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Do it yourself
Measuring human energy expenditure and metabolic function: basic principles and methods

William R. Leonard

Laboratory for Human Biology Research, Department of Anthropology, Northwestern University, 1810 Hinman Avenue, Evanston, IL 60208, U.S.A.
e-mail: w-leonard1@northwestern.edu

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Introduction

Biological anthropologists have become increasingly interested in using an energetics perspective to study human evolution and adaptation (Leonard & Ulijaszek, 2002). Energy dynamics, the acquisition and allocation of metabolic energy over the life course, are important to evolutionary research for a number of reasons. First, energy represents a key interface between organisms and their environment. The search for food energy, its consumption, and ultimately its allocation for biological processes are all critical aspects of an organism's ecology. Additionally, the acquisition and allocation of energy have important adaptive consequences for both survival and reproduction. As shown in Figure 1, maintenance (or respiratory) energy costs (including resting and activity demands) are the components of the energy budget associated with keeping the organism alive on day-to-day basis. Productive energy costs, on the other hand, are those associated with maturing and producing offspring for the next generation.

Comparative analyses have shown that the amount of energy allocated to these different components varies greatly across human populations living in different environments (see Roberts, 1978; Katzmarzyk & Leonard, 1998; Ulijaszek, 1995). Additionally, over the course of an individual's lifespan, the relative allocations will also change (Holliday, 1986)

Over the last 15-20 years, technological and methodological advances have greatly facilitated the measurement of human energy expenditure in both laboratory and field settings. These advances are now allowing human evolutionary biologists to study variation in energy dynamics with much greater accuracy in a wide variety of ecological contexts. This paper presents the basic principles, methods, and equipment for measuring human energy expenditure and work capacity, and discusses some of the important evolutionary issues that can be addressed with these methods.

Principles of calorimetry

The study of energy relies on the principle of calorimetry, the measurement of heat transfer. In food and nutrition, energy is most often

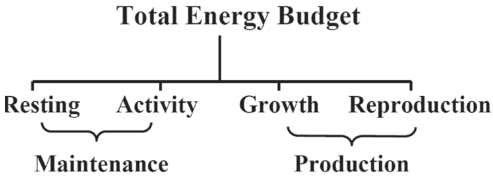

Fig. 1 - Components of an organism's total energy budget. Respiratory (or maintenance) energy costs are those necessary for keeping the individual alive on a daily basis. They include resting energy costs and activity costs. Productive energy costs are those required for growth and development and reproduction.

measured in kilocalories (kcal). One kilocalorie is the amount of heat required to raise the temperature of 1 kilogram (or 1 liter) of water 1°C. Thus, a food item containing 150 kilocalories (e.g., two pieces of bread) has enough stored chemical energy to increase the temperature of 150 liters of water by 1°C. Another common unit for measuring energy is the joule or the kilojoule [1 kilojoule (kJ) = 1,000 joules]. The conversion between calories and joules is:

$$1 \text{ kcal} = 4.184 \text{ kJ}$$

Techniques for measuring energy expenditure 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 & Tobin, 1987). Although quite accurate, direct calorimetry is not widely used because of its expense, technical difficulty, and the limitations placed on a subject's mobility.

Thus, methods of indirect calorimetry are more commonly used to quantify human energy expenditure, particularly under field conditions (Jéquier *et al.,* 1987). The most widely used of these techniques involve measuring oxygen consumption. Because the body's energy production is dependent on oxygen (aerobic respiration), O_2 consumption provides a very accurate indirect way of measuring a person's energy expenditure. Every liter of O_2 consumed by the body is equivalent to energy cost of approximately 5 kcal (see Tab. 1; McArdle *et al.,* 2001). Consequently, by measuring O_2 use while a person is performing a particular task (e.g., standing, walking, 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 studies of ecological energetics. The subject breathes in ambient air, which has constant concentrations of oxygen (20.93%), carbon dioxide (0.03%) and nitrogen (N_2: 79.04%). Upon exhalation, the subject's rate of breathing (i.e, 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 (ATP). 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 CO_2 (3-5%).

The raw measurements of breathing (respiratory) rate and gas concentrations are used to calculate the following variables:

- *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 – Oxygen consumption (l O_2/min).* Liters of oxygen per minute used by the body (corrected for STPD).
- *VCO_2 – Carbon dioxide production (l CO_2/min).* Liters of carbon dioxide per minute produced by the body (corrected for STPD).

Tab. 1 - *Estimated energetic equivalents (kcal) per 1 liter 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)

- *RQ – Respiratory Quotient (VCO_2/VO_2).* The ratio of carbon dioxide production to oxygen consumption. Under non–steady state conditions, this measure is referred to as the Respiratory Exchange Ratio (RER).

Detailed information on the calculation of these metabolic parameters is presented in Appendix D of McArdle *et al.* (2001, pp. 1117-1120). Under steady-state conditions, the RQ ranges from 0.7 to 1.0, and provides useful index for determining the type of fuel being used for metabolism (i.e., fat, protein, carbohydrates), and the amount of energy being liberated for each liter of O_2 consumed. Due to the differences in the chemical structure of fat, protein and carbohydrates, different amounts of oxygen are required to completely metabolize each. Complete breakdown of carbohydrates is associated with an RQ of 1.0, because each molecule O_2 consumed results in one molecule of CO_2 being produced. In contrast, fat metabolism requires greater amounts of oxygen, 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).

Using measures of RQ and VO_2, energy expenditure (kcal/min) can be calculated using the caloric conversions presented in Table 1. Note that the caloric equivalent for each liter of oxygen consumed varies as a function RQ. For an RQ of 0.71, each liter of oxygen used yields 4.690 kcal, whereas an RQ of 1.0 has an energetic equivalent is 5.047. Thus, for a subject with a resting VO_2 of 0.25 liters/min and an RQ of 0.80, their resting energy expenditure (REE) would be calculated as:

$$\textit{REE (kcal/day)} = (4.801\ \text{kcal/l}\ O_2)(0.25\ \text{l}\ O_2/\text{min}) = 1.20\ \text{kcal/min} = 1728\ \text{kcal/day}$$

Equipment for measuring energy expenditure: metabolic carts

Advances in computer technology have greatly facilitated the measurement of human energy expenditure in both laboratory and field settings. All standard computerized metabolic carts contain the same basic components: (1) oxygen and carbon dioxide 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. Figures 2 a and b show examples of a computerized system for measuring energy expenditure under resting and exercising conditions. 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 3a shows a standard printout of a metabolic test under resting conditions. The graph shows changes in VO_2, VCO_2, and REE over the 8 minutes of the test, with the shaded area denoting the predicted REE +/-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 REE across subjects, determining whether subjects may have relatively sluggish or elevated metabolic rates. Figure 3b 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/min) are monitored at increasing exercise levels (speeds and inclines). This type of test provides insights into

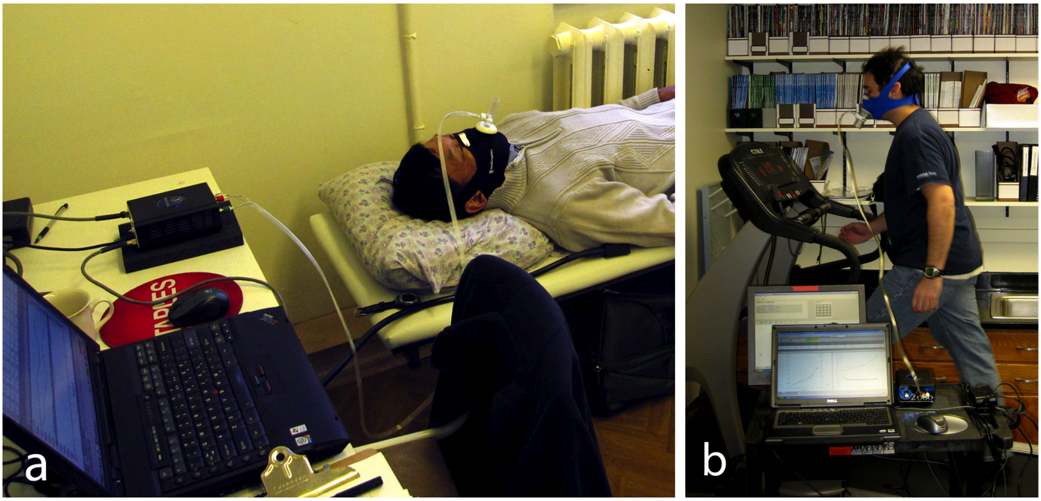

Fig. 2 - Measurement of energy expenditure under (a) resting and (b) exercising conditions (while walking on a treadmill).

energy costs at different workloads, and allows for the estimation of a subject's maximal working capacity (VO_{2max} or VO_{2peak}) (Cooper & 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 Tab. 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, both), (2) whether the unit will be used in a lab 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 nutritional 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 oxygen analyzers are used in metabolic analysis systems: paramagnetic, fuel cell, and zirconium oxide (see Cooper & Storer, 2001). Of these, the paramagnetic analyzers are among the most common. These analyzers align oxygen molecules within a magnetic field inside a mixing chamber. Changes in oxygen concentration are directly correlated with changes in the magnetic field.

In an electrochemical or fuel cell analyzer, oxygen molecules pass through a sensing membrane and then through a thin layer of electrolyte. A chemical reaction occurs within the cell in which the oxygen 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 oxygen 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" oxygen 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 oxygen ions from a higher to lower concentrations of oxygen. The movement of these ions across the zirconium oxide produces a voltage that is proportional to the differences in oxygen concentration. These analyzers respond quickly to changes in oxygen concentration, making them suitable for breath by breath analysis.

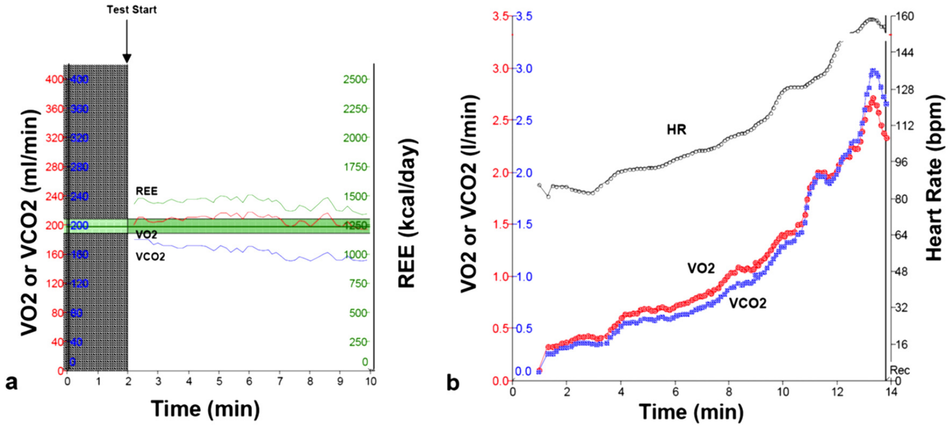

Fig. 3 - Standard graphs of metabolic tests under (a) resting and (b) exercising conditions. For the resting test, the subject's VO2 (l/min), VCO2 (l/min), and REE (kcal/day) are plotted vs. time (min) over the duration of the test. The shaded area in resting graph denotes the predicted REE (+/-5%) based on age, sex, height and weight using the Harris and Benedict (1918) equations. For the exercise test, the subject's VO2, VCO2 and HR are plotted over time in response to increasing workloads while walking on a treadmill.

Most carbon dioxide analyzers are non-dispersive 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 carbon dioxide (Cooper & Storer, 2001).

To measure rates of ventilation, the two most commonly used devices are pneumotachometers and turbine flow meters (Cooper & 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 (eg., children vs. adults) and levels of exertions (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 energetics lab. These additional components include the following: (1) calibration gases and syringe, (2) thermometer, barometer and hygrometer, (3) subject interface (e.g., mouthpiece, facemask), (4) heart rate monitors, (5) an exercise device (e.g., treadmill, ergometer), and (6) anthropometric equipment (e.g., stadiometer, scale, 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 oxygen and carbon dioxide levels. Typically, calibration gases contain 15-16% O_2 and 3-5% CO_2, similar to the levels

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

Category/item	Estimated Costs (US$)
Metabolic cart	12,000 – 45,000
Calibration supplies:	
Calibration gases	200-300/tank; 250-300 regulator
Calibration syringe	300-400
Environmental monitoring (thermometer, barometer, hygrometer)	200-400
Subject interface[a]:	
Mouthpiece/noseclip/valve	100-400
Face mask/valve	100-400
Canopy interface & system modifications	6,000-7,000
HR monitor	100-400
Exercise devices:	
Treadmill	5,000-25,000
Cycle ergometer	1,000-5,000
Step test	100-200
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.

observed in expired air samples. To calibrate the volume or flow measuring devices, a large, 3-liter 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 liters/min), simulating the breathing pattern of a subject.

Equipment for measuring environmental conditions

Since 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 insure 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 REE. 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 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 number of different protocols for measuring energy demands in response to increasing workload for the both the treadmill and ergometer (see Cooper & Storer, 2001, pp. 241-243; ACSM, 2006). 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). In our field studies, we have found the modified Canadian Aerobic Fitness Test (mCAFT) to be quite good for providing a wide range of works loads to accommodate populations of variable body size and fitness level (Katzmarzyk *et al.,* 1996; Leonard *et al.,* 1995, 1997).

Anthropometric equipment

Measurement of basic anthropometric dimensions is important in metabolic studies, because body size is one of primary determinants of an individual's energy expenditure. Minimally, height (cm) and weight (kg) should be measured, since these are key variables used to predict energy costs under resting and exercising conditions (Harris & Benedict, 1918; Schofield, 1985; ACSM, 2006). 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.

Concluding remarks

Advances in the measurement of energy expenditure are providing biological anthropologists with new insights into a wide variety human adaptive strategies. Until recently, most of what we knew about variation in human energy expenditure was based on studies from the US and other industrialized nations. With the expansion of energetic studies in anthropological research, we are now gaining a broader appreciation of the range and correlates of metabolic variation within our species.

Recent work has clearly documented the important influence that climate plays in shaping variation in REE among human populations around the world (Froehle, 2008; Leonard *et al.,* 2002, 2005). 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. Similarly, the study of exercising/working energy expenditure has underscored the remarkable variation in efficiency of work and locomotion across diverse human groups (Heglund *et al.,* 1995; Bastien *et al.,* 2005; Panter-Brick, 1992; Steudel-Numbrer & Tilkins, 2004).

The expanded array of techniques for measuring total energy expenditure under "free-living" conditions is now providing us with a much better understanding of the variation in daily work loads across human societies (see Leonard, 2008; Dufour & Piperata, 2008). Methods such as daily HR monitoring calibrated versus oxygen consumption (Spurr *et al.,* 1996; Leonard, 2003) and accelerometry (Bharathi *et al.,* 2010; Madimenos *et al.,* 2009) have now been applied in fieldwork settings, providing a clearer picture of patterns of variation in TEE among subsistence-level populations and insights into how daily workloads change with the shift to a market-oriented economy. Newly-developed portable units for simultaneously

Info on the web

Metabolic equipment and related supplies

http://www.aeitechnologies.com/
AEI Techonologies

http://www.cosmed.it/
Cosmed

http://www.medgraphics.com/
Medical Graphics

http://www.parvo.com/
Parvomedics

http://www.sensormedics.com/
Sensormedics/VIASYS

http://www.vacumed.com/
Vacumed

Anthropometric equipment and heart rate monitors

https://www.chponline.com/store/cart.php
Creative Health Products

http://www.perspectiveent.com/
Perspective Enterprises

http://www.seritex.com/instruments.html
Seritex

General information on metabolic testing

http://www.acsm.org/
American College of Sports Medicine (ACSM)

http://www.csep.ca/english/View.asp?x=1
Canadian Society for Exercise Physiology (CSEP)

measuring HR, motion (with accelerometry) and heat flux (with skin temperature sensors) offer to provide greater accuracy in measurement of TEE, overcoming some of the limitations associated with HR monitoring or accelerometry alone (Cole *et al.*, 2004; St.-Onge *et al.*, 2007).

More broadly, energetic methods are also allowing us to the study important dimensions of human life history, specifically considering how ecological constraints shape variation in the allocation of energy to maintenance vs. growth and reproduction in different environmental contexts (Reiches *et al.*, 2009). Clearly, the wider application of energetic approaches in biological anthropology offers to provide critical data for addressing important issues in human evolution.

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