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NUTRITIONAL ENERGETICS OF ANIMALS

R. L. Baldwin and A. C. Bywater

Department of Animal Science, University of California, Davis, California 95616

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INTRODUCTION

Energy, generally defined in terms of potential capacity to perform work, is an abstraction that can be measured only in its transformation from one form to another (32). Animal nutritionists are concerned primarily with two forms of energy, chemical and heat. Energy supplied to animals in chemical form can be transformed to heat when utilized in support of vital life processes, stored in chemical form as in growth or fattening, transferred in chemical form to a second animal as in pregnancy and lactation, or transferred to surroundings as in work (3). Quantifying these energy transactions in animals is the focus of the field of nutritional energetics.

The first and second laws of thermodynamics hold that all forms of energy are quantitatively convertible to heat. Classically, all measurements of energy transactions made by animal nutritionists were made and expressed in terms

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of heat energy or calories (3). Although Kleiber (31) strongly urged that the calorie be retained as the basic unit of heat energy, the joule (J) was adopted in the International System of Units and by the US National Bureau of Standards as the preferred unit for expression of electrical, mechanical, and chemical energy (45). Subsequently, most nutrition journals adopted the joule as the basic unit for expressing energy. The joule is defined in terms of the International Metric System as one kg-m^2/sec^2 or 10^7 erg. The nutritional calorie is defined as 4.184 J. Because all measurements of energy are defined in terms of the fundamental metric units of mass (kg), distance (m), and time (sec), joules are readily converted to calories and vice versa. In this presentation, the calorie is the basic unit used to express heat energy.

The major objective of nutritional energetics is to devise a convenient and accurate system to predict the energy balance of individuals based on body weight, sex, activity, physiological state, environment, and amount and nutritive value of feed eaten (11). Committees commissioned by the National Research Council (NRC) and the British Agricultural Research Council (ARC) have reviewed the great mass of experimental data on energy metabolism in a wide range of species including man, and have formulated systems to predict the energy and feed requirements of these species (1, 2, 43–45). These committees have published summaries on the effects of body weight, composition of foods and feeds, composition of products such as meat and milk, age, environment, and other factors, and have proposed feeding systems that accommodate these factors. Partial efficiencies of use of alternate nutrients for various processes have been considered and compromises adopted, often in view of apparently conflicting views and data (1, 2, 43–45). Some of the systems work extremely well when applied carefully and with due consideration of limitations imposed by compromises made in development. Most systems are repeatedly updated based upon new information, and generally systems that yield improved predictions of energy requirements for a given species are adopted when available (22). No currently available system yields accurate estimates, even within a single species, under all conditions, and no current system has universal applicability. Thus, the general objectives of nutritional energetics are to devise more generally applicable systems and to formulate diets that optimize production efficiencies.

The large amount of data available on efficiencies and feed values is summarized comprehensively in ARC, NRC and European Association for Animal Production (EAAP) publications (1, 2, 43–45), and is not reviewed here. Rather, this review focuses on the sources of variation in energy requirements that limit general application of current feeding systems, the research directed at identification of underlying physiologic and metabolic causes of this variation, and early attempts to quantify and accommodate this variance in computer models of animal growth and metabolism.

TERMINOLOGY OF NUTRITIONAL ENERGETICS

Since the original *Quantitation of Combustion* in a living system by Lavoisier, many terms have been invented and applied to describe the types of energy transactions that occur in animals (3, 37). Historical terms such as "specific dynamic action" (of food) have appeal and are still used, even though they imply nothing about underlying relationships; others, including "work of digestion," have specific but incorrect implications regarding underlying relationships. Different schools of nutritionists have tended to adopt and defend alternative systems of nomenclature to describe the partition of energy in animals. The triennial symposia on energy metabolism of the EAAP (12, 18, 43, 55) have helped remove many disparities from the terminology. Recently, a subcommittee of the Committee on Animal Nutrition of the NRC was appointed to develop a systematic terminology for description of energy utilization by animals which is consistent with feeding systems in current use in the US and terminology applied in other countries (45). This system is presented diagrammatically in Figure 1.

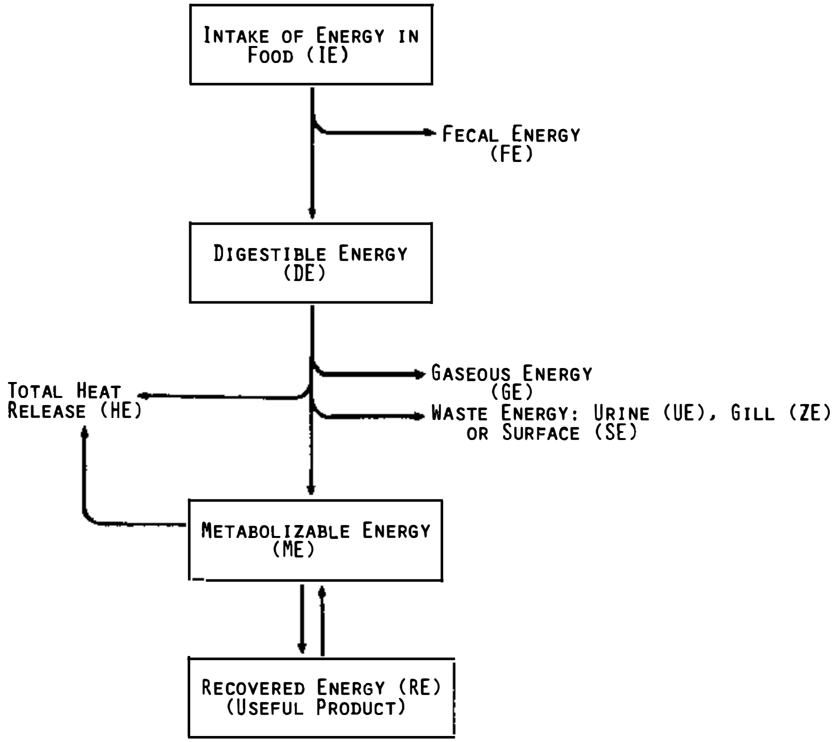

Figure 1. Partition of energy in animals. Adapted from NRC (45).

Description of Energy Transactions in the Animal

The classical term gross energy intake has been replaced by the term total intake of energy (IE) or ingested energy, which is defined as the amount of food consumed (I) times gross energy per unit of food (E). Conventional definitions of apparent digestible energy (DE = IE − FE) and metabolizable energy (ME = DE − GE − UE) are retained (see Figure 1 for definitions of terms). Energy in excreta can be from nonutilized compounds in ingested (sub i) food (F_iE, U_iE) or of endogenous (sub e) or metabolic (sub m) origin (F_eE, F_mE, U_eE, U_mE) so that true digestible energy (TDE) equals $IE - FE + F_eE + F_mE - H_fE - GE$, where H_fE is heat released in fermentation during digestion. Similarly, true metabolizable energy (TME) equals $TDE - UE + U_eE$. Waste products excreted via the gills of fish (ZE) or from the exterior surface of the animal (SE) are treated similarly to urine. The term recovered energy (RE) replaces the older, collective term Net Energy in Product (NE_p) and identifies energy recovered in useful products such as tissue (TE), milk (LE), eggs (OE), conceptus (YE), and wool, hair or feathers (VE). Use of the term RE obviates confusion between NE values assigned feeds (discussed below) and energy transactions in the animal.

Partition of total heat production (HE) into meaningful physiologic or metabolic components is the most complex and controversial aspect of all systems of nomenclature. This is due in part to (*a*) a lack of knowledge and quantification of the physiologic and metabolic processes that contribute to total heat production; (*b*) systematic differences among estimates of components of heat production that should be identical on mathematical grounds or by definition, but which differ because alternate methodologies may aggregate energy expenditures associated with somewhat different metabolic processes; and (*c*) the attempt to reconcile terminology with academic or research goals and the pragmatic goal that the terminology accommodate current and future feeding systems (22, 45). These problems will be elaborated upon in subsequent sections.

Components of total heat production explicitly identified in the NRC system (45) are basal or fasting metabolism (H_eE), heat of voluntary activity (H_jE), heat of product formation (H_rE), heats of digestion, absorption, and assimilation (H_dE), heat of thermal regulation (H_cE), heat of fermentation (H_fE), and heat of waste formation and excretion (H_wE). H_rE, H_dE, H_fE and H_wE can be referred to in aggregate as heat increments (H_iE) of maintenance and production.

The terms defined above allow description of energy transactions within an animal in accord with the first two laws of thermodynamics. For example, a lactating, growing animal might partition ingested energy as follows: $IE = FE + GE + UE + SE + HE + RE$, where $RE = TE + LE$, and if desired, $HE = H_eE + H_jE + H_rE + H_cE + H_dE + H_wE + H_fE$. Further partition, for example of H_rE into costs of milk lactose, protein and fat synthesis, and body fat and lean synthesis, is permissible as long as the equality of input and output remains satisfied.

Expression of Animal Energy Requirements and Feed Energy Values

Animal energy requirements and feed energy values must be expressed in compatible terms. Early in this century, the limitations of systems based upon gross energy—variability in digestibility—and digestible energy—variability in urinary and gaseous losses—were recognized and several systems based upon metabolizable energy concepts were developed (3). Among these were the Physiological Fuel Value (PFV) and Total Digestible Nutrient (TDN) systems, which are still in use. Specific limitations of these ME-based systems are that protein is undervalued in fast-growing animals and efficiencies of ME use for various physiological processes vary systematically with chemical and physical properties of feeds including caloric density (ME/kg). These limitations led to the development of net energy (NE) systems which value feeds in terms of their efficiency of use for specific processes based upon the identity $NE = \Delta RE/\Delta I$, where RE can be a positive or negative quantity, and I is feed intake in grams. In animals fed at or below maintenance (energy balance ≤ 0), the net energy value of a feed for maintenance (NE_m) equals the amount of body energy spared (ΔTE) by an increment (ΔI) of feed ($NE_m = \Delta TE/\Delta I$). In a growing animal fed above maintenance, the net energy value of a feed for growth (NE_g) is equal to the amount of body energy stored (ΔTE) due to provision of an additional increment (ΔI) of feed ($NE_g = \Delta TE/\Delta I = \Delta R_gE/\Delta I$). Thus, net energy values of feeds for maintenance, growth, fattening, lactation, egg production, etc can be estimated and tabulated. The net energy requirements of an animal can be calculated as the sum of functions for which energy is required. For example, for a growing, pregnant, lactating animal, $NE_{mr} = NE_m + TE + LE + YE$, where NE_m equals fasting catabolism or basal metabolism plus endogenous and metabolic losses in urine and feces and from the surface and, by convention, normal activity ($NE_m = H_eE + U_{em}E + F_{em}E + S_eE + H_jE$).

NE and ME systems are highly compatible because feed values and animal requirements expressed according to one system can be converted readily to the other based on the efficiency with which metabolizable energy from a feed is used for specific functions. For example, efficiencies of ME use for maintenance (K_m) and growth (K_g) can be calculated as $K_m = NE_m/ME_m$ and $K_g = NE_g$ or $TE/(MEI - ME_m)$, where ME_m is the amount of metabolizable energy from a feed required to maintain energy balance ($EB = 0$) and MEI is metabolizable energy intake. Costs of digestion, absorbtion and assimilation (H_dE) and of product synthesis (H_rE) can be aggregated as H_iE such that ME_{mr}

$= NE_m + NE_g + H_iE$ and $ME_{mr} = NE_m/K_m + NE_g/K_g$. The latter four equations provide a quantitative link among current feeding systems such as the ARC system (2) wherein feed values and animal requirements are expressed on a ME basis, and the NRC systems, which are based on NE (43).

The above discussion summarizes current terminology in nutritional energetics and the underlying conceptual frame upon which the terminology and most current feeding systems are based. The major problems encountered in application of the concepts and feeding systems are that estimates of parameters such as H_eE, K_m, K_g, etc. can vary greatly among animals, feeds, and methods of estimation. Subsequent sections examine sources or causes of this variation.

BASAL METABOLISM AND MAINTENANCE REQUIREMENTS

Late in the last century, Rubner (11, 37) noted that basal metabolism, or heat production, was not a linear function of body weight (BW) either within or between species, but rather, varied as an approximate function of surface area, $BW^{2/3}$. Subsequently, Brody (13) and Kleiber (32) reported that the best statistical fit between body weight and basal or resting heat production in young adults across species was obtained with the equation $y = a \times BW_{kg}^{0.7-0.75}$, where y is basal heat production in kcal/day, a is a coefficient with units of kcal/(day $\times BW_{kg}^{0.7-0.75}$)and $BW_{kg}^{0.7-0.75}$ is metabolic body weight (MBW). At an early EAAP Conference on Energy Metabolism (12), the well known equation $BMR = 70 \times BW_{kg}^{0.75}$ was adopted for estimation of basal heat production in kcal/day in young adults on an interspecific basis. Both Brody (13) and Kleiber (32) recognized and, indeed, emphasized that the relationship they reported was mathematical or empirical rather than theoretical, as was Rubner's suggestion that $BW^{2/3}$ be used. They also noted that the best empirical fits to data within species were obtained with exponents other than 0.75. This latter fact has been reemphasized recently by Thonney et al (54), Geers & Michels (23) and others. The decision to set the exponent at 0.75 by convention was pragmatic. One reason was to facilitate comparisons among data produced in different laboratories where exponents ranging from 0.65–0.75 were then in use. A second, perhaps implicit, reason was that there was no theoretical explanation of why the empirical, interspecific exponent (0.75) differs from 0.66. Further, there was no explanation of why exponents deduced statistically from intraspecific data on basal heat production ranged from 0.4–0.85 (54). In view of this uncertainty it seemed rational, as a start, to fix the exponent in the allometric equation, thereby forcing all variance into estimates of the coefficient a, to examine factors that caused the coefficient to vary, and, later, to devise an appropriate mathematical formula. This approach was adopted in developing subsequent discussion of basal heat production. This is in conformance with convention. An exponent of 1.0 would have had equal utility, since in most cases animal weights compared are similar. When accurate predictions of basal heat productions within species are desired and there is sufficient data available to define both coefficient and exponent in the allometric equation, these values should be deduced and applied to that species. Forcing the exponent to 0.75 usually introduces systematic errors of prediction; the tendency is to underpredict basal in young animals and overpredict in older animals (13, 25, 26).

Sources of Variation in Basal Metabolism

Brody (13) noted long ago that resting heat production (H_eE) per unit MBW in producing and working animals was higher than in comparable nonworking (e.g. pregnant and lactating) animals. He suggested use of the term "working maintenance" to designate this phenomenon and to quantify maintenance requirements of producing animals appropriately. Speculations regarding causes of these differences in apparent maintenance costs were general at that time and cited endocrine, physiologic, and metabolic differences essential to the productive process (13). During the next several decades, observations accumulated that supported the view that apparent maintenance requirements vary considerably with plane of nutrition, physiological state, age, level of productivity, environment, and other possible factors. Reported coefficients *a* for the allometric equation defining basal heat production range from 40–140 kcal ME/(day × $BW^{0.75}$) (16, 35, 41). Limited research was directed at defining underlying physiologic and metabolic changes that cause this variance. However, considerable controversy arose. First, many argued that the concept of maintenance, which is explicitly incorporated into all current feeding systems, was inadequate in view of this variance and should be discarded or replaced (38, 51, 60). Others argued that since we know, for example, that the apparent maintenance requirements of growing steers and lactating cows are 110 kcal ME/(day × $BW^{0.75}$) and 140 kcal ME/(day × $BW^{0.75}$), respectively, there is no problem; we only need use these values (22, 41). A third, ongoing argument is that the increase in apparent maintenance in producing animals is really a cost of production and should be reflected in estimates of net efficiency of production rather than in maintenance; maintenance requirements should be considered a constant (4).

VARIATION IN ENERGY EXPENDITURES PER UNIT MASS OF ORGANS

Investigation of the underlying sources of variance in rates of basal heat production has received increasing attention over the last decade. A first step was identifying and at least semiquantitatively defining the contributions to basal heat production of various energy-requiring maintenance functions. These have been summarized (5, 8, 60). In general, these divide into (*a*) service functions essential to maintenance of an integrated organism, such as heart and liver work, respiration, ion and metabolite resorption by kidney, and nervous and endocrine functions related to integration, and (*b*) tissue and cellular level functions such as ion transport for maintenance of membrane potential, and macromolecule resynthesis (turnover or repair). Each type of function accounts for 35–50% of basal energy expenditure (5, 8). Milligan (39) was one of the first to emphasize that energy expenditures in ion (Na^+) transport are major, amounting to about 30% of basal energy expenditure, and that they may vary significantly with physiologic and endocrine status. The latter suggestion was reinforced by observations by Ismail-Beigi & Edelman (29) that energy expenditure in tissues varies significantly with thyroid status as a result of the role of thyroxin in regulating activity of the ouabain-sensitive (Na^+,K^+)-ATPase. Recently, Gregg & Milligan (26) partitioned energy expenditures in muscle from cold-exposed, two- and seven-week old lambs and lactating and nonlactating ewes into (Na^+,K^+)-ATPase–dependent and –independent respiration. They found that the increase in respiration in muscle after exposure to cold was largely (Na^+,K^+)-ATPase–dependent, in agreement with previous reports (27). Respiration rates were 32% greater in lactating than in control ewes, and 67% of this increase was (Na^+,K^+)-ATPase–dependent. Respiration rates of muscle from two- and seven-week-old lambs were 50% and 20% greater than in muscle from control ewes. The decrease in muscle respiration with age in the lambs was due to equal proportional decreases in the (Na^+, K^+)-ATPase–dependent and –independent components. The difference in respiration rates between the seven-week-old lambs and the adult ewes was almost entirely independent of (Na^+,K^+)-ATPase. The specific nature of the (Na^+,K^+)-ATPase–independent functions that differ are not known, although the authors speculated that differences in protein synthesis are only a minor component (26). In a related series of experiments, Canas et al (17) observed that rates of palmitate oxidation in liver and heart slices from pregnant and lactating rats were 64% and 120%, and 30% and 75% greater than those observed in samples from age-paired control rats. It is clear that a portion of changes in apparent maintenance requirements due to plane of nutrition (25), age (26), pregnancy (40, 47), and lactation (41) can be attributed to changes in basal energy expenditures in tissues. Further, some of these are due to changes in activity of the (Na^+,K^+)-ATPase. Considerable additional work will be required to identify affected functions other than ion transport, and to relate these quantitatively to changes in whole-animal energy expenditures. Further, it is essential that dietary, endocrine, and other physiologic and metabolic processes that affect energy expenditure in tissues are identified and their effects quantified (57).

VARIATION DUE TO DIFFERENCES IN RELATIVE ORGAN WEIGHTS Productive functions including growth, pregnancy, and lactation are accompanied by significant increases in food intake. Webster (60) and others

(6) have reported that energy expenditures in visceral organs such as liver and gut contribute 25–30% of basal heat production. One might expect that relative weights of these organs would increase at high feed intakes. Similarly, the relative weights of several organs with high energy expenditures per unit mass are much greater in young animals than in adults. Holliday et al (28) addressed the possibility that the high metabolic rates of infants could be explained on the basis of the high relative weights of brain and visceral organs in infants as compared to adults. Using the assumption that energy expenditures per unit mass of tissue do not differ between infants and adults, they estimated that over 50% of the difference in heat production per unit MBW in infants compared to adults could be explained on the basis of differences in relative organ weights. Based on the same assumption, Smith & Baldwin (52) and Canas et al (17) estimated that about 50% of the increase in apparent maintenance requirements in lactating as compared to nonlactating cows and rats could be the result of increases in relative weights of liver, gastrointestinal tract, and heart. Koong and his colleagues (34, 35) have reported a series of experiments with rats, pigs, and sheep designed to bring animals of each species to the same final weights at the same age at differing planes of nutrition. For example, in the pig experiment, one group (HL) was fed to gain 19 kg in the first 35-day feeding period and to lose 5 kg during a second 35-day period; a second group (MM) was fed to gain 7 kg during each period; a third group (LH) was fed to lose 5 kg in the first period and to gain 19 kg in the second period. Fasting heat productions/MBW (FHP) in the MM and LH groups were 20% and 40% greater than in the HL group, clearly illustrating the magnitude of the effect of plane of nutrition on basal metabolism. Liver weights in the MM and LH groups were 20% and 45% greater than in the HL group. Positive and significant correlations between FHP and weights of liver, gastrointestinal tract, pancreas, and kidney were found. Observations with rats and sheep were comparable (35). Pathway analyses indicate that a large proportion of variance in FHP can be accounted for by changes in relative weights of vital organs and possibly correlated with changes in respiration per unit weight of tissue (L. J. Koong, personal communication). If the effects of plane of nutrition upon vital organ weights are essentially linear and highly correlated with FHP, as suggested by the reports of Koong et al (34, 35) and Canas et al (16, 17), resolution of observed variance in apparent maintenance requirements could be straightforward. Unfortunately, many additional factors contribute. Effects of age, physiologic, and endocrine state on energy expenditure per unit weight of tissue were discussed above. Farid et al (19) reported that diet has significant effects on the increases in liver weight that accompany lactation and/or the attendant high feed intakes. This is compatible with reports of interactions between diet and FHP (18, 25). Webster (61), Ferrell et al (20), and Vermorel et al (59) have reported significant sex, seasonal, and breed effects upon FHP. Until all of the causal relationships that lead to variation in apparent mainte-

nance have been sorted out and quantified, users of current feeding systems will be restricted to careful selection of maintenance estimates best suited for the animals they wish to feed.

PRODUCTIVE PROCESSES

Accurate estimates of animal performance based upon consideration of feed intake, body weight, environment, physiological state, and productive function require not only accurate estimates of maintenance requirements, but also accurate estimates of efficiency of conversion of metabolizable energy to product. The equations presented above, $NE = \Delta RE/\Delta I$ and $K_g = \Delta RE/\Delta MEI$, are the basis for such estimates, with the restrictions that the two amounts of feed intake (I_1 and I_2) and of metabolizable energy intake (MEI_1 and MEI_2) used to calculate ΔI and ΔMEI are at or above the amounts required for maintenance. Changes in recovered energy (ΔRE) can be estimated in two ways. Since by definition, $\Delta MEI = \Delta RE + \Delta HE$, one can measure ΔHE using direct or indirect calorimetry (11, 15) and calculate ΔRE by difference, or one can measure ΔRE directly (36). There are advantages and disadvantages inherent in each approach. Equipment for both direct and indirect calorimetry is expensive; an investigator has a limited number of units, so his estimates are usually short in duration and involve limited numbers of animals. Direct measurement of ΔRE in growing animals, for example, requires that ΔRE be large relative to errors in measurement of initial and final body energy contents. This approach can be inexpensive and large numbers of animals can be used, but studies must be long in duration—weeks in rats and months in cattle. Unfortunately, results obtained using the two methods tend to differ. Comparison of the ARC (2) and NRC (43) feeding systems for growing cattle, which are based on indirect calorimetry and comparative slaughter data, respectively, illustrates this. ARC estimates of K_m for various feeds exceed NRC estimates by 10–15% while estimates of K_g are 25–30% greater. A result of these differences is that recommended energy requirements for 200- and 400-kg cattle growing at the rate of 1 kg/day calculated according to the NRC system are 18% and 26% greater, respectively, than those calculated according to the ARC system (2, 43). Some of these differences can be explained on the basis of differences in climate, livestock management practices in the two countries, energy losses from surface (SE), insensible nitrogen losses not accounted for in indirect calorimetry, and activity differences—movements are somewhat restricted in indirect calorimetry chambers. However, much of the difference remains to be explained since the equation $\Delta ME = \Delta RE + \Delta HE$ is theoretically sound and absolute. One can speculate that the difference lies in duration of the two types of studies leading to assessment of somewhat different physiologic or metabolic processes. These processes include aspects of turnover of macromolecules and physiological adaptations to changes in plane of nutrition (discussed above) which require several weeks to occur and, as a result, are not evaluated in short-term respiration studies. Graham (25) addressed these issues well and concluded: "... this discrepancy and associated variation in predicted feed requirements occur because there is, in the immature animal, an appreciable energy expenditure which is associated with its physiological state and which responds rather slowly to feed intake. This is not allowed full expression in short-term studies and failure to identify it in long-term trials is prejudicial to their general applicability." Graham (25) emphasized that a great number of rigorous investigations will be required to resolve questions regarding variance in estimates of basal heat production, apparent maintenance, and apparent efficiencies of productive processes. He also implied that the degree of complexity involved will require development of more sophisticated models than those used in current systems for prediction of energy requirements, models that capture the wide range of cause-and-effect relationships that must be accommodated.

MATHEMATICAL ANALYSIS OF ENERGY BALANCE DATA

The primary statistical method employed in evaluations of energy balance studies has been multiple regression using models (30, 50) of the general form $\mathrm{MEI} = a + \mathrm{K_g} \times \mathrm{R_gE}$ and $\mathrm{MEI} = a + b \times \mathrm{R_pE} + c \times \mathrm{R_fE}$, where a is the maintenance requirement and b and c are efficiencies of protein and fat accretion, respectively. Most of the estimates of a and $\mathrm{K_g}$ discussed above were obtained using the first equation. The second equation is an extension of the method, and requires that protein and fat accretion be determined separately rather than in aggregate as RE in energy balance studies. The basic models are straightforward, but the associated statistics can become very sophisticated, especially for lactating animals, which gain or lose body protein and fat as well as producing milk (41, 56, 58). A major problem in application of the second equation has been that deduced values for b and c range from 15–80% and 30–90% respectively, varying with diet, age, species, plane of nutrition, and probably a number of unknown metabolic factors (21, 49). Roux et al (50) addressed this problem using ridge and principal component regression procedures and concluded that a great deal of the variance or instability in estimates of partial efficiencies of protein and fat accretion is due to multicolinearity in accretion of these components. Koong (33) and Roux and his colleagues (38, 51) have proposed alternate analytical procedures that merit further investigation since they yield more stable and apparently realistic estimates. However, neither approach has sufficient dimension to yield estimates of such parameters as partial efficiencies of protein and fat accretion that are unique, apply generally, or enable accommodation of the effects of age, diet, and the like.

Two types of mathematical modeling approaches have been used in recent years to aid resolution of problems of variations in maintenance and productive efficiencies. The first approach is the use of research models to evaluate current concepts and data for quantitative and dynamic adequacy and to identify and interpret critical experiments. This approach and the underlying physiologic and metabolic processes that are appropriately considered in analyses of animal energy expenditures and partitioning of nutrients were reviewed recently (7, 8, 53). Research models characteristically are highly theoretical (causal) and incorporate considerable physiologic and metabolic detail. As a result, they are too complex and expensive to use as predictive models or as components of feeding or management systems. However, they can be used to identify and characterize elements for incorporation into more empirical, predictive models for use under applied conditions (7, 14, 46).

The second approach has been development of predictive models of energy transactions in animals. These models are more highly aggregated and empirical than research models, but they incorporate primary determinant elements to the extent that they are far less empirical than models upon which current feeding systems are based. These models generally consider the digestion of feed components and metabolism of absorbed nutrients explicitly rather than in the aggregate as energy and crude protein (9, 24, 48; M. Gill, personal communication). In addition, they often consider the turnover of macromolecules in the animal and partitioning of nutrients among tissues and functions within the animal (8, 10, 46). These elements enable accommodation of a large portion of variance in apparent maintenance and productive efficiencies due to diet composition, composition of body energy gain or loss, age, and physiological state of the animal. Above all, unlike current systems, such models are dynamic and therefore may contain equations to represent the effects of plane of nutrition over time on basal heat production (25). By and large, the philosophy and methodology for development and verification of rigorous predictive models are relatively new, and the few models available require further refinement (9, 14). However, when enough is known about animal systems and responses, predictive models containing provisions for handling greater variance in animal energy expenditures and efficiencies will become an integral part of feeding systems, improving both the accuracy and general applicability of current systems (22). The availability and relatively low cost of microcomputers are likely to accelerate developments in this area and to provide the necessary vehicle for practical use of such models. We must be cautious about implementing these models, however. The tendency is to accept them readily because such systems are generally more sound on academic grounds; however, their capacity to reduce errors of prediction compared to current systems should be demonstrated before they are adopted (22). An important feature of the NRC nomenclature (45) discussed above is that it is compatible with the introduction of prediction models, so as the latter mature and are proven, they can be incorporated readily.

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