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SYMPOSIUM ON 'ASSESSING RESPONSES TO NUTRIENTS BY RUMINANTS'

An historical perspective: the development of methods for assessing nutrient requirements

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Interest in the assessment of the nutrient requirements of ruminants arises from the practical need to sustain or manipulate the production of meat, milk or wool. A difficulty in making such an assessment has always been the definition of what constitutes a nutrient (see Blaxter, 1977). This is well illustrated by the history of attempts to express the nutritive value of feeds as sources of energy and to relate these to energy-demanding processes of both the rumen and the body proper.

Crude biological assays

The earliest work on the nutrient requirements of ruminants was based on the practical observations of Captain Middleton, summarized by Young (1793) and later by Albrecht Thaer (see Tyler, 1975). A crude type of biological assay was used in which both feed values and feed requirements were expressed in terms of hay; hardly a precisely defined standard. A later version of this approach was that devised in the 1880s by Winkel & Fjord (see Eskedal, 1954) in Scandinavia. Barley was used as the standard and animal needs were expressed as feed units, one feed unit being equivalent to 1 kg barley. A still later version of the biological assay principle was the attempt of Kleiber *et al.* (1941) to express nutrient needs and feed values in terms of glucose/casein equivalents.

Definition in terms of crude constituents

In the early 19th century attempts were made to place these assays on a firmer chemical basis. The problem was that knowledge of animal metabolism was meagre at that time and much of what was accepted as true was wrong. von Liebig (1840), acknowledged to be the pre-eminent agricultural chemist of the time, contended that carbohydrate and fat simply acted as substrates for respiratory metabolism and that protein was the only substrate for growth and for sustaining muscular work. The former contention was refuted by Lawes & Gilbert (1853) and the latter by Fick & Wisclicenus (1856). At the time the several attempts to express Thaer's hay equivalents more precisely emphasized protein. Examples are the estimates made by Boussingault (1843) and Grouven (1858) of the amounts of fat, carbohydrate and protein required by cattle.

Definition in terms of digested nutrients

The next step in assessing nutrient requirements was taken at Weende (Gottingen) by Henneberg & Stohmann (1860, 1870). They not only devised the analytical scheme for feeds which is still in use today, but conducted numerous digestion trials. Woolff (1874) at Mockern (Leipzig) expressed their results and his own in terms of the amounts of the digested proximate principles required by stock, and these standards of nutrient need were published annually by Woolff until 1898 when responsibility for them rested on Lehmann. These same standards expressed as total digestible nutrients (TDN), in which the digested nutrients were summed with digested diethyl ether exctractives multiplied by 2·25, were the basis of Haecker's (1907) standards in the USA. They were incorporated in the standard text book published first by Henry (1898) and then by Morrison (1947) and the TDN system was for a long time the basis of the energy requirements employed by the National Research Council of the USA. The standards were simply the amounts of TDN thought to be needed by different classes of stock producing at different rates, and were mainly based on a judicious selection of results from feeding trials.

The net energy principle

A major advance was then made at Mockern by Kuhn (1894) and his successor Kellner (1908) and also by Armsby (1917) at Pennsylvania State College. At both centres attempts were made to measure by calorimetry the change in energy retention following changes in diet intake. At Mockern, Kuhn (1894) and Kellner (1908) both gave 'pure nutrients' as additions to a basal diet and measured the increase in retention. The nutrients were starch, sucrose, gluten, vegetable oil and fibre as extracted straw. It was found, and subsequently confirmed by Hoffman *et al.* (1962), that the amounts of energy retained from the digested pure nutrients could be precisely determined. When, however, the resultant 'pure nutrient factors' were applied to these digested nutrients in feeds, there were serious discrepancies, particularly severe for roughages. This did not deter Kellner (1908); he stated that feeds could be assessed in terms of their ability to promote energy retention in the mature animal and that requirements could all be expressed in these terms. In fact, he devised his feeding system, the starch equivalent system, by expressing values of feeds and requirements relative to the net energy of starch.

Armsby's (1917) experiments were mostly conducted at lower intakes of feed than were Kellner's (1908), but his conclusions were much the same. Both centres thus concluded that animal requirements could be expressed in terms of the enthalpy of combustion of the tissue gained or of any milk secreted together with an amount of energy necessary to meet maintenance needs. The latter was theoretically equivalent to the enthalpy of the tissues lost when no feed was given. Neither Arsmby (1917) nor Kellner (1908) measured the fasting metabolism; maintenance needs were simply the amounts of feed needed for zero balance expressed as the net energy for fattening the animal.

Some difficulties

On looking back, there had been immense progress by the 1920s. A crude assessment of nutrient needs in terms of hay or its equivalent had been replaced by one based on the chemical classes of energy-yielding constituents. These were then replaced by the amounts of these constituents which were apparently digested and later by their weighted sum. Finally the net energy system and particularly the starch equivalent system appeared to provide a simple, additive and non-colligative scheme for dealing with the practical problem of feeding ruminants, for it expressed requirements in terms of the energy of what was added to or removed from the body.

The completeness of the net energy scheme, coupled perhaps with the cost of calorimetric work, probably inhibited progress in the next 30 years and little work was done. Some was undertaken, however, to reveal considerable shortcomings. Armsby's successor, Forbes, showed that the net energy of feeds varied and he concluded (Forbes, 1933) that the net energy of a feed was only fully expressed when it was part of a balanced ration given in 'quantitatively sufficient amounts'. Mitchell (1934) came to the same conclusion, while Kriss (1942) and Reid (1962) concluded that for all intents and purposes the net availability of metabolizable energy for growth and fattening could be taken as constant, a conclusion which implied that the TDN system was a correct one.

More practical studies, however, showed that the net energy system did not work in practice. For example, Dodsworth (1959) demonstrated that the actual gains made by fattening cattle ranged from 60 to 210% of those predicted from the UK standards of net energy (starch equivalent) requirement. Furthermore, the anomalies which Kellner (1908) had shown when he compared results from his digested pure nutrients with those for natural feeds had not been resolved, nor had his finding that starch and fibre had virtually the same net energy values been explained. It was again the meagre nature of knowledge about animal metabolism that inhibited progress, just as it had been so a century before.

The metabolizable energy system

The impetus for new work arose from the findings at Cambridge (Barcroft *et al.* 1944) about the significance of the steam volatile fatty acids in ruminant metabolism, as well as from an increasingly expressed dissatisfaction with the Kellner (1908) system. At the Hannah Institute in the 1950s, we undertook calorimetric work which led to the metabolizable energy system (Blaxter, 1962), which was adopted by the Agricultural Research Council (1965, 1980) and by the UK agricultural departments (Ministry of Agriculture, Fisheries and Food;

Department of Agriculture and Fisheries, Scotland; and Department of Agriculture, Northern Ireland (MAFF, DAFS and DANI), 1975). This system states that requirements of energy are defined by the enthalpies of combustion of the tissues deposited or the milk secreted and by the enthalpy of combustion of the tissues lost on fasting, that is it adheres to the net energy principle. However, feed is used with variable efficiency in meeting these primary needs, varying with feeding level, type of production and the nature of the total diet. These efficiencies can be predicted.

The metabolizable energy system exemplifies the problem of defining a nutrient. Metabolizable energy is not a nutrient in a primary sense since it is not directly related to an animal requirement with a one-to-one concordance. This is well illustrated by the derivative 'variable net energy system' (MAFF, DAFS and DANI, 1975); feeds have variable net energy values or, alternatively, requirements for metabolizable energy are variable.

It has been said (France & Thornley, 1984) that the Agricultural Research Council scheme is deterministic, empirical and static. It is obviously deterministic and not stochastic; whether it is empirical depends on the depth of understanding required in a practical model. It is certainly not static since the values are time rates and the differential equation can be integrated numerically. When this is done for fattening animals (Blaxter, 1980), there is no discernible bias and residual errors are those to be expected in estimating gain from initial and final weighings. For gains of 300 kg estimated from initial weight and feed intake over periods of up to 680 d, the standard deviations of differences between observed and calculated gain for individual animals was only 20–30 kg.

End-products of digestion

The work at the Hannah Institute also involved study of the energy value of the products of digestion. Steam volatile and higher fatty acids were given by rumen infusion and glucose and proteins by ways which avoided subsequent rumen fermentation. These studies showed that digestion products replaced one another for maintenance in proportion to the ATP calculated to be produced on their dissimilation, provided that sufficient oxaloacetate was available to enable C_2 fragments to enter the Krebs cycle (Blaxter, 1961; Armstrong, 1969). Above maintenance, the stoichiometric calculations agreed with experiments showing that acetic acid was utilized less efficiently than glucose when the basal level was roughage. Studies, notably by Ørskov & Allen (1966*a*,*b*,*c*), showed, however, that acetic acid added to grain rations was efficiently utilized. It was subsequently shown that the type of ration (roughage or grain) affected the efficiency with which acetic acid was used (Tyrrell *et al.* 1976), high values being associated with grain feeding and low ones with roughage diets. This again emphasized that glucose or glucose precursors were necessary for efficient utilization of acetate. The results obtained by Ørskov *et al.* (1979) from complete intra-gastric nutrition studies showed no effect of an increase in acetate relative to propionate; the diets,

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however, contained large amounts of protein and glucogenic amino acids to furnish reduced NADP.

This work which showed that unique single-valued energy coefficients could not be assigned to the products of digestion which were absorbed, was in line with the studies which led to the metabolizable energy system and its recognition that the metabolizable energy of feeds (a rough approximation to the energy of absorbed nutrients but including heat arising from fermentation and hydrolyses in the digestive tract) was used with varying efficiency. Much current modelling is concerned with describing the complex interactions between nutrients and of nutrients with the synthetic and degradative processes controlled by the endocrine mechanisms of the body. Such tasks are formidable and their formulation massive in scale; the simple model of Gill *et al.* (1984), for example, involves 158 equations and well over fifty parameters. This model deals with the metabolism of absorbed energy-yielding nutrients only; it does not include the rumen dimension. These attempts to systematize knowledge are interesting. They do not add to knowledge and it is doubtful if, in the immediate future, they will allow a greater precision to be obtained in the practical task of feeding animals.

Some present problems in assessing nutrient demands

There is a number of real problems related to the assessment of nutrient responses, or perhaps better in view of the difficulties in defining nutrients, feed responses, that remain to be resolved. Some are clearly of practical importance in arriving at better predictions of responses in commodity output from ruminant animal industries. Others relate to the adequacy of present conceptual frameworks of idea.

A distinction has emerged in the practical approach to the energy metabolism of pigs in that the efficiency of use of dietary energy for net synthesis of protein is recognized to be less than it is for body fat. In the Agricultural Research Council's (1981) *The Nutrient Requirements of Pigs*, the preferred value for the efficiency of utilization of metabolizable energy for fat synthesis is 0·74 and for protein synthesis 0·54. Investigations with ruminants have given a wide range of values (for example, see Geay, 1984). Whether in growing ruminants it will be possible to assess energy requirements for protein deposition separately from those for lipid deposition and yet retain the clear relation between type of diet and its utilization remains to be seen.

A second problem equally relates to the separation of net energy into components, namely that of nutritional effects on the partition of fat and protein between milk and body gain or loss. The work commenced by Yates *et al.* (1942) showing that additional feed was partitioned and the work that followed (Blaxter, 1966; Broster, 1972; Broster & Broster, 1984) has yet to be explained in physiological terms.

A third problem relates to the variation between animals in their fasting metabolism and hence maintenance needs. This variation is real and occurs in other species (Blaxter, 1985) and suggests that there are individual differences in the work they do in a thermodynamic sense. To achieve any further refinement of feeding systems an identification of animals with high or low metabolic rates seems essential, as essential as identifying those with high or low rates of tissue protein deposition.

Finally, one of the major problems in ruminant nutrition still relates to the reason for the high heat increments associated with roughage feeding compared with concentrate feeding. This was first uncovered by Zuntz & Hagemann (1898), was exemplified by Kellner's (1908) studies with pure nutrients and normal feeds and appears to be only partly explained by the hypothesis that acetic acid can only be utilized efficiently in the presence of glucogenic material.

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