Measurement of energy metabolism

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Measurement of Energy Metabolism

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INTRODUCTION

There are a vast number of publications describing the measurement of energy metabolism in farm animals and the interpretation of the measurements obtained. A few are referenced within the following chapter, which is intended as an overview of the subject for those who do not work actively in the area. The result is far from complete, but will hopefully provide a starting point for further investigation. Measurements of energy metabolism are the basis of current rationing systems for feeding energy to livestock, which many believe to be inadequate. This is not unlike the situation when the current systems were developed some 30 years ago. Energy is the first limiting 'nutrient' in most animal production systems, thus the need for an accurate and precise feed rationing system which can budget energy balances, and predict responses, will remain. There are many who feel that the classical techniques for the study of energy metabolism have reached the end of their useful life, to borrow the words of Sir Kenneth Blaxter (Blaxter and Graham,1955), that the approach and the information obtained have been 'sucked dry'. Time will tell. In the mean time, an enlightened understanding of the current energy feeding systems and their basis is needed for them be improved, or replaced.

HISTORICAL PERSPECTIVES

Limitations of existing systems for feed evaluation and ration formulation in the 'post-war' boom of agricultural research of the 1950's and 1960's lead to the development of a number of 'new' feeding systems based on measurements of energy metabolism using balance trials or comparative body composition methodology. Some of the systems in place, such as the total digestible nutrient (TDN) approach, tended to overestimate the feeding value of forages (e.g. lucerne hay) compared to concentrates (e.g. maize meal) by not accounting for differences in their net energy value. Debate arising over this specific comparison was a driving force behind the establishment of 6 respiration calorimeters for dairy cows at the US Department of Agriculture's Research Center in Beltsville, Maryland (Flatt *et al.*, 1958; Van Soest, 1992). A sustained program of research on the energy metabolism of lactating dairy cattle at this facility, and others in Europe, lead to the development of a Net Energy for Lactation (NE$_l$) system for describing the nutrient requirements of dairy cattle and the energy value of feeds (Moe *et al.*, 1972; NRC, 1989). In Europe, similar concerns about the Starch Equivalent systems in use (Blaxter, 1986) lead to the simultaneous and conjoint development of various metabolizable energy (ARC, 1965) and net energy (Vermorel and Coulon, 1998) systems for ruminant livestock. Similar systems were also developed for pigs and poultry, although in these species the effects of forages on the suitability of digestible energy (DE) as a basis for rationing energy are of less concern. Current systems for rationing energy for pigs are effectively based on DE (Chapter 9), whilst a metabolizable energy (ME) system is widely used for poultry as faeces and urine are not separated in the measurement of digestion (Chapter 10; McDonald *et al.*, 1995).

Although the current systems were developed on the back of a profusion of new measurements of energy metabolism, the concepts on which they are based and the techniques used for measurements of energy metabolism and feeding value of ration components have a long history. The work of Kellner in Germany and Armsby in the US led to the development of net energy (NE) approaches for describing feed energy utilisation by ruminants at the turn of the century. However, the NE values published by Armsby (Armsby, 1917) were expressed as therms, whilst Kellner's system expressed the energy value of feeds in terms of Starch Equivalents (Kellner, 1926). Due to the difficulty of obtaining measurements of the NE value of individual feeds, both used values for a large proportion of feeds which were estimated from their digestible nutrient content (Morrison, 1954; McDonald *et al.*, 1995). The starch Equivalent system was used widely in Europe until replaced by more refined NE systems. In the US, Armsby's NE system tended to be used as a supplement to the TDN system, which later incorporated Morrison's own estimated NE values, so called 'corn equivalents', which were derived from feeding trials (Morrison, 1954). The period between the ground breaking experimentation of Kellner, Zuntz, Rubner, Armsby and others and the larger scale studies 60 years later was not devoid of research in energy metabolism of farm animals. Work continued at a number of locations (NRC, 1935; van Es, 1994) and substantial contributions were made, but a working NE system was never achieved, largely due to the limited number of measurements of feed utilisation which the technology of the day could produce.

One concern with the number of facilities operating independently in the area of energy metabolism was a lack of standardisation of approach and terminology. In 1935 many of the scientists working in the area of energy metabolism (S. Brody, Missouri; E. B. Forbes, Pennsylvania; M. Klieber, California; T. S. Hamilton and H. H. Mitchell, Illinois; E. G. Ritzman, New Hampshire) met at State College, Pennsylvania, site of the Armsby calorimeter, to discuss and debate current findings and approaches. The meeting was held under the auspices of the Committee on Animal Nutrition of the National Research Council, the organisation which co-ordinates the publication of current feeding standards in the US. This Conference on Energy Metabolism provided an early opportunity for standardisation of terminology, methodology and conceptual frameworks such as maintenance energy requirements and metabolic body size (NRC, 1935). Similarly, the European Association of Animal Production held a symposium on Energy Metabolism in Farm Animals in 1958 to provide a forum for comparison and discussion of energy metabolism methodology. This symposium, held every 3 years (Table 1), has also contributed to the standardisation of terminology and approaches used, such as the formulae for calculating heat production from respiratory exchange (Brouwer, 1965). In spite of the success of this symposium in achieving these objectives, many of the feeding standards developed in individual countries have used varied approaches, assumptions and terminology. This has lead to confusion amongst those seeking to compare the relative merits and weaknesses of the individual systems. In addition, the lack of understanding of the historical basis for the assumptions and approaches used in studies of energy metabolism has led to misinterpretations of results and comparisons of data obtained using differing methodologies.

TERMINOLOGY AND ASSUMPTIONS

There are a variety of units for the expression of the energy value of feeds and animal products. The calorie has been the term of choice in the US, but the internationally accepted term is now the Joule. In the US, the NRC published (Harris, 1966) and later revised (NRC, 1981) a glossary of terms for describing the components of energy metabolism. This glossary gives a comprehensive breakdown of the various components of mammalian energetics, along with a suggested acronym for each component. However, these terms and acronyms have not been universally adopted. Terminology differs between energy feeding systems used in different countries and between systems used for different species as well, and as in the present chapter, is subject to the interpretation of individual authors. This is especially true for the various efficiency constants, which can be particularly confusing for the uninitiated. Differences in terminology between countries using different language are to be expected. However, in comparing energy feeding standards, the problems arising from the use of different assumptions and calculations for individual terms is made worse by the lack of universally accepted terminology and/or abbreviations. Editorial boards for scientific journals can establish 'acceptable' terminology for measurements of energy metabolism, but acceptable terminology varies between journals. In reviewing the literature, one should be aware that the terminology used to report measurement of energy metabolism has evolved with time as well.

Calculations and Abbreviations

The idealised flow of energy through animals suggested by the NRC (1981) is shown in figure 1. All energy-feeding systems begin with gross energy, the total energy in food provided to the animal. Gross energy intake, or intake energy (IE), is the total amount of energy consumed. Apparently digested energy (DE) is measured by subtracting faecal energy (FE) from IE. This is distinguished from true digested energy (TDE), which accounts for metabolic faecal energy (F_mE) and heat of fermentation (H_fE). Subtracting urine and gaseous energy (mainly methane) gives metabolizable energy (ME), which is in a sense a net measurement as the energy in urine is partly a consequence of metabolism. True metabolizable energy (TME) then is the energy truly available for metabolism, which is obtained by accounting for endogenous urine energy (U_eE) not of food origin. True ME is used in evaluating poultry feeds by comparing the energy voided in fasted (or glucose fed) birds and birds fed a test meal (McDonald *et al*., 1995). In other species the effects of body protein loss (or gain) on U_eE losses can be obtained by adjusting to zero nitrogen retention, giving nitrogen-corrected ME (M_nE).

On a net basis, ME can be lost as heat energy (HE) or recovered as energy in specific products (RE), such as lactation energy (LE) or body tissue energy (TE), the sum of recovered energy representing 'energy balance' in many publications.   This subdivision requires the measurement of either HE or RE. In growing animals, energy is retained as TE, whilst in dairy cows milk energy production must also be measured. Historically NE was a term applied to total energy balance at a given level of food intake (Armsby, 1917; Morrison, 1954), or ME minus HE. However, in the glossary proposed by NRC (1981) the term NE is specifically applied to the change in recovered energy relative to a change in IE, which represents an incremental efficiency. Incremental efficiencies are often represented by 'k' values, or 'partial' efficiency constants, which can be calculated for a variety of products and inputs. For example, k_m, k_g and k_l represent the partial efficiencies of ME use for maintenance,

TE gain and lactation energy, respectively, which are calculated as the increase in energy recovered in these products with increasing ME. These efficiency constants are typically derived using linear regression, although one should never assume absolute linearity for any biological response. Certainly, the relationship between retained energy (or conversely HE) and ME is different above and below maintenance. This relationship is often described by 2 straight lines, intersecting at the point where ME = HE, although there is evidence that the response is curvilinear (Blaxter, 1989; NRC, 1996).

The Concept of Maintenance

The manner in which maintenance energy requirements are described and accounted for varies between feeding systems (Moe and Tyrrell, 1973; Moe, 1981). In energetic terms, maintenance represents the state of retained energy (energy balance) being zero, thus the point where ME = HE. The total NE requirement for maintenance is theoretically equal to the heat production at zero food intake, or fasting metabolism, whilst NE for maintenance (NE_m) represents the relationship between energy balance (which is negative) and ME below maintenance. Thus k_m is equal to fasting HE divided by maintenance ME (ME_m). Alternatively, NE for production (recovered energy) represents the relationship between energy balance (which is positive) and ME above maintenance. The partial efficiency of ME use for energy recovered in a given product is ideally calculated with corrections for ME_m (i.e. ME - ME_m). If NE_m and NE for production are expressed as a combined, linear function which theoretically intersects fasting HE, then at higher intakes (as occur in lactating dairy cows at production intakes), the slope is more similar to the one for NE for production than NE_m (Moe and Tyrrell, 1973). Alternatively, at lower intakes the slope becomes more similar to the regression for NE_m. This is one reason that systems used for describing energy requirements and feed values for ruminants fed at lower intakes tend to use separate terms for NE_m and NE for production, whilst systems in use for lactating dairy cows use a single combined NE term (Moe and Tyrrell, 1973). This is also justified on the basis that measurements of energy metabolism of lactating cows at lower intakes or fasting are difficult to obtain and considered irrelevant to the lactating cow consuming 3 to 4 times her ME_m (Moe *et al.*, 1972).

Whilst older systems assumed a constant efficiency of DE or ME use for production, virtually all the major energy rationing systems in use today assume a variable efficiency of ME use. This results in the use of different efficiency constants for calculating RE from ME, or the assignment of different NE values for feeds. An alternative approach, used in the Australian energy feeding system for ruminants (Australian Standing Committee on Agriculture, 1990), includes a variable maintenance cost that increases with higher intakes, rather than varying K_g as done in the current UK system. In reality, these systems differ more in terms of application rather than underlying scientific principle, but problems of application are an important consideration in the development of any effective feeding system (Moe and Tyrrell, 1973).

Net Energy for Lactation

In the US system for feeding energy to dairy cows (NRC, 1989), nutrient requirements and feed energy value is expressed in terms of NE_l, which is LE with

corrections for tissue energy loss or gain, energy costs of gestation and energy cost of excess protein intake (Moe *et al.*, 1972). The corrections for tissue energy loss or gain are not simply energy balance (milk plus tissue energy), but include adjustments based on the efficiency of conversion of tissue energy into milk energy obtained using multiple regression (Moe *et al.*, 1971). As the system is based on describing the net energy value of feeds for milk energy production, this correction is also applied to retained tissue energy to reflect the energetic value of body tissue for milk synthesis. This logic applies even if the tissue energy is not converted into milk energy until the rising phase of a subsequent lactation. The adjustments for gestation energy (Moe and Tyrrell, 1972) and the cost of excess protein (Tyrrell *et al.*, 1970) were also based on relationships derived from regression procedures. These adjustments are applied to account for effects of physiological state or biochemical responses to ration imbalances on the energetic value of individual feeds. The calculation of NE_l then is as follows:

$$NE_l \text{ (MJ)} = \text{milk energy} + \text{adjusted TE} + .0301(\text{excess N}) + .1841(\text{foetal tissues})$$

Where:
a. adjusted TE = TE/1.14 if TE > 0 or
            = TE(0.84) if TE < 0
b. foetal tissues = (cow live weight/600)$\exp^{0.0174t}$, where t = days pregnant and the exponential equation is assumed to be for a 600 kg cow and vary linearly with cow live weight
c. excess N (g) = digested N – milk N – foetal N – 0.456(cow live weight$^{0.75}$), where foetal N = .3259(foetal tissues) and cow tissue N requirements are assumed to be 0.456 g/kg live weight$^{0.75}$

As for earlier NE systems, in the absence of measured NE_l values for many feeds, tabular values were obtained from TDN values using regression (Moe *et al.*, 1972). In this regard, corrections are applied to data obtained at lower levels of intake to account for depressions in digestibility or metabolizability (NRC, 1989). Thus in using tables of feed composition, uncorrected ME values should not be directly compared to corrected NE_l values. In this regard, extreme care must be exercised in using tabular values of the digestible nutrient content of feeds obtained using sheep or nonlactating animals to estimate ME or NE content of feeds fed to lactating cows (Moe and Tyrrell, 1975; Tyrrell and Moe, 1975; Sutton *et al.*, 1997).

MEASUREMENT OF ENERGY METABOLISM

There are numerous reviews, detailed descriptions and interpretations published of the techniques used for the measurement of energy metabolism in farm animals and humans (e.g. Blaxter, 1967; Blaxter, 1971; Blaxter, 1989; Flatt, 1969; McLean and Tobin, 1987; McDonald *et al.*, 1995). The series of symposia on Energy Metabolism in Farm Animals (Table 1) is also an excellent source of information on the subject. It is beyond the scope of this chapter to provide a detailed shopping list for the initiation of a program of energy metabolism research using classical methodology. The approaches used are indeed relatively simple, but complex in the number of measurements required, and have changed little since the 'Determination of the Source of Animal Heat' by Despretz and Dulong in 1822 (see McLean and Tobin,

1987). What has changed is the technology available for obtaining these measurements, making measurements of respiratory exchange and heat production more precise and less labour intensive. Indeed, advancements in technology for obtaining and recording measurements and calculation of results enabled the onslaught of energy metabolism studies coinciding with the initiation of the EAAP Energy Metabolism Symposia. Technology for calorimetric measurements of energy metabolism continues to evolve and result in modifications to the particular approaches used, but those undertaking research in this area should not ignore the volumes of archived material describing the work of their predecessors.

Measurement of Heat Energy

Measurements of heat production can be obtained either directly or indirectly using calorimeters. As the name implies, direct calorimeters measure heat (both non-evaporative and evaporative) produced by an animal within them directly, using thermocouples or changes in the amount of heat produced in cooling the chamber. Types of direct calorimeters include isothermal, heat sink, convection and differential, which are all described in the exhaustive book on calorimetry by McLean and Tobin (1987). The calorimeter used by Armsby was a heat-sink calorimeter that was accurate, as well as responsive to acute changes in heat production, but very complex and labour intensive to operate. Although modern gradient layer calorimeters are now highly automated, their complexity makes them expensive. In order to accurately measure the HE produced, the animal is typically contained within a closed chamber under environmental control. This allows the measurement of respiratory exchange, which can also be used to estimate HE indirectly. Comparison of estimates of HE based on respiratory exchange with direct measurements in the Armsby calorimeter were important in establishing the validity of the respiratory exchange approach (McLean and Tobin, 1987). Owing to the historical complexity of direct calorimeters, the majority of measurements of energy metabolism in farm animals in the last 40 years have been obtained using indirect calorimeters. This is especially true for lactating dairy cows.

There have generally been 2 basic approaches used for indirect calorimetry. In the first, HE is estimated from respiratory exchange based on established relationships between oxygen (O_2) consumption and HE, with adjustments for the proportions of fat and carbohydrate oxidised based on CO_2 production (respiratory quotient), and for amino acid oxidation based on urinary nitrogen excretion. In addition, the incomplete oxidation of nutrients lost as methane is accounted for in ruminants. These calculations were condensed into a single equation using simultaneous equations and effectively standardised by a sub-committee established by the EAAP Energy Symposium and chaired by E. Brouwer. In 1957 Brouwer published a revision of a similar formula developed by Zuntz in 1897 and revised by Forbes and others in the intervening years (Brouwer, 1957). A modification for methane losses was added (Brouwer, 1958) and the equation adopted by the sub-committee in 1965 (Brouwer, 1965) has been universally accepted and used without question by many:

$$HE \ (MJ) = 16.18(O_2) + 5.16(CO_2) - 5.90(UN) - 2.42(CH_4)$$

In the equation, gasses are expressed in litres and UN, representing urinary nitrogen excretion, is expressed in g. The measurement of respiratory exchange is usually

obtained whilst animals are housed in a chamber, and 2 approaches can be used. In the closed circuit respiration chamber, an airtight system is maintained with chamber air circulated through scrubbers for removing CO_2 and H_2O, with O_2 introduced into the system. In this system, O_2 use is based on the required input, whilst CO_2 production is obtained from the change in weight of absorbent. These systems are not convenient for measurements of methane production or for use with large animals, thus most measurements of respiratory exchange for large animals are obtained using open circuit respiration chambers. In open circuit systems respiratory exchange is based on the difference in the concentration of gasses entering the chamber in outside air and leaving in chamber exhaust, which is then multiplied by flow rate through the chambers after correction for temperature, humidity and pressure. Chambers are operated under negative pressure, thus do not have to be absolutely air tight, although changes in the gas concentration of air in the room housing the chamber are a concern for a leaky chamber. Modern infrared analysis of CO_2 and CH_4 and paramagnetic analysis of O_2 has greatly reduced the labour required for measuring gas concentrations, and the 'flow-through' open circuit respiration chamber is used widely for measurements of energy metabolism in farm animals. Respiratory exchange can also be measured using head chambers, face masks, tracheal cannulas or mouthpieces (McLean and Tobin, 1987). Brody (1945) used facemasks extensively for measurements of respiratory exchange in farm animals.

Measurement of Recovered Energy

The second indirect approach is to estimate RE energy based on measurements of total carbon and nitrogen balance (Blaxter, 1967). This approach is based on the assumption that energy is stored in the body as fat or protein, with minimal change in body carbohydrate (glycogen) stores in the long term. Protein deposition is estimated from body nitrogen retention, whilst fat storage is estimated from body carbon retention after correction for carbon storage as protein. The amount of energy retained as fat and protein is then estimated using factors derived primarily from muscle analysis, although other approaches have been used (Flatt, 1969). As for estimates of HE by respiratory exchange, formulae for calculating energy balance from measurements of carbon and nitrogen balance were recommended by the Energy Symposium subcommittee on constants chaired by Brouwer (1965). This approach requires the measurement of CO_2 and CH_4 production, but not O_2 consumption, and separates energy retention into fat and protein components. The approach was used widely in the past, but as carbon analysis is required on all inputs and outputs for the animal, adds to the analytical burden of estimating energy balance. Difficulties and cost of carbon analysis compared to measurement of gross energy content using a bomb calorimeter have made the estimation of heat production the preferred indirect approach in recent years.

Another indirect approach used widely in recent years, especially in humans, is to use isotope dilution procedures to estimate respiratory exchange. One approach is to estimate body CO_2 production using dilution of labelled CO_2 in blood. In the other approach, known as the 'Doubly Labelled Water' technique, the turnover of H_2 and O_2 is estimated by following the concentration of $^2H_2$ and ^{18}O in urine after an injection of $^2H_2{}^{18}O$. The difference in their rate of turnover is proportional to the rate of CO_2 production, as H_2 is eliminated as H_2O, whilst O_2 is eliminated as both H_2O and CO_2. The merits and limitations of these approaches have been widely discussed

in the literature (McLean and Tobin, 1987). The major advantage of dilution approaches is that subjects do not have to be confined to a stationary or portable respiration apparatus, thus effects of normal activity on energy metabolism can be included. They also require fewer measurements, but are inherently less accurate than direct measurements of respiratory exchange.

Comparative Slaughter Balance

Another approach for estimating energy retention, which has been applied primarily to growing animals, is to compare the total energy content of groups of animals before and after a sufficient experimental period. The composition of the initial slaughter group is then assumed to be equal to the composition of animals slaughtered at the end of the experiment, and energy retention is calculated as the difference in total body energy content (Flatt, 1969; Blaxter, 1989). As the name implies, this requires slaughter and analysis of the energy content of a representative sample of the total carcass, thus within animal comparisons are impossible and larger numbers of animals are required to account for animal variation. The approach is very precise for smaller animals where the entire carcass can be processed, but carcass processing can be difficult in larger ruminants. Companion digestion trials are also conducted to determine DE and UE, but for ruminants, methane losses (and thus ME) are often estimated from DE and not measured directly.

The difficulty of conducting slaughter balance studies in larger animals, the terminal nature of the approach, and the inability to apply the technique in humans, has lead to the development of a plethora of indirect methods for estimating body composition which do not require the slaughter of experimental subjects. The basis of many of these approaches is that there is an inverse relationship between body fat and water and that within species the proportions of water, protein and ash in the fat-free empty body can be predicted based on the results of large scale slaughter trials (Reid, 1968). Thus if body water or fat content can be estimated, the proportions of the other components can be predicted. The energy content of the body can then be estimated as for the carbon and nitrogen balance technique. A major stumbling block for these approaches is the contributions of gut fill and water to empty body weight, which can be extremely large in ruminants. This makes estimation of empty body weight difficult, but also compromises the use of dilution techniques to estimate body water content (Flatt, 1969). Approaches used to estimate body water content generally involve measurement of the dilution of injected substances that are rapidly and uniformly distributed in body water, wherein lies the problem with gut water contents for ruminants. A variety of compounds have been used, but of those listed by Flatt (1969), deuterium and urea have seen the most attention from animal scientists in recent years (e.g. Andrew *et al.*, 1995). Attempts have been made to address the problem of gut water content by using multiple pool models to relate the dilution of the marker to measured body water in validation studies. However, the resulting equations have not proved accurate in practice (Crooker *et al.*, 1998) and there has not been widespread adoption of these approaches. Although measurements of the body composition of dairy cows at various stages of lactation are needed, and are extremely costly to obtain directly, the flux of water through the gut and mammary gland of a high yielding cow makes the application of these approaches especially difficult. As already mentioned for estimates of CO_2 production, dilution procedures for estimating body composition are inherently less accurate and precise than direct approaches.

Another approach for estimation of carcass water content is the estimation of specific gravity by underwater weighing procedures (Flatt, 1969). Specific gravity can then be used to estimate body water content, which is then used to predict fat, protein and ash content and thus their energy value. This approached was used extensively in the development of the California Net Energy System for rationing beef cattle (Lofgreen and Garret, 1968; NRC, 1996). A major advantage of the approach used is that the system was based on measurements from animals fed under normal industry conditions, rather than the artificial and restrained environment of a respiration chamber.

Other approaches have involved the prediction of body fat from absorption of marker compounds or the prediction of body protein content from estimated body K content. The list of procedures used is long, but there are a number of procedures currently in use for the estimation of body composition based on recently developed technologies, such as nuclear magnetic resonance, CAT scans, ultrasound scanning or more recently dual energy x-ray absorption (Geers *et al.*, 1998). The cost of many of these procedures, the need for subjects to remain perfectly still and the design of the systems for use in humans makes the application of these technologies to larger, less co-operative farm animals difficult. But they have been used to predict the composition of smaller (often anaesthetised) animals or their carcasses. In addition, ultrasound scanning is used widely in animal agriculture and now used to estimate changes in body fat content based on measurements of subcutaneous fat depth, as an adjunct to visual condition scoring approaches.

COMPARISON OF APPROACHES

Comparisons of results from simultaneous measurements of HE and RE obtained using 'balance trials' (direct or indirect calorimetric measurements of HE or RE from carbon and nitrogen balance) were extensive in the early part of this century. At the time, many calorimeters were constructed for the simultaneous use of more than one of these techniques. On the whole, these approaches yielded very similar results when the techniques were rigorously applied and experimental errors were minimised (Blaxter, 1967). Indeed, differences between measured and calculated energy balance from 129 measurements in the Armsby calorimeter resemble a bell shaped curve (Blaxter, 1967). Blaxter concluded that 'there is no reason to suppose' there was any significant inaccuracy or bias in the balance trial approach to measuring energy metabolism. At the time, there were few comparisons of results from energy balance measurements with those obtained using comparative slaughter trials. Comparisons made in chickens have shown good agreement between the 2 approaches (Blaxter, 1967; McDonald *et al.*, 1995). In contrast, direct comparisons of the effects of specific feeds on energy metabolism in ruminants have found that measurements obtained using respiration calorimetry have yielded consistently higher estimates of energy retention and K_g than those obtained using slaughter balance (e.g. Waldo *et al.*, 1990; Webster, 1989). This is similar to the bias observed for measurements of nitrogen retention obtained using short term balance trials, which are frequently higher than direct measures of nitrogen retention by 20% or more (Johnson, 1986). Indeed, for this reason some workers use a correction factor to account for this bias in short term measurements of nitrogen balance. There are a number of reasons for these discrepancies. First, errors of measurement in digestion trials are cumulative

and thus all errors are included in the variable calculated by difference, which is tissue energy or protein retention (Johnson, 1986). Therefore, if any feed, faeces or urine is unaccounted for, the loss is assumed to be included in body tissue. Urine is acidified to prevent ammonia volatilisation, but some losses from urine or faeces are unavoidable. Frequent scraping and attention to faecal collections will greatly reduce this error. In the Beltsville respiration chambers the residual faeces accumulating on collection equipment is accounted for by measuring the energy and nitrogen content of an initial wash (a wet scraping) of the chamber and faecal collection equipment. In addition, hair, scurf and spilled feed are collected from the floor of the chamber and analysed. Other losses can occur after sampling, and great care must be taken to avoid losses of volatile ammonia and energy during sample storage, processing and analysis.

In addition to the accumulation of errors of measurement in balance trials, another consideration when comparing them to comparative slaughter trials is the fact that the animals are restrained in respiration chambers or digestion stalls, thus they have limited activity other than standing and changing position. In addition, the environment of the chamber is controlled. Therefore the energy lost in activity and to a lesser extent temperature regulation is reduced. This is one reason energy retention tends to be lower in slaughter balance trials conducted under practical conditions. In addition, there may be interactions between intake level and activity which differ for the 2 techniques (Webster, 1989).

ADDITIONAL CONSIDERATIONS

Potential sources of error in measurements of energy metabolism are well documented (e.g. Blaxter, 1967 and 1971; Johnson, 1986; McLean and Tobin, 1987). The original publication of what has come to be known as the Brouwer equation contained a number of disclaimers (Brouwer, 1957 and 1958), which should not be ignored by the users. First, the statement that measurements were obtained 'in a not too short experimental period' preceded each list of equations. The primary concern was that short-term changes in body temperature or blood and tissue CO_2 concentrations would compromise the validity of the equation. In most cases the measurements obtained represent daily rates of exchange, typically averaged over a number of days. Certainly this is 'not too short an experimental period'. Adjustments were also included for H_2 production and hippuric acid excretion in urine, but they are seldom used. In addition, the disclaimer specifies that under physiological states leading to incomplete combustion (specifically ketosis), or when specific nutrients such as sucrose or ethanol are oxidised, the equation should be revised (McLean and Toby, 1987). An additional provision was that the equation should not be used if RQ was outside the range of 0.707 and 1.00 (NRC, 1935). Another consideration is that the equation was developed using urinary nitrogen excretion as an indicator of the amount of protein oxidised, whilst in ruminants fed excessive amounts of rumen degradable protein a large portion of urinary nitrogen is derived directly from ammonia absorbed into the portal vein. However, errors of urinary nitrogen excretion have a relatively minor effect on HE compared to errors in airflow and O_2 concentration measurement (Johnson, 1986). In spite of these concerns, the use of alternative equations, derived using other approaches or reference compounds, do not have a dramatic effect on calculated HE (Blaxter, 1967).

Another potential source of error in digestion trials is the use of bladder catheters to collect urine in females. In males, a soft collection funnel suspended from the belly and evacuated by a vacuum is an excellent approach (Varga *et al.*, 1990) and preferred over the use of a metabolism crate. No matter how carefully and aseptically they are established, bladder catheters are a potential source of irritation to the urinary tract which can in many animals increase the volume of urine produced and nitrogen excreted, in addition to the general effects of distress and immune response. The use of urine collection devices attached to the genital region (e.g. Fellner *et al.*, 1988), in combination with plastic chutes for distribution of faeces into collection vessels (see Morrison, 1954), can with experience provide an excellent separation and collection of urine and faeces in females (Sutton *et al.*, 1997). While not completely irritation free for the animal, the system is much preferred to the use of bladder catheters, which in the author's opinion should be avoided vigorously. Although acetone can be used for loosening the cement and removing the collection device without hair loss, the major draw back of this approach is that it should not be used at intervals too frequent to allow adequate hair growth for attaching the device to the genital area.

Other considerations for the use of respiration calorimetry include the adaptation of animals to facilities prior to experimentation, the separation of respiratory exchange and digestion trials, and environmental control. Adaptation of animals to calorimeters is critical to avoid depressions in intake, milk yield and nervous behaviour, all of which can dramatically alter energy metabolism. Nervous behaviour may be obvious in animals that do not settle and are constantly bawling or refuse to lay down, or may be less apparent in some individuals. Regardless, heat energy can be elevated in animals that are not adapted. Having more than one chamber and windows allowing animals in adjacent chambers to see each other can reduce the stress of confinement for many animals. The subject of adaptation and stress of confinement has been the subject of much discussion at the EAAP Energy Symposia (Table 1).

Depending on the construction of respiration chambers, it may not be possible to obtain measurements of respiratory exchange, digestion and urine output simultaneously. If these measurements are obtained separately, then care should be taken to insure that conditions under which the measurements are obtained are as similar as possible. Ideally the animals will be housed under environmental conditions which are similar to those of the chambers. Alternatively, to avoid dramatic changes the temperature of the chambers may be adjusted to that of the housing in which experimental subjects are maintained when they are not in the chambers. Environmental control can be a particular problem in ruminants, and particularly lactating dairy cows that loose large amounts of water through respiration.

Variations in intake can have immediate effects on respiratory exchange, thus if intake is reduced when animals enter the respiration chambers then measurements of heat production will not be quantitatively comparable to measurements of feed digestion and urine nitrogen output. This has serious consequences for the calculation of HE and energy balance. For this reason intakes may be set below ad libitum for a period of time prior to measurements, but this will change the physiological state of the animal. This is especially a problem in the conduct of energy metabolism studies with lactating dairy cows, where restriction of intake below ad libitum can influence the remainder of the lactation curve and the response to dietary perturbations (Blaxter,

1956). Ideally, measurements of DE and HE should be obtained simultaneously to avoid disparities in intake and other conditions during the measurements.

TISSUE 'CALORIMETRY'

The combination of multiple techniques for measuring nutrient metabolism was suggested as an approach which would provide important insights into the mechanisms underlying production responses to variation in diet composition, intake and physiological state in ruminants (Annison, 1964). This view has been echoed repeatedly (Moe, 1981; Webster, 1989). The combination of measurements of HE and RE using calorimetry with measurements of the metabolism of specific nutrients (e.g. using isotopic labelling) or specific tissues has provided important insights into the processes underlying energetic responses to nutrition or changes in physiological state. Measurements of the contribution of individual tissues to body O_2 consumption can be obtained in vivo by the use of multicatheterization procedures (Huntington *et al.*, 1989). Surgical placement of chronic, indwelling catheters enable the measurement of blood flow and venous-arterial concentration difference for O_2, CO_2 and other nutrients and metabolites across specific tissues. The net removal of O_2 from blood or CO_2 release into blood can then be calculated. Combination of these measurements with measurements of body respiratory exchange have shown that the tissues drained by the hepatic portal vein, the portal-drained viscera (PDV), and liver each account for roughly 20 to 25% of body O_2 consumption, whilst accounting for less than 13 % of body mass (Reynolds, 1994). Although the prediction of body HE from O_2 consumption is based on measurements for the whole body (McLean, 1972), the relationship has been used to estimate HE by body tissues. Alternatively, thermocouples have been used to measure transfer of heat into the portal vein directly, accounting for the contribution of H_fE, these measurements agreed reasonably well with measurements of PDV HE based on O_2 consumption (Webster *et al.*, 1975). The high rate of O_2 consumption by these tissues highlights their importance to the maintenance requirement and energy balance of the animal, as well as the energetic response to changes in diet composition and intake (Reynolds *et al.*, 1991). Interpretation of CO_2 production rates by these tissues is compromised by the fact that metabolic processes in the liver use CO_2, whilst CO_2 absorbed into the portal vein can be a product of fermentation or arise from salivary bicarbonate. In addition, CO_2 can also be transferred from blood to the lumen of the gut, and *vice versa* (Hoernicke *et al.*, 1958). For these reasons measurements of CO2 production by the PDV and liver vary considerably and CO2 removal is sometimes measured when very rapid sampling is employed. Thus measurements of tissue RQ, especially for the PDV, must be interpreted with extreme caution.

FUTURE DIRECTIONS

It has been suggested that measurements of fasting metabolism and km are irrelevant to the energy metabolism of animals at production intakes and their importance in estimating maintenance requirements over emphasised (Webster, *et al.*, 1974; Webster, 1989). Similarly, it has been suggested that there has been too much emphasis on obtaining measurements of ME_m and K_g in growing animals, as these terms have no absolute meaning, but are simply components of the linear regression of recovered energy on ME (Webster, 1989; Table 1). In comparing effects of diet or physiological state on energy metabolism, if at equal ME one treatment results in a

higher HE than another, then the increase in HE may the result of a higher maintenance requirement, a reduced efficiency of ME use for production of recovered energy, or both. In many cases, the reduction in efficiency may be due to an increase in the mass of metabolically active tissues such as the gut or liver. Does this increase represent a maintenance cost, or a production cost? For measurements of whole body HE, the design of the trial and the mathematical description of the results have in the past determined the answer. Approaches other than linear regression have been used to resolve energy balance measurements in the past, and in the future more emphasis on the use of alternative models and more enlightened approaches are needed (Moe, 1981).

There are many, and many of them with considerable experience in the field of energy metabolism, who believe measurements of energy metabolism using classical approaches are nearing (or well past) the end of their useful life. Certainly a limitation, but also a strength, of current feeding systems based on measurements of energy metabolism is that DE or ME is not a nutrient per se, but the sum of a number of processes resulting in the assimilation of specific energy yielding nutrients. For the past 30 years those involved in the development of the feeding systems in use today have recognised the need for feeding systems based on a clearer understanding of the role of specific absorbed nutrients and their metabolism in determining productive responses of farm animals (Moe, 1981; Webster, 1989). Forty years ago animal nutritionists were criticising the day's feeding standards, and worked hard to improve them. Today the current energy feeding standards, which were built on the back of 200 years of energy metabolism research, are being challenged and criticised, largely for their inability to predict productive responses. For dairy cattle, a major concern is the ability to predict the partition of ME use between milk and body tissue. Newer systems based on models of digestion are now in use and being refined, but they are being used to predict ME, not specific energy yielding substrates (Sniffen *et al.*, 1993). In practice, the ability to predict the absorption of specific nutrients and their metabolism may be limited by the ability to obtain adequate measurements of the food characteristics needed to 'feed' predictive models. More mechanistic models of nutrient absorption and metabolism are also in use, but need more refinement to achieve practical application (e.g. Chapter 14). Any new feeding system must be flexible and adaptable to the circumstances confronting the user. Today's nutritionist has access to a variety of rationing systems, and may use different systems depending on the application. In addition, many develop their own 'customised' feeding system using components of individual systems with modifications based on experience. Depending on the end user, new rationing systems should allow that flexibility, but in today's research environment copyright restrictions may limit this versatility.

FINALLY

In calling the Conference on Energy Metabolism (NRC, 1935), P. E. Howe, the chairman of the Committee on Animal Nutrition, presented the following statement of the problem, which is reproduced verbatim:

Studies of energy, energy metabolism, and efficiency of feed utilization have a relationship to agriculture in establishing:
a) Fundamental concepts of the energy requirements of animal of different ages, sexes, and conditions of production, including work

b) Fundamentals of the utilization of feed, the nutritive elements in feed and the interrelation of the various feed stuffs.
c) The characteristics of animals.

The last 65 years has seen considerable progress in addressing these issues, and improvements in feeding standards. However, future rationing systems will benefit from a greater insight into the effects of nutrition on the utilization of specific energy yielding nutrients within the body. Perhaps more importantly, the ability to predict responses and the partition of absorbed nutrients will only be achieved by an enlightened representation of the characteristics of animals which determine their productive response to feeds, and applicable measurements of the components of feed that determine those responses.

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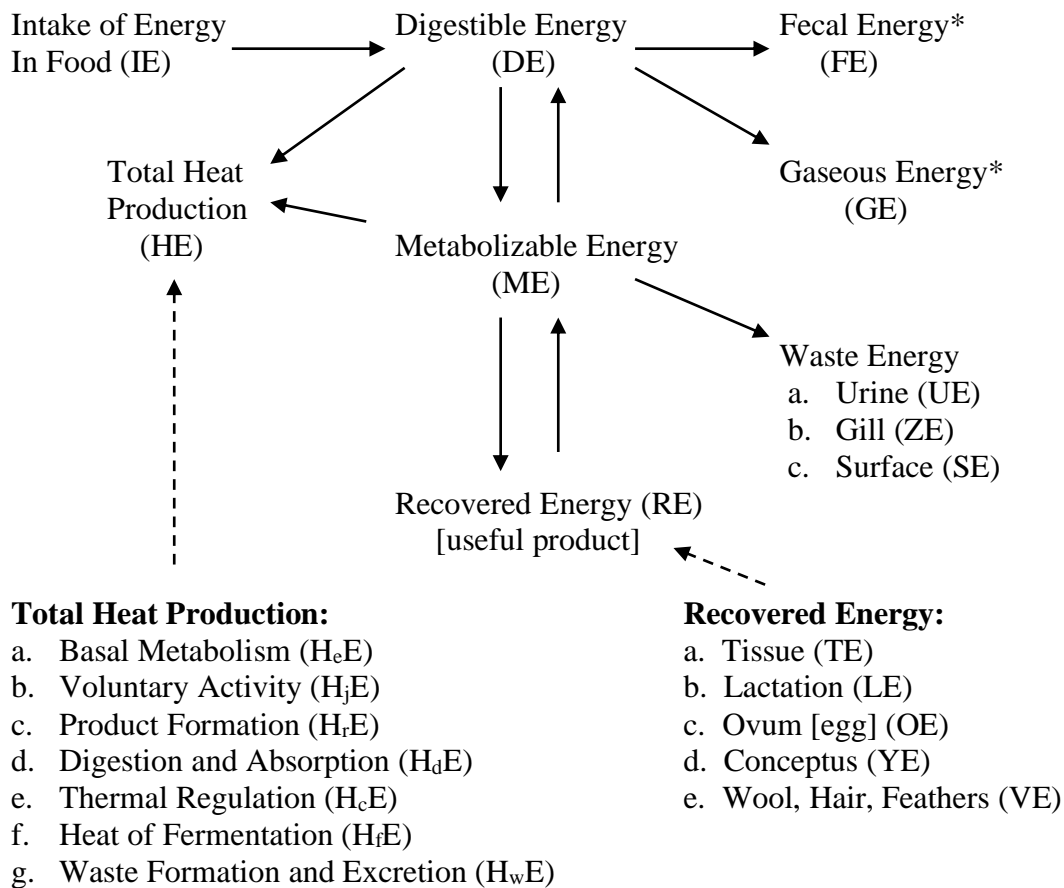
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Table 1. Symposia on energy metabolism of farm animals sponsored by the European Association of Animal Production (Moe, 1981). For a brief history see Van Es, 1994.

No	Year	Site	Reference
*	1935	USA	Report of the conference on energy metabolism held at State College, Pennsylvania (1935) NRC, Washington, DC
1	1958	Denmark	Symposium on Energy Metabolism. Principles, Methods, and General Aspects (1958) Thorbek, G. and Aersoe, H. (eds) EAAP Publ. No. 8. Statens Husdyrugsudvalg, Copenhagen.
2	1961	Netherlands	Symposium on Energy Metabolism. Mehods and Results of Experiments with Animals (1961) Brouwer, E. and van Es, A. J.H. (eds) EAAP Publ. No. 10.
3	1964	Scotland	Energy Metabolism (1965) Blaxter, K.L. (ed) EAAP Publ. No. 11. Academic Press, London.
4	1967	Poland	Energy Metabolism of Farm Animals (1969) Blaxter, K.L., Kielanowski, J. and Thorbek, G. (eds) EAAP Publ. No. 12. Oriel Press, Newcastle upon Tyne.
5	1970	Switzerland	Energy Metabolism (1970) Schurch, A. and Wenk, C. (eds) EAAP Publ. No. 13. Juris Verlag, Zurich.
6	1973	West Germany	Energy Metabolism of Farm Animals (1974) Menke, K.H., Lantzsch, H.J. and Reichl, J.R. (eds) EAAP Publ. No.14, Universitat Hohenheim Dokumentationsstelle, B.D.R.
7	1976	France	Energy Metabolism of Farm Animals (1976) Vermorel, M. (ed) EAAP Publ. No. 19. G. de Bussac, Clermont-Ferrand, France.
8	1979	England	Energy Metabolism (1979) Mount, L.E. (ed) EAAP Publ. No. 26. Butterworths, London.
9	1982	Norway	Energy Metabolism of Farm Animals (1982) Ekern, A. and Sundstol, R. (eds) EAAP Publ. No. 29. Agricultural University of Norway.
10	1985	USA	Energy Metabolism of Farm Animals (1986) Moe, P.W., Tyrrell, H.F. and Reynolds, P.J. (eds) EAAP Publication No. 32, Rowman and Littlefield, New Jersey.
11	1988	Netherlands	Energy Metabolism of Farm Animals (1989) Close, W.H. and van der Honing, Y. (ed) EAAP Publication No. 43. Pudoc Wageningen, Netherlands.
12	1991	Switzerland	Energy Metabolism of Farm Animals (1991) Wenk, C. and Boessinger, M. (eds) EAAP Publication No. 58. ETH-Zentrum, Zurich.
13	1994	Spain	Energy Metabolism of Farm Animals (1994) Aguilera, J.F. (ed) EAAP Publication No. 76. CSIC, Madrid.
14	1997	Northern Ireland	Energy Metabolism of Farm Animals (1998) McCracken, K.J. Unsworth, E.F. and Wylie, A.R.G. (eds) CABI, Wallingford.

*Early conference sponsored by the National Research Council, Committee on Animal Nutrition, USA.

Figure 1. Energy flow in animals and suggested terms (NRC, 1981)

Intake of Energy In Food (IE) → Digestible Energy (DE) → Fecal Energy* (FE)

Digestible Energy (DE) → Gaseous Energy* (GE)

Total Heat Production (HE)

Metabolizable Energy (ME)

Waste Energy
  a. Urine (UE)
  b. Gill (ZE)
  c. Surface (SE)

Recovered Energy (RE) [useful product]

Total Heat Production:
a. Basal Metabolism (H_eE)
b. Voluntary Activity (H_jE)
c. Product Formation (H_rE)
d. Digestion and Absorption (H_dE)
e. Thermal Regulation (H_cE)
f. Heat of Fermentation (H_fE)
g. Waste Formation and Excretion (H_wE)

Recovered Energy:
a. Tissue (TE)
b. Lactation (LE)
c. Ovum [egg] (OE)
d. Conceptus (YE)
e. Wool, Hair, Feathers (VE)

*May be considered useful.