13 ENERGY METABOLISM

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INTRODUCTION

In the living animal energy is required to perform the "work" of living. A mature fasting sheep weighing 70 kg loses about 1,600 Kcal of heat daily. Body tissues must be metabolized to produce this heat. About 1.2 kg of a moderate quality feed is required daily to maintain body weight and composition of this animal, that is, to offset the body tissue loss. This amount of feed contains about 5,300 Kcal of gross energy (heat of combustion). Of the gross energy consumed, about 2,400 Kcal are lost as feces, 600 Kcal are lost as urine and combustible gases and 2,300 Kcal are lost as heat. Of course, in domestic species it is hoped that animals do more than simply maintain themselves. Thus, animals require feed not only for maintenance but also to support the work of production, e.g., growth fattening, gestation, and lactation. For example, in a beef production cycle feed is required for maintenance of the cow, gestation, lactation and maintenance, growth and fattening of the calf. Of the total gross energy required in this system, about 45% is lost as heat, 40% is lost as feces, 10% is lost as urine and combustible gases and only 5% is retained in the calf to be slaughtered. Of the 5% retained, less than half is edible.

These examples have been presented to emphasize three important points. First, to supply energy to an animal is more costly both biologically and economically than supplying any other nutrient. Second, the primary factors that determine the efficiency of utilization of feed energy are the amounts lost as feces and as heat. Finally, the efficiency of converting feed energy to products for human consumption by ruminants is very low.

Three classic books are available that relate specifically to energy metabolism of animals (1, 2, 3). These books provide a historical perspective as well as an excellent foundation to the field of energy metabolism. Proceedings of the triennial symposium on energy metabolism (beginning in 1958) sponsored by the European Association of Animal Production are available and chronicle the research that has occurred over the last several years. In addition a recent publication of the Agricultural Research Council (4) provides an excellent technical review of many facets of energy utilization and requirements of ruminant livestock.

DEFINITIONS AND ABBREVIATIONS

Energy is defined as the potential to perform work. Energy is an abstraction that can be measured only in reference to defined, standard conditions. Thus, all defined units to measure energy are equally absolute. The joule is the preferred unit for expressing electrical, mechanical and chemical energy. The joule can be converted to ergs, watt-seconds and calories; the converse is also true. The calorie is related to the joule by the expression: 1 calorie = 4.184 joules, and is defined as the heat required to raise the temperature of one gram of water from 16.5° to 17.5°C.

Many of the energy requirements of animals are expressed in terms of energy requirements per unit time. The energy requirements for maintenance of a steer might be expressed as 12 Mcal/d, 50 MJ/d or 580 watts. The joule is used as the standard unit of energy for nutritional work in many countries, however, the calorie is presently used as the standard unit in the USA, thus, will be used throughout this chapter. In practice the calorie is so small that nutritionists work with multiple units. For this reason the kilocalorie (1 Kcal = 1,000 calories) and megacalorie (1 Mcal = 1,000 Kcal) will be used.

A number of abbreviations have been used to describe energy fractions in the animal system. The abbreviations used throughout this chapter are those recommended by the NRC (5). The first measurement in a nutritional evaluation of energy exchange is gross energy. Gross energy (E) or heat of combustion is the energy released as heat when an organic substance is completely oxidized to carbon dioxide and water.

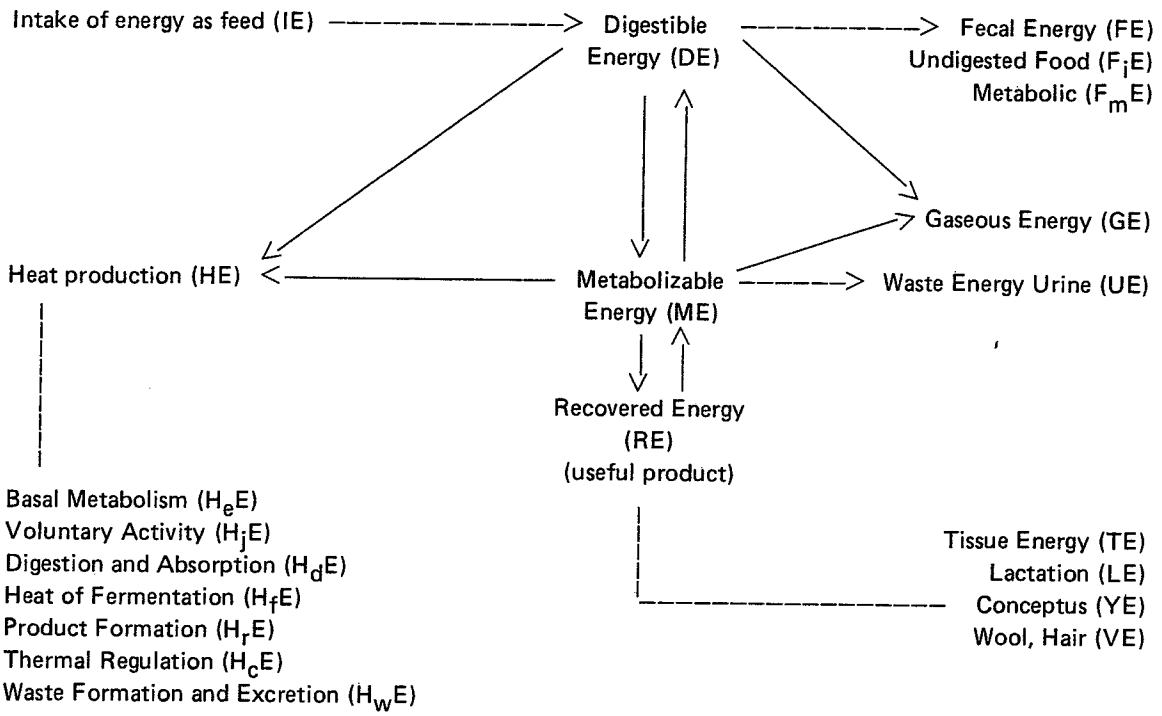

Figure 13-1. Flow of energy through the animal. From NRC (5).

The flow of energy, as outlined by NRC (5), is shown in Fig. 13-1. Definitions and abbreviations of terms used have been described in detail in that publication. Briefly, intake of food energy (IE) is the gross energy of the food consumed. A substantial portion of IE is lost from the animal as fecal energy (FE) and the difference (IE–FE) is termed apparently digested energy (DE). Portions of IE are also lost as urinary energy (UE) and gaseous energy (GE). The remainder (IE–FE–UE–GE) is termed metabolizable energy (ME). ME may be recovered as a useful product (RE) such as tissue energy (TE), milk energy (LE), conceptus energy (YE) or wool or hair (VE) or may be lost as heat. Energy lost as heat (HE) may be the results of a variety of functions including basal metabolism (H_eE), activity (H_jE), digestion and absorption (H_dE), fermentation (H_fE), product formation (H_rE), thermal regulation (H_cE) and waste formation and excretion (H_wE). An increase in heat production following consumption of food is termed heat increment (H_iE) and includes H_dE, H_fE, H_rE and H_wE.

PARTITION OF ENERGY

The laws of thermodynamics and the law of Hess state the fundamental principles on which bioenergetics (the study of energy transformations in biological systems) is based. Simply stated, these laws assert that (a) energy can be neither created nor destroyed but may be converted from one form to another, (b) all forms of energy can be quantitatively converted to heat, and (c) heat generated in a net transformation is independent of the path of conversion.

The basis of bioenergetics as defined by these laws and application to animal nutritional energetics may be stated by use of terminology defined earlier: IE = FE + GE + UE + HE + RE. This identity partitions the food energy consumed by an animal into the major components associated with animal energetics. It can be expanded to include a few or many of the intermediate steps involved and each component can be divided into component parts. For example, in a young, lactating, pregnant heifer, RE may be replaced by

TE + LE + YE. The expression will remain compatible with the laws described above, that is, the inclusion or exclusion of more detailed information on intermediate transformations does not prejudice the balance of the equation. All energy balance techniques and all systems used to describe the relationship between the animal's requirement for energy and the usefulness of a food to supply those needs are related to this classical energy balance identity.

Gross energy intake (IE) or the total energy contained in a feedstuff provides little useful information in assessing the value of a particular diet or dietary component as a source of energy for an animal. Gross energy expressed per unit weight may give some index of the potential of a substance to furnish energy. For example, carbohydrates have an E of about 4.2 Kcal/g, thus a feedstuff consisting primarily of carbohydrates might have a similar E, whereas one containing a large amount of protein or fat might have a higher E and one containing a large amount of inorganic substances might have a lower E. Regardless of this, a gross energy value does not provide any information as to how available the energy is to the animal.

DE has some value for the assessment of an animal's requirements and for feed evaluation because the energy lost as feces (FE) is associated with the ability of a diet to meet an animal's need for energy. The major weakness of DE as a basis for a feeding system of ruminants is that it overestimates the value of high-fiber diets in relation to low-fiber diets. This weakness is of less importance in nonruminant diets because the range in DE or fiber contents of the diets is much less.

ME is of greater value than DE for the assessment of energy values and requirements because it considers gaseous and urinary energy losses. Thus, ME is an estimate of dietary energy available to the animal. However, ME has many of the same weaknesses as DE. Energy lost as UE and GE are highly predictable from DE, thus DE and ME are highly correlated. For most forages and mixtures of forages and cereal grains, the ratio of ME to DE is about 0.82. The definition of ME and the energy balance identity indicate ME can appear only as HE or RE. Thus, ME = HE + RE. As indicated by this relationship, a major value of ME is as a reference unit and as a starting point for most systems based on the net energy (NE) concept.

The NE of a feed or diet has classically been illustrated by the equality: $NE = \Delta RE \div \Delta IE$. The value of food energy for the promotion of energy retention is measured by determining the RE at two amounts of IE. Determination of NE by this method assumes the relationship between retained energy and food intake is linear. Actually the relationship is curvilinear. This curvilinear relationship is conventionally approximated by two straight lines (Fig. 13-2). The intersection of the two lines is the point at which RE = 0 and is defined as maintenance (M). The relationship between food intake and body tissue loss (negative RE) comprises one portion of the curve and the relationship between food intake and body tissue gain (positive RE) comprises a second portion of the curve. The heat production at zero food intake (H_eE) is equivalent to the animal's NE requirement for maintenance. The ability of the food consumed to meet the NE requirement for maintenance is expressed as NE_m and is represented by the following expression: $NE_m = H_eE/I_m$, where I_m is the amount of food consumed at RE = 0. Similarly, the ability of food consumed to promote energy retention is represented by the expression NE_r and is determined as: $NE_r = RE/I - I_m$, where $I - I_m$ represents the amount of food consumed above maintenance.

The relationship ME = RE + HE can be rewritten in terms of NE. Thus,

$$ME = RE + H_eE + H_jE + H_iE$$

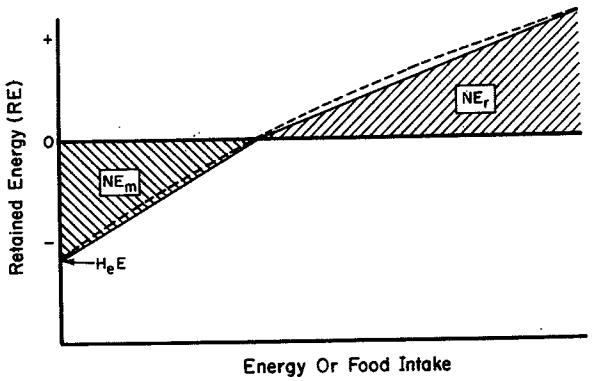

Figure 13-2. The relationship of retained energy to food intake. Adapted from NRC (5).

or, because in practical situations, the heat of activity associated with obtaining food (H_jE) is often included with H_eE, the expression becomes $ME = NE_r + NE_m + H_iE$. The NE_r used in this expression does not distinguish among the different forms in which energy may be retained, e.g., body tissue, milk or tissues of the conceptus. It is not possible to assign a single NE_r value to a food for all productive functions because ME may be used with different efficiencies. Thus, the former expression might be expanded such that in a pregnant, lactating heifer it becomes the following:

$$RE = LE + YE + TE$$

or

$$NE_r = NE_l + NE_y + NE_g,$$

thus,

$$ME = NE_g + NE_l + NE_y + NE_m + H_iE.$$

A portion of the heat increment (H_iE) is associated with the food consumed for maintenance and each of the productive functions. For a NE system to have practical application, multiple NE values must be assigned to each feed. Alternatively, ME values may be adjusted for maintenance and the various productive functions or the animal's energy requirements may be expressed in terms of a single NE value.

It is possible to convert ME values to NE values if the efficiency of ME use (k) for a particular function is known. The efficiency of use of ME for maintenance can be expressed as:

$$k_m = H_eE/ME_m \text{ or } k_m = NE_m/ME_m.$$

Likewise, the efficiency of ME use for tissue energy retention may be expressed as:

$$k_g = TE/ME - ME_m$$

or

$$k_g = NE_g/ME - ME_m.$$

Efficiencies of ME use for other productive functions may be expressed similarly. It is important to note that efficiencies of use of ME vary depending on the source of ME and on function for which it is to be used.

TECHNIQUES FOR THE STUDY OF ENERGY METABOLISM

Balance Studies

Many of the techniques currently used to study energy metabolism have been reviewed recently (6). As indicated previously, a major proportion of IE of an animal is lost as feces. The amount of FE is primarily a function of the physical and chemical characteristics of the food consumed and to a lesser extent the level of intake. As a result the digestion trial has often been used on the basis of many studies (see Ch. 9). From the data obtained the DE content of the diet can be determined. These are very laborious procedures to follow, thus many alternative procedures have been evaluated. These include the use of markers such as chromic oxide, polyethylene glycol or the rare earths, in vitro fermentation, or laboratory analysis of the chemical characteristics of the feedstuff. To date, none of the indirect methods approach the accuracy of the direct approach, but in many situations are useful because the direct approach is impossible or impractical.

In many circumstances energy lost as urine (UE) is determined in conjunction with the determination of FE. This measurement involves the quantitative collection of urine during the collection period and the subsequent determination of its gross energy content by bomb calorimetry. An assessment of the gaseous energy loss (GE) in conjunction with these measurements allows the assessment of the ME content of the diet. The measurement of GE is usually determined by respiratory exchange in a respiration calorimeter.

In addition to the above measurements, some researchers have, by determining the C and N contents of the feed, feces, urine and respired gases, obtained estimates of C and N balance of the animal. From those estimates RE may be calculated. Alternatively, calorimetry may be used to estimate heat loss as described below.

Calorimetry

Techniques of calorimetry have been discussed in detail by Blaxter (3), and in the proceedings of the 4th symposium on energy

metabolism (7), thus only a brief description of the procedures involved will be included in this chapter. An animal loses heat to the environment as sensible heat or as evaporative heat. Sensible heat is lost through convection, conduction and radiation, and evaporative heat is lost through the excreta, or via the skin and respiratory tract. Heat loss can be measured directly (direct calorimetry) using either heat sink or gradient layer calorimeters. In the heat sink calorimeter, sensible heat loss is measured as a rise in temperature of an absorbing medium such as the air stream ventilating the chamber or water circulating outside its walls. Evaporative heat loss can be determined from the increase in humidity of the ventilating air. The gradient layer calorimeter measures sensible heat loss from the temperature differences across a conducting layer between the animal and a constant temperature source. Evaporative heat loss can be measured with precision as the heat balance across the air conditioning system for the chamber. Because of the extremely high costs of these types of systems, few are presently in operation.

Indirect calorimetry is based on the principle that metabolic heat production is the result of oxidation of organic compounds. Thus, if all compounds were completely oxidized, heat production could be readily calculated from the amounts of O_2 consumed and the amount of CO_2 produced. However, in the animal, incomplete oxidation of protein results in combustible nitrogenous compounds, primarily urea, that are excreted in the urine. In addition, anaerobic fermentation yields combustible gases, primarily CH_4. For ruminants, the equation to estimate heat production is:

$$HE = 3.886\ O_2 + 1.200\ CO_2 - 0.518\ CH_4 - 1.431\ N,$$

where HE is in Kcal, O_2, CO_2 and CH_4 refer to gaseous exchange in liters and N refers to urinary N in grams (8). The contribution of CH_4 and N to the above equation is small. It is often sufficient to estimate HE from O_2 and CO_2 or even from O_2 alone.

Indirect or respiration calorimeters may be of the closed circuit or open circuit type. In the closed circuit type the animal is enclosed in a temperature controlled chamber. The air in the chamber is continuously circulated through an absorbant such as silica gel or KOH which removes water and CO_2. Constant pressure is maintained within the system by a supply of pure O_2. CH_4 is allowed to accumulate within the chamber. CH_4 production is calculated as the concentration difference between the beginning and end of the test period times the volume of the system.

The most common type of calorimeter is the open circuit indirect calorimeter. In this type of system, a mask, hood or animal chamber may be used. Air is drawn past the animal at a precisely determined rate. O_2, CO_2 and CH_4 concentrations must be accurately determined in both the incoming and outgoing air. Rates of consumption or production of these gases are calculated as the difference in concentration between incoming and outgoing air times the flow rate. This type of system is relatively inexpensive and easy to construct but is susceptible to error because of the high degree of accuracy required in the measurement of air flow and gas concentrations.

The CO_2 entry rate technique is based on principles similar to those of indirect calorimetry. This technique involves the infusion of $NaH^{14}CO_3$ at a constant rate into the animal and observation of the specific activity of CO_2 in the body. After the $NaH^{14}CO_3$ has reached equilibrium with the body pool of CO_2, the CO_2 entry rate is calculated from the ratio of the infused radioactivity to the specific activity of CO_2 in the body. Energy expenditures are then estimated using a previously determined relationship between energy expenditures and CO_2 entry rate. This procedure generally is less accurate than other procedures based on gaseous exchange, but has an advantage in that it can be applied to unrestrained animals, e.g., animals on pasture.

Various physiological variables have been proposed for use as indices of energy expenditures in unrestrained animals. Perhaps one of the more viable of these is heart rate. However, it appears that the individual animal's relationship between heart rate and energy expenditure must be calibrated for each situation.

Comparative Slaughter

In contrast to calorimetry, in which ME intake and HE are determined and RE estimated by difference, comparative slaughter

procedures measure RE directly. Briefly, a uniform group of animals are fed a common ration for a minimum of two weeks. At the end of the adaptation period, a sample of the animals is slaughtered and the body energy content is determined. The remaining animals undergo predetermined treatments for a period of time, and are then slaughtered and energy contents of the bodies are determined. The RE is then calculated as the difference in body energy contents between the initial and final slaughter groups. These techniques have advantages over the calorimetric techniques because they usually allow experiments to be conducted under situations more similar to those found in the livestock industries. They must be conducted over an extended time period, however, to allow accurate assessment of body energy changes.

Body energy content has often been determined by the accurate but expensive technique of whole body grindings and chemical analysis. This technique is expensive, laborious and destructive (i.e., an animal can be used only once). Thus, this technique is often used to calibrate other less expensive techniques such as carcass density or specific gravity. The search for non-destructive, inexpensive methods of estimation of body composition (hence, energy retention) has led to the evaluation of numerous methods including various water dilution procedures, ultrasonic scanning, ^{40}K counting, three dimensional photography, nuclear magnetic resonance and computer assisted tomography. Although several of these methods show promise, each has limitations that have restricted their application.

Other Techniques

The techniques briefly described above have been used to study energy metabolism in th whole animal. However, it should be noted that studies of energy metabolism at lower levels may facilitate greater understanding of the origins and source of heat production or energy expenditures in the animal. To present a detailed description of the numerous techniques that have been employed to study energy metabolism at the organ or tissue, cellular or subcellular level is beyond the scope of this chapter. However, a few of the procedures will be presented briefly to indicate that several techniques are available and are useful for the study of energy metabolism.

Blood flow has been used as an index of energy expenditures by various body organs or tissues. Thus, blood flow to a specific tissue as a proportion of cardiac output has been used as a relative index of the energy expenditure of that tissue. Measurement of O_2 arterial-venous concentration difference or blood temperature difference across a specific tissue in conjunction with blood flow, allows a direct quantitation of the energy use or the heat output of that tissue. These approaches have facilitated assessment of the relative importance of different body tissues as they contribute to heat production or energy expenditures of the whole animal. These approaches have been used, for example, to measure and separate heat generated from the digestive tract into anaerobic and aerobic origins and have been used successfully to measure energy expenditures or substrate flux across the digestive tract, liver, gravid uterus, fetus, and hind limb. In vitro tissue preparations or isolated cell preparations have proven useful to evaluate treatment effects on tissue energy expenditures and to assess the relative energy costs of various metabolic processes. For example, these techniques have been useful for the assessment of energy costs associated with protein synthesis and with ion pumping.

As much as these types of approaches have contributed to the understanding of energy metabolism within the animal, their contribution is relatively small compared to that potentially available from studies of physiological and biochemical mechanisms associated with energy expenditure at the cellular or subcellular level. For example, numerous catabolic (e.g., glucose-glucose-6-phosphate; pyruvate-phosphoenolypyruvate), anabolic (e.g., triglyceride-fatty acid+glycerol; protein-amino acid) and translocation (Na pump; Ca pump) cycles are known to exist in the animal body. The energy costs of these types of cycles and how they impinge on energy transactions of the animal are only beginning to be understood. Their importance is suggested, for example, by observations that the Na-K pump may account for 20-30% of basal energy expenditures. Other observations suggest that increased rate of cycling of the

triglyceride-fatty acid cycle in response to feeding may be equivalent to 10% of the H_eE.

Obviously, intuitive integration of knowledge of energy expending processes at the subcellular level for application to the animal level is difficult, if not impossible. Mathematical modeling is proving to be a useful, objective and quantitative tool to bridge that gap. This approach is proving useful not only to integrate knowledge, but to identify critical areas in which information or concepts are deficient or inaccurate. The usefulness and some of the limitations of this tool are indicated in a recent publication edited by Baldwin and Bywater (9).

DIGESTIBILITY AND METABOLIZABILITY

In the ruminant retained energy increases as the amount of feed given increases; however, this relationship is not linear and, as shown in Fig. 13-3, the relationship varies with type of diet. The reasons for these types of response are not completely understood, but involve, in part, differences in rate and extent of digestion, amounts and proportions of energy-yielding products of digestion, efficiency of energy utilization when body tissues are being oxidized versus use of food energy for energy retention, rate of body metabolism associated with level of feeding and efficiency of synthesis of different products (eg., protein vs fat).

The rate and extent of digestion as well as ciency of synthesis of different products are primarily influenced by the chemical and physical nature of the diet. For example, fecal losses contain about 13% metabolic fecal components plus 2% from the non-structural components plus 10-90% of the structural components (depending on lignification and physical structure) of the feedstuff. Thus, in general, feedstuffs such as grains that contain a low proportion of structural components are highly digestible whereas those such as straws that contain a high proportion of structural components are of lower digestibility. Digestibilities may be depressed under conditions in which rate of passage is increased or when fiber digestion is depressed as in high starch diets. The fecal loss form non-structural components may be much greater than expected for unprocessed

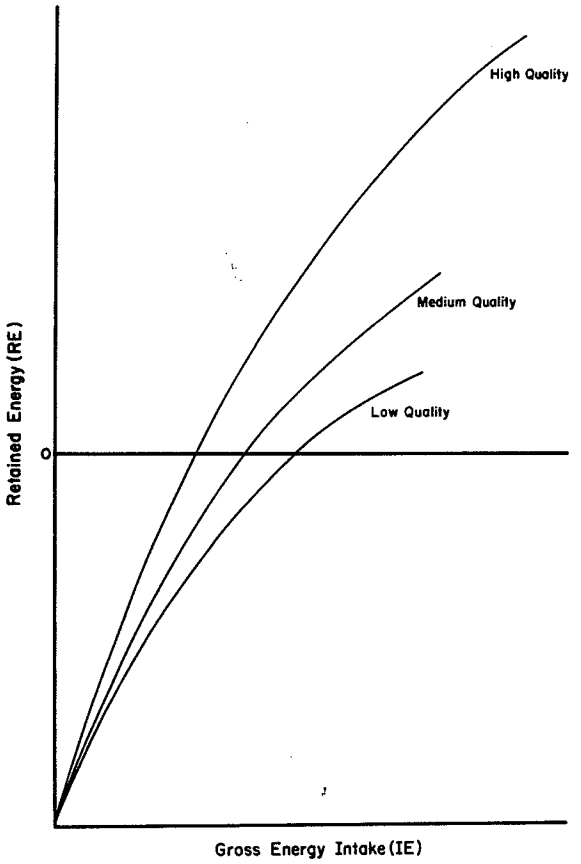

Figure 13-3. Relationship between retained energy and gross energy intake for foods of differing qualities. From ARC (4).

or minimally processed grains in grain-forage mixed diets, especially at high intakes. The numerous factors influencing the digestibility of feedstuffs have been discussed in greater detail in Chapter 9 and in the proceedings of the symposium on physiology of digestion and metabolism in the ruminant, held every five years beginning in 1959.

Differences in digestibility within species and between breeds are negligible. For example, in studies cited by Wainman (10), no differences in digestibility were found when six breeds of sheep were compared, when *Bos indicus* and *Bos taurus* breeds of cattle were compared or when different breeds of *Bos taurus* cattle were compared. Only small differences have been observed when different species of ruminants have been compared. Goats appear to digest low-protein diets with slightly greater efficiency than sheep or cattle. Food appears to be retained in the digestive tract of red deer for a shorter time than

in the digestive tract of sheep. This is associated with lower digestibility of the fibrous components of the diet. Although the data are limited, bison appear to digest low quality forage diets slightly better than cattle; however, this difference has not been observed with higher quality forages. Again, it should be noted that differences in these comparisons have been small. Thus, tables of DE or ME for ruminants can be applied to all ruminant species of economic importance with reasonable confidence.

Intake Level

In ruminants, when the amount of food ingested is increased, the proportion of IE lost as feces increases and the apparent digestibility decreases. The depression in apparent digestibility is greater for finely ground forages and for mixed diets containing grain than for long forages and may be greater for less digestible grains (or less processed grains). The ARC (4) concluded the decrease in apparent digestibility depended on the digestibility of the diet determined at the maintenance level. Thus, the change in digestibility (Δd_e) associated with a change in feeding level, expressed as a multiple of maintenance, was expressed relative to the digestibility (d_e) of the diet by the equation: $\Delta d_e = 0.107 - 0.113\ d_e$. This equation implies, for example, that a diet having a digestibility of 0.70 at maintenance would have a digestibility of 0.70 - (0.107 - 0.113*0.70) or 0.672 at twice maintenance and 0.561 at five times maintenance. The depression in digestibility may not be of major importance in a growing-finishing animal in which intake rarely exceeds three times maintenance, but can become quite meaningful in lactating dairy cows where intake may exceed five times maintenance.

The proportional losses of energy as CH_4 and in urine decrease as level of intake or digestibility decreases. Thus, an increase in the proportion of energy lost as feces tends to be compensated for by decreased losses as CH_4 and in the urine. The net effect is that metabolizability or ME is less affected by intake than is digestibility or DE. For example, the metabolizability of a diet having a digestibility of 0.70 is expected to be about 0.57 at maintenance. At two and five times maintenance the metabolizability is expected to be about 0.56 and 0.53, respectively. Thus, an increase in feed consumption of a diet of this type from maintenance to five times maintenance is expected to result in a decrease in metabolizability of less than 7% whereas a decrease in digestibility of about 20% is expected. In most practical situations, diets used for growing or finishing ruminants are of sufficient quality and food consumption sufficiently low (3X maintenance) that correction of ME for feeding level is not necessary. Correction for feeding level may be recommended if poor quality diets are used or if food consumption is extremely high.

Associative Effects

In most feeding systems the ME content of different feedstuffs are considered to be additive. Thus, if foods A and B have ME contents of 3.00 and 1.50 Mcal/kg, then a diet containing equal amounts of A and B is expected to contain 2.25 [(3.00 x 1.50)/2] Mcal/kg. The term "associative effect" is used in reference to the influence one food has on the utilization of another when the two are fed in combination. Thus, any deviation from additivity is considered an associative effect; however, the term is most commonly used when one food has a negative effect on the utilization of another, i.e., a negative associative effect. A schematic representation of additivity and negative associative effects is shown in Fig. 13-4.

An associative effect can be considered only in conjunction with the term balanced diet. A balanced diet may be defined as one in which all nutrients are present in amounts which do not limit the utilization of other nutrients. However, in ruminants this concept is complicated by the presence of ruminal digestion. For example, a given diet may contain adequate amounts of protein; however, if inadequate amounts of protein are available to the rumen microbes at the proper time, growth of the microbes and, as a result, microbial digestion of fibrous components of the diet may be depressed. As a result of this type of phenomenon, many of the observed negative associative effects may be in fact attributable to dietary imbalance. Negative associative effects between grains and forages are most likely to occur with high intakes and may occur, in part, due to low ruminal pH

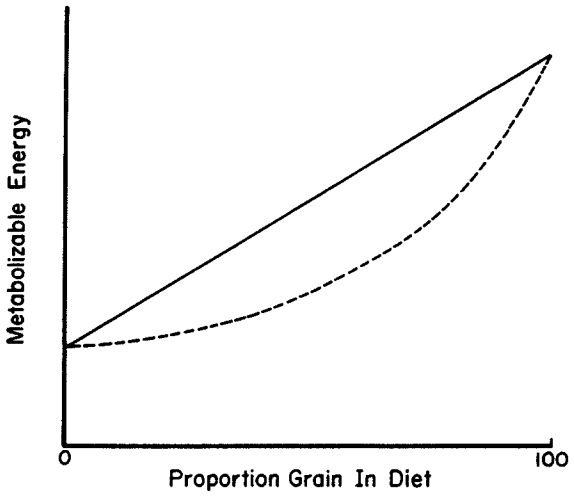

Figure 13-4. Schematic representation of additivity (—) and negative associative effects (— —).

and increased rate of passage. A depressing effect of certain types of fiber on starch digestion overall or an amylase function is a possibility that has received some support.

Feed Additives

Ruminants lose, as combustible gases (primarily CH_4) from 5-12% of the dietary energy ingested, depending on the nature of the diet and the level of intake (11). Many compounds such as chloroform, fatty acids or their analogs or halogenated methane analogs are known to suppress methanogenesis. The same compounds influence the fermentation pattern by increasing the proportion of propionate and reducing the proportion acetate. Thus, potential benefits could result from a reduction of the energy loss as CH_4 and, with some diets, increased gluconeogenic precursors. However, to date, addition of CH_4 inhibitors has resulted in little practical benefit. In some studies additions of CH_4 inhibitors have resulted in decreased food consumption. In others the microbiol population has apparently adapted to the inhibitor over time such that the CH_4 production and other fermentation products have returned to normal patterns within a few weeks.

Monensin and lasalocid are antibiotic feed additives that have been used effectively with ruminants. In general, feed consumption is reduced when these compounds are added to the diet whereas rate of gain is usually not affected, resulting in increased feed efficiency. The mechanisms of action of these compounds have not been fully elucidated, however, part of the benefit of these compounds may result from a reduction in methanogenesis and an increase in the propionate to acetate ratio. These effects are similar to those of other methane-inhibiting compounds. In addition, some evidence is available indicating ruminal lactic acid production is decreased and ruminal pH is increased when these compounds are added to high-grain diets. This effect may be of substantial benefit in situations conducive to chronic or subacute acidosis (see Ch. 23). These compounds appear to have no major effect on digestibility. However, additional benefits of these compounds may result from a reduction in maintenance requirements by altering the flux of Na and K in tissues, thus decreasing the energy expenditures for Na transport.

UTILIZATION OF ME

The animal uses ME for maintenance, tissue gain, gestation, lactation and muscular activity. Energy expenditures and efficiency of energy utilization vary within and among each of these functions. Some of the factors contributing to energy expenditures and efficiencies of ME utilization will be addressed in the following paragraphs.

Maintenance

The ME requirement for maintenance (ME_m) is defined as the ME intake at which RE = 0, thus ME_m is equivalent to fasting heat production (H_eE) plus the heat increment of the food consumed (H_iE). The importance of maintenance energy requirements to the overall animal economy is demonstrated by the observation that 65-70% of the ME needed for beef production is utilized to meet the needs of maintenance functions (12). Thus, an understanding of the factors contributing to maintenance energy expenditures and to efficiencies (or conversely inefficiencies) of energy use for maintenance is a necessary part of developing an understanding of the animal's energy economy.

As the above definition of maintenance indicates, ME_m is a function of H_eE and H_iE or, expressed in a different manner, ME_m is a function of the energy required for essential life processes and the efficiency with which

the ME from food is used to meet those requirements. Thus, both the animal and food source contribute to the amount of ME required for maintenance.

To be precise, the term maintenance should be used to refer to the amount of energy required to keep a non-pregnant, non-lactating adult (i.e., non-productive) in energy balance. Brody (1) and Kleiber (2) have shown that H_eE in different species of adult, non-productive mammals is about 70 $Kcal/kg^{-0.75}/d$. In practice, the term maintenance has been used frequently to apply to productive animals, that is growing, pregnant and/or lactating animals, as well as non-productive adults. When so used the meaning and measurement of maintenance become less clear. For example, a growing animal may gain structural components and body weight but lose tissue energy; a lactating cow generally produces milk at the expense of tissue energy. Body weight in kilograms raised to the 0.75 power, often referred to as metabolic body size, was originally used to confer proportionality on measurements of H_eE made in species differing considerably in mature weight (i.e., mice to elephants), but has been adopted with varying degrees of success for use in expressing H_eE and food energy requirements of animals within a species. In fact H_eE even in adult ruminants may differ substantially from 70 $Kcal/kg^{0.75}/d$. This value varies among species and has a mean value of about 60 for sheep and about 80 for cattle.

Elements of the animal's maintenance requirements (H_eE) may be viewed as being of two types: service functions and functions associated with cell maintenance. Service functions include functions that are performed by tissues or organs for the benefit of the entire, integrated organism. Included in these functions are the work of circulation and respiration, liver and kidney work (eg., detoxification, maintenance of body osmolarity and pH) and nervous functions. In total these functions account for about 35-50% of H_eE (13).

Major components of cell maintenance are ion transport (especially Na and Ca transport), protein turnover and lipid turnover (Table 13-1). These metabolic functions are examples of what is often referred to as substrate or futile cycles. These three cycles alone may account for as much as 30-50% of H_eE. Other

Table 13-1. Contributions of substrate cycles to maintenance energy expenditures.[a]

Cycle	Percentage contribution
Ion transport	20-30
Protein turnover	10-20
Triacyglycerol turnover	2-3
Glucose, glucose-6-phosphate	2
Pyruvate, Phophoenolypyruvate	1
Fructose-6-phosphate, Fructose-1,6-bisphosphate	2

[a]Adapted from Baldwin and Bauman (13)

substrate cycles such as those indicated in Table 13-1 contribute further to H_eE, but appear to be of lower energetic cost. Although these types of processes contribute significantly to H_eE and, in the case of protein, to the apparent costs of protein accretion, their role in the animal's rapid adaptation to constantly changing internal and external environments is essential to life. Other metabolic processes such as glycogen turnover, gluconeogenesis, ketogenesis, urea synthesis, RNA and DNA synthesis, among many others, require the expenditure of energy, thus contribute to the animal's maintenance energy expenditures.

Maintenance energy expenditures vary with age, body weight, breed or species, sex, physiological state, season, temperature and previous nutrition (12). The reasons are complex and have not been explained fully. However, part of this variation may be explained by differences in rates of substrate cycles. For example, energy expenditure for ion transport varies among tissues and is apparently greater in lactating than in non-lactating animals, is higher in young than in mature animals and is greater in cold-adapted animals than in those not cold-adapted (14). Similarly, protein turnover rates vary tremendously among tissues, are higher in young than in mature animals and decrease in response to lower planes of nutrition. Triacylglyceride turnover, likewise increases in response to increased plane of nutrition.

Variation in H_eE may also be explained, in part, by variation in proportions of various body tissues or organs. Table 13-2 shows typical masses, as proportions of body weight,

of the various body organs or tissues, the relative proportion of cardiac output they receive and an estimate of their relative energy expenditures. These estimates illustrate that although the combined masses of nervous tissue, heart, kidney, digestive tract and liver account for less than 10% of body mass, they receive about 55% of cardiac output and account for about 50-60% of H_eE. The high energy expenditures of these tissues may be partially explained by high rates of protein turnover and ion transport activities as well as the numerous other metabolic and service functions they perform. It is obvious that energy expenditures of these tissues per unit mass are considerably above the average of all body tissues. A change in the proportion of these tissues may have a large impact on overall animal H_eE. Proportions of liver and digestive tract tissues and, to a lesser extent, kidney and heart differ in response to nutritional level, physiological state and breed. As shown in Table 13-3, changes in masses of these tissues appear to account for a large proportion of the change in H_eE associated with nutritional manipulations. In other studies, changes in the proportion of liver, heart and digestive tract of lactating as compared to non-lactating animals, were sufficiently large to account for a 24% increase in maintenance. Proportions of certain metabolically active internal organs have also been shown to vary among cattle breeds (12).

The proportions of protein and fat in the body may also contribute to variations in H_eE. Several reports have shown that H_eE or ME_m is highly correlated with body lean or protein mass and less highly correlated with body fat mass. Further, genetically lean animals generally have higher maintenance requirements than genetically obese animals. These observations may reflect, in part, strong

Table 13-2. Estimated mass, blood flow and energy expenditures of tissue and organ systems of a ruminant 24 h post-feeding.[a]

Tissue	Mass, % of empty body weight	Cardiac output, %	Total energy expenditures, %
Nervous tissue	2.0	10.0	12.0
Skin	6.3	8.0	2.7
Heart	0.4	4.1	10.0
Kidney	0.3	13.4	5.0
Digestive tract	4.0	23.0	15.0
Liver	1.5	27.0	20.5
Muscle	41.0	18.0	23.0
Adipose tissue	15.0	9.6	7.0
Other (skeleton, etc.)	29.5	9.9	4.8

[a]Adapted with modifications from Smith (15). Liver percentage of cardiac output includes venous blood flow from the digestive tract as well as arterial flow.

Table 13-3. Effect of nutritional treatment on organ weight and fasting heat production.[a]

Nutritional treatment	Body weight, kg	Digestive tract, g	Liver, g	Kidney, g	Heart, g	Fasting heat production, Kcal/d
High	44.0	1.889	668	121	155	1,674
Medium	47.2	1.653	625	114	143	1,549
Low	39.9	1,304	428	93	126	1,143
Very low	34.4	1,162	350	83	130	966

[a]Adopted from Ferrell and Jenkins (12)

relationships between body lean and energetically expensive metabolic processes such as certain substrate cycles and between body lean mass and energy required for service functions as well as higher energy expenses of maintenance of lean tissues as compared to adipose tissues.

Numerous other factors may effect H_eE. To discuss all or even a major part of the potential sources of variation in H_eE is beyond the scope of this chapter. In any case, many of the contributors to variation in H_eE are only beginning to be understood and the magnitude of their contribution is yet to be appreciated.

The ME requirement for maintenance varies as a function of H_iE or k_m as well as H_eE. Over the range of ME concentrations fed to beef cattle, for example, of 2.0 to 3.0 Mcal/kg, the k_m increases about 10 percentage units, i.e., from about 65-75% (17). Thus, a 450-kg steer having a daily maintenance requirement of 13 Mcal ME when fed a diet containing 2.0 Mcal ME/kg would require about 11 Mcal ME when fed a diet containing 3.0 Mcal ME/kg. The change in H_iE due to diet is, in part, related to the nutrients available to the animal. This is because nutrients do not replace one another in proportion to their heats of combustion, but rather to the extent that they provide free energy to the cells of the body. The efficiency with which energy is trapped and becomes available to the cell as high-energy phosphate bonds varies among different metabolic pathways and can be calculated for different nutrients from the stoichiometry of the pathways involved. For example, if the relative value of glucose is set at 100%, acetate, proprionate, butyrate, stearate and proteins have values of 85, 87, 91, 95 and 76-79%, respectively (13). These estimates imply that ME_m can vary by as much as 20-25% depending on the nutrients available to the animal.

In actuality, this range in efficiencies due to nutrient source is rarely observable in the ruminant animal; mixtures of these and other nutrients are presented to the animal. In the ruminant animal particular attention must be given to the efficiency of utilization VFA because their heats of combustion account for about 65% of the energy absorbed from the digestive tract. In general the molar proportions of acetate and butyrate are higher on high-forage diets and lower on high-concentrate diets. Conversely, the molar proportion of proprionate is lower on forage diets and higher on concentrate diets. The range in k_m that can be attributed to varying proportions of VFA observed with diets typically consumed by ruminants is about 5%. Additional energy is supplied from the diet primarily as longer chain fatty acids, lactate and proteins. The proportions of these nutrients available also contribute to differences in k_m.

In addition to the varying efficiencies of utilization of nutrients to supply free energy to cells, the k_m of diets differ as a result of differing heats of fermentation and differing amounts of work required for prehension, mastication and rumination and to propel the food through the digestive tract (4). Evidence to date indicates that inefficiencies of nutrient metabolism account for about 65-70%, the energy costs of eating and rumination account for about 20-25% and the work of digestion accounts for about 10% of H_iE.

Tissue Gain

It should be recognized at the outset of this discussion that separation of energy retention (whether energy retention is in the form of tissue gain, conceptive tissue development or milk production) from maintenance is strictly artificial. In the animal these are highly integrated, interrelated processes; the separation is for simplicity and for "accounting" purposes. With this thought in mind, it is of considerable advantage to view the process of growth as the net result of synthesis and degradation rather than as simple accretion of body water, protein, fat and minerals. Taken in this context many of the concepts relating to energy retention represent extensions of concepts discussed previously in regards to maintenance.

In considering factors that influence the efficiency of utilization of ME for tissue energy gain, it is instructive to first consider the normal pattern of growth as determined by the net result of protein and fat synthesis and degradation. A schematic of the typical relationship between body protein and fat as growth proceeds with reasonably good nutrition is shown in Fig. 13-5. There have been numerous experiments with cattle and sheep on how nutrition can shift the normal pattern of growth. In general, protein levels below

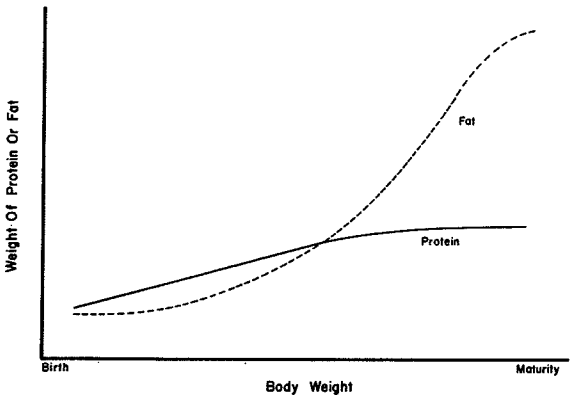

Figure 13-5. Schematic representation of the protein and fat contents of the body. Adopted from Garrett (17).

that which permits expression of the genetic potential for growth may result in a measurable difference in the composition of the animal. These differences, when observed, have been relatively small. Protein intakes above that necessary to permit protein deposition to the animal's genetic potential does not stimulate protein deposition. Several studies have shown that feeding of high-concentrate diets to appetite from weaning may result in animals being fatter at a given weight than those fed diets having lower energy densities. However, in some studies no effect of energy density of the diet on body composition has been observed. Overall, assuming reasonably good nutrition, nutritional manipulations have a relatively small influence on the body composition of the animal at a given weight as compared to differences that may be achieved through selection of genotype. That is, with reasonably good nutrition, the genotype of the animal is the primary determinant of body composition and composition of body tissue gain. This is not to say that body composition cannot ,be altered substantially by severe nutritional treatment, however, nutritional manipulations beyond the range normally feasible due to economic restraints are required.

The efficiency of utilization of ME above maintenance for tissue energy gain (k_g) is a function of an array of metabolic functions within the animal and the ability of absorbed nutrients to meet those metabolic demands. It is possible to calculate, with a knowledge of the metabolic pathways involved, estimates of the theoretical maximum efficiencies by which animals can perform productive functions. Using this approach Baldwin and coworkers (13) have estimated the theoretical maximum efficiency of growth of ruminants to be 70-80%. Estimates of k_g in growing ruminants has been in the range of 30-60%, however. These observations are used to indicate that few animals achieve theoretically maximum efficiencies and there is wide variation in efficiencies among animals.

In the previous section, turnover and repair were discussed as elements of maintenance. The energy costs of turnover also contribute substantially to the apparent inefficiencies of tissue accretion. The data presented in Table 13-4 emphasize that turnover rates of protein vary considerably among body tissues. For example, in the growing animal as much as 70% of the protein of the jejunum must be replaced each day. In addition to varying among tissues, protein turnover rates have been shown to vary with age, body size, physiological state and level of nutrition. High protein turnover rates certainly lower

Table 13-4. Fractional rate of protein synthesis and proportion of total protein synthesis of different tissues of the pig.[a]

Tissue	Fractional rate, %/d	Percentage of total synthesis
Stomach	22.9	
Duodenum	45.2	
Jejunum	70.0	19.4-22.6
Ileum	42.5	
Caecum	57.2	
Colon	44.0	
Liver	28.0	
Pancreas	88.0	16.5-17.0
Kidney cortex	15.1	
Kidney medulla	15.7	
Gastrocnemius muscle	3.6	
Soleus muscle	4.7	24.1-27.6
Heart	5.9	
Skin	8.6	6.0-6.9
Other		30

[a]From Simon et al (16)

the net efficiency with which protein accretion can occur. For example, if protein accretion only required the digestion, absorption, transport and uptake of amino acids and the synthesis of the peptide bond, net efficiency of protein accretion would be in the 75-85% range (13). Turnover of protein alone can reduce this efficiency by 15-40%. Factors in addition to turnover that might reduce the net efficiency of protein accretion include the use of amino acids as energy sources and rearrangements among non-essential amino acids that might be required to match the balance of amino acids in the protein being synthesized. As a result of these and other factors as well as turnover, the net efficiency of protein accretion in ruminants has been observed to be 12-40%.

Estimates of the net efficiency of fat accretion have been relatively similar to theoretical estimates of efficiencies of fat synthesis in ruminants. Estimates of the efficiency of fat accretion have been in the 60-80% range and average about 70%. The apparently high efficiency of fat accretion may be the result of relatively low rates of turnover and relatively high efficiency of synthesis from the nutrients available.

Also associated with the apparent inefficiencies are the increases in other substrate cycles such as ion transport with increases in feed intake. Work associated with service functions such as liver, kidney, and digestive tract work and possibly the work associated with respiration must increase in response to increased nutrition. Some of the differences among animals may be attributed to differences in rates of the substrate cycles and other metabolic functions as well as differing amounts of energy required for service functions.

The source of ME certainly has a marked influence on k_g. In general, k_g decreases as ME concentration in the diet decreases. As can be seen in Fig. 13-6, not only is k_g lower than k_m, the change in k_g varies more with ME than does k_m. Over the range of ME concentrations of diets commonly fed to growing cattle (2.0 to 3.0 Mcal/kg), this decrease in k_g associated with diets lower in ME indicates that a 300-kg steer depositing 5.0 Mcal of energy per day would have to consume 15.6 Mcal ME above maintenance of a diet containing 2.0 Mcal/kg versus 10.2 Mcal ME of a diet

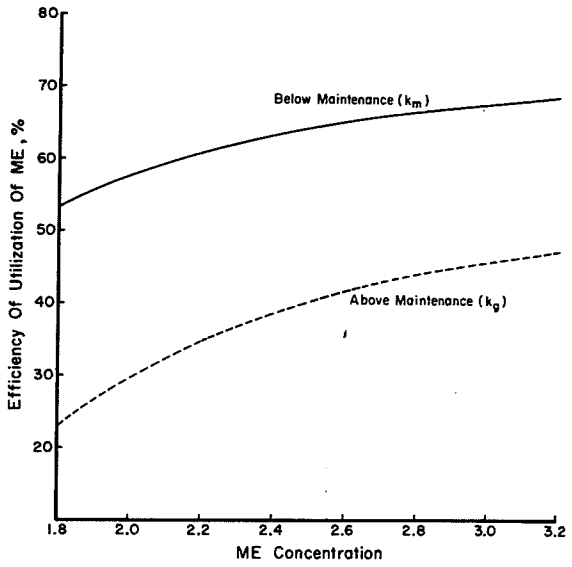

Figure 13-6. The effect of ME concentration in the diet on the efficiency of utilization of ME for maintenance and tissue energy gain in cattle. After NCR (25).

containing 3.0 Mcal/kg (17). Available evidence suggests only a small proportion of the differences in k_g can be attributed to the work of ingestion and digestion. The primary reasons for these differences appear to relate to the nature of the substrates made available to the animal and the metabolic decisions made within the animal for use of the substrates that are available. For example, efficiencies of 30-60% have been observed when acetate is used for fatty acid synthesis. In comparison, efficiencies of 60-80% have been reported when glucose was used and 90% or greater have been reported when dietary fat was used for fatty acid synthesis. Similarly, gluconeogenesis is much more efficient when propionate or lactate is available as glucose precursors than when amino acids must be used. The pattern of nutrient use within the animal can have an impact on apparent k_g. If, for example, VFA are used for fat synthesis and fatty acids are used for maintenance functions versus the reverse, heat increment can vary about two fold (13).

Gestation

The growth of the tissues of the gravid uterus (uterus, fetus, placenta and fetal fluids) together with the mammary gland represents a high priority requirement for energy in

animals. Growth of these tissues can be modified only to a limited extent by diet, sheep being more susceptible to modification than cattle. Energy accretion in the tissues of the gravid uterus has been determined in several serial slaughter experiments and estimated from respiration calorimetry trials with sheep and cattle. A typical energy accretion curve for cattle is shown in Fig. 13-7.

The efficiency of energy utilization for growth of gravid uterine tissues (k_Y) is usually defined as energy recovered in these tissues divided by the ME used for growth of those tissues. When this definition is used, k_Y has been relatively uniform and low (i.e., 10-20%) and average about 13%. Some of this variation is possibly of dietary origin. A review of data in sheep (18) suggests the evidence would tentatively justify the hypothesis that k_Y is related to the ME concntration in the diet in a similar way as k_m or k_g. Robinson et al (18) also suggested ME from diets containing less than 2.4 Mcal/kg were used with less efficiency than were body tissues.

Recent evidence indicates that about half of the increase in heat production during gestation is the result of increased maternal energy expenditures. Presumably, a large part of this is attributable to increased work of service functions, e.g., increased cardiac output and increased liver and kidney work. In addition, a large proportion of the energy actually used by the tissues of the gravid uterus is used by the uterus and placenta. These tissues account for 50-80% of the energy expenditures of the gravid uterus. Although the reasons for the high energy expenditures of these tissues have not been fully elucidated, they, in general, may be viewed as service functions necessary to maintain an optimum intra-uterine environment for fetal growth. Of the energy actually made available to the fetus for growth and maintenance, about 35-40% is retained in fetal tissues. The reasons for the loss of 60-65% of the energy available to the fetus are similar to those discussed previously in relation to efficiencies of maintenance and tissue energy gain.

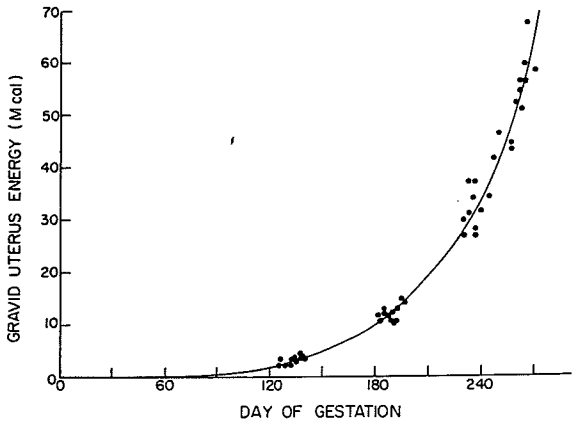

Figure 13-7. Relationship between energy content of the gravid uterus and day of gestation in cattle.

Lactation

The efficiency of utilization of ME was defined previously as the increase in energy retention as a result of a unit increase in the ME supplied. Assuming change in body composition can be measured, this can be determined in the growing animal in which energy is retained as tissues. However, in the lactating animal milk is produced although the animal may be losing, maintaining or gaining tissue energy. Thus, in the lactating animal three efficiency terms may be defined as (a) efficiency of utilization of body constituents for milk production when ME intake is less than needed to achieve maintenance of body tissues, (b) efficiency of utilization of ME for milk production in the absence of body tissue energy change and (c) utilization of ME for tissue energy gain and milk production simultaneously.

Estimates of the efficiency of utilization of body tissues for milk production have been consistently high and average about 84% (4). Efficiency of utilization of ME for milk production in the absence of tissue energy change varies around 62%. This efficiency varies linearly with the metabolizability (q) of the diet (k_l = 0.35 q + 0.42) (ARC, 4), e.g., k_l increases from 56-67% when q increases from 0.40 to 0.70. The concomitant deposition of energy in body tissues is more efficient than that which occurs in the non-lactating animal and appears to be about 95% of k_l, that is about 53-64%. The apparent costs of milk synthesis when ME intake is below that necessary to maintain body energy equilibrium have been partitioned among biosynthetic costs (50%), changes in physiological work such as work of circulation and respiration (17%), change in the costs of ion transport (17%) and decreases in the energy costs of

body component (primarily protein) resynthesis (16%) which accompany increasing rates of body energy loss (19). Partition of apparent costs for milk production when ME intake is sufficient or in excess of that required for tissue energy equilibrium may be similar.

It should be noted that the above discussion of the efficiency of utilization of energy for milk production was based primarily on data obtained by the use of dairy cows. Only limited information is available with other species or with non-dairy breeds of cattle. Insufficient information is available on how these efficiencies vary among species or among breeds within species. Data are available to suggest that k_1 may vary by as much as 35% (i.e., from 40-75%) within a breed of dairy cows, thus considerable variation among individuals, breeds or species is expected.

Muscular Activity

Determination of the efficiency of utilization of ME for muscular activity is difficult because it involves measurement of the amount of work done by an animal in moving its body. However, the amount of work done in ascent can be estimated from the mass of the body, the vertical distance and the acceleration due to gravity. The energy expended can be calculated as the difference between walking on the level and walking on a grade and the efficiency of muscular work can be calculated as the ratio of work done to the energy expended (4). Values obtained in this manner with several species indicate the efficiency of muscular activity to be about 0.30.

The other types of work done such as standing or walking can best be expressed in terms of an energy expenditure. The ARC (4) has concluded the energy costs of standing over lying to be about 2.4 Kcal/kg/d for cattle and sheep. For sheep, horizontal movement and vertical movements were estimated to require 0.6 and 6.7 cal/kg/m, respectively. Horizontal and vertical movements of cattle were estimated to require 0.5 and 6.7 cal per kg/m. Energy expenditures for eating appear to depend primarily on the time spent for that activity. It should be noted that these estimates are based on a very limited amount of data. Energy costs of muscular activity may be quite important to the energy economy of ruminant animals, especially in a range environment. For example, if a 500-kg cow travels 5 km (about 3.1 mile) horizontally and ascends 500 m during a day, her ME requirements would be about 2.9 Mcal or 23% greater than those of a similar, confined animal.

FEEDING SYSTEMS

All feeding systems seek to match the supply of feed energy to the energy requirements of the animal. As have been shown previously, the capacity of a feed to meet the requirements of the animal depends on the chemical and physical nature of the feed, the requirements of the animal and how the feed is used to meet those requirements. Most nutritionists would agree that the dynamics and complexity of the relationships involved in animal metabolism make the term "constant" a misnomer when applied to feeds or to animal requirements. Energy values of feeds or energy requirements can only be constants in a relative way. The chief limitation to all systems is in the application of general concepts and relationships to specific, practical situations (6).

Essentially all currently recommended feeding systems are based on NE concepts, but the procedures by which these concepts are applied to practical conditions vary. Descriptions of the systems currently recommended in France, Germany, Great Britain, the Netherlands, Switzerland and the United States can be found in the publications of INRA (20), Nehring and Haenlein (21), ARC (4), Van Es (22), Bickel and Landis (23), and NRC (24, 25). In the following paragraphs the ARC (4) and the NRC (25) systems will be discussed briefly to show two different approaches to the application of NE concepts to practical situations.

The equations used by the ARC (4) and NRC (25) to obtain estimates of the energy requirements of beef cattle are shown in Table 13-5. The ARC has retained ME as the unit of measure; the ME content of the diet and the metabolizability (q) of the diet are determined at maintenance intake, thus are standardized. As can be seen, the ARC system includes explicit corrections for activity on ME requirements for maintenance, tissue gain and lactation. These estimates are also explicitly adjusted for efficiency of utilization

Table 13-5. Calculations to estimate energy requirements of beef cattle.

ARC[a]	NRC[b,c]
Maintenance	
1) $H_eE = 0.53\ (W/1.08)^{0.67}$	ME = 0.82 DE
2) $H_jE = 0.0043\ W$	$NE_m = 1.37\ ME - 0.138\ ME^2 + 0.0105\ ME^3 - 1.12$
3) $Z = H_eE + H_jE$	$NE_g = 1.42\ ME - 0.174\ ME^2 + 0.0122\ ME^3 - 1.65$
4) $k_m = 0.35\ q + 0.503$	
5) Maintenance = Z/k_m	Retained Energy (RE)
	steers: $RE = 0.0635\ W^{0.75}\ EBG^{1.097}$
	heifers: $RE = 0.0783\ W^{0.75}\ EBG^{1.119}$
Tissue Gain	
1) Heat of combustion of live weight gain (Hc) $= (4.1+0.0322\ W-0.000009\ W^2)/(1-0.1475\ W)$	Maintenance: NE_m requirement = 77 Kcal/$W^{0.75}$
2) $R = H_c \times W/Z$	
3) $k_f = 0.78\ q + 0.006$ (at L = 2)	
4) $B = k_m/(k_m-k_f)$	Tissue Gain: $NE_g = RE$
5) $p = k_m \log_e(k_m/k_f)$	
6) Requirement = $Z/p \log_e[B/(B-R-1)]$	
Pregnancy	
1) For a 40-kg calf, daily energy retention (RE/day) = $E(t) \times 0.0201 \exp(-0.0000576\ t)$ where $\log_{10} E(t) = 151.665 - 151.64 \times \exp(-0.0000576\ t)$ and t is the number of days from conception.	Pregnancy: NE_m = birth weight $(0.0149-0.0000407\ t) \times \exp(0.05883\ t-0.0000804\ t^2)$
2) $k_y = 0.133$	
3) Requirement = $(RE/d)/k_y$	
Lactation	
1) R = milk yield X [(1.509+0.0406 X (g fat/kg)]	Lactation: NE_m = milk yield X [0.1(percent fat)+0.35]
2) $k_1 = 0.35\ q + 0.420$	
3) Approximate feeding level $L = 1 + (R/k_1)/Z/k_m$	
4) Correction for feeding level = 1 + 0.018(L-1)	
5) Requirement = $[1+0.018(L-1)]\ (R/k_1+Z/k_m)$	

[a] All requirements are in MJ/d; W and ΔW are live weight (kg) and change in live weight (kg/d).

[b] All requirements are expressed in Kcal or Mcal units; W is digesta free body weight (empty body weight in kg) and EBG is empty body weight gain (kg/d).

[c] Requirements for tissue gain are adjusted to a live weight gain (LWG) basis by use of the following equations: EBG = LWG X 0.956 and MEBW = MLW X 0.891 where MEBW and MLW are mean empty body and live weights, respectively.

of ME for those functions and the influence of q on those efficiencies. Explicit corrections for feeding level are also included in estimates of requirements for tissue gain and lactation.

Conversely, although based on similar concepts, the NRC (25) expresses the energy content of feeds in NE_m or NE_g units. These have been defined earlier in the chapter. In contrast to the ARC in which estimates of parameters used in the equations are based on calorimetric studies and on ME determined at maintenance, estimates of feed energy values and requirements have been determined by the use of comparative slaughter studies in which animals were housed outdoors and fed at least two levels of feed above maintenance. As a result, influences of activity, feeding level and diet quality are implicitly and explicitly accounted for in the estimates of

the energy value of the feed and in the estimates of animal requirements. Some differences between the two systems are inherent because of the different data bases that were used to develop the systems. Adjustments to the estimates for differences in mature size of the animal and sex condition are suggested by both the ARC (4) and NRC (25). The NRC (25) further suggests corrections for previous nutrition. The NRC (25) has expressed requirements for pregnancy and lactation in NE_m units for the sake of simplicity and because of the similarity between k_m and k_1. Tables of requirements, feed energy contents and examples of how to use the systems in practice are provided in the above publications.

In many cases, the series of equations used by the ARC (4) and NRC (25) result in similar estimates of energy requirements. For example, a typical "British" breed of steer weighing 400 kg (live weight) and consuming a diet having a q of 0.65 (ME = 2.8 Mcal/kg) and gaining 1.0 kg/d would require 40.5 MJ/d or 3.46 kg/d for maintenance and 37.9 MJ/d or 3.23 kg/d for gain based on the ARC equations (Table 13-5). NE_m and NE_g values of this diet are 1.86 and 1.23 Mcal/kg, respectively, and the requirement for maintenance would be 6.32 Mcal NE_m or 3.39 kg and for gain would be 4.96 Mcal NE_g or 4.03 kg. Thus, total requirements estimated by the ARC (6.69 kg/d) are about 10% lower than those estimated by the NRC (7.42 kg/d). This difference results primarily from the difference in the estimates of the energy content of live weight gain. Part of the difference may be attributed to differences in k_f estimated by the two systems, i.e., from the ARC equation, $k_f = 0.51$ whereas k_f in the NRC system $(NE_g/ME) = 0.44$. These types of differences relate, primarily, to the different data bases used in the development of the two systems.

Estimates of the extra feed requirement for pregnancy in cattle differ substantially between the two systems. For example, at 280 d postmating, assuming a 40-kg calf weight at birth, the requirements for pregnancy estimated by the ARC are 3.59 kg of the diet described above. This is about 80% greater than the requirements estimated by NRC (1.96 kg of the above diet). Both assume ME is utilized with an efficiency of 13%, however the ARC based their estimates on rates of energy accretion in tissues of the gravid uterus (uterus, placenta, fetal fluids and fetus), whereas the NRC based their estimates on rates of energy retention in the concepts (placenta, fetal fluids and fetus). In essence the ARC estimate is based on the rate of energy accretion in tissues directly due to pregnancy, whereas the NRC estimate is based on the rate or energy accretion in tissues (directly due to pregnancy) that are lost from the maternal system at parturition.

SUMMARY

Many of the systems currently in use for the expression of the energy requirements of ruminants and the energy contents of feedstuffs are based on similar principles. They differ to varying degrees on how those principles are applied to the production situation. Although all of the systems have limitations, reasonably good estimates of the animal's requirements and energy values of feedstuffs are obtained from most systems currently in use if proper consideration is given to the adaptation of those recommendations to the situations in which they are to be applied.

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