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Integration of human and animal concepts of energy metabolism

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Energy metabolism research has been conducted with both animals and man for well over a century. The value of research findings from other species is undeniable. Yet it is important to recognize the substantial differences in the usual experimental approaches and in the energy systems which are applied in practice. Experimentation with farm animals is usually done with animals in a steady-state, i.e. consuming a fixed amount of a well-defined diet for several weeks. Human studies are more commonly done with rotating diets and with less rigid control. The energy systems for farm animals describe the amount of energy required for each of several physiological functions, i.e. maintenance, growth, milk production, pregnancy. Energy is usually expressed as metabolizable energy (ME). The requirement for production is derived from the amount of product formed and the partial efficiency of ME used for its formation. With humans, the energy requirement is expressed in terms of ME directly. Questions of efficiency are usually less important for humans because the formation of new tissue is a relatively small proportion of total energy requirements. Although the terminology is different and the primary sources of variation different when human and animal systems are compared, the fundamental principles remain constant and much valuable information can be exchanged.

ANIMAL ENERGY SYSTEMS

Animal feeding systems are based on a wide array of units of expression and with substantial variation in assumptions. That such variation exists is less due to any disagreement on questions of energy use by animals than to considerations required to ensure understandable communication to the end user at the farm. A controversy existed for many years regarding energy systems for animals concerning the desirability of systems based on ME *v.* those based on net energy (NE), where NE is the energy contained in the product formed. Central to the discussion was the question regarding the extent to which the heat increment (HI) of feeds differed among feeds and among physiological functions. The frequently unstated assumption behind this debate was that there was a 'best' feeding standard or feeding system which was superior to all others. It was necessary to identify what this best system was. The question generated research in energy metabolism of farm animals. Such research was greatly accelerated in the 1950s. By the early 1970s there was general agreement on the fundamental role of ME as the basis for expressing the potential energy value of feeds, and when combined with partial efficiency of product formation, ME served equally well to describe the requirements of animals. Agreement was not so good on which units should be used at the farm level. In addition to the classical energy terms of digestible energy (DE), ME and NE, terms such as the oat unit, starch equivalent, barley unit, etc., were in common use. A great deal of effort was expended in comparisons of the various feeding systems under a variety of conditions. It was finally recognized that practical feeding systems must involve considerations which are of local origin, and, although based on scientifically sound principles, could be expressed in whatever units could be most easily understood. This recognition prompted an informal agreement at the 6th Symposium on Energy Metabolism of Farm Animals in 1973 to restrict future discussions to topics of energy metabolism and energy use by animals rather than the development of feeding systems for local use.

Statement of energy requirements. The nutrient requirements of farm animals are based on the goal of maximum economic efficiency, feeding for maximum profit. Rations are typically formulated using linear programming techniques to identify least cost mixtures of available feed ingredients. Because production rates vary so widely it is convenient to partition the total requirement of animals into the costs for maintenance plus the individual costs for production. Table 1 shows the relative energy requirements for several species. The total requirement of a high-producing dairy cow may be several times the maintenance requirement, whereas the total requirement of even a hard-working human is seldom twice that needed for maintenance alone. Whether the requirements are stated as NE: net energy for gain (NE_g), net energy for lactation (NE_l), net energy for maintenance (NE_m), or ME combined with partial efficiencies, the requirements incorporate the variation in partial energetic efficiency for different physiological functions. A source of difficulty in use of partial efficiencies to compute energy needs was the possibility that these efficiencies were not constant but varied with rate of production. Curvilinear responses had been observed between intake of ME and

Table 1. *Scaled metabolizable energy (ME) and total ME requirements of man and several species of farm animals producing at substantial but not remarkable rates*

	ME requirement	
	kJ/kg body-wt$^{0.75}$	kJ/d
Man, 70 kg, survival	377	9138
Man, 70 kg, heavy work	628	15 117
Steer, large frame 300 kg, 1·2 kg gain/d*	1159	83 680
Pig, 35 kg, 700 g gain/d†	1800	26 000
Dairy cow, 650 kg, 45 kg milk at 3·5% fat‡	2243	289 000

* National Research Council (1984).
† National Research Council (1988).
‡ National Research Council (1989).

energy gain in growing animals. A major step in resolving this difficulty was the identification by Kielanowski & Kotarbinska (1970) of different partial efficiencies for ME used for protein and fat deposition. They found the energy cost of protein deposition was much higher than that of fat deposition in terms of energetic efficiency. The curvilinear response in growth could now be explained by changes in the partial rates of deposition of protein and fat which are known to occur in response to age and energy intake. This was a departure from the traditional understanding of efficiency of growth being higher when protein deposition was greatest and decreased as fat deposition increased.

The concept of maintenance. Maintenance can be carefully defined for an adult of any species that is in energy or weight equilibrium. This is the usual situation for most adult humans but is a situation which almost never exists for farm animals. Animals are usually growing, producing a product of economic importance, i.e. milk, eggs, wool, or are pregnant. Although the condition of maintenance rarely exists with farm animals, a mathematical concept of maintenance has proved very useful. The cost of production can be arbitrarily defined as the amount of energy required in excess of that needed for maintenance. This can be measured for milk production and wool growth but is less well defined for growing animals. Still, it is possible to extrapolate by various mathematical means to zero growth rates to identify a maintenance component. If this hypothetical maintenance component is accepted as a mathematical entity rather than a physiological one, many conceptual problems can be avoided. The net energy for maintenance is taken to be equal to fasting heat production (FHP), i.e. the amount of energy expended when maintenance needs are met by metabolism of body tissue. It has been emphasized (van Es, 1972) that the use of an NE_m is for mathematical convenience and an NE_m should not be compared with NE of product formation. The ratio, FHP:ME required for maintenance represents the relative efficiency of meeting maintenance needs from dietary energy compared with those needs being met by metabolism of body tissue. This is in contrast to the partial efficiency of ME used for tissue gain or milk production in which efficiency is properly computed by the ratio, product formed:the amount of ME required for its formation. It is also useful to stress that the curvilinear responses to changing energy intake whether in lactation or growth are largely eliminated when proper recognition is given to changes in the product formed. In lactation, the relationship between ME intake and milk production is strikingly linear when body energy changes are minimized. In growth, the total energy costs of growth can be identified as the sum of protein and fat gain each of which occurs at variable rates and each of which occurs with different but constant partial efficiency. The implication is that evidence to support large variations in efficiency of energy use by humans will not come from observed variation in production efficiency among farm animals.

HUMAN ENERGY SYSTEMS

The definition of energy requirements for humans is stated by World Health Organization (1985) as follows: ‘The energy requirement of an individual is the level of energy intake from food that will balance energy expenditure (EE) when the individual has a body size and composition, and level of physical activity, consistent with long-term good health; and that will allow for the maintenance of economically necessary and socially desirable physical activity. In children and pregnant or lactating women the energy requirement includes the energy needs associated with the deposition of tissues or the secretion of milk at rates consistent with good health.' Human energy systems developed in a climate almost totally free of challenges to the use of ME as the unit of expression of energy values of foods since advanced by Atwater at the beginning of this century. Although based on ME, the method of derivation of energy requirements for humans differs substantially from that of animals. Human energy requirements are based on the time spent on and the energy cost of different activities during the day. Typically this is done by estimating the amount of time spent sleeping, sitting, walking, or working at a specific activity and multiplying those times by a tabulated rate of EE for each. In practice the total requirements for all activities are combined into a single factor which is multiplied by the basal metabolic rate (BMR). For example, 1·27 × BMR is the requirement for minimal activity in a survival mode and 2·14 for a person involved with heavy work. An example of the World Health Organization (1985) method is shown in Table 2.

HEAT INCREMENT *v*. THERMIC EFFECTS

The translation of results of animal energy metabolism research to humans requires attention to the differences in usual experimental approaches between the two. Most animal research from which the requirements for maintenance and partial efficiencies of production were derived were done under steady-state conditions. The differences between HI and thermic effects of food (TEF) illustrate the differences between the systems. The HI of a diet is the difference in heat production at two different intakes above maintenance where each measurement is made over a minimum of 24 h and after adaptation to the diet. The HI is a computation based on the difference in EE between two steady-states. The increase in EE represents the total change in EE and includes not only the specific cost of metabolic synthesis of new body tissue or other product, but it also includes all the additional costs related to the larger food intake, increased digestive tract mass and activity as well as marginal increases in the work of the heart, etc. HI,

Table 2. *Energy requirement of a male office clerk (light activity work)*

Age 25 years, weight 65 kg, height 1·72 m, body mass index (weight/height^2) 22, estimated basal metabolic rate 290 kJ(70 kcal)/h

		Energy requirement	
	Time spent (h)	kcal	kJ
In bed at 1·0 × BMR	8	560	2340
Occupational activities at 1·7 × BMR	6	710	2970
Discretionary activities:			
Socially desirable and household tasks at 3.0 × BMR	2	420	1760
Cardiovascular and muscular maintenance at 6 × BMR	⅓	140	580
For residual time, energy needs at 1·4 × BMR	7⅔	750	3140
Total, 1·54 × BMR	24	2580	10 780

BMR, basal metabolic rate.

therefore, should be thought of as the sum total of all costs associated with increased product formation, not just the metabolic cost of the product synthesis. The increment of ME intake is partitioned into HI and new product. The measurement of HI, therefore, allows the computation of a partial efficiency of energy use for product gain. Because the measurement is made under steady-state conditions, the result is not influenced by any time delay in the EE associated with the nutrients derived from any particular meal.

The thermic effect of foods or diet-induced thermogenesis (DIT) is substantially different from HI in that it is not measured in a steady-state. It is most commonly measured in man by measuring the increase in EE following consumption of a meal. Although the rise in EE following consumption of a meal is easily detected, it cannot be easily quantified. The usual procedure is to establish a fasting baseline followed by consumption of the test meal and measurement of EE until either (a) the EE returns to the baseline level or (b) an arbitrary time limit is reached. Many measurements are restricted to 3 h. This is in marked contrast to the universally accepted requirement of 12 h fast preceding measurement of BMR to avoid the effects of the previous meal. Although the measurement of TEF is useful in studies of questions relating to the timing of metabolic events, it is not useful as a component in the development of total energy requirements. This limitation is because the measurement relates only to the substitution of food energy for body energy in the fasted individual. The EE which is measured as TEF cannot be separated from the EE which occurs as a consequence of physical activity by an individual. Energy is expended because of physical activity, and food is consumed to provide the required energy. The energy expended in the process cannot be arbitrarily assigned to intake or activity.

FHP *v*. BMR

Another difference is that of FHP in animals and BMR in humans. Because EE measurements with animals are not made under restraint, FHP usually includes an activity component. Animals are able to stand or lie at will and are generally about as active as animals studied in the fed state. Fasting measurements are, thus, reasonably comparable with measurements of fed animals in terms of the relationship between fed and fasted at similar activity levels. In humans, the BMR is measured following an overnight fast while the subject is awake but at complete rest. BMR is, thus, intended to represent a condition in which all voluntary activity is eliminated. Because movement is restricted, the BMR is measured for only a brief period of time, generally less than 90 min. There is little comparable data from 24 h measurements. Because BMR includes no voluntary activity it does not bear the same relationship to 'maintenance' energy needs of free-living individuals that FHP of animals does.

APPLICATION OF KNOWLEDGE FROM ANIMAL STUDIES

Though the systems for describing energy needs of animals and people may appear substantially different, the underlying biology is basically the same and much information derived from animal experimentation is put to good use. As an example, a question of intensive interest in human nutrition is the search for metabolic explanations for obesity. The search is based on indications derived largely from intake studies of great variation in the amount of food required for individuals that are apparently quite similar in mass, etc., to maintain body-weight. With the exception of diseased states, it is likely that this search will fail. There is meagre evidence from extensive animal energetic experiments that the efficiency with which given metabolic precursors are used to synthesize identical products is subject to significant variation. There are very large differences in the composition of products formed and large differences in the rate of product formation; and it is these differences that account for the observed variation in energy use. It is my contention that observed differences in partial efficiency of product formation are the result of inexact assumptions regarding maintenance rather than a real biological difference in efficiency of product formation.

One frequently overlooked source of variation in energy use in humans is the effect of previous nutrition on BMR. Experiments with swine and sheep (e.g. Koong & Ferrell, 1990) have demonstrated that the FHP of animals is influenced by previous plane of nutrition, the FHP being higher when measured following a period of higher feed intake. Some studies directly link the increased FHP to a greater mass of liver and digestive tract tissue. It has also been shown that the oxygen uptake by the portal-drained viscera is greatly increased during periods of increased feed intake. Reynolds *et al.* (1991) found that 44 and 72% of the HI in growing heifers was due to O_2 consumption by the splanchnic tissues on high-concentrate and high-forage diets respectively. Table 3 shows the effects of previous level of nutrition on organ size and FHP in pigs from a study by Koong & Ferrell (1990). FHP was 40% greater for the animals that finished the experiment at the high intake level than those that finished at the low intake level. The relationship between intake and organ mass is important to the interpretation of BMR measurements in humans. The establishment of weight equilibrium for 2–3 weeks would be necessary to eliminate the possibility of previous plane of nutrition having an influence on the measured BMR. It is likely that some data in the literature indicating an adaptation to decreased intake by humans are due to measurements of BMR which were influenced by changes in organ size due to previous intake level.

SUMMARY AND CONCLUSIONS

With relatively few limitations, findings derived from the study of the energetics of farm animals provide extremely valuable information in the application of human energetics

Table 3. *Energy of nutritional status on organ size and fasting heat production in pigs (data from Koong & Ferrell, 1990)*

Nutritional status . . .	Low	Medium	High
Body-wt (kg)	40·7	40·9	40·5
Stomach (g)	263	287	338
Small intestine (g)	669	853	1013
Large intestine (g)	451	492	588
Pancreas (g)	52	63	79
Liver (g)	447	537	646
Heart (g)	165	157	155
Kidneys (g)	112	120	139
Spleen (g)	53	51	49
Fasting heat production (kJ/d)	4515	5431	6355
Weight gain (g/d)	−142	200	542

to the solution of dietary questions. The nature of the body's response to variation in energy intake and the nature of variation among individuals are good examples. It is important to appreciate the differences in the usual experimental constraints of studies with animals and humans. Human requirements are based on the summation of the energy costs of several different activities performed throughout the day whereas animal requirements are based on steady-state conditions at various production levels. Although the factors which influence specific biochemical or physiological events may be very similar, the manner in which those effects are incorporated into energy systems and the terminology used to describe them may differ substantially.

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