ANIMAL RESPONSE INDICATORS

RECENT ADVANCES IN QUANTIFYING RUMINANT DIGESTION

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Introduction

Historically, the problem of understanding the biological mechanisms of an animal was approached by simply subdividing the complete organism into functional units, or organ systems. Such systems were then studied separately. This logical process was followed inexorably to molecular level, spawning many new and independent branches of biology such as biochemistry, biophysics and molecular biology. In the process, some fundamental mechanisms such as the genetic code have been elucidated. However, it is now becoming clear that the whole is more than simply the sum of its parts. As a result, integrative physiology is becoming increasingly important in order to understand the intact organism. The process, which started when Harvey elucidated the role of the heart in pumping blood around the body, has now come full circle. The organism was approached as a "Black Box" which consumed feed, processed this to extract useful energy, and excreted the waste products. By ignoring the mechanisms inside the "Black Box", it was possible to build up an extensive body of knowledge concerning the interactions between input (intake of feed and water) and output (maintenance + production + waste products), which is unfortunately purely descriptive in nature. The ideal towards which all animal science research should be directed, is to obtain a predictive model which may be used to optimise animal production. The problem with purely empirical models is that solutions that fall outside the original parameters are usually unpredictable. And so another round of experiments are carried out in an attempt to include the new circumstances. It is only by examining actual mechanisms that truly predictive models can be constructed, and valid conclusions can be made which will take into account the extensive variation inherent in biological systems.

When Jan van Riebeeck landed at the Cape to establish a provisioning station for the Dutch East India Company, he obtained most of his animal products from the indigenous Koi peoples. As the settlement grew, and as people pushed into the hinterland, so the perception arose that the "superior" breeds from Europe should be brought in to "improve" the local stock belonging to the local people, who were, after all, ignorant of the theory and advantages of breeding programmes. This perception grew into an entrenched paradigm, that led to the virtual extinction of many local breeds of sheep and cattle. At the same time, vast herds of wild herbivores thrived on the same grasslands of Southern Africa despite regular periods of low rainfall. Most of the total land area of Southern Africa (102 272 323 and 17 192 709 hectares for the RSA and the homeland areas respectively) is taken up by farms (83 064 408 and 16 111 523 hectares respectively). However, only a small fraction of this farmland is arable (15 927 198 and 2 034 648 respectively), leaving vast tracts suitable only for grazing ruminants. Many grasses contain little protein during winter, which corresponds to the driest period of the year. As a result, grazing herbivores often have to contend with a protein content (crude protein referred to as CP) of less than 3% ('t Mannetje 1984). The grazing ruminant may remain in a positive nitrogen balance at CP levels above 6%, in contrast to most monogastric mammals which require about 12% CP or more.

In order to answer this type of question it is necessary to adopt new technologies and approaches, which will enable the mechanisms to be more deeply probed. In this review, I propose to examine this process in terms of understanding digestion and its contribution to the nitrogen metabolism of the whole animal. Current knowledge of the processes involved in the digestion and utilisation of food to support growth, reproduction and production is extensive. The gross metabolism of the major metabolites has been elucidated, and it is unlikely that significant metabolic pathways remain to be revealed. In addition, much is known of the hormonal regulation of nutrient utilisation (Bray 1986; Gibbs & Smith 1986; Vernon 1986; Tucker & Merkel 1986). However, effective manipulation of the metabolism to improve livestock production must be based on quantitative data, which may be obtained from a combination of isotope dilution and arteriovenous difference studies.

Whole body turnover of key metabolites may be estimated in the conscious, undisturbed animal by isotope dilution procedures (Shipley & Clark 1972). Important assumptions of this approach include the use of a labelled substrate of high specific radioactivity and of insufficient mass to provoke a hormonal response, adequate mixing of the labelled substance with the body pool of substrate, and steady state conditions. Using this approach, considerable data has been obtained on the whole-body metabolism of metabolites such as acetate (Pethick *et al.* 1981), glucose (Bergman 1964; Bergman 1963; Baird *et al.* 1983), long-chain fatty acids (Pethick *et al.* 1983; Pethick *et al.* 1987), ketone bodies (Bergman *et al.* 1963), glycerol (Bergman *et al.* 1968), volatile fatty acids (Bergman *et al.* 1965; Bergman *et al.* 1966), amino acids (Bergman 1986; Bergman & Heitmann 1978; Wolff & Bergman 1972), to name but a few. Recent advances in this field include the use of stable isotopes, to minimise the environmental risk associated with radioactive isotopes. For example, 13C-labelled compounds have been used to determine the whole-body turnover of metabolites such as acetate, glucose and alanine (Bertoni *et al.* 1994), while 15N has been used for some time to follow the metabolism of amino acids and urea (Dixon & Nolan 1986; Nolan & Stachiw 1979). Whole-body protein content may be estimated by measuring the plasma creatine concentration,

which correlates well with body condition score (Bertoni *et al.* 1994).

Digestive tract

Initially, this organ system was treated as a "Black Box" by animal scientists only interested in what disappeared during passage of the digesta through the digestive tract. Earlier studies were carried out on a whole-body basis, and provided data only on apparent digestibility. Soon it was realised that the output data (faeces) was contaminated by contributions from bacterial fermentation in the large intestine, luminal secretions, serosal cells, etc. Techniques were adapted to compensate for these factors, resulting in more accurate estimates of "true" digestibility (Green *et al.* 1987; Huisman *et al.* 1992; Bayourthe *et al.* 1993).

The disappearance of a nutrient across a specific segment of the digestive tract may be estimated by measuring the difference between input and output from that segment. Although simple in conception, the actual estimate of partial digestion may be confounded by several factors such as accurate determination of digesta flow rate, the addition of that nutrient by the wall of the digestive tract to the digesta and other metabolites that may interfere with the accurate determination of the nutrient in question. Of all the factors that bedevil in vivo partial digestion studies, the one that contributes most to the uncertainty of the results is the determination of digesta flow. Since the total flow of nutrient is calculated from the product of digesta flow and concentration difference, it is clear that any significant discrepancy in the estimate of digesta flow will be reflected in the calculation of nutrient flow. Despite the practical difficulties involved with cannulated animals, marker stabilities, differential liquid and solid flow rates, etc., a considerable body of knowledge has been accumulated using these techniques. Obtaining similar data on free-ranging animals is considerably more difficult, and it is not surprising that so little of this data exists. As an example of what has been obtained in this manner, the following data on protein digestion and metabolism in the small and large intestines of ruminants is given.

Nitrogenous compounds may enter with the digesta flowing from the abomasum (1.76-2.29 g N/d/kg $^{0.75}$), or may be added with the bile or pancreatic juices (0.09-0.20g N/d/kg $^{0.75}$), or may be added via the succus entericus and endothelial sloughing (0.9-1.06 g N/d/kg $^{0.75}$), as estimated for an intake of about 1 g N/d/kg$^{0.75}$ via the feed (Van der Walt & Meyer 1988). Of this nitrogen, a large proportion (64-69%) is in the alpha-amino-linked form (Clarke *et al.* 1966), and is therefore available for absorption from the small intestine.

While the concentration of alpha-amino-linked compounds arriving at the duodenum is relatively constant (4.1-5.5 g N/100 g dry matter (Harrison *et al.* 1973), the flux increases (0.60-1.36 g N/d/kg $^{0.75}$) with the amount of nitrogen taken with the feed (0.34-1.65 g N/d/kg $^{0.75}$) (Bunting *et al.* 1987; Clarke *et al.* 1966). The greatest increase is in the amount of amino acids derived from unfermented feed (50% as compared to 15% for microbial N (Bunting *et al.* 1987). The greatest increase in concentration of individual amino acids in digesta arriving at the duodenum is in methionine, lysine, tryptophan, cysteine and isoleucine (Coelho da Silva *et al.* 1972). The apparent digestibility of the total amount of à-amino-linked material passing down the small intestine is between 66% and 72%, while individual values range from 47% for histidine to 80% for methionine (Coelho da Silva *et al.* 1972). Using regression analysis, true digestibilities have been shown to be somewhat higher, with a mean of 70%, ranging from 52% for cystine to 86% for arginine (Lindsay *et al.*. 1980). The following groups of amino acids are absorbed at descending rates: (a) isoleucine, arginine, methionine, valine; (b) leucine, lysine, phenylalanine; © aspartate, serine, tyrosine, alanine; (d) alanine, proline, threonine; (e) proline, threonine, glutamate, histidine; and (f) glycine (Armstrong & Hutton 1975). Although it was initially assumed that organic nitrogen is assimilated from the small intestine solely in the form of amino acids, relatively large amounts of small peptides are also absorbed (Armstrong & Hutton 1975). Amino acids appear to be absorbed mainly from mid to lower ileum (Johns & Bergen 1973), although the highest rate of absorption occurs in mid-jejunum (Ben-Ghedalia *et al.* 1974). The caecum and proximal colon appear to be the major sites of fermentation and absorption of fermentation end-products in the large intestine (Dixon & Nolan 1982). The recycling of nitrogen within this region and between the large intestine and the rumen has received most of the research attention.

A total of about 0.6-0.9 g N/d/kg $^{0.75}$ enters the caecum as amino acids (40-60%), urea (15%), nucleic acids (3-4%) and ammonia (1-13%) of sheep fed 800 g Lucerne hay per day (Clarke *et al.* 1966; Coelho da Silva *et al.* 1972). About 0.15 g N/d/kg $^{0.75}$ urea may diffuse from the blood into the caecum, adding to the nitrogen pool (Dixon & Milligan 1984). Hindgut fermentation appears to be limited by the availability of readily-fermentable carbohydrate (Oncuer *et al.* 1990; Orskov *et al.* 1970). Increasing the energy supply increases faecal nitrogen output while decreasing the excretion of nitrogen via the urine (Orskov *et al.* 1970; Thornton *et al.* 1970). This implies that nitrogen is sequestrated by microbial anabolism, fuelled by the additional energy, thereby removing it from the urea/ammonia pool and trapping it as microbial protein, to be largely excreted in the faeces. Recent advances in improving the accuracy and precision of digestibility determinations include the possible use of purines as microbial markers (Stangassinger *et al.* 1994). The practical application of this techniques is complicated by the problems associated with assessing the endogenous purine contribution. On the other hand, the use of the long-chain alkanes have been identified as the best markers for organic matter intake (C33), faecal output (C32) and intake (C32 + C33) (Mannerkorpi *et al.* 1994). The measurement of in vitro fermentation rate may be automated (Cone 1994), thereby allowing greater precision to be attained, as well as increasing the amount of data that can be collected by any one person. Sonographic techniques have been coupled to video technology to record reticulo-rumen contractions in cattle, sheep and goats (Midasch *et al.* 1994), while the omasum may be directly sampled from the ruminal cannula (Huhtanen *et al.* 1994). The amount and composition of saliva may be determined by means of a direct cannulation method, using the technology developed by clinicians for human surgery (Goritz *et al.* 1994). Near-infrared spectrometry may be used to estimate the degree of microbial nitrogen contamination of nylon bags incubated in the rumen (Lecomte *et al.* 1994).

Nutrient utilisation

The next phase in following the uptake of nutrients through the wall of the digestive tract requires new techniques that will allow the metabolism of the enteric cells to be determined and the

portal/mesenteric appearance of metabolites to be measured. Nutrients that are absorbed from the lumen of the tract pass through the cells that make up the wall of the tract en route to the portal circulation. In order to quantitatively measure this flux, it is necessary to examine the metabolism of this organ system. Nutrients may reach these cells via the lumen-portal or arterial-portal route. As a result, any quantitative investigation of in vivo digestive tract metabolism must examine the actual uptake and output rates via both of these routes, necessitating the use of radio-active markers. In this review, I will concentrate on data obtained via the arterial-portal model, as very little data has been obtained using the alternative approach. This is one of the avenues that requires further investigation.

Aside from determining the difference in nutrient concentration between the arterial and venous vessels, it is also essential that the blood flow through the portal-drained viscera and its constituent parts be estimated as accurately as possible. When combined with the arteriovenous technique, the use of labelled metabolites may be used to obtain quantitative data on the uptake and output of these compounds and their immediate metabolic products from any organ system which has a clearly defined arterial input and venous drainage (Bickerstaffe *et al.* 1974). Much of the current knowledge of the metabolism of the mammary gland (Annison & Linzell 1964), hind-limb (Oddy *et al.* 1985), liver (Bergman & Wolfe 1971; Brockman *et al.* 1975; Peters *et al.* 1983) and the portal-drained viscera (Bergman & Wolfe 1971; Bergman 1986; Van der Walt *et al.* 1983) has been obtained in this way. Blood flow in these earlier studies was measured by means of a dye-dilution principle (Schambye 1955; Huntington *et al.* 1990) (usually p-amino hippuric acid, sometimes indocyanin green), which gives an average flow rate over the period of the infusion. More recent studies using the transit time Doppler principle allows the flow to be continuously recorded during the experiment and has shown that such flows may be quite variable, even during so-called steady state conditions (Giles *et al.* 1989). This technological advance will allow the effect of short-term changes to be followed and quantitatively expressed.

Blood flow

The development of techniques to measure this flow illustrates the influence of technology on progress. Methods that have been commonly used include dye dilution, more specifically p-amino hippurate (PAH) (Heitmann & Bergman 1978a; Pell *et al.* 1983; Bergman 1986; Bergman & Heitmann, 1978; Wolff & Bergman 1972; Wolff *et al.* 1972; Heitmann & Bergman 1978b; Tagari & Bergman 1978), radiolabelled microbeads (Barnes *et al.* 1983a; Barnes *et al.* 1981) and transit-time ultrasound (Doppler) (Barnes *et al.* 1983b). The dye-dilution method provides an average flow over the experimental period, and assumes that the flow, like the metabolic status of the animal is at steady state. This is the value usually required to calculate nutrient flux. The microbead approach, on the other hand, determines the flow in a particular tissue at a point in time, i.e. the time of injection. While this may not be suitable for most flux calculations, it allows the distribution of blood flow to various regions of the organ under investigation to be measured at the time of injection. The last mentioned method, the Doppler technique, requires that a probe be implanted around the vessel supplying (or draining) the organ under investigation, and will give a continuous record of the blood flow during the entire course of the experiment.

Although the splanchnic bed only constitutes 7-13% of total body mass, it takes 30-40% of the cardiac output. This substantial partitioning of the cardiac output to the splanchnic bed is all the more remarkable when compared to the relative size of the organs making up the splanchnic bed (Huntington 1990). Furthermore, the metabolic importance of this region is suggested by the oxygen demand, which may amount to 40-60% of the total body uptake of oxygen (Huntington 1990; Burrin *et al.* 1989). Within this tract, the liver is most remarkable, with a mass of only 1-2% of total body mass, yet taking up 22-35% of the total oxygen uptake (Huntington & Reynolds 1987). The sheer magnitude of this oxidative demand highlights the importance of hepatic intermediary metabolism to the animal.

As mentioned above, the splanchnic bed of fed cattle is perfused by about 38% of the total cardiac output (Huntington *et al.* 1990), a value which may decline to about 32% during fasting. The actual flow, when expressed in terms of metabolic mass, through the portal-drained viscera (PDV) would appear to be about 125 ml/min/kg $^{0.75}$ in non-pregnant, non-lactating cattle fed close to maintenance (Reynolds & Huntington, 1988). A similar value has been obtained in sheep under similar circumstances (Lush & Gooden 1988; Mineo *et al.* 1991), i.e. 102-133 ml/min/kg $^{0.75}$. Total hepatic flow is made up of a portal (ca 80%) and an arterial component (hepatic artery, ca 20%) (Mineo *et al.* 1991; Reynolds *et al.* 1988). The portal component may be further subdivided into that coming from the anterior mesenteric vein (53 ml/min/kg $^{0.75}$, or ca 42% of the PDV flow) and that draining the rumen (53 ml/min/kg $^{0.75}$) (Reynolds & Huntington 1988). The flow of blood through this region has been shown to be proportional to the level of feed intake in both sheep (Lush & Gooden 1988) and cattle (McGuire *et al.* 1989). In sheep, portal flow declined from 126 to 95 and to 69 ml/min/kg $^{0.75}$ when the intake of chopped lucerne hay was reduced from 1000g to 75% and then 50% of maintenance. In lactating dairy cattle, the flow fell from 229 to 127 ml/min/kg $^{0.75}$ when dry matter intake was restricted from 15.7 to 9.9 kg/day. Splanchnic flow may also be affected by lactation, values ranging from 216 (Huntington 1984) to 229 (McGuire *et al.* 1989) to 257 (Reynolds *et al.* 1988) ml/min/kg $^{0.75}$ have been recorded for lactating dairy cows, values which are almost double those found in dry cows. While some of this increase may be due to the concomitant increase in intake, at least some appears to be due to a direct effect of lactation. The effect of pregnancy is not clear; a value of 124 ml/min/kg $^{0.75}$ was obtained from one study (Van der Walt *et al.* 1983) comparing pregnant to lactating ewes falling within the range for non-pregnant sheep (102-133 ml/min/kg $^{0.75}$). A factor that has not been investigated in ruminants, is the effect of ammonia in the portal circulation. In rabbits, however, an infusion of ammonia into the portal vein that results in a slow, small rise in the peripheral concentration of ammonia causes a significant decrease in portal flow (Debski & Pierzynowski 1985). This has also been demonstrated in sheep (Orzechowski *et al.* 1987).

Gut wall metabolism

Examination of the metabolism of amino acids across the portal-drained viscera illustrates the metabolic complexity of this area, and underlines the inadequacy of current, overly simplistic models.

Small Intestine

The small intestine is the most important site of protein digestion

and absorption of the resultant peptides and amino acids (Tagari & Bergman 1978). While numerous studies have obtained quantitative data for the disappearance of amino acids from the lumen (Clarke *et al.* 1966; Bunting *et al.* 1987; Coelho da Silva *et al.* 1972), the metabolism of these in passage through the gut wall ensures that the mixture of amino acids that appear in the portal circulation will bear little resemblance to that absorbed. For example, the mucosal cells of the small intestine extract glutamine from both the lumen and the arterial blood supply. The rate of uptake is equal to that of glucose, and it is even more important than glucose as an oxidative fuel (Souba 1991). Although it ismainly amino acids that appear on the serosal side of the gut wall, it is now well established that significant amounts of small peptides, chiefly dipeptides, are also transported by systems in the brush border of these cells (Matthews 1972). It is not clear whether the uptake is mediated by specific carriers, or whether the dipeptides are hydrolysed by membrane-bound enzymes, as in the liver (Plauth *et al.* 1991).

Amino acids (and possibly some peptides) are transported via specific carrier systems, most of which may be classified as of the secondary active type. Peptides and amino acids undergo considerable metabolic changes in passage through the wall of the small intestine. Reports suggest that up to 67-71% and 55-57% of amino acids absorbed may be metabolised in the gut wall of sheep fed a high (19.8% crude protein=CP) or a low (15.6% CP) protein diet respectively (Macrae 1978; Tagari & Bergman 1978). Complicating any such analysis, is the uptake of considerable amounts of amino acids from the arterial circulation, which complement the metabolism of lumen derived amino acids. For example, while there is a net absorption of most amino acids from the small intestine, glutamine is removed in large quantities by the tissues of the small intestine of sheep fed at maintenance (Heitmann & Bergman 1978b; Wolff & Bergman 1972), growing lambs fed at maintenance and ad libitum (Burrin *et al.* 1991) and lactating Holstein dairy cows, 8 weeks postpartum (Reynolds *et al.* 1988). Expressed in terms of metabolic mass, the magnitude of this uptake by the tissues of the PDV ranged from about 30 to 56 to 114 to 240 mg N/d/kg $^{0.75}$ respectively. In the latter study, the same cows at 4 weeks postpartum were exporting net amounts of glutamine from the portal-drained viscera. In rats, enterocytes metabolise the carbon skeleton of glutamine to CO_2 (64%) and lactate (11%), and the nitrogen is exported as ammonia (38%), citrulline (28%) and alanine (24%), thus providing a major energy source for these tissues (Windmueller 1982; Windmueller & Spaeth 1974; Windmueller & Spaeth 1975; Windmueller & Spaeth 1980). Furthermore, as much as 33% of this glutamine uptake is transaminated and released as alanine. It is likely that similar reactions occur in ruminant tissues, since both sheep and lambs showed a net export of both alanine and citrulline from portal-drained viscera (Burrin *et al.* 1991; Heitmann & Bergman 1978b; Wolff & Bergman 1972).

Although substantial quantities of urea (up to 85% of all urea transferred to the entire gastro-intestinal Tract (Varady *et al.* 1979) appear to enter the small intestine, in proportion to the blood urea concentration (Engelhardt & Hinderer 1976; Norton *et al.* 1978; Kennedy 1980), lack of any urease activity in the tissues of the small intestine and little activity in the digesta (Egan *et al.* 1986) suggests that most is reabsorbed back into the portal circulation. Little passes on to the large intestine (about 2 g N/d, (Dixon & Milligan 1984), although there are significant amounts of ammonia in ileal digesta (roughly equal to the amount added to the caecal pool from blood urea (Nolan *et al.* 1973).

Large Intestine

Nitrogen is absorbed in net amounts (0.04-0.16 g N/d/kg $^{0.75}$) from this region (Clarke *et al.* 1966; Hecker 1971). Amino acids may well be actively transported across the wall of the caecum and colon, since this has been demonstrated in the rabbit (Hoover & Heitmann 1975) and the horse (Slade *et al.* 1971). The mucosa of the hindgut may also take up amino acids from the blood, as demonstrated in sheep for amino-isobutyric acid (Scharrer 1978). However, it has been suggested that the uptake of amino acids into the blood may be quantitatively unimportant (Wrong *et al.* 1981), compared to the uptake of ammonia (ca 0.15 gN/d/kg $^{0.75}$, (Nolan & Stachiw 1979; Nolan & Leng 1972)). Carbon skeletons of amino acids are rapidly absorbed from the large intestine of rats (Fordtran *et al.* 1964). Volatile fatty acids are absorbed from the caecum of sheep (Argenzio *et al.* 1975), either as passive transport in the dissociated form (in the guinea pig (Engelhardt *et al.* 1989) or as anions in an antiport mechanism driven by bicarbonate (in humans, (Soergel *et al.* 1989)). These fatty acids contribute about 70% and glucose about 30% towards the energy metabolism of the rat colon (Roediger 1989). It is entirely likely that mechanisms similar to that in the rat exist for the absorption of keto and hydroxy acids in sheep.

Portal Flux

Aspects of digestive tract metabolism that have been investigated quantitatively include glucose (Van der Walt *et al.* 1983), lactate (Van der Walt *et al.* 1983), volatile fatty acids (Bergman & Wolfe 1971), ketone bodies (Roe *et al.* 1966), long chain fatty acids (Katz & Bergman 1969), and the amino acids (Wolff *et al.* 1972). These studies have concentrated either on the partial digestion or metabolite turnover approaches. In very few studies have both approaches been used simultaneously. However, the digestion of alpha-linked polysaccharides in the small intestine was investigated by Armstrong and his group (Janes *et al.* 1985), and amino acids (Tagari & Bergman 1978) using the combined technique.

When the net uptake or production of ammonia, urea and à-linked amino acids by the PDV is measured, remarkably constant values of 0.47 to 0.71, -0.39 to -1.12 and 0.26 to 0.54 g N/d/kg $^{0.75}$ respectively, were found in beef steers and lambs fed between 0.74 and 2.90 g N/d/kg $^{0.75}$ (Guerino *et al.* 1991; Burrin *et al.* 1991; Huntington, 1989; Reynolds & Huntington, 1988). When N intake was increased, as a result of post-ruminally added protein (Guerino *et al.* 1991) or lactation-induced increase in dry matter intake (Reynolds *et al.* 1988), the amount of ammonia produced by the PDV increased proportionately, with a good correlation (r^2=0.81, df=9). In the case of the casein infusion, the additional ammonia probably resulted from an increased metabolism of amino acids in transit through the gut wall. A similar relationship was found for the amount of urea taken up by the PDV, although the correlation was much worse (r^2=0.40, df=9), as can be seen in Fig. 1. When the production of alpha-linked amino acids by the PDV is similarly examined, it would appear that the absorption of these was also proportional to intake, although the correlation is not as clear (r^2=0.51, df=9) as that for ammonia, although somewhat better than that obtained for urea. This data seems to suggest that the uptake of amino acids from the PDV only

increases significantly at nitrogen intakes above about 1.8 g N/d/kg $^{0.75}$ (See Fig. 2). The quantitative role of peptide transport between the PDV and the liver does not seem to have enjoyed serious attention.

When the portal transport of individual amino acids is examined, it is apparent that most are absorbed in net amounts from the PDV. In order to simplify analysis of the more than 20 amino acids that occur in plasma, it is helpful to classify them into the 5 groups suggested by Bergman (Bergman 1986; Bergman & Heitmann 1978), namely alanine and glycine/serine representing the glucogenic amino acids, arginine/citrulline/ornithine representing the urea cycle acids, leucine/isoleucine/valine representing the essential acids and glutamine/glutamate which are major energy substrates for the PDV. The net uptake of the glucogenic acids seems to be proportional to the intake of feed, increasing in magnitude from the fasting (in sheep) to the fed state (in steers) (Wolff *et al.* 1972; Burrin *et al.* 1991; Huntington & Prior 1985).

A similar pattern was found for the essential amino acids, most strongly shown by valine, whose flux increased from a slight utilisation of 3.48 to a net production of 53.5 mg N/d/kg $^{0.75}$. In another study of leucine metabolism in beef heifers (Hammond *et al.* 1987), similar values obtained for the uptake of leucine from the PDV (21.1 or 48.5 mg N/d/kg $^{0.75}$) of steers fed at low or high intake levels respectively. Of the urea cycle amino acids, arginine and citrulline appeared to respond positively to an increase in feed intake in 2 studies (Wolff *et al.* 1972; Burrin *et al.* 1991), while ornithine uptake declined in one (Burrin *et al.* 1991) and increased in another (Wolff *et al.* 1972). Most of these changes were quantitatively low compared to the glucogenic amino acids.

The outstanding exception to the net output of most amino acids from the PDV is glutamine, which was taken up by the PDV in proportion to the intake of feed. When additional amino acids were supplied by means of abomasal infusion (Guerino *et al.* 1991) into steers, the PDV exported net amounts of glutamine. The fate of glutamate was not so clearly defined; in one study (Wolff *et al.* 1972), the PDV utilised glutamate, while in another (Burrin *et al.* 1991) it produced this acid. Glutamate metabolism is intimately related to that of glutamine and ammonia, and the amount released from the gut will depend on the proportion being used for energy metabolism. As much as 33% of the glutamine uptake may be transaminated to alanine, thereby contributing to the net production of alanine by the PDV (Windmueller 1982; Windmueller & Spaeth 1974).

A new approach that may make a significant contribution to this field, is the isolated intestinal loop technique (Kato *et al.* 1994; Kohn *et al.* 1993). One or more loops of suitable small intestine are selected in an animal under general anaesthesia, and isolated from the rest of the gut by clamping the lumen closed at either end of the segment, and by catheterising the venous outflow from that segment. In this way, selected solutions may be perfused through the lumen of the segment, while the total venous outflow is collected. The possibilities for quantitatively investigating the metabolism of the tract wall are considerably expanded by means of this approach.

Energy metabolism

The future development of ultrasound Doppler techniques to determine instantaneous blood flow coupled with the simultaneous determination of oxygen and carbon dioxide concentrations in blood, will allow the direct calculation of energy metabolism. The introduction of this new technology to an old principle will allow short term data to be collected. The history of this field illustrates the impact of new technology very clearly.

Many of the basic principles of the energy metabolism of animals emerged from the use of simple calorimeters by Lavoisier and Laplace in the 18th Century. The heat produced by the animal was measured by the increase in temperature of a surrounding medium, which was usually water. These early systems were surprisingly precise, and represented the first steps in quantitative animal nutrition, representing the classical "Black Box" approach. The next advance came in the form of indirect calorimetry, which has provided data over a wide range of nutritional and physiological states of the whole animal. Indeed, the economic importance of the efficient use of feed stuffs, and biological interest in the factors which influence energy expenditure, has led to the series of symposia on the energy metabolism of farm animals (EAAP Publications). While most groups up to now have used automated open-circuit respiration chambers, combined with improved gas analysers and computerised data acquisition, the equipment costs are high and measurements must be made over periods of at least 24 hours, after the animals have adapted to the chambers. Other technical problems such as the stress of strange surroundings, the use of hoods or face masks, all limit the value of the data thus obtained. However, by careful adaptation of these techniques, indirect calorimetry may provide extensive data under field conditions, such as in the Bedouin goat kept outdoors in small camps. Core temperatures were monitored telemetrically, while oxygen uptake rates and carbon dioxide output rates were used to calculate total energy metabolism (Shkolnik & Chosniak 1994). The results of this study showed that the dark coat colour did not increase the heat stress on these animals, when compared to light-coloured goats, provided that the goats were allowed to react to their surroundings. In fact, the dark colour enabled these goats to absorb early morning sunlight more efficiently during the winter months, thus providing the evolutionary advantage over the lighter goats.

The alternative approach depends on the direct measurement of oxygen consumption, calculated by the Fick principle, from cardiac output and the difference in blood oxygen content across the lungs. Key features that make this technique possible are the continuous measurement of blood flow and the oxygen content of mixed venous blood. Blood flow is determined by means of a new ultrasound technique which is independent of blood vessel size, alignment or flow profile, and represents a considerable advance over earlier models of the same type. The development of fibre-optic catheter technology, largely for use in human medicine, has made it possible to monitor continuously the oxygen content of blood. When applied to a specific organ system, e.g. the portal-drained viscera, this technique allows the energy metabolism of that organ to be determined.

The grazing animal

The challenge for the future, particularly in the "New" South Africa, will be to obtain this data from free-ranging ruminants, since these constitute the greater proportion of ruminants in the country. Not only is the experimental animal not under the precisely set conditions of the research laboratory, it is subject to all the extraneous influences of the climate, season, pasture

composition, etc. Furthermore, it is much more difficult to obtain samples from an unrestrained animal, which is free to select from a wide choice of grasses and clovers. Several technological advances have appeared lately which may point the way to the future.

In order to realise the ideal, it is necessary to utilise telemetry to collect data from free-ranging animals, with the minimum of restraint. A transmitter has recently been developed (Reese 1994), based on a 4 channel, 8 bit computer, with analogue/digital communications, a Schmidt trigger input and running on 2 to 6 V, 15 micro A. The device holds a 1Kx14 bit program, with 36x8 bit registers and may be interfaced to a standard PC via a serial port. Transducers that are currently under development include pH, ammonia, pressure, temperature, motion and acceleration. A similar approach has been used to collect data from free-ranging Przewalski horses, fitted with identity collars, which collect data every second and transmit every 30 minutes (Berger 1994). This system tracks not only water intake, but also the activity of each horse. The addition of radio control to a mechanically opened oesophageal cannula has allowed the selection of feed material by free ranging goats to be determined without the physical intervention of the researcher and its concomitant consequences. The same principle may be used to obtain blood samples from experimental animals. In practice, the principle of collecting blood samples by remote control is fraught with difficulties, not least of which is the prevention of coagulation in the sampling catheters.

Another approach to the grazing animal is to more clearly delineate the problem by modelling some aspect of the system, thereby identifying the unknown parameters. By examining the relationship between climate and grazing pressure, (Ma & Steinbach 1994) have suggested that the response surface is discontinuous, and that a catastrophic collapse is inherent in the system, particularly at rainfall levels below 390 mm per annum. Such an observation is counter-intuitive, and would not have been easily described without the sophisticated modelling techniques employed. Another approach has been used to model the use of grazing land using the Spatial Bayes Network (Kothmann & Pittroff 1994) and satellite photographs. Predictions show good agreement with the photographs, particularly when geographical and sociological constraints are added to the model.

The previous lack of suitable technology has seriously hampered research on the free-ranging ruminant in the past. The successful solution to this technological barrier will provide the necessary stimulus to the next quantum leap in research into the ruminant-pasture interaction.

Conclusions

Contrary to popular belief, scientific progress does not occur via the steady but slow accretion of myriads of facts which eventually build up to a new hypothesis or even a theory, but by the explosive, quantum leap of insight that leads to a new paradigms. Usually, such quantum advances are triggered by or result from the application of new technology that enables new avenues to be investigated and new approaches to be tried.

Most of the so-called scientific research that takes place between these major advances amounts to dotting the i's and crossing the t's. Examining the historical record gives numerous examples of such major changes in the prevailing paradigm that leads to new insights and advances; the change from an Earth-centred to a Sun-centred solar system, acquired to inherited genetic characteristics, etc.

The science of measuring quantitatively the nutrition of domestic animals has progressed by reducing the size of the "Black Box" from a large one encompassing the entire animal (everything between the mouth and the anus) to many small ones representing organs and even individual cells in certain cases. Continuing that progress requires that animal scientists delve ever deeper into the detail of the metabolic processes that underlie the physiology of the animal.

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THE USE OF BLOOD PROFILES AS ANIMAL RESPONSE INDICATORS

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Abstract

Blood metabolite concentrations are the end result of a complex web of factors which interact to maintain homeostasis and homeorhesis. Despite the uses to which blood metabolite profiles have been applied in overseas commercial dairying systems, little attempt has been made to investigate whether or not this technique could be applied to alternative (indigenous) genotypes under local (free-ranging) conditions. Some blood metabolites which may merit attention in this context are discussed.

Introduction

The use of blood metabolite concentrations in the diagnosis of acute nutritional imbalances such as clinical ketosis and pregnancy toxaemia is well established and validated (Foster 1988). As sub-clinical ketosis and other less acute nutritional imbalances are of potentially greater economic significance than the clinical forms of metabolic diseases in high producing dairy cows, considerable attention has been given to the use of blood metabolite profiles to predict more subtle nutrient imbalances. The Compton Metabolic Profile is an example of such a system which has been used with dairy cows in the UK (Payne 1978). As a continuation of this concept, it is reasonable to enquire whether blood profiles could be used to determine the nutritional intake or status of free-ranging indigenous livestock under extensive and communal farming conditions. The use of blood metabolite concentrations as an index of nutrient intake would have a significant practical impact in this context, as alternative techniques for estimating the intake of herbage and its nutrient value under field conditions are laborious, expensive and are associated with considerable error. Furthermore, the use of blood metabolite concentrations which reflect the balance between environmental supply and animal demand for nutrients would also be of great value, as the nutrient requirements

of local indigenous genotypes are poorly defined. Several comprehensive reviews dealing with blood profiles in dairy herds are available (Payne 1978; Rowlands 1980; Ingraham & Kappel 1988); the following discussion will be directed at the potential use of blood profiles in indigenous genotypes under free-ranging grazing conditions.

Factors affecting the concentration of blood metabolites

Most nutrients do not enter the blood directly, but are extensively modified by the rumen microbiota, the gut tissues and the liver before they appear as blood metabolites in the peripheral circulation. The entry rate of metabolites into the peripheral blood pool may also include a contribution from endogenous sources. The concentration of a nutrient in the peripheral (venous) circulatory system is determined not only by the rate of intake of that nutrient, but by the volume through which it is distributed (volume of distribution) and the capacity of body tissues for storage (pool size), catabolism (oxidation rate), recirculation or synthesis to other intermediates (Figure 1a).

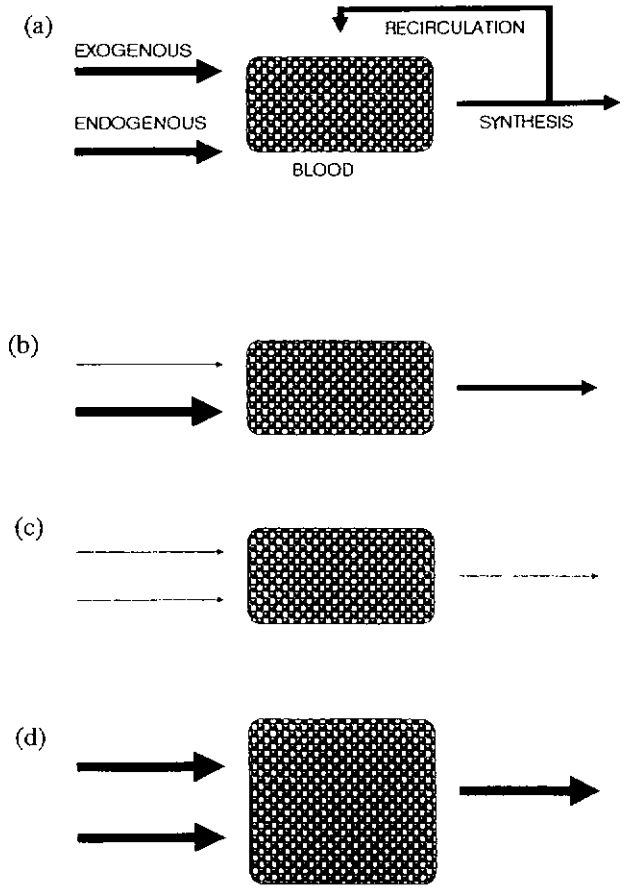


Figure 1 Factors affecting blood metabolite concentrations (a). Diagrams (b), (c) and (d) illustrate how a constant blood concentration may be maintained despite changes in nutrient supply by adjustments of other factors (the relative flow of nutrients through pathways is indicated by the width of arrows). (See text for further details)

Blood metabolite concentrations may not necessarily reflect exogenous nutrient supply: Constant blood concentrations may be maintained if exogenous supply increases in response to decreased exogenous supply (Figure 1b); if the rate of removal from the blood (synthesis) decreases in response to a decrease in nutrient supply (Figure 1c), or if the pool size is increased in response to increased nutrient supply (Figure 1d). In most instances, it is advantageous for the body to present a constant concentration of blood metabolites to the tissues, and elaborate control mechanisms exist to prevent deviations from the norm.

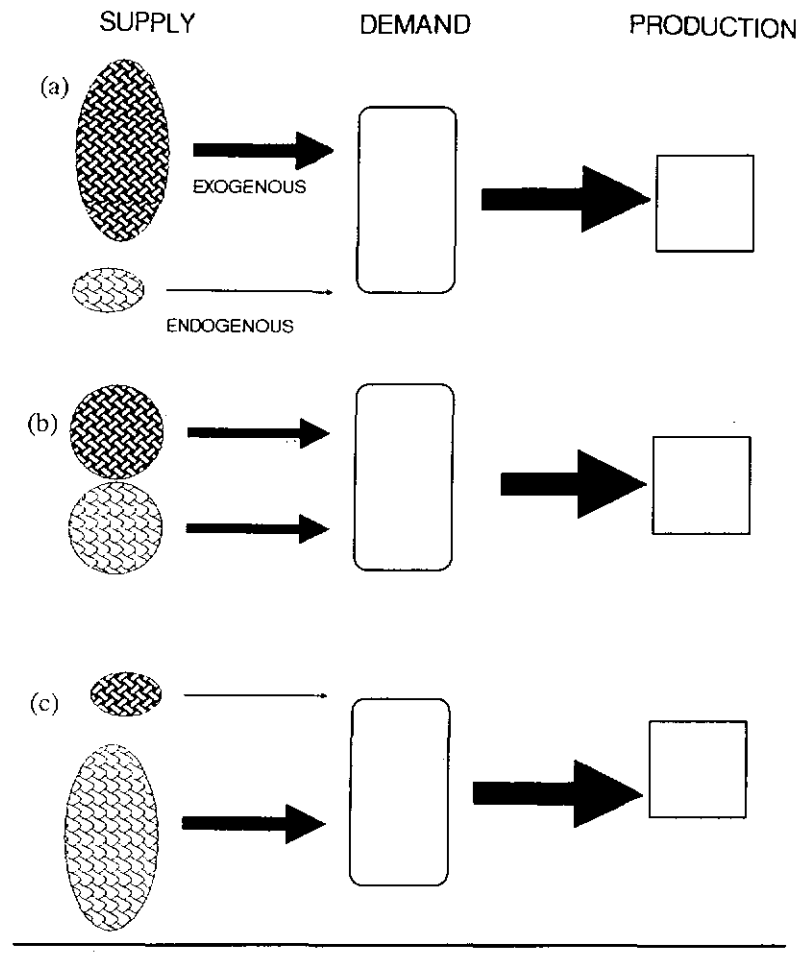
The maintenance of this physiological equilibrium is called homeostasis (Bauman & Currie 1980), and is mediated by various mechanisms including hormone secretion, activity, receptor site number and sensitivity, and also by pacemaker enzymes. The advantage to the body of a constant blood metabolite concentration lies in the fact that most biochemical reactions in the body are catalyzed by enzymes: Although enzymes can function over a wide range of substrate concentrations, the most efficient use of an enzyme is obtained at a specific substrate concentration (K_m). Outside of this substrate concentration, either the velocity of the reaction or its control will be impaired. Most enzymes are built with affinities for their substrates such that their K_m values will lie within an order of magnitude of the physiological concentrations of their substrates. Thus, under most conditions, increased substrate supply will induce increased conversion of substrate to product, effectively maintaining relatively constant blood metabolite concentrations. It is apparent from the above that the blood concentrations of most blood metabolites will be relatively insensitive to variations in precursor intake at normal levels of feeding, i.e.: in excess of maintenance requirements.

Blood metabolite concentrations are more likely to be of diagnostic value when imbalances exist between substrate supply and demand. A nutrient deficit may result either from a shortage of nutrient *inputs*, or from an increased *demand* for nutrients. Within a genotype, the usefulness of a blood metabolite profile would probably differ according to the prevalent physiological state: Growth rate is readily adapted to variations in nutrient supply, making it less likely that blood metabolites will be of any great predictive value except under extreme conditions. On the other hand, blood metabolites are likely to be at their most sensitive as indicators of nutritional adequacy during pregnancy, as nutrient demands are largely directed by the foetus itself with little scope for maternal adaptation.

The sensitivity of blood metabolites as animal response indicators during lactation is likely to be intermediate between the latter two physiological states. The co-ordination of metabolism in various tissues to support a physiological state is called homeorhesis (Bauman & Currie 1980). Homeorhetic control of nutrient partitioning is mediated by hormones, and large differences are known to exist between genotypes with regard to the priorities of different tissues for nutrients. Years of selection for milk production are likely to have changed nutrient priorities in the modern dairy cow to favour milk production at the expense of body reserves. In this case a decrease in exogenous nutrient supply would be accompanied by an increase in concentrations of endogenous metabolites as the body attempts to maintain homeostasis (Figure 2).

In the hypothetical example illustrated (Figure 2), milk production provides the driving force for the mobilization of endogenous reserves, and the concentration of the endogenous blood metabolite could serve as a useful index of nutritional supply. However, this situation may only be approached in

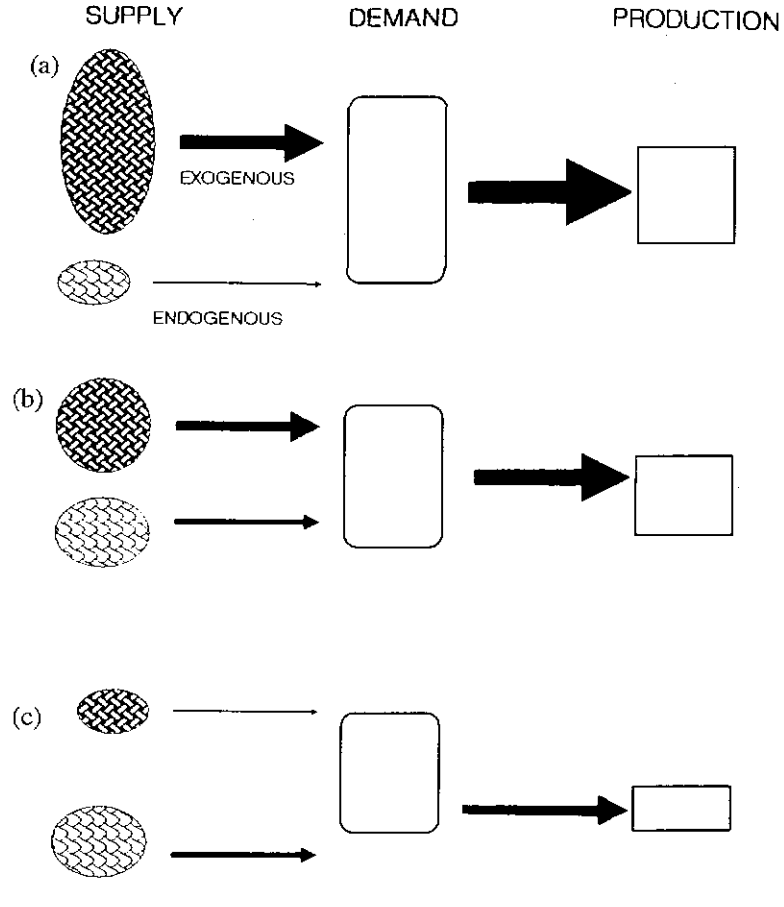
Figure 2 →
Interaction between exogenous and endogenous nutrients at levels of nutrition which are adequate (a); sub-optimal (b); and inadequate (c) in a genotype where the maintenance of production levels is accorded a high priority. (Magnitude of nutrient flow corresponds to the width of arrows)



genotypes where milk production is accorded a very high priority over other body functions. Where the maintenance of endogenous body reserves is accorded a higher priority than that of mammary tissue, milk production rates may be decreased in accordance with the decrease in nutrient supply (Figure 3).

In the hypothetical extreme illustrated in Figure 3, the extent of endogenous reserves provides the driving force for milk production, and not vice versa as in the previous example (Figure 2). This situation may be approached in animals adapted to milk production is likely to have a lower priority for endogenous reserves because excessive depletion of these reserves would reduce the probability of reconception following lactation. Although nutrient partitioning in most genotypes will probably lie somewhere in-between the two extremes illustrated above, it is evident that the usefulness of blood metabolite profiles as animal response indicators will depend very much on genotype-directed priorities for different productive functions. The effect of changes in tissue priorities resulting from genetic selection pressure for milk production is reflected in the higher incidence of pregnancy ketosis, hypocalcaemia and hypomagnesaemia in cattle bred exclusively for milk production than in their counterparts, beef cattle. The complexity of homeorhetic control of nutrient partitioning is evident from a trial in which low- vs high- yielding dairy cows were compared: Nielson *et al.* (1983) found that the fattest animals at calving in the low milk-producing group lost the least body condition after calving and produced the least milk, while the fattest animals in the high milk producing group lost harsh nutritional conditions: Under these circumstances the main pressure of natural selection is to increase reproductive fitness: the most condition and produced the most milk. In sheep, ewes producing the most milk when available food was restricted also lost the most body weight (Owen & Ingleton 1963). An example of the potential extent of differences in

Figure 3 →
Interaction between exogenous and endogenous nutrients at levels of nutrition which are adequate (a); sub-optimal (b); and inadequate (c) in an animal where the maintenance of non-essential production levels is accorded a low priority. (Magnitude of nutrient flow corresponds to the width of arrows).



nutrient partitioning is given by Bauman *et al.* (1985), who fed equal amounts of an identical diet to two heifers of equal livemass: One animal produced 26 kg milk daily and lost 52 kg body mass during lactation, while the other produced only 12 kg milk but gained 39 kg bodymass. Given the above evidence for genotype related differences in nutrient partitioning, it is surprising that, in his review of blood metabolite profiles, Rowlands (1980) came to the conclusion that "for the application of metabolic profile tests, breed differences can be neglected". In contrast to this, Andersson (1988) has presented evidence indicating that selection for higher milk yield could result in cows with an increased disposition to ketosis, and suggests that this problem could be avoided by the inclusion of milk acetone concentrations in selection indices. If substantial differences in nutrient partitioning do exist between genotypes, then differences in blood metabolite concentrations should also exist between genotypes. Genotype-related differences have been reported for many metabolite and hormone blood concentrations. In the case of urea, various authors have shown that differences in blood concentrations exist between high fleece-producing *vs* unselected sheep (McCutcheon *et al.* 1987; Clark *et al.* 1989), between Friesian calves of high *vs* low genetic merit for milk production (Tilakaratne *et al.* 1980; Sinnett-Smith *et al.* 1987), between lean *vs* obese pigs (Mersman *et al.* 1984), and between low *vs* high backfat lines of sheep (Bremmers *et al.* 1988; Carter *et al.* 1989). Several papers have been published on the relationship of various blood metabolites to production parameters, many with differing or even contradictory results. Several reviews have attempted to reconcile these differences (Payne 1978; Rowlands 1980; Ingraham & Kappel 1988), and there has been much debate as to what constitutes abnormal concentrations for different blood metabolites. Even within the relatively narrow confines of commercial UK dairy herds, Rowlands (1980) found that the relationship between milk yield and blood composition was not consistent, but varied from herd to herd, both in magnitude and direction. The apparent contradictions and inconsistencies reported in the literature can to a large extent probably be reconciled by genotype-related differences in respect of the priorities of different productive functions for exogenous and endogenous nutrients. This being the case, it is evident that blood metabolite profile systems based on generalized normal reference standards for blood metabolites without regard for animal genotype will at best represent a compromise between accuracy and expediency. Blood metabolite profiles will be most effectively utilized if samples are taken in a sequential manner over time (e.g. monthly) and comparisons are made within genotype, age and physiological state. For this reason, only cursory reference will be made to existing results, and the following discussion will concentrate on principles relevant to several blood metabolites which have

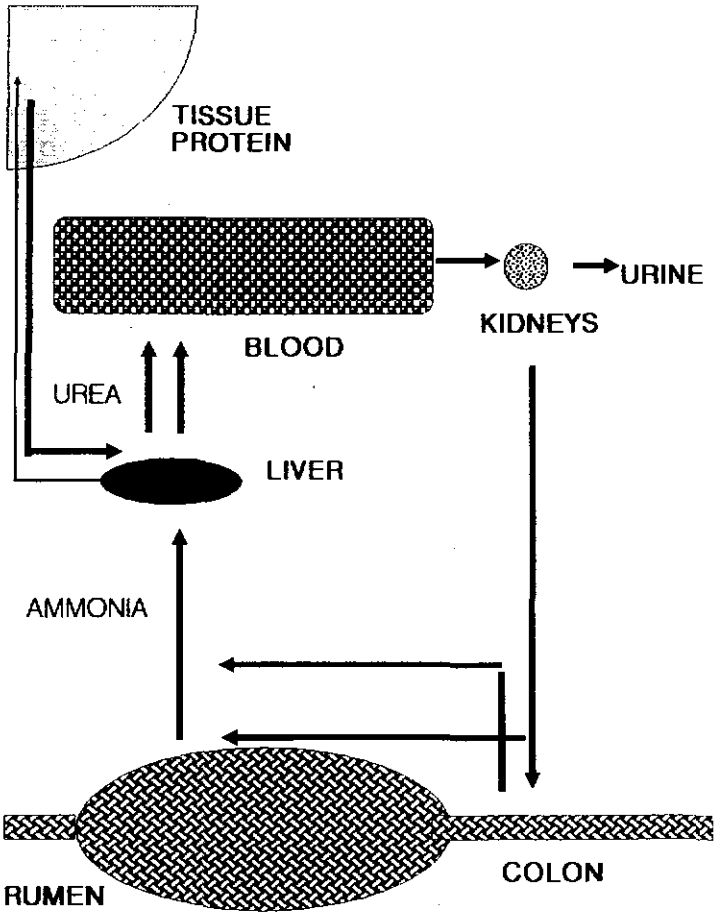


Figure 4 Urea metabolism in the ruminant.

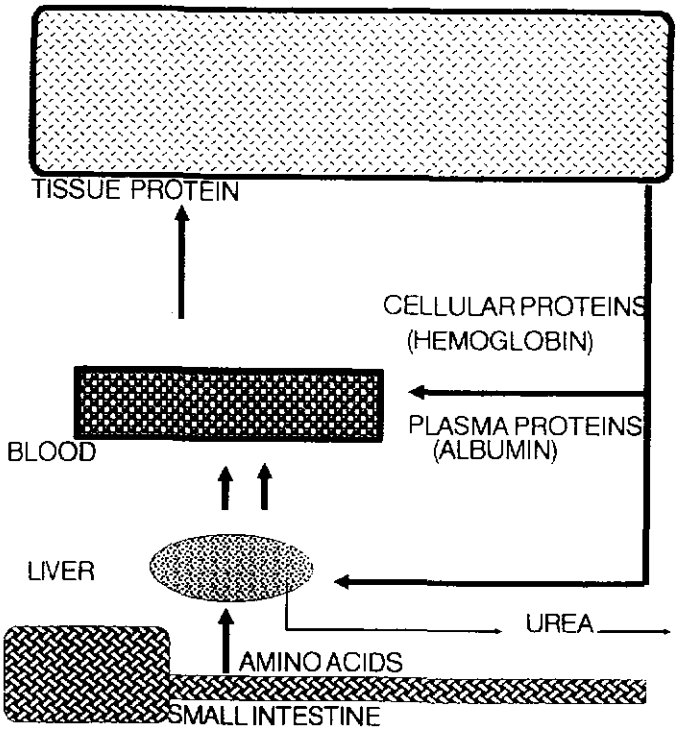


Figure 5 Protein metabolism in the ruminant

shown potential as animal response indicators.

Blood metabolites associated with protein metabolism

In the ruminant animal, dietary protein is extensively modified by microbial fermentation in the rumen, so that the form in which such material is absorbed from the gut differs substantially from the form in which it was ingested. The principal fates of dietary nitrogenous compounds are (a) degradation to ammonia in the rumen; (b) incorporation into microbial protein in the rumen; (c) transit through the rumen to the lower gastro-intestinal tract. Most of the ammonia produced in the rumen is transported through the rumen epithelium, taken up by the portal venous system and transported to the liver (Figure 4). Although ammonia nitrogen can contribute to the synthesis of non-essential amino acids in the liver, most is converted to urea and exported to the general circulatory system via the hepatic vein. Most urea is excreted by the kidneys, although urea may be re-circulated back to the gut. In addition to exogenous precursors, urea may be derived from the catabolism of endogenous proteins. Proteins from microbial cells which have been washed out of the rumen together with those from plant material which have escaped ruminal microbial degradation are hydrolised to peptides and amino acids by proteases in the abomasum and small intestine. After absorption and further deamination in the mucosa of the small intestine, the products (mainly amino acids) are transported to the liver via the portal blood system and enter the general circulation. The free amino acid pool of the body has no precise physical location and is in a state of continual and rapid flux: amino acids are continually withdrawn for protein synthesis by various tissues, and are added to the pool by protein degradation (Figure 5).

K_m values for enzymes initiating amino acid degradation are typically ten times higher than concentrations of blood amino acids (Krebs, 1972). In addition to this, increases in blood amino acid concentrations will induce changes in enzyme activity which may increase by up to 300-fold. For this reason, blood amino acid concentrations are not sensitive to variations in exogenous supply.

From the above, it can be deduced that the most significant blood metabolites associated with protein metabolism in the ruminant are likely to be urea and proteins.

Urea

Urea can be detected in blood, milk or urine. According to Rowlands (1980), urea is a sensitive indicator of dietary digestible crude protein intake in dairy cattle. Others (Biddle *et al.* 1975; Richardson & Kegel 1980; Richardson 1984) found that blood urea concentrations are linearly related to nitrogen intake in growing cattle. In growing lambs Preston *et al.* (1965) reported a very close relationship ($r = 0.986$) between blood urea nitrogen and protein intake. Although there is no doubt that urea concentrations are related to protein intake, several other factors may modify blood urea concentrations: The amount and form of dietary energy may influence rumen ammonia concentration and thus blood urea concentrations through its effect on ruminal microbial activity. Similarly, qualitative differences in the susceptibility of different sources of protein to ruminal degradation will be reflected in different rumen ammonia production rates and hence blood urea levels. Despite numerous other factors such as internal parasites, biological value of dietary protein and intake of glucose precursors, which may affect blood urea concentrations, blood urea concentrations are regarded as useful indicators of nitrogen intake in grazing animals Sykes (1978).

Blood proteins

Proteins in blood may occur in cellular components such as erythrocytes, leukocytes and platelets, or in the fluid component (plasma). The principal cellular protein of interest in the present context is haemoglobin, which occurs in erythrocytes and is responsible for oxygen transport. More than 100 plasma proteins have been identified, but the most important are albumin, globulin and fibrinogen of which only albumin will be discussed here. With the exception of the immunoglubulins, all plasma proteins are synthesised by the liver, and catabolised by metabolically active tissues.

Cellular proteins

The mature erythrocyte is devoid of nuclei and ribosomes, and lacks a significant portion of the metabolic machinery characteristic of all nucleated cells. As a result, erythrocytes are entirely dependant on the functioning of performed enzymes for their survival and have a characteristic life-span (130-160d in sheep and cattle), after which they are removed from the circulation by macrophages. Anaemia occurs when the rate of removal of erythrocytes exceeds the rate of synthesis by bone marrow, and results in a decreased blood erythrocyte concentration. Although a lowered erythrocyte count will result from protein deficiency, other factors such as dietary iron, copper, vitamins or intestinal parasites will also cause anaemia. In practice, blood erythrocyte concentration is most commonly estimated as blood haemoglobin concentration or as packed cell volume (PCV). The latter is expressed as the percentage (by volume) of whole blood that is constituted by erythrocytes following centrifugation. PCV is probably one of the simplest and most economical indicators of nitrogen deficiency, and good results were reported by Biddle *et al.* (1975) in growing cattle. Blood haemoglobin concentration may be a slightly more precise indicator than PCV, but analysis is more time consuming and less easy to interpret. A combination of PCV as indicator of hematocrit and haemoglobin as indicator of dietary Fe adequacy are recommended by Nikokyris *et al.* (1991) for studies concerned with the physiological status of the growing animal.

Plasma Proteins

Albumin is a globular protein which constitutes 35-55% of blood plasma protein. Albumin is a major contributor to the colloid osmotic pressure of blood which is important for fluid balance. Albumin is also important as a transport protein; substances such as free fatty acids which would otherwise be only sparingly soluble in body fluids are solubilized by binding to albumin. Albumin also represents a storage reservoir of protein and transporter of amino acids. Unlike urea, which has a half-life in the body of only a few hours, albumin has a half-life of 13-18 days (Sykes 1978). Albumin will therefore be more useful as an indicator of long-term protein deficiency, while urea concentrations will reflect short term protein intake. Thus, when low concentrations of albumin and urea occur together, particularly in mid-lactation, they are likely to indicate inadequate protein intake. In the experiments of Sykes (1978) with pregnant sheep, blood albumin concentrations accounted for 64% of the variation in body N content loss. Low albumin concentrations have been associated with poor milk production and solid-non-fat (SNF) content of milk (Rowlands

1980). A low albumin concentration may also be caused by parasite infestation, particularly liver fluke, which may reduce the capacity of the liver to synthesise albumin. During infectious disease, increased globulin concentrations may depress albumin concentrations (Rowlands 1980).

Cholesterol

While the exact nature of the causal relationship between cholesterol and protein metabolism is not entirely clear, several reports have suggested that this blood metabolite may be of some use as an animal response indicator. In studies with growing ruminant animals and lactating cows, a reciprocal relationship has been reported (Park 1985) between the dietary protein level and plasma cholesterol concentration. This relationship suggests that the amount of dietary protein acts as a regulator of plasma cholesterol by exerting its influence upon rates of cholesterolgenesis. Ruegg *et al.* (1992) found that cholesterol concentrations were lower in cows which lost the most condition during lactation, and suggested that cholesterol concentrations may reflect the availability of endogenous energy reserves. As indicated earlier, one of the main stumbling blocks to the accurate interpretation of most blood metabolite profiles lies in the fact that it is rarely possible to separate endogenous from exogenous contributions to the blood pool. Blood cholesterol concentrations hold exciting possibilities in this regard, but further research needs to be done.

Blood metabolites associated with energy metabolism

The main sources of exogenous energy for the ruminant are volatile fatty acids (VFA) which are absorbed from the rumen and carbohydrates (mainly starch) which escape rumen fermentation and are absorbed from the small intestine (Figure 6).

The main VFA arising from rumen fermentation are propionate, acetate and butyrate. Propionate entering the portal vein is almost quantitatively converted to glucose by the liver, which then enters the general circulation where it is used as an energy source by tissues such as the brain and central nervous system, the fetus and the mammary gland. Acetate passes unchanged through the liver to tissues such as muscle or is used for fat synthesis system, the fetus and the mammary gland. According to Lindsay (1978), acetate is in principle quite unable as an index of the adequacy of feed intake, but has not been evaluated for this purpose. Blood acetate concentrations deserve further investigation, as there is evidence of concentration-related responses to the addition of dietary propionate in sheep (Cronjé *et al.* 1991). Butyrate is converted by the rumen epithelium and liver to ketones, especially ß-hydroxyl butyrate, which are used as energy substrates by extrahepatic tissues such as the heart and mammary gland. Glucose absorbed from the small intestine is rapidly oxidised

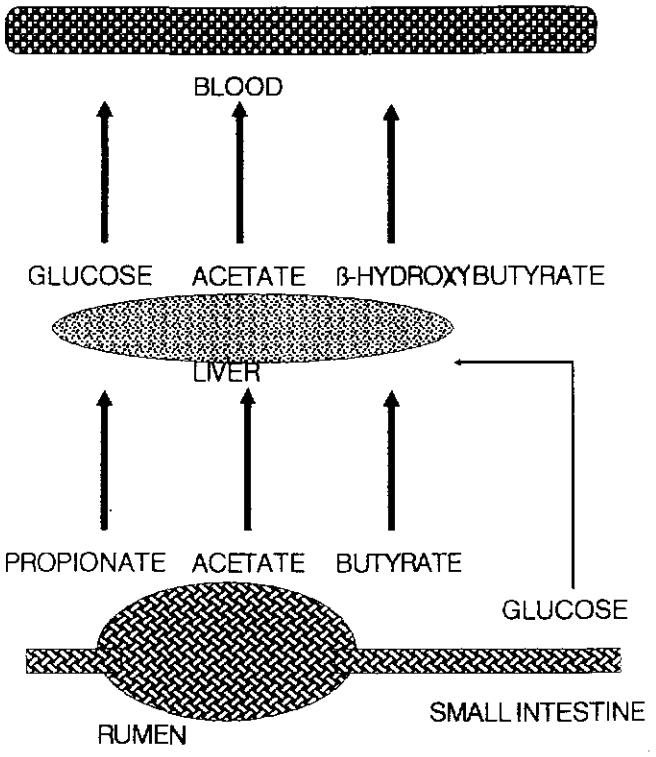


Figure 6 Energy metabolism in the ruminant

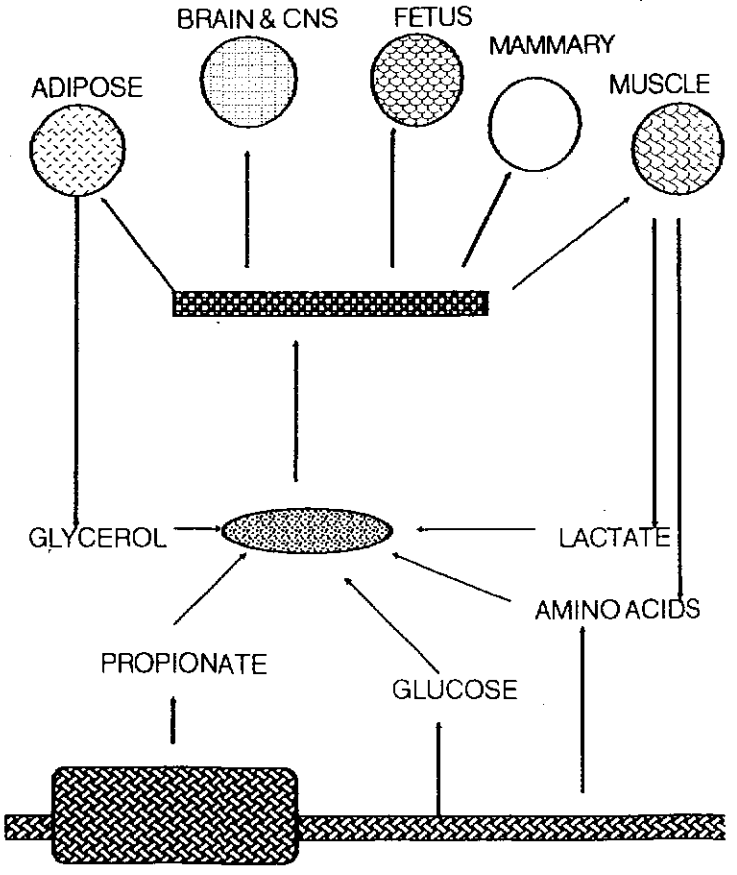


Figure 7 Glucose metabolism in the ruminant

by gut epithelium, and contributes little to glucose turnover in the ruminant under normal grazing conditions. The main endogenous energy reserves in the ruminant are fat (lipogenic energy) and protein (glycogenic energy). Triglycerides in fat depots are broken down to fatty acids in the adipocyte and enter the blood as non-esterified fatty acids for transport to other organs such as the liver and muscle. Nonesterified fatty acids are frequently referred to as free fatty acids, but this is technically incorrect, as the majority are in fact bound to albumin or lipoproteins. Under certain circumstances, when the fatty acid release exceeds the capacity for oxidation, fatty acids may be converted to ketones, and ß-hydroxy butyrate, acetoacetate and acetone may accumulate in the blood. The main indicator metabolites associated with energy metabolism are thus glucose, non-esterified fatty acids and the ketones of which ß-hydroxybutyrate is the most preferable.

Glucose

Glucose metabolism is illustrated in Figure 7. Because of the central role played by glucose in many important metabolic reactions, the blood concentration of glucose is tightly regulated. The high K_m of liver hexokinase enzymes represents a sensitive, high capacity control mechanism for regulating circulating glucose concentrations. For this reason, blood glucose concentrations are maintained within narrow limits and are relatively insensitive to dietary changes. In addition to this the secretion of epinephrine by the adrenal in response to stress associated with blood sampling may induce large transitory increases in blood glucose concentration. Blood glucose is considered to be one of the poorest of indicators (Lindsay 1978).

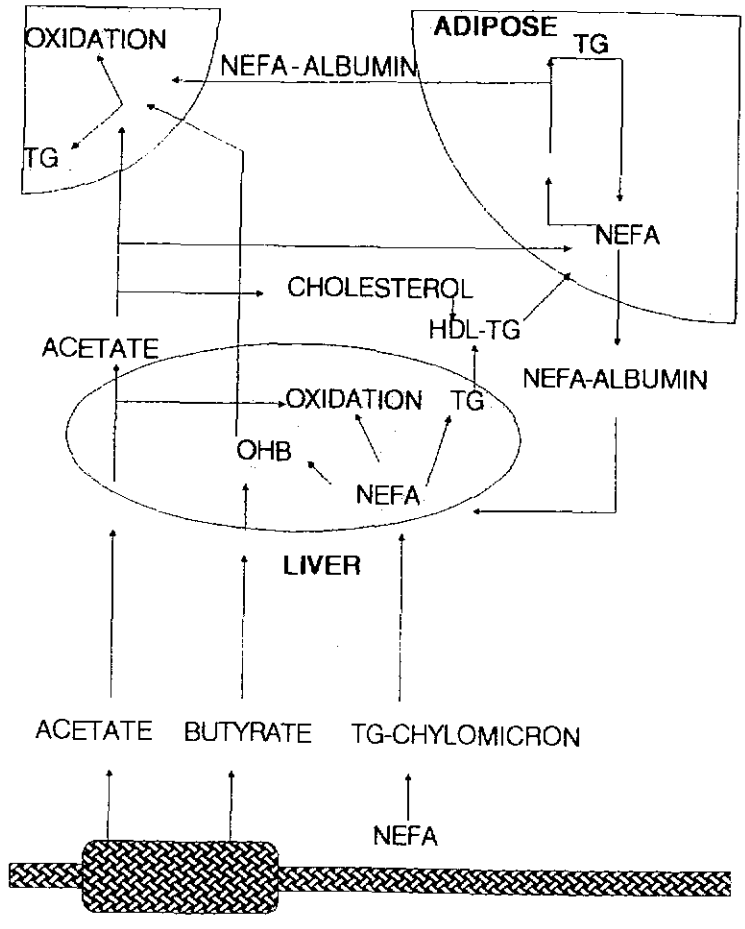


Figure 8 Lipid metabolism in the ruminant

Non-esterified fatty acids

As an increased energy deficit relative to requirements will result in increased fat mobilization (Figure 8), blood non-esterified fatty acid concentrations may be useful animal response indicators.

According to Russel (1978) and Lindsay (1978), blood non-esterified fatty acid concentrations represent the parameter of choice for characterizing moderate degrees of undernourishment. However, blood concentrations do plateau at more severe levels of undernourishment, which limits their usefulness. Rowlands (1980) suggested that plasma FFA are most useful as an index of the degree of undernourishment over a range of approximately 800 - 1200 µeq/l. As in the case of glucose, blood non-esterified fatty acid concentrations will be affected by epinephrine secretion in animals not accustomed to frequent handling (Russel 1978), and this is regarded as one of the major disadvantages of this metabolite (Lindsay 1978). Substantial variation in blood non-esterifed fatty acid concentrations due to time of feeding has also been reported (see Bowden 1971).

ß-hydroxybutyrate

FFA are catabolised in the liver to produce acetyl Co-A and ketone bodies such as ß-hydroxybutyrate (OHB) (Figure 8). Ketones are normally catabolized to carbon dioxide and water in extrahepatic tissues, but will accumulate in the blood at high rates of fat catabolism, thus providing an index of the extent of mobilization of endogenous reserves and hence of nutritional stress. Ketone body concentrations such as ß-hydroxybutyrate are not subject to as much variation as fatty acids, but responses to moderate levels of undernourishment are relatively small (Russel 1978). ß-hydroxybutyrate concentrations are therefore more valuable during relatively severe degrees of undernourishment, and are more appropriate than non-esterified fatty acids in circumstances where the animals are unaccustomed to blood sampling. The efficacy of ß-hydroxybutyrate as a meaningful index of nutritional stress is well illustrated by the experiment of Russel *et al.* (1977), in which birth masses of twin lambs from Greyface ewes with blood ß-hydroxybutyrate concentrations of 1.1 or 1.6 mmol/l were 8% and 26% lower when compared to those of adequately nourished ewes (ß-hydroxybutyrate concentration of below 0.7 mmol/l). Lamb mortality at birth is also higher in ewes with elevated blood ß-hydroxybutyrate concentrations at parturition (1.07 mmol/l) than in ewes fed ad lib (0.53 mmol/l) (Lynch & Jackson 1983). It has been reported (Russel 1984) that the nutrition of several flocks of experimental sheep at the Hill Farming Research Organisation (UK) has been successfully regulated during late pregnancy for a number of years on the basis of blood ß-hydroxybutyrate concentrations. This system is based on a formula relating ß-hydroxybutyrate concentration to energy status (i.e. the difference between energy requirements and intake), and has been expanded to include a formula for calculating the amount of supplementary

energy required to decrease measured ß-hydroxybutyrate concentrations to a desired optimum (0.8 mmol/l).

Conclusions

Energy from endogenous fat reserves may constitute 4-59% of the energy content of milk produced by the ewe (Robinson 1988). The magnitude of this source of nutrients limits the accuracy of attempts to quantify the adequacy of nutrients available to free grazing animals from measurements of intake and nutrient concentration. In addition to this, the latter approach is limited by the fact that few estimates of nutrient requirements exist for local indigenous genotypes. The use of production traits such as milk production to quantify nutritional adequacy is difficult under field conditions - especially with small stock. The use of body mass is complicated by the presence of multiple foetuses in sheep in goats, and by changes in gut fill in all classes of livestock - particularly during pregnancy. A limitation to the use of body condition score as an index of nutritional adequacy is that it provides information only in hindsight: By the time an excessive loss of condition score has been recognised, an irreparable production penalty may have been occurred (Russel 1985). What is needed is an integrated measure of nutritional status. This measure should provide, in a single value, the net sum of the balance between all sources of nutrient supply, both exogenous and endogenous, and the nutrient requirement of the animal as dictated by its genetic makeup. Blood metabolite profiles, appropriately interpreted may provide a key tool for matching nutritional supply to requirements in local indigenous animals under free-grazing conditions.

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AVAILABLE BIOMASS & CARRYING CAPACITY

RANGE MANAGEMENT: OPTIMIZING FORAGE PRODUCTION AND QUALITY

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Abstract

Range management involves optimizing forage production and quality, both in the short-term and in the long-term. In the short-term, forage production and quality is strongly influenced, *inter alia* by temporal climatic variability, stocking rate, grazing system, fire, animal type and spatial variability. On the other hand, long-term optimization requires prevention of range deterioration. The nature of this process seems to be profoundly different between humid and arid rangelands. In the former, changes are relatively predictable, with overgrazing resulting in gradual deterioration. In the latter, change is event driven, providing the grazier with long periods of system inertia interspersed randomly by risks and opportunities to cause or prevent community change from one state to another. Management for long-term sustainability often requires sacrifice of short-term welfare. The benefits of such management may even be beyond the planning horizon of the grazier. Implementing conservation thus requires altruism on the part of the grazier - an unlikely option. If society requires such conservation, it may need to amend its values, and either provide the grazier with an incentive, or outlaw overgrazing.

Keywords
Management, production, quality, range, short-term, sustainability

Introduction

Range management is the process whereby graziers examine the probable consequences of different management actions, and select those which, in their opinion, have the highest chance of attaining their objectives (adapted from Provenza 1991). Grazier objectives are driven largely by socio-economic conditions. Since these are diverse (nowhere more evident than in the first world/third world dichotomy of southern Africa), management actions will vary, even where conditions and resources for plant growth are similar.

Despite the diversity of grazier objectives, under domestic pastoralism, they usually relate directly to some aspect of animal performance, and only indirectly to range performance. Range management actions would thus be taken only in so far as they affect animal performance. Such performance would be a function of the quantity and quality of forage consumed by animals. Range management thus translates, essentially, to optimizing productivity and quality of forage, both in the short- and long-term, the optimum being determined by grazier objectives.

The role of the range scientist in this process is not to prescribe what the grazier's objectives should be, but rather to provide reliable predictions of the consequences of management actions. The various combinations of enterprises and other management actions from which the grazier might choose are almost endless. Clearly, the range scientist cannot hope to address all possible permutations through empirical experimentation, and is forced to develop conceptual models, and hence management principles, to assist in prediction. These will rely as far as possible on quantitative research, but will, of necessity, also draw heavily on conventional wisdom, observed successes and failures of graziers, untested hypotheses and intuition.

In this paper we address a few range management principles that affect the quantity and quality of forage production, and consequently animal performance. We draw largely on southern African experience, but attempt to evaluate this in a broader perspective.

Short-term and long-term objectives

Differentiation between short- and long-term grazier objectives is arbitrary. The former refer essentially to the current- and near future welfare of the grazier, while the latter refer to welfare at a later stage, which may, or may not, require some sacrifice of short-term welfare. The comparison, on a time scale, is relative rather than absolute. In both instances they must fall within the planning horizon of the individual grazier. Management actions aimed beyond this horizon would be society goals and not grazier objectives.

Short-term welfare must be complied with, at least to a critical minimum level, before long-term welfare can be addressed. This applies to both subsistence and commercial pastoralism. In the former, short-term welfare must at least exceed that required for healthy physical existence, and in the latter, the grazier must be able to maintain financial liquidity. Below these "critical" levels, pastoral operations would fail before long-term objectives could be attained. Above these critical levels, graziers are in a position to consider long-term options that may not, but very often do, require investment or sacrifice of at least some short-term welfare.

In the ensuing discussion we differentiate between

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