because of its expense, technical difficulty, and the limitations placed on a subject's mobility.

Consequently, methods of indirect calorimetry are more commonly used to quantify human EE, particularly under field conditions (Jéquier et al., 1987). The most widely used of these techniques involve measuring O_2 consumption. Because the body's energy production is dependent on O_2 (aerobic respiration), O_2 consumption provides a very accurate indirect way of measuring a person's EE. Each liter of O_2 consumed by the body is equivalent to ~5 kcal (see Table 1; McArdle et al., 2001). Consequently, by measuring O_2 use while a person is performing a particular task (e.g., standing, walking, and running on a treadmill), the energy cost of the task can be determined.

The open-circuit method for measuring O_2 consumption is the most straightforward and is the technique most widely used in human energetics. The subject breathes in ambient air, which has constant concentrations of O_2 (20.93%), CO_2 (0.03%), and nitrogen (79.04%). Upon exhalation, the subject's breathing rate (liters of air/min) and the O_2 and CO_2 concentrations of the expired air samples are determined. In the presence of O_2, the body's primary fuel sources (carbohydrates, fats, or protein) are broken down into CO_2 and water (H_2O), liberating energy in the form of adenosine triphosphate. Thus, the amount of energy that the subject is using for aerobic respiration is directly reflected by the differences in O_2 and CO_2 levels between the inspired and expired air. Relative to the ambient air, expired air samples have lower levels of O_2 (about 15–17%) and higher levels of CO_2 (3–5%).

The raw measurements of breathing (respiratory) rate and gas concentrations are used to calculation of these variables.[1]

- V_E—ventilatory rate (l/min). The rate of breathing, adjusted for "standard" environmental conditions (STPD: standard temperature of 0°C; barometric pressure of 760 mm Hg, and no water vapor [dry]).
- VO_2—O_2 consumption (l O_2/min). Liters of O_2 per minute used by the body (corrected for STPD).
- VCO_2 —CO_2 production (l CO_2/min). Liters of CO_2 per minute produced by the body (corrected for STPD).
- RQ—respiratory quotient (VCO_2/ VO_2). The ratio of CO_2 production to O_2 consumption. Under nonsteady-state conditions, this measure is referred to as the respiratory exchange ratio.

Under steady-state conditions, the RQ values range from 0.7 to 1.0 and provide a useful index for determining the type of fuel being used for metabolism (i.e., fat, protein, and carbohydrates) and the amount of energy being liberated for each liter of O_2 consumed. Because of the differences in the chemical structure of fat, protein, and carbohydrates, different amounts of O_2 are required to completely metabolize each. Complete breakdown of carbohydrates is associated with an RQ of 1.0, because each molecule of O_2 consumed results in one molecule of CO_2 being produced. In contrast, fat metabolism requires greater amounts of O_2 and is thus associated with low RQs of ~0.70 (i.e., more O_2 consumed per CO_2 produced; Consolazio et al., 1963; McArdle et al., 2001).

From VO_2 and RQ, EE (kcal/min) can be calculated using the caloric conversions presented in Table 1. Note that the caloric equivalent for each liter of O_2 consumed varies as a function RQ. For an RQ of 0.71, each liter of O_2 used yields 4.690 kcal, whereas an RQ of 1.0 has an energetic equivalent of 5.047. Thus, for a subject with a resting VO_2 of 0.25 l/min and an RQ of 0.80, their resting EE (RMR) would be calculated as follows:

$$\text{RMR (kcal/day)} = 4.801 \text{ kcal/l } O_2)(0.251 \text{ } O_2\text{/min})$$
$$= 1728 \text{ kcal/day}$$

EQUIPMENT FOR MEASURING ENERGY EXPENDITURE

Metabolic carts

Technological advances have facilitated the measurement of human EE in both laboratory and field settings. All standard computerized metabolic carts contain the same basic components: (1) O_2 and CO_2 analyzers, (2) a device for measuring breathing (ventilation) rates, (3) a gas sampling system, and (4) a computer interface that allows for the transfer of the raw data (McArdle et al., 2001). Once the data are acquired by the computer, standard software applications perform the metabolic calculations noted in the previous section. Energy costs are assessed on a continuous basis by measuring the volume and the O_2 and CO_2 concentrations of expired air samples.

Figure 1a shows a standard printout of a metabolic test under resting conditions. The graph shows changes in VO_2, VCO_2, and RMR over the 8 min of the test, with the shaded area denoting the predicted RMR ±5%, for the subject based on the subject's age, sex, height, and weight (from Harris and Benedict, 1918). Such a test can be used to assess variation in RMR across subjects, determining whether subjects may have relatively sluggish or elevated metabolic rates. Figure 1b shows a similar printout for an exercise test on a treadmill. In this case, changes in VO_2, VCO_2, and heart rate (HR; beats per minute) are monitored at increasing exercise levels (speeds and inclines). This type of test provides insights into energy costs at different workloads and allows for the estimation of a subject's maximal working capacity ($VO_{2\ max}$ or $VO_{2\ peak}$; Cooper and Storer, 2001; McArdle et al., 2001).

Metabolic carts vary considerably in price depending on several factors, including the type of gas analyzers used and the size and portability of the unit (see Table 2). In choosing an appropriate metabolic analysis system, some important issues to consider include: (1) what types of tests to be performed (i.e., resting, exercising, or both), (2) whether the unit will be used in a laboratory or transported to field locations, and (3) whether the system will be used primarily for research or teaching. Reviews of the accuracy and performance of several widely used metabolic systems have recently been published in the nutri-

[1]Detailed information on the calculation of these metabolic parameters is presented in Appendix D of McArdle et al. (2001: 1117–1120).

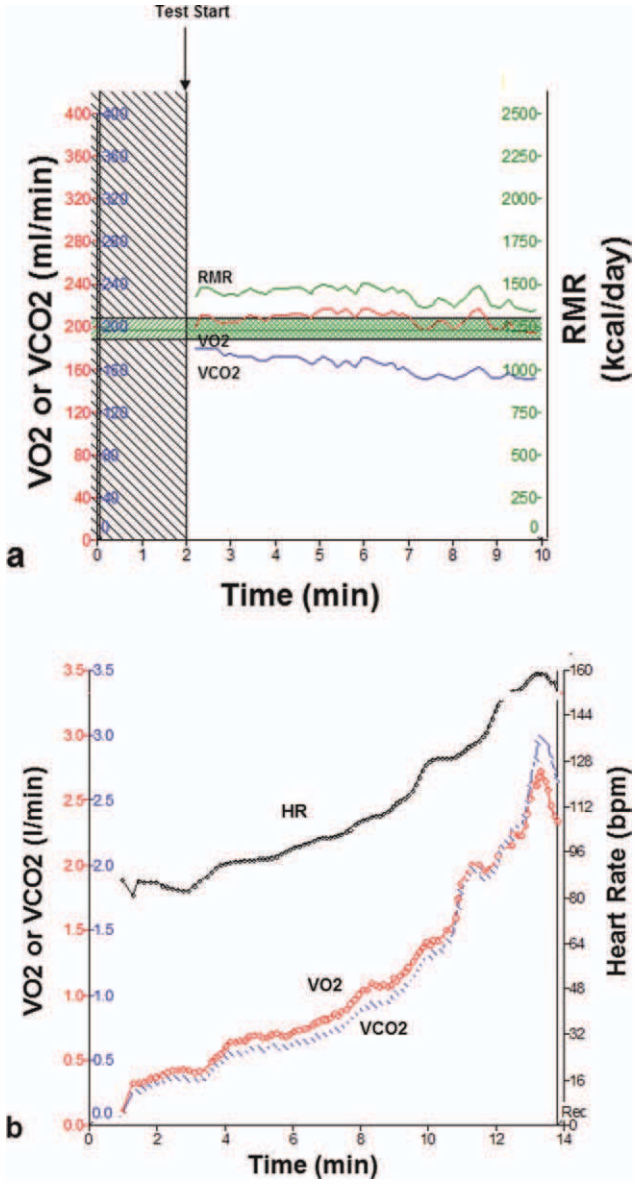

Fig. 1. Standard graphs of metabolic tests under (a) resting and (b) exercising conditions. For the resting test, the subject's VO_2 (l/min), VCO_2 (l/min), and RMR (kcal/day) are plotted versus time (min) over the duration of the test. The shaded area in resting graph denotes the predicted RMR (±5%) based on age, sex, height, and weight using the Harris and Benedict (1918) equations. For the exercise test, the subject's VO_2, VCO_2 and HR are plotted over time in response to increasing workloads while walking on a treadmill. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

tional science and exercise science literature (e.g., Cooper et al., 2009; Macfarlane, 2001; Meyer et al., 2005; Wahrlich et al., 2006).

Three different types of electronic O_2 analyzers are used in metabolic analysis systems: paramagnetic, fuel cell, and zirconium oxide (see Cooper and Storer, 2001). Of these, the paramagnetic analyzers are among the most common. These analyzers align O_2 molecules within a magnetic field inside a mixing chamber. Changes in O_2 concentration are directly correlated with changes in the magnetic field.

TABLE 2. Estimated costs for equipment and supplies necessary for measuring human energy expenditure

Category/item	Estimated costs ($)
1. Metabolic cart	12,000–45,000
2. Calibration supplies:	
Calibration gases	200–300 per tank; 250–300 regulator
Calibration syringe	300–400
3. Environmental monitoring (thermometer, barometer, and hygrometer)	200–400
4. Subject interface[a]:	
Mouthpiece/noseclip/valve	100–400
Face mask/valve	100–400
Canopy interface and system modifications	6,000–7,000
HR monitor	100–400
5. Exercise devices:	
Treadmill	5,000–25,000
Cycle ergometer	1,000–5,000
Step test	100–200
6. Anthropometric equipment (basic):	
Stadiometer	100–2,700
Scale	100–400
Skinfold calipers	200–400

[a]Costs for patient interface includes costs for tubes, valves, or pneumotachometers necessary for linking subject to the metabolic cart.

In an electrochemical or fuel cell analyzer, O_2 molecules pass through a sensing membrane and then through a thin layer of electrolyte. A chemical reaction occurs within the cell in which the O_2 molecules are reduced, gaining electrons. The transfer of electrons from the lead anode to gold-plated cathode creates an electrical current that is proportional to the concentration of O_2 in the air sample. Fuel cell sensors become weaker with continued use and, thus, must be replaced every 1–3 years.

Zirconium oxide analyzers are sometimes referred to as "high-temperature" O_2 sensors. In these sensors, the expired air sample surrounds the zirconium oxide cell, while the cell's interior is exposed to ambient air. When heated to temperatures of 650°C and above, the zirconium oxide ceramic material becomes porous, allowing the movement of O_2 ions from a higher to lower concentrations of O_2. The movement of these ions across the zirconium oxide produces a voltage that is proportional to the differences in O_2 concentration. These analyzers respond quickly to changes in O_2 concentration, making them suitable for breath by breath analysis.

Most CO_2 analyzers are nondispersive infrared sensors that direct a beam of infrared light alternately through a reference sample and a sample of expired gas. A detector senses differences in the absorption of selected infrared wavelengths between the two samples. The differences in infrared absorption are proportional to the differences in the concentration of CO_2 (Cooper and Storer, 2001).

To measure the rates of ventilation, the two most commonly used devices are pneumotachometers and turbine flow meters (Cooper and Storer, 2001; McArdle et al., 2001). Pneumotachometers assess the rate of airflow by measuring the pressure drop across obstructions placed within a breathing tube. These devices come in different sizes to accommodate variation in rates of airflow associated with differences in body size (e.g., children vs. adults) and levels of exertion (e.g., resting vs. exercising). Turbine flow meters, on the other hand, rely on a rotor mounted inside of a breathing tube. The rate at which the rotor

spins thus provides a measure of the speed of airflow while breathing.

Additional equipment for metabolic testing

In addition to the metabolic system itself, other equipment and supplies are also required in setting up and maintaining a human energetic laboratory. These additional components include the following: (1) calibration gases and syringe, (2) thermometer, barometer, and hygrometer, (3) subject interface (e.g., mouthpiece and facemask), (4) HR monitors, (5) an exercise device (e.g., treadmill and ergometer), and (6) anthropometric equipment (e.g., stadiometer, scale, and skinfold calipers). Each of these items is discussed below. The estimated costs for each of these items are presented in Table 2.

Calibration equipment and supplies. To insure accurate measurements, both the gas analyzers and volume measuring systems need to be calibrated. The gas analyzers are calibrated with compressed gases of known O_2 and CO_2 levels. Typically, calibration gases contain 15–16% O_2 and 3–5% CO_2, similar to the levels observed in expired air samples.

To calibrate the volume or flow measuring devices, a large, 3-l syringe is typically used. This device allows for a known volume of air to be pushed through the system in a specified unit of time (X l/min), simulating the breathing pattern of a subject.

Environmental monitoring. As all metabolic measurements are adjusted to "standard" environmental conditions (STPD; see above), it is important to know the temperature, barometric pressure, and relative humidity at the testing location. Some metabolic carts have barometers and thermometers built in, whereas others require the environmental conditions be input directly.

Subject interfaces. There are a variety of different breathing devices used for connecting a subject to the metabolic cart. The most commonly used is the mouthpiece and nose clip system, in which the subject breathes entirely through his/her mouth. This system is usually quite effective, but extended mouth breathing can become uncomfortable for subjects.

Silicone or neoprene face masks represent a common alternative to mouthpieces and nose clips. These masks fit snugly over a subject's lower face, typically allowing the person to breathe through both their nose and mouth. Subjects often find the masks to be preferable to the mouthpieces/nose clips, especially for prolonged tests. However, care must be taken to ensure that the mask fits tightly on the subject's face, and that expired air is not leaking out of the sides.

Another recent innovation has been the development of a canopy interface, specifically designed for measuring RMR. This system involves placing a hard plastic "bubble" over the subject's entire upper body and having a pump draw the expired air into the metabolic cart at a constant rate.

Heart rate monitors. Heart rate is a key variable that is typically monitored in both resting and exercise tests. The most commonly used monitors have an electrode chest strap that transmits a HR signal to a wrist watch or other receiver where the data are stored. Most metabolic carts have interfaces that allow for direct up HR data from the chest transmitters.

Exercise devices. For the measurement of energy costs in response to exercise, treadmills or cycle ergometers are commonly used to establish standardized work loads. In the exercise physiology literature, there are a number of different protocols for measuring energy demands in response to increasing workload for both the treadmill and ergometer (see ACSM, 2006; Cooper and Storer, 2001:241-243).

Another exercise option that is particularly useful in remote field settings is a graded step test. A standard step test allows for workloads to be determined based on the weight of the subject, height of the steps, and rate of ascent/descent. As with treadmills and ergometers, a number of step-test protocols have been developed over the years (see ACSM, 2006; CSEP, 2003).

Anthropometric equipment. Measurement of basic anthropometric dimensions is important in metabolic studies, because body size is one of the primary determinants of an individual's EE. Minimally, height (cm) and weight (kg) should be measured, as these are key variables used to predict energy costs under resting and exercising conditions (ACSM, 2006; Harris and Benedict, 1918; Schofield, 1985). Depending on the research questions being addressed, additional measures commonly collected include: (1) sitting height (cm), (2) arm and leg length (cm), (3) chest, waist, and hip circumferences (cm), (4) selected skinfold measures (mm), and (5) measurement of body fatness (%) by bioelectrical impedance.

MEASURING VARIATION IN HUMAN ENERGY EXPENDITURE

Resting metabolic rate

RMR represents the minimum amount of energy necessary to keep a person alive. Resting metabolism is measured under controlled, thermoneutral conditions while a subject is lying in a relaxed and fasted state (at least 10 h after a meal; see McLean and Tobin, 1987; Schofield, 1985). Measurements are typically taken for 10–20 min, with the RMR being determined as the average energy costs over the entire measurement period. Before each measurement, the O_2 and CO_2 analyzers are calibrated, and the subject is fitted with both a HR monitor and the interface with the metabolic cart (e.g., face mask, mouthpiece, or canopy). After the subject is comfortably situated and acclimated to the equipment, V_E, VO_2, VCO_2, and the RQ are monitored over the entire measurement period. Energy expenditure (kcal/day) is then calculated from the average VO_2 measures and are then converted into energetic equivalents (RMR, kcal/day) based on the measured RQ (after Weir, 1949; see Table 1). Figures 2a and b show examples of measurement of RMR using face mask and canopy systems.

The utility of measuring metabolic rate under such controlled conditions is that allows for direct comparison both within and among different species. Since the early 20th century, the determinants of variation in RMR have been widely studied across mammalian species and within humans (Benedict, 1938; Brody, 1945; Kleiber, 1932). Both

Fig. 2. Measurement of resting metabolic rates using (a) face mask and (b) canopy interfaces. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

within and between species, the strongest correlate of variation in RMR is body mass. Across mammalian species of different size, variation is often described by the "Kleiber relationship" in which RMR scales to ~3/4th power of body mass:

$$\text{RMR (kcal/day)} = 70 \times \text{M}^{0.75} \text{ (from Kleiber, 1975)}$$

The implications of this negative allometric relationship are that smaller animals have higher mass-specific energy cost (kcal/kg mass). These differences in metabolic turnover are central determinants of broad differences in life history and feeding strategies across mammals of different sizes. Higher rates of metabolic turnover in small mammals are associated with faster life histories (e.g., earlier maturation and shorter life spans) and the need for high-quality, energy-rich diets. In contrast, larger mammals live life at a slower pace and can meet their energy demands by subsisting on lower quality foods (see Leonard, 2012).

Within human biology, a number of different predictive equations have been developed for estimating RMR over the last century. Selected examples are presented in Table 3. Among the oldest and mostly widely used are the Harris and Benedict (1918) equations, which estimate RMR in adult men and women based on age, height, and weight. In 1985, the World Health Organization (WHO) commissioned the development of a set of predictive equations based on age, sex, and body weight, derived from studies of RMR conducted around the world (Schofield, 1985). The WHO continues to advocate the use of these equations in their current recommendations on human energy requirements (FAO/WHO/UNU, 2004). Most recently, work in nutritional science has advocated the use of predictive equations based on "fat-free mass" (FFM = body weight − fat mass; see Cunningham, 1991), recognizing the considerable variation that exists in human body composition. Indeed, norms based on FFM are preferred when comparing individuals or populations with markedly different levels of body fatness.

TABLE 3. Selected predictive equations for estimating resting metabolic rate (RMR, kcal/day) in adults

Reference	Sex	Age (years)	Equation
Harris and Benedict (1918)	M	–	66.5 + 13.7(Wt) + 5.0(St) − 6.8 (Age)
	F	–	655.1 + 9.6(Wt) + 1.8(St) − 4.7(Age)
FAO/WHO/UNU (2004)	M	18–29	15.1(Wt) + 692
		30–59	11.5(Wt) + 873
		60 and older	11.7(Wt) + 588
	F	18–29	14.8(Wt) + 487
		30–59	8.1(Wt) + 846
		60 and older	9.1(Wt) + 659
Cunningham (1991)	M/F	–	21.6(FFM) + 371

Wt, weight (kg); St, stature (cm); FFM, fat-free mass (kg).

Although body mass is a strong predictor of RMR in all humans, there exists substantial interpopulational variation in RMR. For example, in his classic work, *Climate and Human Variability*, Roberts (1978) demonstrated a strong negative correlation between RMR and mean annual temperature, suggesting that metabolic variation may partly reflect adaptations to local or regional climatic stressors. More recent work has confirmed many of Roberts' insights, finding that climatic variables play an important role in shaping variation in RMR among human populations around the world (Froehle, 2008; Leonard et al., 2002, 2005; Rode and Shephard, 1995; Snodgrass et al., 2005). Figure 3 shows the relationship between RMR and FFM in indigenous Siberian men and women compared with predicted RMR values using the Cunningham (1991) equation. Both men and women show significant elevations in measured RMRs relative to predicted levels (+16.5% in men and +17.6% in women; $P < 0.001$). Ongoing research is now exploring the extent to which these population differences are related to genetic differences and/or shorter term physiological or developmental adaptations (Leonard et al., 2005; Mishmar et al., 2003; Ruiz-Pesini et al., 2004).

In addition to being of theoretical importance to human biologists, interpopulational differences in RMR also have important nutritional and public health implications. Recent work among the Pima Indians indicates that low RMRs are strong contributors to their high rates of obesity and adult-onset diabetes (Howard et al., 1991; Knowler et al., 1983, 1991). Whether low RMRs are a primary contributor to the high rates of obesity in the United States and other western countries remains a major point of debate and ongoing research in human nutrition (cf. Armellini et al., 1992; Landsberg et al., 2009; Ravussin et al., 1988; Welle et al., 1992; Westrate et al., 1990).

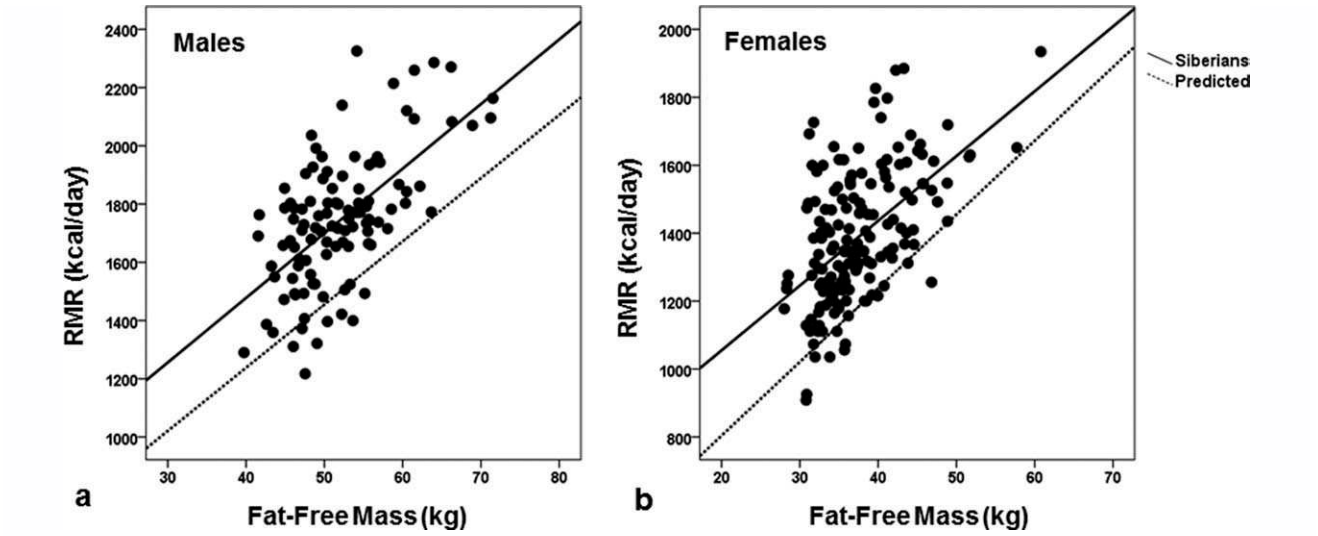

Fig. 3. Resting metabolic rate (RMR, kcal/day) versus fat-free mass (FFM, kg) for indigenous Siberian (a) men and (b) women. Solid lines denote the best fit regression lines for RMR versus FFM, whereas the dotted line denoted predicted RMR values based on the equation of Cunningham (1991). Measured RMR values are significantly greater than those predicted based on FFM in both men and women (+16.5% and +17.6%, respectively; $P < 0.001$). Adapted from Leonard et al. (2005).

Exercising/Working EE

The study of exercising EE has also shown remarkable variation in the costs of work across diverse human groups (Bastien et al., 2005; Heglund et al., 1995; Panter-Brick, 1992; Steudel-Numbers and Tilkins, 2004). Within human biology this type of research typically involves either (1) measuring the energy costs associated with a particular task (e.g., load carrying, cutting sugar cane, and pounding rice) or (2) measuring EE in response to a standardized work/exercise protocol (e.g., step test; treadmill and bicycle ergometer). The advantage of using a standardized exercise protocol is that it allows for human energy costs to be calibrated against known levels of physical work output. Figures 4a and b show the measurement of exercising EE using step test and treadmill protocols.

In our fieldwork in Siberia and Latin America, we have used a step-test protocol, the Canadian Aerobic Fitness Test (CAFT; CSEP, 2003), in part, because of its portability ease of use in remote conditions. Additionally, the CAFT provides a wide range of work loads to accommodate populations of variable body size and fitness level (Katzmarzyk et al., 1996; Leonard et al., 1995, 1997). The CAFT is a standard submaximal exercise test in which subjects step up and down on a portable two-step stair set (each 20.3 cm high) at a marked cadence. Each subject performs three 3-min bouts of exercise at increasing stepping rates. There are six different work levels (stages) of the CAFT; the starting level for each subject is determined by their age, sex, and general health.

During each of the three exercise bouts, HR and the standard metabolic parameters (V_E, VO_2, and VCO_2) are measured continuously. The HR and energy cost associated with each work level are then calculated as the average values over the last minute of the exercise bout (Leonard et al., 1997). Data on exercise energy costs (kcal/min) of indigenous men of Siberia and highland and coastal Ecuador are shown in Figure 5 (from Katzmarzyk et al., 1996).

These types of data can then be used to evaluate variation in both the economy and efficiency for work/exercise. The economy of work refers to the total amount of energy expended to perform a task of given intensity. To standardize for differences in body size, task-specific energy costs are typically standardized relative to RMR as "physical activity ratios" (PAR = task EE [kcal/min]/RMR [kcal/min]). Thus, PARs measure energy costs as multiples of RMR, and range from a minimum of 1.0 (sleeping) up to values as high as 8 to 10 for very intense physical work. Table 4 presents the examples of PARs for selected activities based on the WHO's most recent recommendations on human energy requirements (FAO/WHO/UNU, 2004).

In contrast to economy, work (mechanical) efficiency reflects the percentage of metabolic EE that results in physical work (McArdle et al., 2001). Efficiency can be evaluated in a number of ways, including (1) gross efficiency (GE), (2) net efficiency (NE), and (3) delta efficiency (DE). GE is calculated as the external work output relative to the total metabolic energy costs for performing that work:

$$\text{GE}\,(\%) = 100 \times (\text{External work [kcal]})/(\text{Metabolic Energy Costs [kcal]})$$

NE reflects work output relative to metabolic costs above RMR:

$$\text{NE}(\%) = 100 \times (\text{External work [kcal]})/(\text{Metabolic Energy Costs [kcal]} - \text{RMR[kcal]})$$

DE is determined by measuring the *change* in work output from one exercise level to another versus the *change* in metabolic energy costs:

$$\text{DE}(\%) = 100 \times (\Delta\ \text{External work [kcal]})/(\Delta\ \text{Metabolic Energy Costs [kcal]})$$

Table 5 presents an example of how each of the measures of efficiency are calculated for a 70 kg man exercising

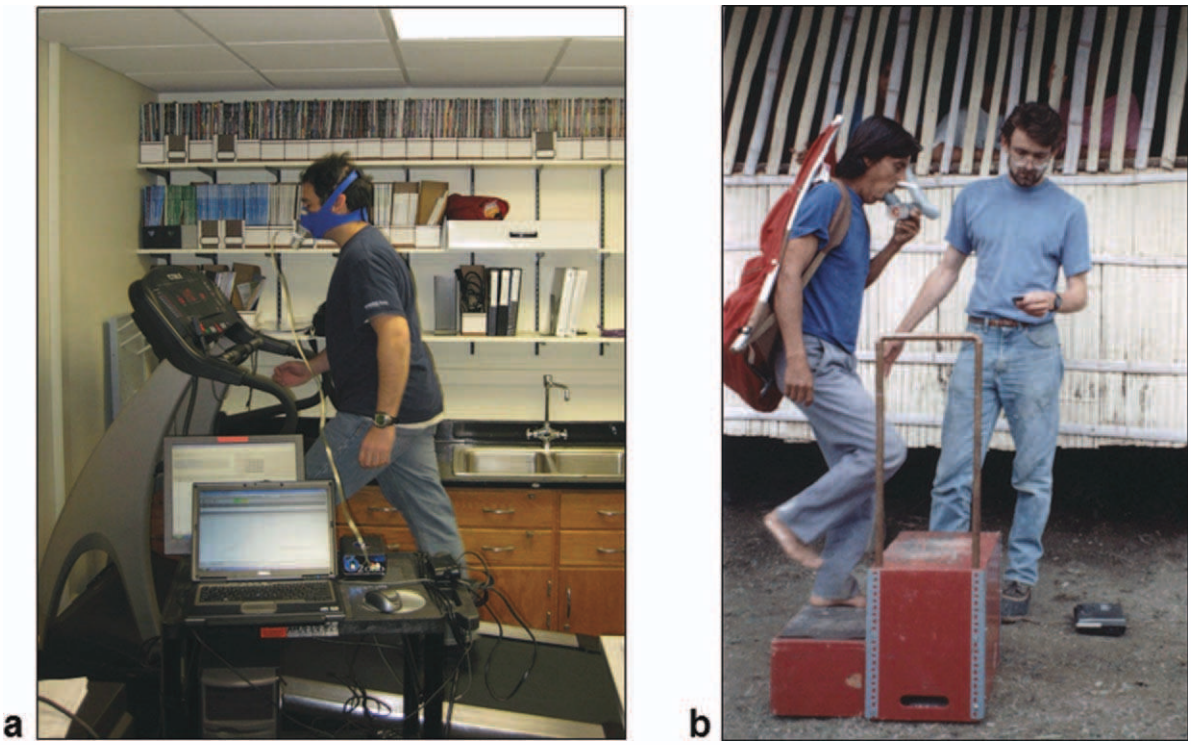

Fig. 4. Measurement of exercising energy expenditure (a) while walking on a treadmill and (b) while performing a step test (the Canadian Aerobic Fitness Test). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

on a bicycle ergometer at work loads of 100 and 200 W. Based on the measured VO_2 and RQ values, the total energy costs for working at the two exercise levels are calculated as 7.39 and 14.36 kcal/min. Converting watts into kcal/min, we find that the external work rates are 1.433 and 2.866 kcal/min. Thus, the GEs at the 100 and 200 W loads are estimated at 19.4% and 20.0%, respectively. Adjusting for an RMR of 1.21 kcal/min, the calculated NE levels are slightly higher, 23.2% and 21.8%. Finally, we use the changes in total and external work rates (6.97 and 1.433 kcal/min, respectively) to calculate DE as 20.6%.

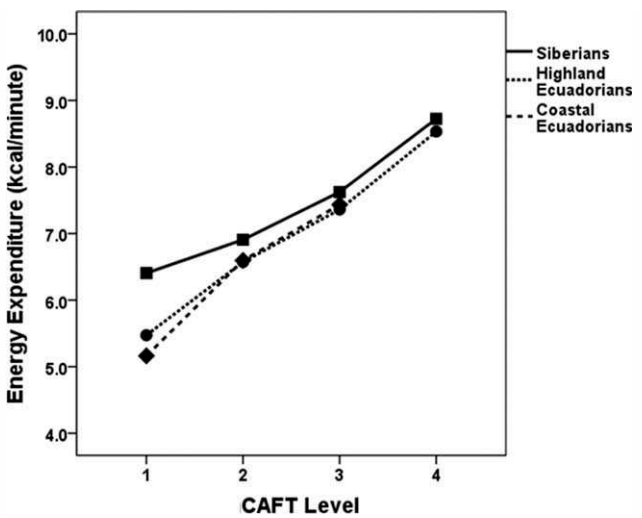

Fig. 5. Mean exercising energy costs (kcal/min) for men of three different populations performing levels 1 through 4 of the Canadian Aerobic Fitness Test (CAFT). Adapted from Katzmarzyk et al. (1996).

Different types of mechanical work are associated with different levels of average efficiency. For the CAFT step-test protocol, the level of physical work performed (i.e., moving one's weight against gravity) is calculated based on the weight of the subject, height of the steps, and the rate of ascent. The NEs for the groups shown in Figure 5 average between 15 and 17% and are comparable to those measured for young Canadian men using the same protocol (see Katzmarzyk et al., 1996).

Similar research has explored variation in work efficiency among indigenous and nonindigenous Andean populations living at high altitude. This research has explicitly tested whether adaptations to hypoxic stress among

TABLE 4. Physical activity ratio (PAR) values for selected activities in adult men and women

	Males		Females	
Activity	Mean PAR	PAR range	Mean PAR	PAR range
Sleeping	1.0		1.0	
Lying	1.2		1.2	
Sitting quietly	1.2		1.2	
Standing	1.4		1.5	
Walking (leisurely pace)	2.1	2.0–2.2	2.5	2.1–2.9
Running (distance)	6.3		6.6	
Dancing	5.0		5.1	
Harvesting potatoes	4.4	3.5–5.7	3.0	2.8–3.4
Harvesting rice	3.5	2.4–4.2	3.8	3.5–4.4
Cutting sugarcane	7.0	6.6–7.9	–	
Pounding rice	–		5.6	5.0–6.3

From FAO/WHO/UNU (2004:92-96).

TABLE 5. Sample calculations of gross efficiency (GE, %), net efficiency (NE, %), and delta efficiency (DE, %) for a 70 kg man exercising on an ergometer at work loads of 100 and 200 W

Level	Work load (W [kcal/min])	VO_2 (l/min)	RQ	EE (kcal/min)	RMR (kcal/min)	GE (%)	NE (%)
1	100 [1.433]	1.50	0.90	7.39	1.21	19.4%	23.1
2	200 [2.866]	2.88	0.95	14.36	1.21	20.0%	21.8
Change	100 [1.433]			6.97			

DE (%) = 100*(1.433/6.970) = 20.6%.

TABLE 6. Physical activity levels (PAL) associated with different lifestyles in adult men and women

	Sedentary or light activity lifestyle	Moderately activity lifestyle	Vigorously active lifestyle
Range	1.4–1.69	1.70–1.99	2.00–2.40
Midpoint	1.55	1.85	2.20

From FAO/WHO/UNU (2004:38).

TABLE 7. Sample calculations of total energy expenditure (TEE, kcal/day) for a 30-year-old man (70 kg) and a 30-year-old woman (60 kg) with identical activity profiles shown below

Activity category (PAR)	Time (h)	PAR × Time
Sleeping (1.0)	8.5	8.5
Sitting (1.2)	6.0	7.2
Standing (1.4)	1.5	2.1
Light–moderate activities (2.1)	5.0	10.5
Moderate work (2.8)	2.5	7.0
Intense exercise (5.1)	0.5	2.55
Total	24.0	37.85

A. Estimate resting metabolic rate (RMR, kcal/day):
RMR_{man} = 11.5(70) + 873 = 1678 kcal/day
RMR_{woman} = 8.1(60) + 846 = 1332 kcal/day
B. Calculate 24-h physical activity level (PAL) from activity data:
PAL = 37.85/24 = 1.58
C. Calculate total energy expenditure (TEE, kcal/day):
TEE_{man} = (1.58)(1678) = 2651 kcal/day
TEE_{woman} = (1.58)(1332) = 2105 kcal/day
D. Additional energy costs associated with reproductive status:
Pregnancy: +85 kcal/day (1st trimester); +285 kcal/day (2nd trimester); +475 kcal/day (3rd trimester)
Lactation: +675 kcal/day (<6 months; exclusive breastfeeding); +460 kcal/day (≥6 months; partial)
from: FAO/WHO/UNU (2004: 59, 65).

Andean natives are associated with increased metabolic efficiency relative to non-natives. To date, these studies have provided mixed results, with some showing significantly greater work efficiency among indigenous highlanders, compared with lowland control subjects (e.g., Haas et al., 1983; Hochachka et al., 1991), whereas others have shown no differences (e.g., Brutsaert et al., 2004; Mazess, 1969). These conflicting results are likely attributable to several factors, including differences in sample composition and protocols being used, and the fact that overall work efficiency may be shaped by a variety of physiological and health parameters (e.g., nutritional status).

Total EE

Most important for human biologists are the techniques used for measuring variation in TEE under "free-living" (i.e., real world) conditions. Regardless of which technique is used to measure daily energy costs, a person's physical activity level (PAL) is typically assessed by expressing TEE relative to RMR (PAL = TEE/RMR; FAO/WHO/UNU, 2004). PAL values range from ~1.2 in very sedentary, bed-ridden populations, up to ~5.0 among elite, endurance athletes (Black et al., 1996; Westerterp, 2001). The PAL ranges associated with different lifestyles for adult men and women are presented in Table 6 (from FAO/WHO/UNU, 2004). The PAL values for sedentary and light activity lifestyles range from 1.4 to 1.69. Individuals with "moderate to active" lifestyles have PALs of 1.70–1.99. This group includes individuals with sedentary occupations who regularly exercise or individuals in occupations that require greater physical activity (e.g., construction workers). "Vigorous or vigorously active lifestyles" are associated with PALs of 2.0 or greater and include individuals who are involved in strenuous work activities (e.g., nonmechanized subsistence farming) or rigorous recreational activities (e.g., dancing or swimming for 2 h/day).

Factorial method. The most commonly used technique for measuring TEE in real-world conditions is the factorial method. This technique involves using time allocation data to first determine the amount of time that person spends on different activities of the course of a day. This type of time use data may be collected through direct observation, spot checks, activity diaries, or 24-h recalls (see Gross, 1984; Johnson, 1975; Suda, 1994; Thomas, 1976). Individual activities are then assigned PAR values (see Table 4), reflecting the metabolic intensity of the task. For each of the activity categories, the amount of time spent per day on those tasks is multiplied by the PAR value for those tasks. These values are then summed for all activity categories and then divided by the total time/day (24 h) to provide an estimate of the PAL for the entire day:

$$PAL = \sum[PAR_i(t_i)]/24$$

where PAR_i is the physical activity ratio of each activity category "i" and t_i is the time (hours) spent in each activity category "i."

Table 7 provides an example of how TEE is estimated using the factorial method recommended by the WHO (FAO/WHO/UNU, 1985, 2004; James and Schofield, 1990) for a 30-year-old man (70 kg) and a 30-year-old woman (60 kg), each with the same activity profiles. The first step is to estimate RMR using the WHO predictive equations shown in Table 3. For the man, resting energy costs are 1,678 kcal/day when compared with 1,332 kcal/day for the women. The daily activity profile shown in Table 7 divides activities into six categories ranging in metabolic intensity from PARs of 1.0 (sleeping) to 5.1 (intense exercise/activity). From this

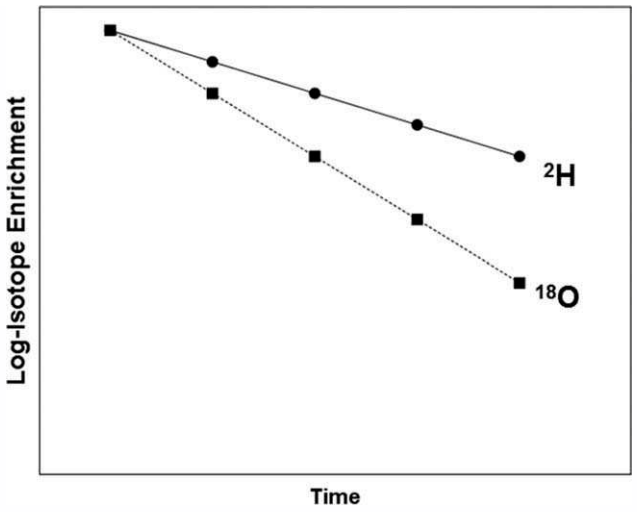

Fig. 6. Graph depicting the basic principles for measuring total energy expenditure (TEE) using the doubly labeled water (DLW) method. Subjects consume a dose of water enriched with the stable isotopes ^{2}H and ^{18}O. After the isotopes are allowed to spread through the body, the washout rates of the isotopes are monitored from urine samples. The difference in the rates of decline in ^{2}H and ^{18}O allows for the determination of carbon dioxide production (VCO_2) and TEE over the measurement period.

activity profile, the estimated PAL for the entire day is 1.58, in the "sedentary" lifestyle category according to WHO guidelines (see Table 6). With this level of daily activity, the man would require 2,651 kcal/day, whereas the woman would require about 500 kcal less (2,105 kcal/day).

For the woman, the estimate assumes that she is not pregnant or lactating. As shown in Table 7, the metabolic costs associated with reproduction can substantially raise a woman's daily energy demands. For example, the WHO estimates that during the third trimester of pregnancy, a woman's energy needs increase by ~475 kcal/day. For a woman who is exclusively breast feeding her infant, the metabolic demands are even greater, an additional ~675 kcal/day (FAO/WHO/UNU, 2004).

Overall, the factorial method represents an effective and relatively low cost approach for estimating energy needs in nonlaboratory, field settings. Indeed, most of the pioneering studies of daily EE in foraging (Godin and Shephard, 1974; Hill et al., 1984; Lee, 1979; Leslie et al., 1984), subsistence farming (Dufour, 1984; Montgomery and Johnson, 1977; Norgan et al., 1974), and herding populations (Galvin, 1985; Thomas, 1976) utilized time allocation/factorial methods to estimate TEE. The main difficulties associated with the factorial approaches include the heavy measurement burden on subjects for studies involving direct observation of daily activities. The use of surveys and activity recalls lower measurement burden, but potentially introduce error and bias in the estimation of the duration and intensity of daily activities (Leonard et al., 1995, 1997). In addition, interpopulational differences in the task-specific energy costs may represent another source of error in factorial estimates of TEE. Nonetheless, in spite of these limitations, the factorial approach represents an important tool for estimating energy needs and assessing physical activity levels in population-based studies.

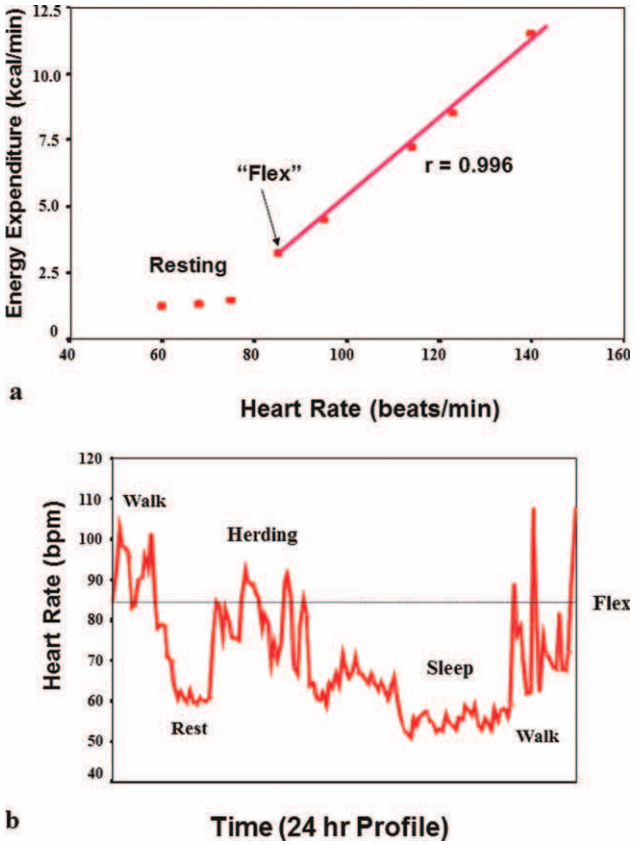

Fig. 7. Components required for estimating a subject's total energy expenditure (TEE, kcal/day) using the flex-HR method. (a) An energy expenditure (EE, kcal/min) versus HR (beats/min) calibration relationship for resting and exercising conditions. The "flex-HR" is calculated as the average of the highest resting and lowest exercising HR. (b) A daily 24-h HR profile. During the waking day, HRs less than or equal to the flex value are assigned an EE equal to the average of the three resting values. Energy costs for waking HRs above the flex point are determined by the EE versus HR regression for the exercising data. Energy costs while sleeping are set at RMR levels. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Doubly labeled water. Currently, the doubly labeled water (DLW) method is regarded as the gold standard for measuring TEE in real-world conditions (Schoeller, 1988, 1999; Speakman, 1997). This technique involves having subjects ingest known amounts of water enriched with stable isotopes of both hydrogen (^{2}H; deuterium) and O_2 (^{18}O). After the labeled water is allowed to distribute throughout the body, changes in isotope levels are then monitored for the next 8–14 days from urine samples. Over the measurement period, the concentrations of both isotopes decline because of water loss and aerobic respiration. However, the ^{18}O isotope levels decrease more rapidly because it is lost in both CO_2 and H_2O, whereas deuterium is lost only in H_2O (see Fig. 6). The differences in washout rates between the ^{18}O and ^{2}H isotopes allow for the calculation of VCO_2 for the entire measurement period. By assuming an average RQ for this period (often based on dietary habits), total VO_2 and overall EE (kcal/day) can be determined.

Validation studies of DLW relative to direct calorimetry have shown this technique to be quite accurate for meas-

uring individual-level EE (±%2–3%). Consequently, DLW has become the preferred choice for measuring TEE and energy balance in nutritional science and obesity research (Schoeller, 2008). Recent recommendations on energy requirements by the WHO (FAO/WHO/UNU, 2004) and the US Institute of Medicine (2005) have increasingly relied on DLW studies, particularly for better defining the energy needs of infants and young children (Butte et al., 2000). DLW is also being more widely used to measure TEE in non-Western population (e.g., Coward, 1998; Diaz et al., 1991; Kashiwazaki et al., 1995, 2009; Snodgrass et al., 2006), providing us with a better understanding of the range of variation in human EE across populations.

To date, the main limitation on wider use of DLW has been the expense of obtaining enriched ^{18}O and of the specialized equipment and training for analyses using isotope ratio mass spectrometry (IRMS). Recent technological advancements now offer to reduce the costs associated with DLW analyses. Specifically, cavity ring-down spectroscopy (CRDS) provides a lower cost alternative to IRMS for measuring deuterium and ^{18}O that also requires less technical training (Brand et al., 2009). Thorsen et al. (2011) recently compared DLW estimates of TEE obtained from both IRMS and CRDS analyses and found that two measures were within 0.5% of one another. These findings suggest that CRDS can provide accurate and unbiased measures of TEE comparable to those obtained from standard IRMS analyses.

Heart rate monitoring and accelerometry. In addition to DLW, techniques such as HR monitoring and accelerometry are now being more widely used in human biology research to provide insights into variation in EE among subsistence-level and urbanizing populations. HR monitoring calibrated versus O_2 consumption has become a popular method for measuring TEE and activity levels in field situations. The best known of these approaches is the "flex-HR" method developed by Spurr et al. (1988). This method involves establishing individual-level calibrations between HR and EE for each subject to address the problem of between-subject variability in HR. For each subject, HR and EE are measured under resting conditions and during a standardized submaximal exercise protocol using the methods noted in the previous sections. Figure 7a shows an example of an individual EE versus HR relationship.

This approach exploits the fact that at an individual level, EE is strongly correlated with HR over a wide range of activity levels. However, at low levels of exertion the relationship between HR and EE breaks down. To address this problem, the flex-HR method establishes HR thresholds for discriminating between "resting" and "active" levels of EE. This point of differentiation (the "flex-HR") is typically defined as the average of the highest resting HR value and the lowest exercising HR. For HRs during the waking day that are greater than the flex point, EE is predicted based on the individual linear regression of EE versus HR for the exercise values. For waking HRs less than or equal to the flex point, EE is determined as the average for the three resting postures. Energy costs while sleeping are set at RMR levels (Spurr, 1990).

Once the calibration relationship has been established, the subject then wears a HR monitor for one or more days. Figure 7b shows a daily HR profile for the same subject whose EE–HR relationship is depicted in Figure 7a. Using the subject's calibration data, individual minute-by-minute HRs are converted into energy equivalents to determine the subject's TEE over the course of the day.

Since it was initially introduced in the late 1980s, the flex-HR method has been validated versus DLW in a number of different populations (e.g., Livingstone et al., 1990, 1992; Lovelady et al., 1993; Maffeis et al., 1995; Spurr et al., 1996; Morio et al., 1997). It is quite accurate at measuring group-level EE (±3% relative to DLW) but so less at the individual level. The use of this technique around the world has provided important insights into changes in TEE associated with lifestyle change and the transition from subsistence to wage-market economies (Leonard, 2003). The main difficulty with daily HR monitoring remains the subject burden associated with establishing individual HR–EE calibrations.

Accelerometers represent another lower-cost and less-invasive technique for measuring daily activity and EE by assessing the body's motion in a single or multiple planes. The more recently developed units are substantially better than earlier models in having the ability to measure acceleration in multiple planes and having much larger storage capacity. Accelerometers are typically worn around the waist and measure raw activity counts over specified time intervals. These counts are then converted into EE using a specific algorithm for the unit. A number of different accelerometers have been validated against DLW, with correlations generally being high, but variable across different models (Hoos et al., 2003; Plasqui and Westerterp, 2007).

Accelerometers are now beginning to be more widely used human biology research to explore variation in activity patterns among non-Western populations (e.g., Bharathi et al., 2010; Madimenos et al., 2011; Snodgrass, 2012). Research to date suggests that they offer great promise for population-based studies. Yet, although accelerometers do a good job of quantifying variation in physical activity, challenges remain in developing algorithms that accurately estimate EE for different types of activity.

Greater accuracy in estimating EE has been achieved by combining accelerometry with HR monitoring (e.g., Moon and Butte, 1996; Strath et al., 2001, 2002; Treuth et al., 1998). These combined approaches have, in some cases, achieved accuracy levels approaching that of DLW (Moon and Butte, 1996; Treuth et al., 1998). Newly-developed portable units for simultaneously measuring HR, accelerometry, and heat flux (with skin temperature sensors) offer to provide additional parameters for estimating TEE, overcoming some of the limitations associated with HR monitoring or accelerometry alone (Cole et al., 2004; St.-Onge et al., 2007). With the increasing number of options for assessing physical activity and EE under free-living conditions, much ongoing work in exercise science and public health is now exploring the accuracy and precision of different monitoring systems to develop guidelines on best practices (see Butte et al., 2012; Matthews et al., 2012).

SUMMARY

Advances in the measurement of EE offer to provide human biologists with important new insights into a variety of questions on human adaptability and health. Until recently, most of what we knew about variation in human EE was based on studies from industrialized nations, often from clinical populations or elite athletes. Newer technologies and improved methodologies have now made it more feasible to study human energy dynamics in a broad

range of environmental contexts (see Box 1 for additional information). We are now gaining a much better understanding of how ecological factors influence both RMR and TEE and the consequences of this variation for health and reproductive function (Piperata and Dufour, 2007; Snodgrass et al., 2008). Additionally, studies of populations shifting from a subsistence to a wage/market economy are providing critical insights into how changes in energy balance are influencing nutritional health around the world (Dufour and Piperata, 2008; Leonard, 2003; Madimenos et al., 2011; Snodgrass et al., 2006). Energetic methods are also allowing us to more broadly apply life history theory to the study of human biology, specifically considering how ecological constraints shape variation in the allocation of energy to maintenance versus growth and reproduction (Reiches et al., 2009). Thus, the expansion of energetic studies in human biology research should provide a greater appreciation of the range and correlates of metabolic variation within our species.

ACKNOWLEDGMENTS

The author is most grateful to Dr. Marcia Robertson and two anonymous reviewers for their comments and suggestions on the manuscript.

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Box 1: Additional Information

Metabolic equipment and related supplies:
- AEI Technologies: http://www.aeitechnologies.com/
- Cosmed: http://www.cosmed.it/
- Medical Graphics: http://www.medgraphics.com/
- Parvomedics: http://www.parvo.com/
- Sensormedics/VIASYS: http://www.sensormedics.com/
- Vacumed: http://www.vacumed.com/

Anthropometric equipment, heart rate monitors, and accelerometers:
- Creative Health Products: https://www.chponline.com/store/cart.php
- Perspective Enterprises: http://www.perspectiveent.com/
- Seritex: http://www.seritex.com/instruments.html
- Actical accelerometers: http://www.healthcare.philips.com/us_en/homehealth/sleep/actical/

General information, references, and data sets:
- American College of Sports Medicine (ACSM): http://www.acsm.org/
- Canadian Society for Exercise Physiology (CSEP): http://www.csep.ca/english/View.asp?x=1
- International Society for Physical Activity and Health (ISPAH): http://www.ispah.org/
- FAO/WHO/UNU 2004 report on Human Energy Requirements: http://www.fao.org/docrep/007/y5686e/y5686e00.htm
- Institute of Medicine's Dietary Reference Intakes for Energy: http://www.nap.edu/openbook.php?isbn=0309085373
- Institute of Medicine's doubly labeled water data used for US Dietary References for Energy: http://www.iom.edu/Home/Global/News%20Announcements/DRI