Host animal—rumen relationships

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In nutritional terms, the ruminant can benefit from microbial fermentative and synthetic processes which transform 'non-nutrients' (e.g. cellulose, non-protein-nitrogen) to nutritionally useful substances; but it suffers simultaneously from some less beneficial consequences of microbial fermentation which may degrade or alter dietary nutrients. The nature and amount of food eaten by the animal affects directly the substrate supply to the microbes and hence the amounts and proportions of end-products digested and absorbed. The duration of fermentation and the extent to which fermentation proceeds are affected by rates of digesta flow, influenced in turn by both dietary and animal characteristics which are variable. This, in turn, introduces variability in nature and proportions of products of fermentation, and in the sites of digestion of protein and carbohydrate, particularly those that have significant consequences for the nutrition of the host animal (Egan, 1980).

This paper examines three aspects of the host animal—rumen inter-dependencies and interactions which have major significance in the protein nutrition of the ruminant; the recycling of nitrogenous substances to the reticulo-rumen, the relationship between 'physical' and 'metabolic' factors which affect level of feed intake, and the 'biological value' of microbial protein in nutrition of the host animal.

The effectiveness of recycling of nitrogen to the rumen

There is ample evidence that on many roughage and concentrate diets, there is a net gain in N between the mouth and the duodenum (Table 1). The magnitude of this gain cannot yet be adequately predicted, but as has been recognized for many years, represents a potentially important contribution to the N economy of the ruminant. Protein yield at the duodenum is the functional term to describe protein supply for the host ruminant animal. If we are to take maximum advantage of the potential which exists for efficient use of dietary N, the understanding and prediction of effective N recycling are of major significance. Reliable physiological determinants and biochemical stoichiometries in the use of recycled N in microbial protein synthesis have not yet been established with sufficient accuracy to allow prediction. As much as 6 g of extra N (Beever *et al.* 1969) has been measured in flow of digesta to the duodenum but generally values for the recycled N contribution are a modest 1 or 2 g (Egan, 1974).

The source, nature and magnitude of these N additions has been debated during the last 20 years (Houpt, 1959; Somers, 1961; Egan, 1965*a*; Nolan & Leng, 1972; Allen & Miller, 1976; MacRae & Re ds, 1979) and the views range from

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Table 1. *Intake and net gain in nitrogen (as non-ammonia-N) between mouth and duodenum for a range of diets fed to sheep (g N/d)*

Diet	Intake	Net gain	Characteristic considered important by authors	
Hay	5·1	3·6	Low N:DOM	Clarke *et al.* (1966)
Hay and maize	7·3	4·3	High fermentable CHO	Clarke *et al.* (1966)
Forage oats	6·2	3·7	Low N:DOM	Hogan & Weston (1969)
Dried grass	27·0	5·5	Low solubility of diet N	Beever *et al.* (1969)
Wild oat	1·8	0·6	Low N:DOM, low intake	Egan (1974)
Wheat hay	5·7	0·9	Low N:DOM	Egan (1974)
Sainfoin	20·2	2·6	Low solubility of diet N	Egan & Ulyatt (1980)
Hay	11·0	4·6	Low N:DOM, endogenous protein	Nolan & Leng (1972); Beever *et al.* (1969); MacRae & Reeds (1979)
Heather	5·0	3·4	Low N:DOM, endogenous protein	R. C. Siddons (unpublished results)

enthusiasm about the potential, to doubts about significance. The quantitative measurements can be made only by judicious use of tracer isotopes (Cocimano & Leng, 1967; Nolan & Leng, 1972; Kennedy & Milligan, 1978). However, the nature of the processes involved allows for significant departures from the ideal conditions of mixing (assumed to operate in isotope studies) and thus leads to uncertainty about the direct and indirect influences, particularly of the blood urea-N contribution, to rumen N metabolism. Different techniques used in measurement also present a source of apparent contradictions. In general terms, major gains in N

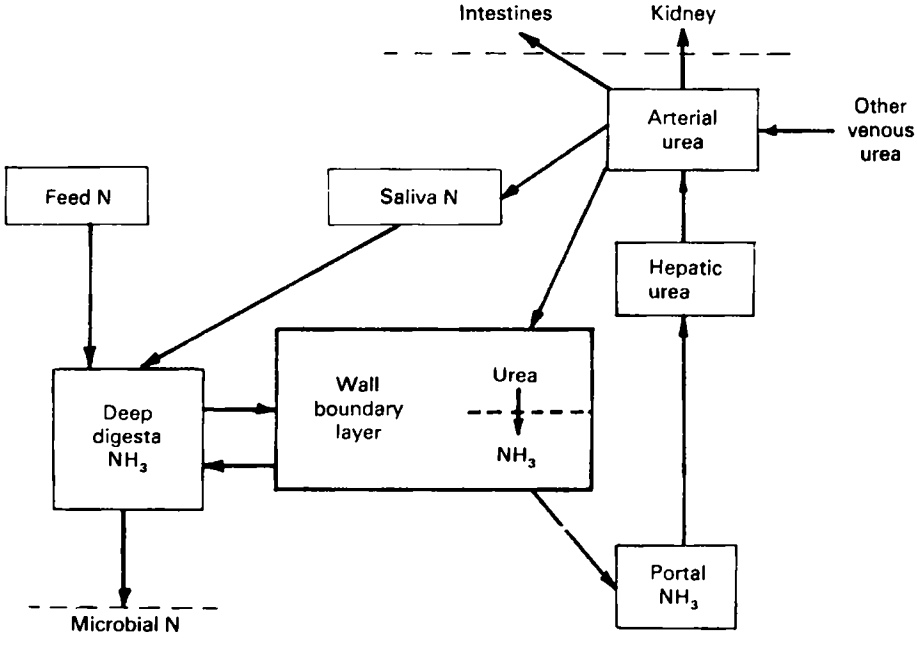

Fig. 1. Flow diagram for nitrogen recycling to the reticulo-rumen.

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between the mouth and the duodenum appear to be associated with use of salivary N and significant capture of blood urea N when degradability of dietary N is low, or when the efficiency of N capture associated with rapid fermentation rates is high, usually in the presence of starch or sugar. The 'model' proposed in Fig. 1 is a representation of the processes involved which would account for all observations made so far.

In this model there are three levels of control, (1) the potential, which depends on the level of urea in the blood and of nitrogenous components in the saliva, (2) the translocation, which depends upon mixing of saliva with digesta, rumen wall permeability to urea, the diffusion gradients and mixing of NH_3 derived from recycled urea, (3) the efficiency of capture, which depends on microbial affinity for ammonia. When these are treated as mixed variables, considering only irreversible loss values and transfer quotients for isotopic labels, the potential for animal factors to intervene disappears particularly as this affects mixing of NH_3 with the digesta. It is clear that the rate of production of urea and the proportional distribution to alternative pathways of excretion is important (Egan & Ulyatt, 1980). On different diets, however, differences in urea production (measured by [^{14}C]urea irreversible loss rate) are not simply paralleled by differences in plasma urea concentration; (Cocimano & Leng, 1967; Weston & Hogan, 1967; Egan & Ulyatt, 1980) nor is urea clearance across the kidney simply related to urea concentration (Thornton, 1970; Egan & Ulyatt, 1980). Consequently the potential for urea movement into digesta or into the fluids which enter the digestive tract (if related to urea concentration in plasma) is not solely a function of rate of urea production from NH_3 absorption or amino acid catabolism, though both these inputs will affect urea production rates. It is clear that [^{14}C] and [^{15}N]urea provide different types of measurement. [^{14}C]urea, when hydrolysed in the gut by micro-organisms, yields $^{14}CO_2$ to a large pool with little likelihood of reincorporation into urea. Therefore the difference between [^{14}C]urea irreversible loss and urea excretion in urine is a measure of the entry of urea into the digestive tract. [^{15}N]urea, when hydrolysed, yields $^{15}NH_3$ into the pool for reabsorption or capture by micro-organisms; most reabsorbed $^{15}NH_3$ will reappear in urea, thus giving a lower irreversible loss than occurs with [^{14}C]urea. Capture by bacteria that adhere to rumen epithelium will defer admixture of newly synthesized microbial protein until the bacteria or the epithelial cells are shed, resulting in another mixing and timing problem of significance.

The extent of movement of urea into the tract depends upon its clearance into the digestive secretions and its movement across the wall in various regions of the gastrointestinal tract. There are many ways in which the total urea movement and the distribution of movement of urea to various sectors of the gut can vary. Relative permeability of the rumen wall has been suggested to vary (Engelhardt *et al.* 1978), and it has been suggested that the entry of urea into the reticulo-rumen is enhanced when ruminal ammonia concentration is low (Houpt, 1970; Kennedy & Milligan, 1978). Fig. 1 shows the ways in which net urea entry may be inhibited by high ruminal NH_3 concentration. This also provides the means

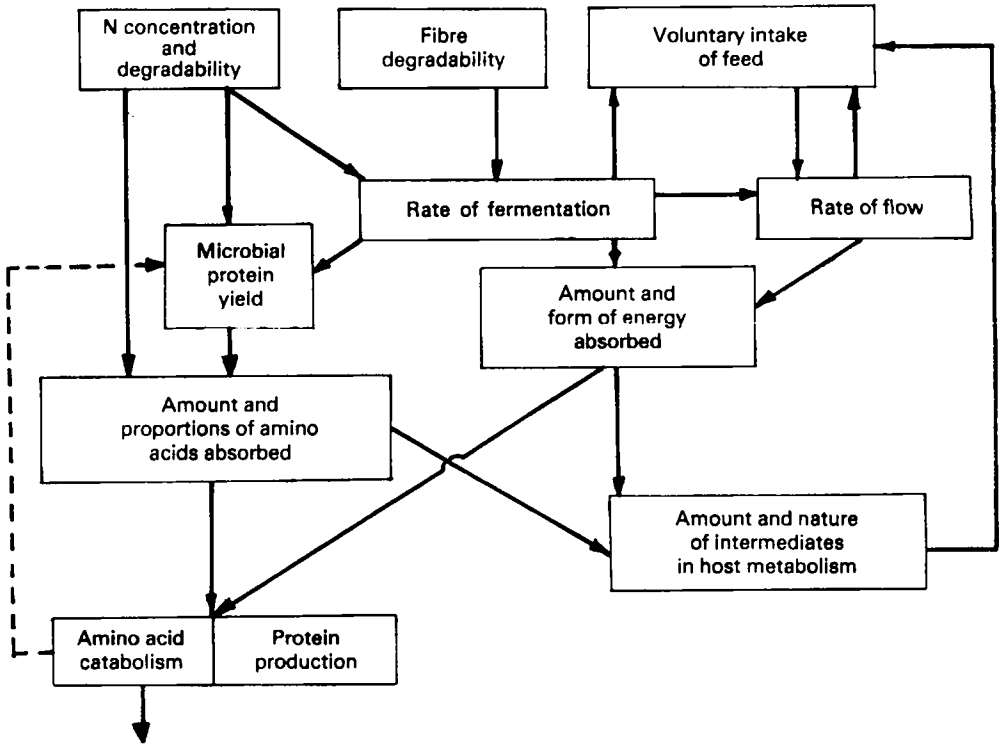

Fig. 2. Flow diagram for factors involved in control of voluntary intake in ruminants.

whereby virtually total reabsorption of plasma urea-derived NH_3 (carrying ^{15}N label, if present) can occur, but the efficiency of use of 'deep digesta' NH_3 may be improved. The potential for more effective N capture can be seen to exist if (1) the mixing of digesta is made more effective or (2) the 'deep' ruminal ammonia concentration is reduced, thus increasing the diffusion gradient from the 'wall boundary layer' of urea-derived NH_3. Mechanisms probably exist to allow increased redirection of the total urea production across the gut wall (Egan & Ulyatt, 1980), to increase the proportion which goes to the reticulo-rumen rather than to other sections of the gut and to improve the efficiency of capture of urea-derived NH_3 by the micro-organisms of the reticulo-rumen.

N economy and voluntary feed intake

The host animal's response to extra protein provision regardless of its source can be expressed fully only if energy intake is also increased to an appropriate level. Part of the animal's response to improved N provision often involves increased voluntary feed consumption. The factors involved in the control of voluntary feed intake by the ruminant are represented in Fig. 2. The mechanisms operate simultaneously, and interact, though on different diets different individual factors may be dominant. The following are of particular relevance to this discussion. Dietary and digesta N and absorbed products of protein digestion appear to affect

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intake in two ways; (1) effect on digestion and rate of movement of digesta, thus influencing the physical controls of food intake; (2) effect on the protein provision to the animal which influences the metabolic response to the diet and the metabolic controls of food intake. Separation of these two effects is necessary if the nature and amount of dietary N is to be optimized to ensure most efficient use of feed resources for animal production.

Elliot & Topps (1964) drew attention to a close correlation between N concentration in the diet and level of voluntary feed intake for sheep fed on roughage diets. Because dietary N concentration and digestibility are broadly correlated for roughage diets, this might be viewed as an expression of the general positive relationship between digestibility and voluntary consumption of roughage, though intake and digestibility were less well correlated in that study.

The accepted conceptual model assumes that this relationship involves a maximum capacity of the reticulo-rumen for digesta, and a rate of reduction of digesta volume (or mass), which is dependent upon fermentation and particle size reduction. These together limit the rate at which available capacity is created for further intake, and involve an interaction between animal and microbial factors. Changes in metabolism of the host introduce a further factor involved in the relationship between dietary protein and intake. It was noted that in some roughage diets protein infused into the small intestine resulted in enhanced intake (Egan, 1965*b*). The magnitude and consistency of intake responses was often greater when protein or even non-protein-N was provided in the diet. Other studies have provided conflicting results (Bryant *et al.* 1970; Weston, 1967, 1971), but some have extended the scope of these observations and showed similar effects in young sheep (Ørskov *et al.* 1971). It is clear that with some roughage diets of low N content, intestinally-digested protein can have a beneficial effect on intake and this can not be attributed to recycling of N to the reticulo-rumen (Egan, 1965*b*). The response involves an increase in the volume (mass) of reticulo-rumen digesta, despite the fact that in the unsupplemented animals it is impossible to increase the reticulo-ruminal digesta load (Egan, 1970, 1972). This response was interpreted as one associated with making good the deficiency of protein in the host animal and an examination was made of relationships between voluntary feed intake, the yield of protein (both dietary and microbial) at the duodenum per unit digestible energy (DE) intake (P:E value) and the response in voluntary intake to a supplement of protein at the duodenum (Egan, 1977). There was a positive and significant correlation between intake and P:E value. In 4 to 6-months-old sheep, for diets where protein provides about 10% of DE an intake response to additional intestinally-digestible protein is likely. Where protein provides about 14% of DE no response in intake has been observed. Neither of these values appears to coincide with estimated requirements for maximum growth rates (Black, 1971; Egan & Walker, 1975) and intake responses are not consistently related to the magnitude of the protein deficit for diets where protein provides less than 14% DE. This is understandable if the capacity for response to supplements of intestinally available protein is limited by other more or less independent factors such as rate of

reduction of reticulo-ruminal digesta load. While the specific mode of action of protein has not yet been elucidated, the intake of sheep will also respond positively to small amounts of mixtures of essential amino acids (e.g. methionine and threonine) infused into the abomasum (Fennessy, 1976) in dietary circumstances where protein responses had been observed. This supports the view that intake control mechanisms are responsive to amino acid supply to the host animal. Certainly, imbalances of amino acids and the correction of imbalances affects intake in sheep (Egan & Rogers, 1978). Such observations underline the nature of the host animal–rumen interactions in the dietary protein response. For roughage diets, both ruminal N deficit, which may limit the microbial fermentation rate and hence the rate of removal of digesta from the reticulo-rumen, and host animal amino acid insufficiency, which will arise with low efficiency of synthesis of microbiol protein and low contribution from undegraded dietary protein, can act as factors limiting energy intake. The extent to which one of these factors can be limiting without the other being also involved deserves attention, as the relationships may well alter with age and physiological state of the animal, as well as being different in species. Intake response to protein probably depends upon multiple relationships involving, (1) tissue amino acid requirements of the host animal, (2) the rates of provision of amino acids derived from dietary protein not degraded by micro-organisms and from microbial protein, (3) the rates of provision of microbial fermentation end-products and other energy-yielding substrates absorbed, and (4) the rates of removal of digesta load from the reticulo-rumen, the last in turn dependent upon microbial fermentative activity and rumination rate to 'dissolve' and comminute digesta particles.

Amino acid requirements and biological value of microbial protein

Because ruminants start life, as do all mammals, receiving milk proteins which are presumably well balanced in amino acids, this does not mean that relative proportional requirements for amino acids are the same as those of other mammals or that they remain constant throughout life. There are three factors which contribute to this point of view.

First, the proportional rates of turnover and accretion of proteins in body tissues, wool etc. change. This leads to changes in relative requirements for amino acids in most species as animals approach their mature size.

Secondly, the ruminant animal receives a different pattern of energy-yielding substrates and is dependent upon gluconeogenesis to meet the true physiological glucose requirement and upon gluconeogenic substrates to ensure adequacy of three carbon intermediates at the cellular level. The balance of utilization of amino acids in catabolic pathways may well differ, even for essential amino acids, from those found in the non-ruminant.

Thirdly, the ruminant has evolved a mature animal metabolic pattern which may relate to the provision of amino acids in a relatively constant proportional relationship; apparently not well balanced if compared with the patterns required by non-ruminant animals. In particular, the ruminant is likely to receive less than

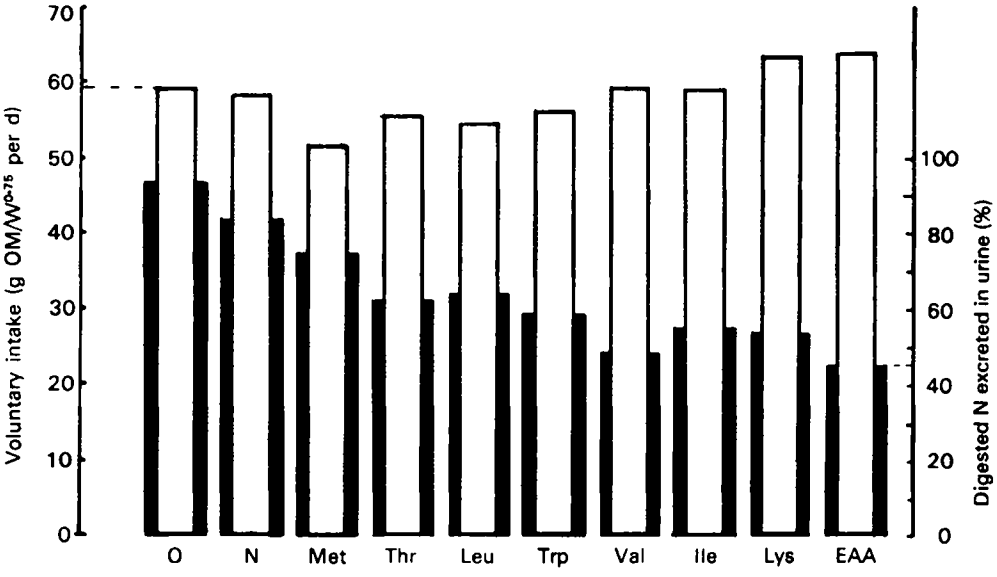

Fig. 3. Responses in (□) intake and (■) nitrogen retention to essential amino acid mixtures infused into the abomasum (2·6 g N/d) of animals fed on chopped wheaten hay (59% digestible; 1·05% nitrogen) EAA mix; Met, Thr, Trp, Lys, Leu, Ile, Val.

estimated needs of methionine and threonine (P. F. Fennessy and A. R. Egan, unpublished results). The ruminant may have gained different adaptive mechanisms or lost some which are important in other species.

For these reasons, the amino acid requirements of the ruminant makes a fascinating study. Estimates of the requirements of young ruminant sheep have been developed through a sequence of approximations derived from infusion experiments and using responses in 7 d N retention as the criteria of efficiency of N use. The latest approximation (A. R. Egan, P. F. Fennessy and J. D. Radcliffe, unpublished results) indicates that microbial and plant proteins are not as poorly balanced as was suspected from our earliest estimates (Egan & Walker, 1975).

This raises the question of the metabolic significance of the adoption by animals of the ruminant herbivore system, an evolutionary process linked to the use of microbial and plant proteins. Are these proteins poorly balanced in amino acid content, relative to the animal's proteins and the need for amino acids to meet anabolic requirements while suffering at the same time differential 'wastage' in catabolism? If they are, which amino acids are required to complement these proteins? If they are not, how are the amino acids available for protein synthesis balanced with respect to the relative rates of amino acid catabolism? Is the ruminant more, or less sensitive than other species to an amino acid imbalance, deficiency or toxicity? In particular, which amino acids are most critical and produce the greatest physiological embarrassment when supplied in inadequate amounts or in excess?

Our latest approximation indicates that microbial protein together with more than one amino acid (and probably 5 or 6, including methionine, threonine, leucine,

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trytophan, isoleucine and lysine) is necessary to maximize N retention on 'protein deficient' microbial–plant protein-yielding diets (Fennessy, 1976).

Methionine toxicity appears in some individual sheep at sufficiently low levels of addition to make it more effective to supply a mixture of methionine, threonine, etc. Provision of cystine appears to have less effect on efficiency of retention of methionine than does provision of extra energy, i.e. cystine has little specific sparing effect on methionine.

The variability between individual sheep within a breed is very great and more so between breeds. However, the important point is that amelioration of a likely insufficiency of a single amino acid may have undesirable effects; and addition of extra protein rather than extra specific amino acid is the safest procedure metabolically and probably the cheapest way of meeting any amino acid inadequacy. This is true even if the protein is of microbial origin because although the efficiency of use of the truly digested amino acids is about 80% and certainly less than 100%, it seems likely that amino acid catabolism can only be marginally reduced by 'improving' essential amino proportions. In other words biological value of proteins for ruminants may not be much better than that attributable to microbial protein; it is possible that no protein digested in the small intestine has a biological value of 100% for the ruminant.

The points which I wish to draw from this are these: firstly, that we know little of the metabolic basis of amino acid use in ruminants, but we assume that microbial and plant protein are of markedly lower biological value than would be some other proteins of different amino acid content. I believe that we are not safe in making that assumption. Secondly, variability between individuals and breeds exists in relation to responsiveness to protein and amino acid mixtures, and to over- or under-supply of individual essential amino acids. This variability may offer scope for selection of lines which use microbial protein more efficiently through higher efficiencies in anabolic use of methionine and threonine which are in short supply. It may also offer scope to select lines which will respond better to alternative protein sources of different amino acid composition.

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