Heart rate measurements as an index of energy expenditure and energy balance in ruminants: A review

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ABSTRACT: A major part of the ME consumed by ruminants (MEI) is dissipated as heat. This fraction, called heat production or energy expenditure (EE), is assayed largely by measuring O₂ consumption (VO₂). Conventional measurement of EE in controlled conditions in chambers does not reflect the complexity of natural, environmental, and social conditions of free-ranging animals. In mammals, most of the measured VO₂ is transferred to the tissues through the heart; therefore, regression of heart rate (HR) against VO₂ can be used to estimate the EE of free-ranging animals. The present article reviews the current knowledge on the use of HR for estimating EE. Energy expenditure can be determined from HR measurements, recorded daily over the course of several days, multiplied by the VO₂ per beat. When an animal does not perform significant exercise, a constant value of VO₂ per beat [O₂ pulse (O₂P)] measured over a short period (10 to 15 min) is used; during exercise, O₂P increases, and the regression equation of VO₂ against HR is used. Under extreme heat load, HR increases to improve heat dissipation, and O₂P decreases; therefore, the effect of heat load on O₂P needs to be taken into account. Cold stress that doubles heat production does not affect O₂P. Heart rate and EE are highly correlated with MEI, but there is significant individual variation in the relationship; therefore, the daily change in the HR of individual animals can be used as an indicator of changes in the individual energy status of a ruminant, and the average HR of the group can serve in the estimation of the energy status of the group. When O₂P is measured, the average group EE is an indication of the energy balance of the whole group. Because the MEI of nondraft animals is the sum of EE and retained energy (RE), the MEI of free-ranging ruminants can be determined by measurement of EE by the HR method and adding the RE. Similarly, the RE can be determined without slaughtering the animals from measurements of EE and MEI. Soon when devices for automatic HR monitoring of domestic ruminants become available at a reasonable price, continuous monitoring of HR might provide producers with a sensitive tool for identifying changes in the energy status of their animals. This will also significantly help to shorten the time needed to identify health problems of individual animals.

Key words: energy balance, energy expenditure, heart rate, review, ruminant

INTRODUCTION

Energy expenditure (EE) of farm animals, also known as heat production (HP), has been determined mostly under controlled, confined conditions. These conditions do not necessarily reflect those of free-ranging animals or of commercial cattle in feedlots. Environmental conditions, feeding level, time spent eating and digesting, tissue and pelage conductance, production level, and season of the year may affect the EE of animals (NRC, 1981).

The major part of the ME consumed (MEI) by homoiothermic animals is lost as HP. The energy product or retained energy (RE) of an animal is the difference between MEI and EE. Significant effort has been invested over the past decades to develop methods for measuring the EE of animals in their natural environments. The modern development of microelectronic and computerized miniaturization offers a wide scope for recording biological data. The O₂ used by mammals is transported to the tissues by the heart; consequently, calibration of heart rate (HR) recording to EE is the greatest candidate for future use of EE measurement of free-ranging animals.
The goal of this article is to review the current knowledge on the use of HR for estimating EE and energy balance (EB) of ruminants.

**DISCUSSION**

**General History and Concepts**

**Methods for Measuring EE of Free-Ranging Animals.** Most of the methods used for measurement of EE of farm animals are based on O\(_2\) consumption (VO\(_2\)) measurements under controlled, confined conditions. However, commercial farm animals, and especially grazing animals, mostly live in uncontrolled conditions. Several methods have been developed for measuring the EE of animals in their natural environment by using indirect measurement of VO\(_2\) or CO\(_2\) production. Both acute tracheal intubation for measurement of VO\(_2\) (Young and Webster, 1963) and infusion of 14C-labeled bicarbonate (Corbett et al., 1971; Young and Corbett, 1972) interfere with normal behavior, have limited field applicability, and are expensive to use on a large animal. According to Nagy (1989), using doubly labeled water (DLW) to predict CO\(_2\) turnover is the preferred method to estimate the metabolic rate of free-ranging animals. The DLW method involves average errors of ±8 to ±11% (interval range of 16 to 22%) and is too expensive for general use on large animals (Schoeller and van Santen, 1982). The above methods are suitable for measuring CO\(_2\) turnover over periods of a day or more but not for short periods; therefore, the short-term effect of the activities of an animal, such as walking, grazing, eating, and social behavior, cannot be evaluated by these methods.

**Use of HR to Measure EE.** In homeothermic animals, most of the O\(_2\) used is transported to the tissues by the action of the heart, which is the motive for using HR for estimating VO\(_2\) and, hence, EE.

The HR method for estimating VO\(_2\) is based on Fick’s convection equation for the cardiovascular system:

\[
\text{VO}_2 = \text{HR} \times [\text{Vs} \times (C_a\text{O}_2 - C_v\text{O}_2)],
\]

where Vs = the stroke volume (amount of blood pumped per heart beat) and C\(_a\)O\(_2\) and C\(_v\)O\(_2\) = the \(\text{O}_2\) contents of arterial blood and mixed venous blood, respectively.

Webster (1967) examined the possibility of determining the EE of sheep from measurements of their HR. He cited the pioneering studies of Henderson and Prince (1914) and of Brody (1945), who had begun to examine the subject.

Butler et al. (2004) reviewed the history and development of the HR method from the first demonstrations of the linear relationship between HR and VO\(_2\) in humans during exercise (Boothby, 1915; Krogh and Lindhard, 1917). According to Butler et al. (2004), the DLW and HR methods are the ones most widely used for measuring EE of free-ranging animals. The above authors compared the pros and cons of the DLW and HR methods and concluded that when HR was calibrated against VO\(_2\), the HR method was superior to the DLW method for animals with BW greater than 1 kg.

**Methods Used for Calibrating HR Measurements to VO\(_2\) and EE.** A literature review of the use of HR methods for measuring EE reveals a surprising divergence between those carried out on humans and those carried out on wild or farm animals.

The flex-HR method, introduced by Spurr et al. (1988), has become a standard tool for measuring daily EE in free-ranging humans (Livingstone, 1997). Leonard (2003) reviewed the development of the use of HR to measure EE, from the recognition of the potential of the method by Booyens and Hervey (1960) to the refining of the flex method to the present time. Yamamoto (1989) was the first to point out the discrepancy between the prediction of VO\(_2\) from HR measurements in exercising animals and the HR:VO\(_2\) relationships determined for sedentary subjects.

The flex method is used to resolve this incompatibility; it is based on 2 equations that represent the HR:EE relationship during exercise and in a sedentary condition, respectively. The HR level at the transition point between the resting and active levels of EE is defined as the flex-HR. Use of the flex-HR method to monitor human EE throughout the day and to determine the daily total EE (TEE) was validated in a many experiments, which were reviewed by Leonard (2003) and Achten and Jeukendrup (2003). The validation trials involved the use of the HR method in parallel with the direct determination of HP from the VO\(_2\), and the use of the DLW method on free-ranging subjects. The effects of the environmental conditions, such as temperature and dehydration, on the HR:EE relationships were cited in the above reviews, but the effects of diet energy concentration and intake level were not addressed.

The use of regressions between EE and HR for estimating EE in free-ranging farm animals (Webster, 1967; Yamamoto et al., 1979; Richards and Lawrence, 1984; Purwanto et al., 1990) and large wild animals (Renecker and Hudson, 1985) has been examined. These studies used linear or logarithmic regression equations to relate VO\(_2\) to HR. In a review on the application of the HR method of estimating HP, Yamamoto (1989) showed the incompatibility between using activity level to form a scale of EE vs. HR on the one hand and, on the other hand, the factors that cause changes in HR and EE during the day under farm conditions. Yamamoto (1989) suggested a new method for calibrating EE vs. HR, based on the relative HR, which is the ratio of the HR to the basal HR. He showed that this method can reduce the effect of individual variation on the estimation and indicated that it is necessary to use the average HR of at least 4 animals to represent the average HP of a group of animals. Yamamoto (1989) concluded that although it is possible to estimate the HP from the HR, physiological considerations limit the usefulness of this method. In particular, the HP vs. HR relationship varies among individuals and is affected
by physiological status; for example, reproduction and the production level itself affect the feed intake. Thus, Yamamoto (1989) concluded that equations for estimating HP that are obtained with animals under given conditions cannot be applied to animals held under different conditions.

The discrepancy between the HR vs. EE relationship that applies during exercise and that is determined with sedentary subjects has also been resolved by using a polynomial prediction equation for growing heifers (Brosh et al., 1998a) and humans (Beghin et al., 2000, 2002). Using a polynomial equation is like using the flex-HR method; the range of HR values within the curving area of the polynomial equation is similar to the HR range of the transition point between the resting and active levels, designated as the flex-HR.

Most of the above-cited studies used measurements during exercise as the basis for determining the regression of VO2 vs. HR. However, this practice appears to be based on the assumption that the activity level is the main determinant of HR and EE. The activity level was used even though some authors were aware of other factors that affect the HR:EE relationship (Yamamoto, 1989). Brosh et al. (1994, 1998a) were the first to show that whether the regression prediction equations were based on monitoring of activity levels or on data from sedentary heifers, the regression equations of EE vs. HR that were calculated for a diet with a relatively high energy concentration could not be used to predict these relationships in heifers that were fed a diet of lower-energy concentration and vice versa. In addition, Brosh et al. (1998a,b) contended that for feedlot cattle, the varying levels of HR and EE throughout the day and the whole-day totals depended mainly on the MEI level and the schedule of feed intake times.

Brosh et al. (1998a) estimated EE from data of VO2 and HR taken from sedentary heifers that were fed diets of 2 ME levels. They measured an average ratio of VO2 to HR – the O2 pulse (O2P) – over a relatively short time and calculated EE by multiplying O2P by the HR values measured throughout the day. Brosh et al. (1998a) found that a change in diet ME that increased MEI by 2.5-fold had relatively little effect (10.5%) on O2P. They also reported that for a wide range of HR, as measured on sedentary heifers, O2P was relatively constant. Therefore, they suggested that EE could be estimated from HR measurements, taken throughout the day, multiplied by short-period measurements of O2P. This is known as the O2P-HR method.

The O2P-HR method offers considerable advantages over the regression methods for estimating EE of wild and farm animals. It eliminates the necessity to calibrate EE vs. HR during exercise, which necessitates the use of specially trained animals and requires a relatively long time and expensive accessories. Moreover, because the main variable that affects the EE of farm animals is the diet ME and, consequently, the MEI, the regression equation method is more likely to introduce an estimation error when the calibration is not carried out under the same nutritional conditions as the experiment. The effect of dietary ME on O2P is relatively small, and therefore, the O2P-HR method is significantly less susceptible than the regression method to dietary ME changes.

**Practical Use of the O2P-HR Method for Measuring EE and EB of Ruminants**

In light of the aforementioned literature, it can be concluded that use of the O2P-HR method for measuring EE has a high potential for exploring the energy metabolism of free-range animals. Thus, the following sections will be dedicated to highlighting subjects of practical significance for future users and to reviewing published and unpublished data regarding validation of the O2P-HR method and the conditions that limit its validity.

**Animal Sensitivity to Measurement Conditions.** The measurement of EE by the O2P-HR method is based on long-term measurement of the HR of free-range animals and on the short-term measurement of O2P in animals that are constricted by a cattle squeeze, head yoke, or hood. Thus, the accuracy of the method primarily depends on the accuracy of these 2 measurements.

Physiological data obtained from measurements on excited or stressed animals probably will be biased. This is especially true for fast-response variables such as HR and VO2. Thus, both HR and O2P should be measured, as far as possible, under conditions that are similar to those with which the animals are familiar. The most important concern in this respect is the presence of humans near the tested animal.

Heart rate is measured on free-range animals; therefore, human interference is a minor concern. However, several rules need to be observed. First, HR recording devices must be mounted comfortably on the animals. Second, during HR measurement, throughout the several representative days, the animals must be treated according to their normal daily routine, without any special interference. Third, for grazed animals that have to be moved to enable mounting and dismounting of the HR devices for data downloading, the data obtained during traveling should be excluded from the representative daily HR records.

At present, the commercially available HR recording devices designed especially for free-range animals are based on electrocardiograph analysis. Some of them are implanted devices (Telonics Inc., Mesa, AZ), which transmit the data continuously by radio, and some are connected externally (Mini Mitter Co., Bend, OR; Polar Electro Oy, Kempele, Finland) and must be downloaded via a removable connection. The implanted devices are well protected from environmental damage and usually are designed for long-term recording. On the other hand, when measurements taken over a few days adequately represent the HR of the animals, the external devices have the advantage of being transferable from
one animal to another so that 1 device can be used for many animals and experiments. In recent years, HR recording devices have become very popular for use by trained individuals. Use of a fitted belt for mounting the devices on the animals enables some of them (e.g., the Polar Wearlink transmitter) to be used on free-range animals.

The diurnal patterns of HR and EE of confined ruminants depend mainly on their hourly patterns of feed intake (Brosh et al., 1998b, 2001; Shargal et al., 2001; Arieli et al., 2002; Barkai et al., 2002; Aharoni et al., 2003, 2005), but measurements with grazing cows have shown that these patterns also depend on other activities (Brosh et al., 2003, 2006b). Therefore, calculation of the daily EE must be based on HR measurements taken over the entire 24 h of several consecutive days.

The average daily HR measurements obtained by Brosh et al. (2004) for 6 grazing cows during 7 d were used in estimating the number of days needed to determine daily HR; the average HR of the 6 cows was 51.9 ± 1.7 beats/min. The analysis showed that for 1 individual cow, the maximum deviation of HR for 1 d from the average of the entire period was 12%. When the recorded HR was averaged over several days, the HR of the cow with the greatest day-to-day deviation, averaged over 3, 4, and 5 d, deviated from the whole-period average by 6, 3, and 1%, respectively. When a similar calculation was applied to the average daily HR (i.e., beats per day) of the 6 cows, the maximum deviation of any 1-d measurement from the period average was 2.2%; the corresponding deviations of the 3-, 4-, and 5-d averages from the whole-period average were 1.3, 0.7, and 0.6%, respectively. A similar calculation by Brosh et al. (2002a) applied to HR measurements on 6 confined cows recorded throughout a period of 7 d showed significantly smaller variations: The 1-d average for an individual cow showed a maximum deviation of 3.6% from the whole-period average HR, and the maximal deviations of the 3-, 4-, and 5-d average HR from the whole-period average were only 1.2, 1.1, and 0.6%, respectively. Therefore, it can be concluded that to obtain a truly representative average daily HR, the measurements should be applied to undisturbed animals throughout 3 to 4 full days.

There is a potential problem regarding calculation of the daily average HR. As mentioned before, HR changes during the day, and therefore the calculated daily average HR should encompass the 24-h cycle of measurements. However, HR recordings can often be missed so that the calculated daily average could be biased if the missing data are different from the average daily HR. Under stable conditions, the behavior of animals throughout the day and, consequently, the diurnal HR pattern, is similar from day to day (Figure 1). Thus, to obtain an unbiased daily average HR, the recorded HR should be averaged for identical, intermediate subperiods of each day. The length of the subperiods can be 0.5 h or more, which depends mainly on the recording frequency and on the number of missing data. For calculating the average daily HR, a representative average HR of each subperiod should be calculated, and the representative average daily HR of each individual animal should be calculated as the average of the HR data for the representative subperiods of the whole day.

O$_2$P. The reliability of the O$_2$P measurement as representative of the whole-day O$_2$P of the animals is the
needed to reach this equilibrium depends mainly on the airflow rate and the volume of the system. To reach an O2 concentration of 19.95% (i.e., a 0.5% error in the VO2 calculation), the time required to reach equilibrium. Increasing the turnover of the metabolized energy gases (CO2 and O2) affects the speed of reduction in the O2 concentration (O2 diff of 1%), for system volumes of 10 or 10 L it will take 318 or 32 s, respectively, to reach an O2 concentration of 19.955% (0.005% above equilibrium; i.e., a 0.5% error in the VO2 calculation).

As the resolution of the O2 analyzer increases, it becomes possible to increase the airflow and so to reduce the time required to reach equilibrium. Increasing the flow rate of a system air sample through a drying column and into the O2 analyzer will decrease the time needed for recording the equilibrated O2 concentration.

Three types of systems are most commonly used for measuring the VO2 for O2P calculation: respiration chambers, head hoods, and face masks.

Respiration chambers are expensive to use, which significantly limits the number of animals used. Also, the volume of the chamber is large; therefore, a long time is required to achieve equilibrium, which makes it difficult to cancel unwanted data obtained from excited or stressed animals. On the other hand, in a respiration chamber, the effect of human presence on the behavior of an animal is expected to be minor.

A head hood may impose less stress on the animals than a respiration chamber or a face mask, but its volume is larger than that of the latter so that the time needed for achieving equilibrium is longer than that with a face mask.

Face masks are cheaper than respiration chambers or head hoods, and, more importantly, a face mask can be incorporated into a portable system and thus can enable the monitoring of many animals in or close to their normal environment (e.g., cows or calves at their feeding trough or grazing cows in a cattle squeeze adjacent to the grazing area). Face mask systems have a negligible volume; therefore, the recorded VO2 reaches equilibrium with the VO2 of the animal in a very short time. For example, in the case of a flow of 300 L/min passing through a face mask on a cow whose BW is 400 kg, when the mask was removed, it took 20 s for the recorded O2 concentration to change from the 20.03% recorded during the measurement procedure to 20.93% and another 20 s to reach the fresh air level of 20.95%.

When a face mask is used, the time needed for O2P measurement decreases significantly as the turnover of the air pumped from the space of the animal within the system to the O2 analyzer increases (i.e., as the pumping flow rate increases) and the volume of the pipes and the air-drying column decreases. In a face mask system, the O2 concentration in the air taken from near the face of the animal is significantly affected by the breathing rate and depth so that the O2 concentration and, consequently, the VO2 and O2P recordings oscillate significantly when they are recorded every 5 s (Figure 2, panel A). When the data are averaged to represent the average of 1-min subperiods, the oscillations are significantly moderated (Figure 2, panel B).

The data presented in Figure 2 represent a relatively excited cow, whose HR ranged from 61 to 88 beats/min. To estimate the minimum time needed to obtain a measured VO2 representative of O2P, the data presented in Figure 2, panel A, over intervals of 1, 2, and 4 min (i.e., 12, 6, and 3 subperiods, respectively) were averaged. The corresponding maximum deviations of the average of any subperiod O2P from the overall average of the data were 3.9, 2.4, and 1.1%, respectively.

In light of the results of many experiments, it appears that O2P is best calculated by averaging over at least
Figure 2. Direct measurement of heart rate (HR; beats/min, ●) and O₂ consumption (VO₂; mL·min⁻¹·kg of BW⁻⁰·₇⁵, □) and the calculated O₂ pulse (O₂P, mL·beat⁻¹·kg of BW⁻⁰·₇⁵, Δ) of 1 cow as it was recorded (panel A) once every 5 s and (panel B) when it was averaged over every 60 s.

5 min, preferably 10 to 15 min. These periods are the net measurement times and do not include the time needed to reach equilibrium at the beginning of the measurement and to return to the ambient-air O₂ concentration at the end.

When O₂P is measured with a face mask, the animals are closely handled by people, and calm handling is crucial for achieving reliable O₂P values. Thus, the behavior and atmosphere around the animals should be calm, and the people who work with them should be sensitive to the feelings of the animals. When a person makes an animal nervous, the HR of the animal increases as the person approaches, even before there is any contact.

Variations in O₂P and Their Relation to HR Level. It can be clearly seen in the previously reviewed literature that changes in HR are positively related to changes in EE. However, to determine an individual EE, the O₂P should be measured under specific conditions. Nevertheless, it is possible that for a specific type of animal, under defined conditions, and to satisfy a particular need, it may suffice to represent the mean EE of the group by multiplying the measured HR by a previously determined O₂P.
Factors that can affect HR and EE of animals and that, consequently, could affect their O$_2$P fall mainly into 3 major types:

i. external, acute, short-term effects, such as daily changes in heat load, exercise, or interfering behaviors;

ii. chronic external effects, such as dietary ME, that affect intake and MEI and low or high environmental temperatures that can affect intake and MEI; and

iii. intrinsic chronic effects of production and reproduction levels that directly affect the EE of the animals and can affect their MEI.

The following paragraphs present possible changes in O$_2$P beyond the individual variation and demonstrate the dependence of calculation of coefficients of O$_2$P on HR and that enable estimation of the EE of a group from its HR recordings within a limited range of conditions.

Brosh et al. (1998a) estimated the effects of several factors on the linear dependency of O$_2$P on HR, concerning diurnal changes in O$_2$P. These factors include the following: solar radiation, time of feeding (morning or afternoon), time of measurement (morning or afternoon), and dietary ME concentration (high or low ME). Throughout the day, the maximum HR was almost double the minimum, but only the time of measurement significantly affected O$_2$P. The extents of the effects were 1.5, 3.2, 7.1, and 0.9%, respectively, of the average O$_2$P for solar radiation, time of feeding, time of measurement, and dietary ME concentration.

Aharoni et al. (2003) performed whole-day monitoring of HR, VO$_2$, and O$_2$P of young growing calves and lambs that were kept in sheds under summer conditions and that were fed a diet with a high ME concentration. They found that for both species, the time of day significantly affected O$_2$P. The extents of the effects were 1.5, 3.2, 7.1, and 0.9%, respectively, of the average O$_2$P for solar radiation, time of feeding, time of measurement, and dietary ME concentration.

Shargal et al. (2001) studied Bedouin goats kept either in the shade or exposed to direct solar radiation during the summer and maintained on 3 levels of feed intake, (40, 55, and 100% of ad libitum). They measured HR, VO$_2$, and O$_2$P throughout 24 h and observed distinct diurnal patterns of HR and VO$_2$ under all treatments ($P < 0.001$). Shargal et al. (2001) found that O$_2$P remained stable throughout the day and was not significantly affected by the level of feed intake, except when the goats received as little as 40% of their ad libitum energy intake (average MEI of 236 (kJ·kg·BW$^{-0.75}$·d$^{-1}$) and were exposed to solar radiation, where the maximal values of the wet bulb globe temperature index (Burr, 1991) and of the thermal humidity index (THI; Thom, 1959) were 33.3 and 88.4, respectively.

It can be concluded that for animals that are not subjected to a high heat load or intensive exercise there is a small variation in O$_2$P during the day; measuring the O$_2$P of an individual animal only once daily could bias the individual EE calculations up to about 5%, but repetitive measurements reduce this bias.

The effect of exercise on cardiovascular functions, including O$_2$P, cardiac output, stroke volume, and arterial and mixed venous blood O$_2$ content, was measured in sheep by Brosh et al. (2002b). Over a continuous range of VO$_2$, corresponding to activity levels ranging from rest to exercise at approximately 60% of the maximal O$_2$ consumption, HR increased from 70 to 200 beats/min, cardiac output was doubled, stroke volume decreased by about 32%, and O$_2$P increased by about 70%; it was also found that during exercise the O$_2$ content in arterial blood increased by about 36%. Despite the above changes, the relationship of VO$_2$ to HR was linear, but it differed from the regression line of VO$_2$ vs. HR of the same sheep at rest. Similarly, Brosh et al. (1998a) found that during exercise, O$_2$P usually increased. Thus, the O$_2$P-HR method should not be used for animals that engage in significant exercise during a significant part of the day. However, previous observations on grazing cows (Brosh et al., 2003) and more recent measurement on grazing cows, whose EE was measured simultaneously with their activity by activity sensors and global positioning system (GPS) devices (Brosh et al., 2006b), and on Alpine doe goats (Berhana et al., 2006) have shown that throughout the day, free-range cows and does do not exercise significantly. In the latter study, Berhana et al. (2006) found that the O$_2$P of a doe goat walking at a grazing pace did not differ from its resting O$_2$P. Thus, it can be concluded that unless animals are forced to exercise intensively, the O$_2$P-HR method can be used to estimate the EE of free-range ruminants, including grazing animals.

The changes in the environmental thermal conditions within the thermoneutral range, whether cooling or warming, affect the blood flow rate and distribution in tissues, and therefore may affect the O$_2$P. For changes beyond this range, the HP increases, and apparently the energy state of the animals may be regarded as appropriate for exercise.
Brosh et al. (1998a) measured the effects of heat load on the O$_2$P of growing heifers that were exposed to or protected from solar radiation in midsummer in Queensland, Australia, and found that the high heat load imposed by solar radiation did not affect O$_2$P. Similarly, Aharoni et al. (2003) found that under summer conditions in Israel, a THI of up to 85 did not affect the O$_2$P in growing calves and lambs, but they found that for high-yielding Holstein dairy cows, a THI above 75 caused moderate reductions in VO$_2$ and O$_2$P. Robertson and Rawson (2001) used intensive exercise to induce severe heat stress in sheep and found that the body temperature of sheep at rest after exercise was elevated and that a 14% increase of their cardiac output was required to dissipate the heat generated by exercise rather than for O$_2$ transport (i.e., the exercise caused O$_2$P to decrease). It can be concluded that the combined effect of high intrinsic and extrinsic heat loads is to increase blood flow to provide cooling, and, consequently, it reduces the O$_2$P. Thus, when EE is determined by the HR method, the effects of heavy heat load on O$_2$P should be taken into account, at least during part of the day.

Cold conditions may affect O$_2$P. Skin wetness, damp bedding, and wind significantly affect heat loss of an animal. Thus, even in a moderate climate, animals may be exposed to cold conditions that probably force them to balance the heat loss by increasing their HP. There is little information on the effect of cold weather on O$_2$P, but the increases in EE caused by cold appear to be similar to those caused by exercise, which increases O$_2$P. Brosh et al. (2002b) cited a study by D. Robertson and R. E. Rawson (Cornell University, Ithaca, NY, unpublished data), in which sheep were exposed to cold conditions by removing their fleece at temperatures ranging from 15 to 24°C. The increase in the VO$_2$ of the sheep at rest and under cold exposure varied from 50 to 70% of their VO$_2$ under warm conditions, but the O$_2$P did not change. Webster (1967) measured the effects of cold and of feed intake on the relationship between HP (i.e., VO$_2$) and HR; he presented a regression equation of HP dependency on HR in 4 sheep (Webster, 1967). From the above regression equation and the known effect of cold on HR, it is possible to calculate the effect of cold on O$_2$P (i.e., the HP:HR ratio; Webster did not calculate it). The calculations show that cold had little effect on O$_2$P. Doubling HP by cold increased O$_2$P by only 5.6% (sheep number 1, which Webster indicated to be a nervous animal, was excluded from the calculation).

Chambers et al. (2000) measured the effects of cold conditions on VO$_2$ and HR of ad libitum-fed rats. The VO$_2$ increased from 15 to approximately 26 mL·min$^{-1}$·kg$^{-1}$ of BW$^{-0.75}$, and HR increased from 300 to 460 beats/min in response to the transition from thermoneutral to cold conditions. Thus, although VO$_2$ increased by 50%, O$_2$P increased by only 1.1%. Froget et al. (2002) exposed penguins to thermoneutral and cold temperatures and found a low critical temperature of ~5°C and a VO$_2$ of 18.5 mL·min$^{-1}$·kg$^{-1}$ of BW in the thermoneutral zone. When they reduced the environmental temperature to ~31°C, VO$_2$ increased by 75% and O$_2$P increased by 20%. For these penguins, the exercise-related, linear regression slope of VO$_2$ dependency on HR was 3 times greater than that related to cold exposure (Froget et al., 2002).

Thus, from the limited data available at present, it can be concluded that the increase in O$_2$P associated with the increases in HR and VO$_2$ caused by cold is significantly less than that caused by exercise and may be regarded as negligible in ruminants.

The productive, reproductive, and physiological states of an animal may influence its O$_2$P, because increased dietary ME causes increases in MEI and EE (Brosh et al., 1998a, 2002a, 2004) unless the animal has reached its upper limit of production or EE (Ketelaars and Tolkamp, 1996). Increased energy requirements, especially in response to lactation or considerable cold, cause increases in feed consumption and MEI.

To study the effects of production level, physiological state, and reproductive state on the relationship between O$_2$P and HR, data from 11 published and unpublished studies that were carried out in different periods were used. The animals were measured repeatedly; this enabled one to distinguish the effects on individuals from those on the groups. The combined data set comprised a total of 803 records collected from a total of 236 animals. In all of these studies, in each replicate, HR was monitored for 3 to 4 d, and the O$_2$P of each animal was determined during a session of 10 to 15 min immediately before or after the HR monitoring period. The types of animals used and the treatment conditions were as follows.

Study 1: Six nonpregnant, nonlactating beef cows were fed simultaneously in confinement on 6 dietary ME levels (on a DM basis), ranging from 4.89 to 9.08 MJ/kg; another 4 similar cows were used as a control group, were fed a constant diet of 9.08 MJ/kg during the entire study, and their HR was measured simultaneously with that of the 6 treated cows (Shargal, 2006). The study began after the cows had been adapted to the diet ME levels (on a DM basis), ranging from 4.89 to 9.08 MJ/kg for 2 wk. Throughout the experiment, diet ME was increased from week to week by 0.84 MJ/kg of DM, allowing 3 d to adapt to the diet and 4 d of HR measurement; O$_2$P was measured twice at the end of each week.

Study 2: Thirty-four beef cows were monitored repeatedly, up to 14 times each, during 15 measurement periods. Measurements were taken during 13 periods from winter to late summer, while the cows were grazing in a heterogeneous Mediterranean grassland, and during 2 periods in confinement, while the cows were not pregnant, lactating, or in advanced pregnancy (Aharoni et al., 2004; Brosh et al., 2004).

Study 3: Six beef cows were monitored during 10 periods throughout the reproduction cycle during 1 yr in confinement; they received 9 diets, with ME levels
(on a DM basis) ranging from 4.41 to 8.26 MJ/kg (Brosh et al., 2002a).

Study 4: Eight beef cows, 7 of them at less than 180 d of pregnancy, and one more at 180 d of pregnancy were monitored. The cows were fed in confinement throughout 5 periods on 5 dietary ME levels (on a DM basis) ranging from 6.28 to 11.30 MJ/kg (Brosh and Aharoni, unpublished data). The study procedure was similar to that of study 1 except that the ME was increased from every week by 1.255 MJ/kg of DM.

Study 5: Six beef cows grazing a Mediterranean woodland area during 3 seasons of the year that encompassed every reproductive and physiological state of the cows were monitored (Brosh et al., 2006a).

Study 6: Forty Holstein, high-yielding dairy cows were each monitored twice, at the beginning and end of a 2-mo interval. These cows were fed the same diet on 2 feeding regimens: a night or a day feeding regimen (Aharoni and Brosh, unpublished data). The study procedures were identical to those presented by Aharoni et al. (2005; study 7).

Study 7: Twenty-one Holstein high-yielding dairy cows were each monitored up to 4 times during a 4-mo summer season, during which they were offered the same diet either during the night or during the day (Aharoni et al., 2005).

Study 8: Eleven growing, intact male Holstein calves were each monitored 3 times during a 3-mo summer season, during which they were fed the same diet on 2 feeding regimens: a night or a day feeding regimen. Portions of these data were published by Brosh et al. (2001).

Studies 9, 10, and 11 (Brosh and Aharoni, unpublished data) used young, intact, male Holstein calves, which were observed from 21 d of age and fed a milk replacement until age 100 d, which was approximately 45 d after weaning. The studies were carried out from November to June throughout 4 yr. The measurements were arranged to represent different ages of the calves. A total of 266 measurements were taken from 98 calves at various ages, with each calf measured up to 3 times. The treatments were as follows: a) night or day feeding in the winter, b) dry feed of concentrate only vs. a total mixed ration, and c) several amounts of milk replacement up to weaning (25 to 38 kg of DM from birth to weaning).

Each of the 803 data records of the 11 studies included the following variables: HR; EE; $O_2\text{P}$; individual animal identification; beef vs. Holstein dairy breed; cow, young calf, or fattening calf; type of study; period and treatment within study; and reproductive and physiological state (all calves were classed as nonlactating and not pregnant).

Because each animal in this data set was measured more than once, some of the total variance in analyses could be attributed to the individual animal effect. Therefore, all of the analyses of linear regression or mixed-model linear regressions that tested different effects on $O_2\text{P}$ used the REML procedure (Genstat software, 7th ed., Lawes Agricultural Trust, 2003), which enables inclusion of a random animal effect in the model. To demonstrate the power of this random effect in reducing the residual error and eliminating possible biases introduced by the wide range of animals and conditions, initially a simple linear regression of $O_2\text{P}$ on HR was used, either with or without the animal random effect. The effect of HR (beats/min) on $O_2\text{P}$ (expressed as $\mu$L·beat$^{-1}$·kg of BW$^{-0.75}$) was weak but significant ($P < 0.001$) in both regressions. It was found to be negative ($-0.472 \pm 0.132$) when the random effect of animals was not included but positive ($0.382 \pm 0.132$; $P = 0.004$) when the random animal effect was included in the model. Therefore, this random effect was included in all subsequent models.

Data from the 11 studies were arranged in 4 sets, which were analyzed separately as follows:

data set 1 included all 803 records from the 11 studies;
data set 2 included all 507 records from studies 1 through 7;
data set 3 included only the 376 records on beef cows from studies 1 through 5; and

data set 4 included the 266 records on young Holstein calves from studies 9 through 11.

The effects on $O_2\text{P}$ of HR and of reproductive and physiological states and the interaction of HR and reproductive and physiological states were highly significant in all 3 data sets (Table 1). The similarity in direction and even magnitude of the estimates among the data sets suggests that the biases caused by the inclusion of several types of animals and conditions in data sets 1 and 2 were relatively small. Heart rate was estimated to exert negative effects on $O_2\text{P}$ in nonpregnant cows and even stronger negative effects on $O_2\text{P}$ in late pregnancy. In contrast, HR had a positive effect on $O_2\text{P}$ in lactating cows.

Data set 3 contained data on confined and grazed beef cows in all 3 reproductive and physiological states; therefore, this set of data enabled comparison of $O_2\text{P}$ between grazing and confined beef cows. The analysis showed that $O_2\text{P}$ of grazing cows was greater ($P < 0.001$) than that of the confined cows by 83.5 $\mu$L·beat$^{-1}$·kg of BW$^{-0.75}$ (Table 2).

The predicted average group $O_2\text{P}$ values of the cows used in the above data sets is presented in Table 2. For similar animals under similar conditions, these $O_2\text{P}$ values can serve as a rough estimate of the group average EE from the group average HR, without measurement of $O_2\text{P}$.

The analyses for data set 4 included the effect of calf age. The daily average HR was 100.6 ± 1.0 beats/min, which increased ($P < 0.001$) by 0.629 ± 0.0403 beats·min$^{-1}$·d$^{-1}$ with increasing age. The daily average EE was $820 ± 10.1$ kJ·kg of BW$^{-0.75}$·d$^{-1}$, which increased ($P < 0.001$) by 7.24 ± 0.404 kJ·kg of BW$^{-0.75}$·d$^{-1}$ per d of age with increasing age. When the combined effect
of age and HR on O₂P was examined, it was found that O₂P increased with age (P < 0.001) by 1.124 ± 0.1489 μL·beat⁻¹·kg of BW⁻⁰.⁷⁵·d⁻¹, but each beat per minute in HR caused a decrease (P < 0.001) of −0.6480 ± 0.16030 μL·beat⁻¹·kg of BW⁻⁰.⁷⁵ in O₂P. No interaction was found between the effects of age and HR on O₂P. Therefore, it can be concluded that for young growing calves from 21 to 100 d of age, the increase in the EE per unit of metabolic BW (BW⁰.⁷⁵) is exhibited as an increase in both HR and O₂P.

It can be concluded that under similar physiological conditions, when changes in dietary ME and MEI are the main causes of the increase in EE, an increase in EE is mainly exhibited as increased HR and not increased O₂P. However, the situation is different when the physiological condition of the animals changes and their demands for energy increase (e.g., because of the change from nonlactation to lactation or because of maturation of their digestive tracts). Another example is that of grazing cows compared with confined cows. In these cases, the increase in EE is also exhibited in increased O₂P. This sustained effect on O₂P is similar in direction to those of the acute, short-term effects of exercise and cold, which were discussed above.

**Validation the O₂P-HR Method by EB Trials.** By definition, in nondraft animals, MEI must be converted into either EE or RE (Wenk et al., 2001). Two experiments were conducted to examine the reliability of the HR method for estimating the EE of an animal by calculating their EB. The null hypothesis of the studies was that EE could be estimated with acceptable precision by the O₂P-HR method if MEI recovery [the ratio of MEI to (EE + RE)] does not differ significantly from 1.0. In addition, attention was paid to the variation among the calculated MEI recovery of the animals (i.e., the SE among individuals). It is important that this variation be small, because a nonsignificant difference could result from a large SE in the data, and such a situation could indicate that the method was not reliable.

**Table 1.** Combined effect of heart rate (HR; beats/min) and reproductive and physiological states¹ (RPST) on O₂ pulse (O₂P; μL·beat⁻¹·kg of BW⁻⁰.⁷⁵)

<table>
<thead>
<tr>
<th>Data set</th>
<th>O₂P</th>
<th>HR effect (P &lt; 0.001)</th>
<th>RPST effect² (P &lt; 0.001)</th>
<th>HR × RPST effect (P &lt; 0.001)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NONLACT</td>
<td>SE</td>
<td>O₂P/beat</td>
<td>SE</td>
</tr>
<tr>
<td>1</td>
<td>324</td>
<td>5</td>
<td>−0.43</td>
<td>0.11</td>
</tr>
<tr>
<td>2</td>
<td>362</td>
<td>6</td>
<td>−0.41</td>
<td>0.38</td>
</tr>
<tr>
<td>3</td>
<td>324</td>
<td>9</td>
<td>−0.35</td>
<td>0.39</td>
</tr>
</tbody>
</table>

¹Reproductive state = lactation (LACT) or late pregnancy (PREG; 181 d of gestation up to calving) compared with non-lactating state (NONLACT; 1 to 181 d of gestation, as well as calves). The observations were estimated from 3 data sets: Data set 1 included all 803 records from the 11 studies with beef cows (confined and grazed), high-yield Holstein dairy cows, and growing intact calves (young suckling and fattening). Data set 2 included all 507 records from studies 1 through 7 with grazed and confined beef cows and high-yielding Holstein dairy cows. Data set 3 included only the 376 records from studies 1 through 5 with grazed and confined beef cows. The individual data values were used for the analysis.

²Pregnancy and lactation compared with non-lactating state. O₂P = O₂ pulse.

**Table 2.** Average heart rate (HR) and predicted O₂ pulse (O₂P) of lactating Holstein cattle and beef cows under grazing and confined conditions in 3 reproductive and physiological states (RPST)

<table>
<thead>
<tr>
<th>Animal REPST</th>
<th>Holstein cows</th>
<th>Beef cows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lactating²</td>
<td>Nonpregnant³</td>
</tr>
<tr>
<td>HR (beats/min)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>—</td>
<td>56.6</td>
</tr>
<tr>
<td>Confined</td>
<td>81.4</td>
<td>58.9</td>
</tr>
<tr>
<td>O₂P (μL·beat⁻¹·kg of BW⁻⁰.⁷⁵)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>—</td>
<td>337ab</td>
</tr>
<tr>
<td>Confined</td>
<td>450d</td>
<td>273a</td>
</tr>
<tr>
<td>SE⁵</td>
<td>14</td>
<td>27</td>
</tr>
</tbody>
</table>

⁴⁵For O₂ pulse, means that do not have a common superscript differ (P < 0.05).

¹As estimated from studies (1 to 8) with grazed and confined beef cows, high-yielding Holstein dairy cows, and growing intact male Holstein calves. The individual data values were used for the analysis.

²Lactating cows, 30 to 160 days in milk.

³Nonpregnant or pregnant up to 180 d of gestation.

⁴Pregnant from 181 d of gestation up to calving.

⁵Standard error of the differences among management (grazing vs. confined), reproductive, and physiological states for beef cows and between beef cows under the presented conditions and Holstein cows for the Holstein SE.
In the first experiment by Brosh et al. (2002a), the EB of 6 confined beef cows was monitored throughout a full reproductive cycle for a wide range of dietary energy concentrations. In the second experiment by Ariel et al. (2002), an EB trial was conducted on 12 growing lambs whose RE was measured by a comparative slaughter technique. The MEI recoveries measured in the EB trials were not significantly different from 1.0, and the SE of the estimated EB was small, 1.062 ± 0.026 for beef cows during 1 yr of their reproductive cycle and 0.957 ± 0.024 for growing lambs.

**EE and HR Dependencies on MEI: Potential Use for Estimation of EB of Animals**

Brosh et al. (2002a, 2004) found a linear relationship between EE and MEI and between HR and MEI in cows that were fed and grazed on large ranges in types of herbage ME; a linear relationship between EE and MEI was also found by Brosh et al. (2006a) in cows that were grazed on narrower ranges of grazed ME. The EB of nondraft animals is defined as MEI = EE + RE (Wenek et al., 2001).

When the dependency of EE on MEI is linear, the regression equation is

\[ \text{EE} = (b \times \text{MEI}) + C. \]

Therefore, the following variables could be calculated: fasting EE (regression intercept \( C \)), heat increment (regression slope \( b \)), energy efficiency (1 – regression slope; i.e., \( 1 - b \)), and maintenance energy requirement \( \text{MEm} \), which is MEI when \( \text{EE} = \text{MEI} \) and is calculated mathematically as: \((\text{fasting EE}) / (1 - \text{heat increment})\).

The coefficients of the linear regressions of the dependencies of EE and HR on MEI that were calculated from several published and unpublished studies are presented in Table 3. The dependency of EE on MEI was found to be high and significant \((P < 0.001)\) in all studies. When changes in MEI were induced by changes in dietary ME (trials 4 and 5), the \( R^2 \) values were larger than 0.9; when other variables and factors affected MEI also, the \( R^2 \) values were smaller. Similar data were found for the \( R^2 \) values of the dependency of HR on MEI, except in trial 2, which extended over only 3 seasons, for 2 of which the average MEI values were similar and the average HR range was narrow, from 62 to 70 beats/min. The increase in EE in trial 2 was mainly caused by lactation, which increased \((P < 0.001)\) \( \text{O}_2\text{P} \).

Fasting EE and MEm calculated from measurements of cows throughout an entire year that encompassed all reproductive and physiological states (trials 1 to 3) seemed to be greater than those obtained in the other 2 trials. Over the entire set of experiments, the calculated HR in fasting cows ranged from 35 to 44 beats/min, whereas the calculated HR in a state of maintenance ranged from 49 to 56 beats/min.

### Table 3. Relationship of energy expenditure (EE; kJ·kg\(^{-1}\)·d\(^{-1}\)) and heart rate (HR; beats/min) to ME intake (MEI; kJ·kg of BW\(^{0.75}\)·d\(^{-1}\)) and the calculated maintenance energy (MEm) and HR at maintenance

<table>
<thead>
<tr>
<th>Item</th>
<th>( R^2 )</th>
<th>Slope</th>
<th>Intercept</th>
<th>MEm</th>
</tr>
</thead>
<tbody>
<tr>
<td>EE to MEI</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing(^1)</td>
<td>0.792</td>
<td>0.375</td>
<td>328</td>
<td>525</td>
</tr>
<tr>
<td>Grazing(^2)</td>
<td>0.794</td>
<td>0.282</td>
<td>342</td>
<td>476</td>
</tr>
<tr>
<td>Confinement(^3)</td>
<td>0.616</td>
<td>0.219</td>
<td>340</td>
<td>435</td>
</tr>
<tr>
<td>Confinement(^4)</td>
<td>0.988</td>
<td>0.299</td>
<td>270</td>
<td>385</td>
</tr>
<tr>
<td>Confinement(^5)</td>
<td>0.925</td>
<td>0.289</td>
<td>266</td>
<td>374</td>
</tr>
<tr>
<td>HR to MEI</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing(^1)</td>
<td>0.838</td>
<td>0.027</td>
<td>35.0</td>
<td>49.0</td>
</tr>
<tr>
<td>Grazing(^2)</td>
<td>0.003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Confinement(^3)</td>
<td>0.353</td>
<td>0.024</td>
<td>44.4</td>
<td>55.0</td>
</tr>
<tr>
<td>Confinement(^4)</td>
<td>0.993</td>
<td>0.030</td>
<td>38.1</td>
<td>49.6</td>
</tr>
<tr>
<td>Confinement(^5)</td>
<td>0.979</td>
<td>0.044</td>
<td>39.3</td>
<td>55.6</td>
</tr>
</tbody>
</table>

\(^1\)Brosh et al. (2004): 10 cows grazed on herbage throughout 2 yr of reproductive cycles; herbage ME ranged from 6.66 to 11.76 MJ/kg of DM. Calculation based on 14 group-average measurement periods.

\(^2\)Brosh and Aharoni (unpublished data): 6 cows in confinement, throughout 1 yr of reproductive cycle on 9 diet ME ranging from 4.59 to 8.10 MJ/kg DM; 9 average group measurement periods were used for the calculation.

\(^3\)Brosh and Aharoni (2002a): 6 nonpregnant cows on 6 dietary ME levels ranging from 4.89 to 9.08 MJ/kg of DM; 6 group-average measurement periods were used for the calculation.

\(^4\)Brosh et al. (2006): 6 cows grazed on Mediterranean woodland during lactation, early pregnancy, and late pregnancy; dietary ME ranged from 6.23 to 8.78 MJ/kg of DM. Three measurement periods were used for the calculation; calculations used all the data of the cows after covariate correction for individual cow effects. Heart rate was not affected by MEI; therefore, the HR dependency, slope, intercept, and estimated HR at MEm were not presented.

\(^5\)Brosh and Aharoni (2002a): 6 cows in confinement, throughout 1 yr of reproductive cycle on 9 diet ME ranging from 4.59 to 8.10 MJ/kg DM; 9 average group measurement periods were used for the calculation.

\(^6\)Brosh and Aharoni (unpublished data): 8 early-pregnant cows on 5 dietary ME levels ranging from 6.25 to 11.30 MJ/kg of DM; 5 group-average measurement periods were used for the calculation.

### Numbers of Individuals Representing the Average EE of a Large Group

As cited before, according to Yamamoto (1989), it is necessary to use the HR of at least 4 animals to represent the average HP of a group of animals. To address this subject directly, it is necessary to use dozens of individual measurements under identical environmental and production conditions. To partly address the subject, we used a set of individual measurements of MEI and EE of 8 nonlactating beef cows on 5 diet ME and compared individual variations in MEI to variation in EE. Data set 8, presented in the section “Variations in \( \text{O}_2\text{P} \) and their Relation to HR Level” was used for the analysis.

The maximal deviation of individual measurement from the treatment average was 26% for both MEI and EE. When the absolute value of the deviation of the group average of 3, 4, 5, and 6 of the average of the 8 cows was tested, the maximal deviations from the group average were 6.7 and 8.7% for the MEI and EE, respectively, and average absolute values of the deviation were not different \((P = 0.135)\) between the MEI and EE.
(3.0 ± 0.9 and 3.8% ± 1.3%, respectively). Consequently, it can be concluded that the number of animals needed to represent the EE of a large group average seems to be not significantly different from the number of animals needed to represent the intake of the animals.

Recent Studies of Grazing Behavior and Energy Cost of Activity

Now it is possible to monitor the activities of animals throughout the day, thanks to the possibility of measuring the EE of animals throughout the day, the recently developed ability to obtain data on the location of an animal and locomotion speed via the GPS, and the ability to monitor the activity of animals (lying down, grazing, or traveling (i.e., walking without grazing)) with a motion sensor (Ungar et al., 2005). It has also become possible to monitor the ways the animals exploit different grazed habitats (Henkin et al., 2003). These new techniques have also enabled researchers to combine information on various activities with data such as locomotion speed and traveling distance, to measure EE over short intervals, and to calculate the energy cost of each specific activity and of distance traveled under diverse grazing conditions (Brosh et al., 2006b). The overall summary of the research cited in this paragraph as is follows:

A. For cows grazing on a Mediterranean, herbaceous habitat, the energy cost of locomotion is similar to that determined in treadmill studies on various animal species and humans, but the cost of grazing is 47% greater because of the activity of gathering feedstuffs.

B. Overall activity costs, in addition to that in the lying-down state, accounted for 5.8 to 11.4% of the TEE across seasons and treatments.

C. Overall activity cost as a proportion of the TEE increased as herbage quality and, consequently, energy intake decreased.

D. In a range of herbage ME of 10.4 to 6.3 MJ/kg of DM and biomass of 3,000 to 450 kg of DM/ha, cows responded to decreases in herbage quality (from a ME of about 7.7 to approximately 6.8 MJ/kg of DM and less) and availability (biomass decrease from approximately 3,000 to 2,300 kg of DM/ha and lower) by decreasing their grazing time, the total energy expended on their activities, and their TEE.

Potential for Future Use of HR

Selection for Increasing Efficiency of Animals. Selection of domestic ruminants is mostly used to increase their production under their specific environmental conditions. Increasing the production rate has indirect positive effects on production efficiency. In the last decade, intensive research has been applied to the selection of domestic ruminants for directly increased efficiency (Arthur et al., 2004). The scientific method more recently used to describe animal efficiency is residual feed intake (RFI; Ngwerume and Mao, 1992), which is defined as observed feed intake minus feed intake as predicted from the production of an animal; negative values indicate greater efficiency. In practice, selection specifically for increasing efficiency in ruminants is still minor, even in developed countries. Selection for specific characteristics should be applied to individual animals, and direct selection for increased efficiency by conventional means necessitates measurement of individual intake, which is an expensive process. It could be worthwhile if selection was applied to males, but it would be impracticable for dairy ruminants, whose selection process would have to be applied to many females.

Measurement of the EE of Holstein dairy cows and of the energy in their milk product, plus estimation of the changes in body RE, enable determination of their individual efficiency without measurement of their individual intakes (Aharoni et al., 2006). Moreover, Brosh and Aharoni (2005) have hypothesized, with the support of preliminary measurements, that lowering the EE in relation to production of an animal is the most promising means of improving the efficiency of an animal, and they suggested that selection of animals and determination of their efficiency be based on measurement of residual EE (REE), which is similar to the RFI. The REE is defined as the observed EE minus the expected EE. Similarly, Aharoni et al. (2006) have tested the efficiency of cows by measuring their residual HP; in this context, the term HP was used instead of the term EE. Schaefer et al. (2005) found lower skin temperature in calves with negative RFI compared with calves with positive RFI. Nkhumah et al. (2006) found that calves with negative RFI had smaller VO2 than those with positive RFI. These findings strongly support the hypothesis that RFI can be replaced with REE in animal efficiency estimations, even though Schaefer et al. (2005) and Nkhumah et al. (2006) did not point out this possibility. Therefore, it can be concluded that if and when the hypothesis of Brosh and Aharoni (2005) is confirmed by a larger number of experiments, it will be more practicable to select domestic ruminants, especially dairy ruminants, for greater efficiency from the REE parameter.

Herd Management. The unique potential of the HR method to explore the HP of farm animals throughout the day has led to the recommendation (Brosh et al., 1994, 1998b) to change the feeding time to the afternoon and night hours so as to increase night feed consumption. In hot environments, night feeding compared with day feeding reduces the heat load and increases the production efficiency of fattening beef and Holstein calves (Brosh et al., 2001) and dairy Holstein cows (Aharoni et al., 2004). Under cold conditions, night suckling instead of day suckling of milk replacement by young Holstein calves has been shown to improve their thermal comfort, save 11% of their TEE, and tended to increase their BW gain (Brosh et al., 1997);
it has also been shown to affect the health of the calves, as expressed in the reduction by half of the incidence of nonkosher calves (Brosh et al., 1998c).

Soon, the development of microelectronic and computerized accessories will enable wide use of HR measurement on farm animals. The HR method has been used for generations as an indicator of health status in both human and veterinary medicine. Obtaining good health treatment for farm animals depends first and foremost on early prediction by the producer. Therefore, the use of continuous HR recordings for automatic and early detection of health problems has a great potential for shortening the treatment time, increasing the recovery rates, and decreasing the use of antibiotics. Moreover, because HR level and its changes depend strongly on intake level and therefore on dietary ME, the environmental heat load and the efficiency of the shed cooling systems can be indicated by the HR level of the animals and changes in their diurnal HR pattern. Thus, continuous monitoring of the HR of farm animals can be used as a herd management tool in addition to its use as an early detector of health problems.

**Overall Conclusions**

The use of HR for daily EE estimation is mainly based on the multiplication of daily HR recording by the calibrated ratio of VO$_2$ to HR. This method is used mainly for humans and usually involves calibrating the HR vs. VO$_2$ by exercise. The EE and HR of free-ranging domestic ruminants are mainly affected by their dietary ME, intake level, production level, and reproductive and physiological states rather than by exercise; in addition, grazing cows seldom engage in intensive activity for a significant part of the day. Dietary ME and lactation significantly affect the regression of VO$_2$ on HR of cattle, and therefore, the calibration by exercise can fail by more than 100% to estimate EE when the dietary ME changes significantly. Moreover, exercise-based calibration is expensive, which limits the number of animals that can be measured.

Many studies have investigated the physiological mechanisms of cardiovascular and O$_2$ mobilization in domestic ruminants in a variety of physiological states (ages, production levels, and reproductive states) under a variety of management practices (grazing vs. confined and differing dietary ME levels and intake times) and under various environmental conditions (heat load, cold conditions). From these studies, it can be concluded that EE can be determined from HR measurements taken over the course of several days multiplied by the amount of O$_2$ pumped by 1 heart beat, as measured over a short time (10 to 15 min). Using only 1 d of HR measurement combined with 1 O$_2$P measurement can cause an error of about 6% in individual EE measurement. Using 4 d of HR recording and 2 O$_2$P measurements reduce the potential error for an individual animal to about 2.5%.

Two long EB trials that used sheep and cows found deviations of about 6% between the classic EB calculation (based on MEI and RE measurements) and EB calculation based on RE and EE, using the O$_2$P-HR method. The method is indirectly validated in 3 experiments on cows by using the regression of EE to MEI and comparing the regression-based coefficients of fasting EE and MEI to the published literature values. It seems that variation among individuals in their EE, estimated by the O$_2$P-HR method, is not different from the variation in individual intake. Consequently, the number of individuals needed to represent a large group average is similar for group intake estimation and for group EE estimation.

When the EE of an individual animal is measured by the O$_2$P-HR method, it is strongly recommended that O$_2$P be measured close to the time of the daily HR measurement; this is especially necessary when the physiological and reproductive state of the animals changes. Extreme heat load, whether as a result of extrinsic heat load or of a combination of intrinsic (production rate) and extrinsic heat load, significantly affects O$_2$P (decreasing it). Therefore, using the O$_2$P-HR method under those conditions requires correction of the O$_2$P during the day. Good animal handling practices during the O$_2$P measurement are a necessary condition for measuring EE reliably.

Energy expenditure and HR are highly dependent on MEI. Therefore, for healthy ruminants, changes in EE and in HR can serve as good indicators of changes in MEI and general energy status. The studies show that RE can be determined by this method during the growing phase, without the need for slaughtering. Determination of the EE from the HR while simultaneously monitoring the activities of the animals with a motion sensor and their locomotion intervals with a GPS receiver enable estimation of the energy cost of the activities of the ruminants during grazing. The O$_2$P-HR method has a great potential for agricultural application, but further research is needed for testing the method in a wider range of species and breeds as well physiological and environment conditions.

Finally, the O$_2$P-HR method is a practicable means of monitoring the EE of many domesticated ruminants; changes in their HR level present reliable indications of changes in their energy status. Soon, the development of microelectronic devices will enable wider use of the HR method to determine EE and energy balance. This will open up new avenues for physiological and agricultural research, with minimal strain on the animals. Continuous monitoring of individual HR also offers great potential as a tool for herd management.

**LITERATURE CITED**


