doi: http://dx.doi.org/10.5016/1806-8774.2008.v10pT33

ARBS Annual Review of Biomedical Sciences

Theme Topic on "Unraveling Animal Welfare"

pdf freely available at http://arbs.biblioteca.unesp.br

2008;10:T33-T50

Nutrition and the Welfare of Ruminants

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Received: 06 October 2008; accepted 13 October 2008
Online on 22 October 2008

Abstract

Hogan JP, Phillips CJC. Nutrition and the Welfare of Ruminants. ARBS Annu Rev Biomed Sci 2008;10:T33-T50. Good nutrition is one of the most fundamental requirements for all animals and has been identified by Australian livestock farmers as the biggest contributor to animal welfare on farms. Ruminant livestock utilize their extensive fermentation capacity in their forestomach to digest coarse roughages that could not provide adequate nutrients for the welfare of monogastric animals. They are therefore most often kept on rangelands, with a diverse range of feeds of low quality and characterized by a large seasonal variability in growth and quality. However, the variation in feed quality and quantity can be partly buffered by the ability of domesticated ruminant livestock to store food energy as fat tissue, for example in the hump of *Bos indicus* cattle and fat tail of sheep, to be utilised when feed availability is low. It is important to determine when ruminant livestock are malnourished so that corrective action can be taken. We propose that this occurs when normal functioning of the animal, including behaviour, physiology and reproduction, is adversely affected by an inadequate supply of nutrients. The sensation of hunger is central to the concept that an animal suffers during malnutrition but is also adaptive to motivate the animal to locate the necessary nutrients. It is concluded that a better understanding of malnutrition in ruminant livestock is essential to maintain high welfare standards.

Keywords: animal welfare, nutrition, ruminants, cattle, sheep

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1. Introduction

Nutrition provides the necessary elements for nearly all of the body's metabolic processes and is therefore the most fundamental welfare need for all animals. A recent survey of Australian cattle and sheep farms found that, even though there have been significant advances in nutritional practices, farmers perceive that nutrition remains the most important welfare problem on farms (Phillips, 2008). As Australia is a region of extreme climatic variability, both between regions and over time, nutrition is likely to be of major significance in relation to welfare in most cattle and sheep farms. Whilst the responses of production animals in their output of meat, milk, wool etc. to varying intake of energy, protein, minerals and vitamins has been well-defined (e.g. AFRC, 1993; Freer *et al.*, 2007), the impacts on other welfare parameters, such as behaviour, of either inadequate supplies of these nutrients, or more rarely excesses, has received little attention. An exception is the impact on feeding behaviour of deficiencies of several elements, in particular sodium, calcium and phosphorus. Inadequate sodium intake leads to excessive licking of the environment in attempts to find alternative sources (Phillips *et al.*, 1999), similarly for phosphorus, inadequate intakes lead to ruminants chewing bones (osteophagia), even though little phosphorus is probably extracted by this process (Bredin *et al.*, 2008). An inability to satiate the appetite through searching for alternative food sources is likely to cause frustration at least, and potentially exhaustion, suggesting that welfare is severely compromised. In addition there may be clinical deficiency symptoms, such as hypocalcaemia, which is common in newly calved dairy cows and also indicates a low welfare state.

Ruminants belong to the Order Artiodactyla, which encompasses an enormous range of sizes, from the 2.5 kg musk deer of south-east Asia to the 1200 kg giraffe, utilizing a similarly wide range of plant species and parts of those plants selected by the different types of animal. Thus under natural conditions, there are species of artiodactyls that have adapted to most natural habitats, and this will assist in maintaining their welfare. However, of these numerous species, only a minority has been domesticated including sheep, cattle, goats, camels, some South American camelids such as the llama, and some species of deer. Although these are suited to many different habitats, they are inevitably utilized in some environments to which they are not well suited. In intensive farming systems domestication has brought some control of the diet offered to the animals and therefore their welfare. However, as Reid (1975) has pointed out, whereas it is usually perceived that farmed ruminants are eating only the grasses and legumes presented in a prepared pasture plus any supplements of energy, protein or minerals provided by the farmer, they may in addition be ingesting parts of trees and shrubs, water plants, bedding, wool, hair, paint and animal carcasses. In addition, there may be the intake of soil, sand, fungi and fungal-generated toxins, other microorganisms, chemicals, fungicides, herbicides and insecticides together with pollutants and contaminants of the water supply or soil. Many of these substances may be inimical to the welfare of the animal. India has the largest population of cattle of any country, many of whom roam the streets eating waste food, paper etc, but also unavoidably consume considerable quantities of plastic, wire and other potentially damaging waste materials (Fox, 1998). In view of the fact that this type of malnutrition can occur under intensive management of animals, it is not surprising that many nutritional problems beset animals raised under conditions of extensive grazing or nomadic husbandry. Malnutrition can occur with green leafy forages containing too little or too much of various minerals, or toxic chemicals or fungal toxins arising from infection of the seed and subsequent development within the plant or as saprophytes growing on dead plant material. Undernutrition occurs not only in consequence of malnutrition, but also when the animal cannot eat sufficient nutrients, either because forage of high nutritive value is in short supply, or probably more frequently because the animal cannot ingest and digest enough dry, mature forage of low nutritional value. This exacerbates the already high-energy cost that the grazing or browsing ruminant must pay in obtaining nutrients in useful forms from fibrous forage.

Ruminant animals, by virtue of an effective fermentation system in the first two compartments of the stomach, are well adapted to derive nutrients from herbage diets. Ideally such herbages are always of adequate nutritional value and available in sufficient amounts. In practice, in most parts of the world such conditions are met during only part of the year and the grazing animal must depend on very short, high quality pasture or increasingly mature forage of lower nutritional value for the rest of the time. Little is known about the impact of inadequate energy or protein supplies on an animal's welfare. Changes in condition and reproductive performance can be predicted with some certainty, and these relate to the animals' welfare (Morgan-Davies *et al.*, 2008), but the impact of prolonged hunger, nutrient deficiencies or toxic elements on the animals' cognition is largely unknown. Feed planning is possible to avoid the worst excesses of malnutrition. This is facilitated by the ability to predict animal production responses factorially from the absorbed nutrients required for maintenance of the animal, with the remainder utilized for growth, pregnancy, production of milk, wool etc (AFRC, 1993; Freer *et al.*, 2007). Minimum nutrient intakes necessary to maintain the animal alive are therefore reasonably well known. If the nutrient concentration of the output is known, as well as the efficiency of nutrient utilization for this purpose, the quantity of outputs can be estimated and ruminant production enterprises can be more efficiently managed. For most nutrients it is not possible to define a requirement as such, since there are continuous responses to increased intake of the nutrient. For example, increasing energy intake will enable bone, muscle and fat production to be increased, in that order but with some overlap, after the maintenance requirements have been met (Berg & Butterfield, 1975). In contrast, supranormal intakes of many vitamins are not utilized or stored in the body, but are excreted, and hence a requirement can be established.

2. Malnutrition

The welfare of animals is threatened by any form of malnutrition, which is defined as a deficit, imbalance or excess of nutrients with consequential adverse effects on health and growth potential. A common type of malnutrition is undernutrition, "a prolonged inadequate supply of nutrients to sustain good health and in the case of immature and underweight animals, growth potential, where prolonged implies that a steady state has been reached" (Agenäs *et al.*, 2006). The human equivalent may be termed 'starvation', but this is not a preferred term for animal populations because of its negative associations with human deprivation. Starvation has been defined as a 'shortage of nutrients or energy such that the animal starts to metabolize functional tissues rather than food reserves' (Broom & Fraser, 2007). However, it is difficult to define any tissue as functional or for food reserves. For example, although adipose tissue may function in part as the body's principal storage tissue, it has numerous physiological functions, especially endocrinological. Some functions support the energy-regulating function of adipose tissue through glucose and lipid homeostasis or by leptin secretion, other output, for example of sex steroids do not (Wang *et al.*, 2008). The endocrine role of adipose tissue may be summarized as adipocyte differentiation, energy metabolism, lipid uptake and transport, immune response and inflammation, vasculature and neuron development, and remodeling of the extracellular matrix (Wang *et al.*, 2008). In addition, catabolisation of adipose tissue through caloric restriction has important consequences on its function, some of which may impact on animal welfare, especially effects on the lymphatic system [negative impact on welfare] (Harvey, 2008), slowing the age-related decline in mitochondrial activity and thermogenesis in brown adipose activity [positive impact on welfare] (Valle *et al.*, 2008) and reducing the animal's ability to endure future nutrient shortages [negative impact on welfare]. Another concern with Broom and Fraser's concept of starvation as depletion of functional tissues is that adipose tissue, which could be seen as more utilized for storage than other tissues, is depleted concurrently with other tissues, albeit at a greater rate in the early stages of caloric restriction (Berg & Butterfield, 1975). This renders a precise point of transition from storage to functional tissue unlikely. Hence, we propose that malnutrition occurs when normal *functioning* of the animal, including behaviour, physiology and reproduction, is adversely affected by an inadequate supply of nutrients. Furthermore we propose that the term 'starvation', if it is utilized to refer to an *unacceptable* level of malnutrition, be restricted to these situations in which the functionality of animals is limited by nutrient supply. An example of this is in impaired reproductive function (Buckley *et al.*, 2003), but behavioral function may also be compromised by caloric restriction, especially through induced lethargy and inability to devote significant time to feeding activities (Tucker *et al.*, 2007). Impairment of function is also likely with pregnant or lactating females and the milk-fed offspring.

Small fluctuations in quantity or quality of feed can be tolerated. For example, when lactating dairy cows are fed mixed concentrate and forage diets, their *ad libitum* forage intake can be reduced for periods of about three weeks by up to 40% without affecting milk production (Phillips & Leaver, 1985). More than this will reduce production, in particular milk protein output, and result in considerable losses in body weight. If weight loss continues, the life of the animal may be threatened. The type of nutrients restricted is important: reduced energy intake can be partially offset by increased catabolism of body fat reserves, but protein reserves are less readily mobilized (Tyrrell *et al.*, 1970; Botts *et al.*, 1979). The cognitive impact of persistent hunger is unknown; indeed it is even unsure to what extent animals do experience persistent hunger. It is to be expected that regular reminders of nutritional state would have adaptive benefit to enable a malnourished animal to continue to seek for feed sources. It is the task of the nutritionist to maximize the nutrient supply from the pasture in a sustainable way, to determine the extent to which nutrient supply meets the needs of an animal in a particular physiological state and to derive strategies of supplementary feeding to ensure the welfare of the animal.

Evidence of undernutrition in farm animals is currently a matter of subjective veterinary judgement. Attempts have been made to standardise the subjective visual assessment of the nutritional status of cattle by developing systems for body condition scoring, e.g. from 1 (emaciated) to 5 (obese) (Lowman *et al.*, 1976; Edmonson *et al.*, 1989). People experienced in condition scoring may be capable of achieving a high degree of repeatability between different occasions, but the reliability is less assured, with a risk of inter-person variation (Calavas *et al.*, 1998; Veerkamp *et al.*, 2002). Attempts to identify indicators of undernutrition in cattle have determined that extremely emaciated cattle exhibit high albumin concentrations in their blood (Agenäs *et al.*, 2006), and probably also low fructosamine concentrations, which reflects average glucose concentration over the preceding two to three weeks (Armbruster, 1987). Also related to body condition is creatinine, a measure of muscle mass, and if depressed below the reference range (Table 1) suggests that animals have been mobilising muscle protein for a considerable period. Reference to these values could be utilized either to prove the body condition status in disputed prosecution cases or as a breeding objective to produce cattle which can withstand restricted feed availability (Agenäs *et al.*, 2006). Other potential responses to undernutrition in early lactation cattle relate mainly to the mobilization of fat tissue, with increases in non-esterified fatty acids and â-hydroxybutyrate (Hartmann & Lascelles, 1965; Baird *et al.*, 1972; Agenäs *et al.*, 2003), and reductions in insulin and glucose (Baird *et al.*, 1972; McGuire *et al.*, 1995).

Table 1. Reference ranges for serum constituent concentrations of relevance to malnutrition in adequately-nourished beef cattle.

Analyte	**Reference Range**	**Units**
Albumin	25.0 - 44.4	g/L
β-hydroxybutyrate	0.12 - 0.61	mmol/L
Creatinine	110 - 225	µmol/L
Fructosamine	183 - 365	µmol/L
Fructosamine/albumin	5.63 - 9.70	µmol/g
Globulin	27.2 - 49.2	g/L
NEFA	176 - 1317	µmol/L
Total protein	59.2 - 87.5	g/L
Urea	1.88 - 7.00	mmol/L

From Agenäs *et al.* (2006).

3. Defining the Optimum Animal Weight

A concept of value in discussing animal welfare is the Standard Reference Weight (SRW), defined as the weight of an animal with the skeleton fully developed and the empty carcass containing 25% fat (SCA, 1990). The latter part of this definition has been modified (Freer *et al.*, 2007) to include visual appraisal of body conformation, introduced above, by which the SRW animal is regarded as grade 3 on a scale of 0 to 5, where grade 0 is an emaciated animal close to death and grade 5 has sufficient subcutaneous fat that spinal processes and rib ends cannot readily be palpated. However, this concept is contentious for sheep and cattle, which may gain 25 to 30 % in body weight above SRW when pastures are of highest nutritional value, yet will also lose the same amount because of seasonal changes in the nutritional value of available herbage (McGregor, undated). This process is normal and the animal appears healthy. However, further weight loss brings animals to a Critical Live Weight (CLW) corresponding to Grade 0, when an animal becomes too weak “to walk, graze or safely obtain drinking water”. McGregor (undated) estimated that for small and large-framed sheep, CLW was 58 to 66 (mean 63) % of SRW, respectively. When the quantity or nutritional value of available pasture causes undernutrition of animals to the extent that CLW is reached, the most pressing welfare need of the animal is the maintenance of life. This may involve moving the animals to better-feed elsewhere or providing supplementary feed. For logistical or economic reasons the amount of feed that can be provided may be merely enough to keep the animal at CLW against the hope that the supply of feed will improve. Conversely, where under normal animal husbandry practice animals may be sent to slaughter for failing to produce meat, milk, wool or offspring at satisfactory rates, any interruption to nutrient supply could be regarded as a threat to life.

4. The Ruminant Diet

The diets of ruminants distributed across most climatic zones of the world reflect the vegetation growing in those zones. Hence the diets available may range from shrubs such as Acacias which, despite containing anti-nutritional substances, provide feed of higher nutritive value than local grasses in desert areas to mosses and lichens, a major source of nutrients to reindeer in arctic regions However, most ruminants eat grasses and forbs, many of which have developed naturally, but also including a substantial number of both annuals and perennials that have been bred or selected to provide feed of higher nutritional value. These all pass through similar phases of development, whether following germination or regeneration. Early growth provides forage that contains relatively low levels of fibre, which comprises varying proportions of the hexose polymer, cellulose, the pentose polymer, hemicellulose and the phenolic polymer, lignin. Immature forage plants also contain high levels of protein, are of high digestibility and hence of high nutritive value. As the plant grows and matures, the level of fibre and its lignification increases to provide more support, and digestibility and the contents of protein and minerals decline. Many of the nutrients are then transferred to the seed that, for a brief period, can provide the animal with a concentrated source of energy and protein. The material remaining following seed removal by animal or machine comprises senescent or dead material, mainly highly lignified fibre with levels of protein and minerals often inadequate to sustain the animal. Rain falling on such material will leach out remaining minerals and may promote fungal growth, thus further reducing nutritional value. Ruminants depending solely on this type of vegetation during its seasonal growth cycle thus commence with highly nutritious feed, which provides energy at levels above maintenance so that growth and fattening occur. As the feed matures, the animal has difficulty obtaining energy above maintenance so that the rate of growth slows and finally ceases. Finally, with the most mature feed, nutrient supply becomes insufficient even for maintenance, and weight loss begins. In this process the animal begins to catabolize its body tissues, with the long chain fatty acids and amino acids obtained from fat and protein, respectively, being used to restore some of the deficit in dietary energy and thus reduce weight loss. The severity of weight loss depends on the energy deficit and on the length of time until seed germination and plant regrowth again present the animal with nutritious feed.

5. Ruminant Nutritional Principles

Digestion in the ruminant animal is fundamentally different from the monogastric animal. The main principles of animal nutrition in both types of animals, but derived from studies with pigs and chickens, are that energy, largely in the form of glucose, is the primary nutrient but the efficiency of its use requires the supply of adequate amounts of the 10 “essential” amino acids plus vitamins, minerals and various minor nutrients. The nutrients derived by non-ruminants can be predicted from information on the composition of their highly digestible diets. Further, if a nutrient in the diet is perceived to be inadequate, the deficit can be corrected by addition to the diet. However, with the ruminant that selects and harvests its own feed from the field, little information is available on the amount of feed eaten or on its composition. Even if the composition of the diet is known, as occurs with cattle held in feedlots, feed analysis cannot directly indicate nutrient supply because of the involvement of microbial fermentation in the rumen. Thus ruminant production systems are inherently less easily managed in terms of the nutrition than pig and poultry production systems, which can increase the risk of malnutrition.

Whereas enzyme systems can hydrolyse the alpha-linkages involved in the glucose molecules that form starch, the most common energy source in high quality, cereal-based feeds used for pig and poultry systems, the breakdown of the beta linked-hexose and pentose molecules in plant fibres selected by ruminants is dependent on the anaerobic fermentative activities of microbes in the rumen and large intestine. The phenolic polymer, lignin, passes through the ruminant digestive tract largely untouched, whereas the other two components are fermented at rates and to degrees that decline with advancing plant maturity, which is therefore important in determining the value of feeds to ruminants. Similarly, the catabolism in the rumen of much of the dietary protein leaves the ruminant dependent for its essential amino acids on the digestion in the small intestine of microbial proteins synthesized in the rumen

The difficulties that farmers have in determining nutrient supply to ruminants and the significant impact of nutrition on ruminant welfare have led to attempts by scientists to develop models to predict nutrient supply and animal performance, based on two types of study. The first involves energy balance, that is the energy stored, estimated as the difference between Gross Energy (GE) intake and energy losses. This process involves the partitioning of energy ingested into Digestible (DE), Metabolizable (ME) and Net (NE) or useful fractions by subtracting from energy intake that wasted respectively in faeces, urine plus fermentation gases, and heat. Wastage of energy as heat further varies, depending on whether NE is used for weight maintenance or for production. Losses of energy can be extensive, with consequent effects on the animal’s welfare. The digestibility of grasses grown under temperate climatic conditions ranges from about 50 to 80%, whereas, for those grown in tropical regions (sometimes referred to as “warm season” grasses) digestibility is on average about 13% less (Minson, 1990). Thus energy wastage in faeces can range from approximately 20-60% of GE intake. Reduced digestibility correspondingly reduces the intake of ME, because over a wide range of feeds, ME is a reasonably constant proportion, approximately 81% of DE. The proportion of energy lost as heat depends on whether the animal is fed at maintenance or above-maintenance levels of energy intake. For instance with a forage of 64% digestibility, Armstrong (1964) showed that the energy produced as heat, which was 14% of intake at a submaintenance level of feeding, reached 31% of intake in animals fed at above maintenance levels, due to the increment of energy needed for production. Thus undernourished animals are more susceptible to cold stress than adequately nourished animals.

A second set of models, based on quantitative studies of digestion in different sections of the tract attempts to explain the reasons for the variation in nutritional value of different feeds. These studies (*e.g.* AFRC 1993; Freer *et al.*, 2007) predict the amounts of metabolites that become available to the animal following fermentation and intestinal digestion of organic matter and crude protein and indicate the limiting factors, that is the minerals and metabolites that contribute to malnutrition by limiting the intake and utilization of a particular diet.

5.1. Energy transactions

Animals receiving inadequate energy levels first allocate energy to the maintenance of their current physiological state, and the energy needed to do this is referred to as the maintenance requirement.

This will differ between, for instance, a castrate male and a pregnant or lactating female, and will alter with the energy costs of maintaining body temperature in cold or warm environments, or of walking to acquire feed on land that is flat or hilly. Any available energy above that needed for maintenance can be stored as weight gain or in a foetus, hair or wool or excreted in milk. The extent of weight gain per unit surplus energy will vary between breeds, and within breeds with the age and physiological state of the animal. For instance, weight gain in the 30 kg lamb contained (g/kg) protein 130 and fat 270, whereas in the 50 kg adult the corresponding values were 90 and 600. There is therefore a transition from protein to fat deposition with increasing age (Berg & Butterfield, 1975). The energy stored in weight gain in the adult sheep, 26 MJ/kg, was almost twice as great as in the lamb (Searle *et al.*, 1972). Although this might at first sight appear to require the feeding of adequate quantities of a high quality diet to the ewe, but not the lamb, reductions in growth rate in the adult actually mean that the reverse is true. Furthermore, with significant recent advances in genetic modification techniques for animals, selection for high output, in particular of milk or wool, will exacerbate the risk of inadequate energy supplies.

When net energy supply fails to meet the maintenance requirement, weight loss begins. During weight loss, protein and fat tend to be mobilized in proportions and quantities similar to those in which they were deposited for each class of animal (Berg & Butterfield, 1975). This means that, for a given energy deficit, weight is lost faster in the young animal than in the adult. Provided that undernutrition is not too severe, the most vulnerable classes of animal, in particular the pregnant or the lactating female, can to some extent moderate the consequences of weight loss. The pregnant animal can divert metabolites mobilized as weight loss to maintain the nutrition of the foetus, so that the birth weight of the young animal can be normal despite an appreciable weight loss in the dam. The welfare of dam and offspring are not necessarily in competition, since under extreme undernutrition, foetuses may be sacrificed to allow the dam an opportunity to breed again when conditions allow. To safeguard against these eventualities, conception is highly dependent on adequate nutrient reserves in the dam. Similarly in what is probably a normal physiological practice, metabolites mobilized during weight loss by the dam in early lactation are diverted into milk so that the offspring grows at a normal rate even though the body condition of the dam is declining. More severe undernutrition can affect the birth weight of the offspring and reduce both mammary gland development and milk production, thus threatening the welfare of the under-weight new born animal. Further, reduction in body weight or condition of the lactating animal can delay return to oestrus and subsequent pregnancy. The resultant decline in the number of offspring produced during the lifetime of a female may be undesirable for farmers but, by permitting the animal to regain body condition before the next pregnancy, the future productivity of the animals may be preserved.

The least vulnerable animals are castrated adult males and non-pregnant, non-lactating females, both of which can survive long periods of energy deficiency provided the diet is reasonably well balanced for protein and minerals. For example, Morris (1968) was able to keep alive for 430 days a group of bullocks originally weighing 412 kg by offering a grass-legume hay diet that supplied energy at about two thirds of maintenance requirements. The cattle lost about 40% of body weight asymptotically during this time and hence at the end of the experiment were within the CLW range, marked by "dejected appearance, reluctance to make unnecessary movements and a reduction in rectal temperature", confirming the adverse effects of calorific restriction on ruminant behaviour (Morris, 1968). Survival was assisted by holding the animals in yards to reduce the energy costs of walking. This type of gradual undernutrition differs in its effect from sudden onset feed deprivation, as might occur following flood, fire or snow. The effect is particularly severe with fat, pregnant ewes, which develop metabolic disorders that lead to the development of fatty livers, hypoglycaemia and hyperketonaemia, often with fatal consequences. With such ewes and with lactating dairy cows, disorders of energy metabolism are frequently complicated by the onset of hypocalcaemia and hypomagnesaemia. It is of interest that with sheep transported aboard ship, problems associated with inappetance were greater among sheep that had been gaining weight pretransport than in those slowly losing weight (Norris, 2005).

The undernourished animal, when given access to feed of high nutritional value usually exhibits a period of accelerated growth called 'compensatory gain" (Mitchell, 2007). By comparison with the response to a given amount of feed by well-fed animals, the depleted animal deposits more weight, protein and water and less fat. It appears (Ryan *et al.*, 1993) that in consequence of the depletion of protein in the liver and viscera, the undernourished animal has a reduced maintenance requirement so that more net energy is available for storage. In addition the depleted animal has an increased level of voluntary feed consumption, which may persist after the depleted proteins have been replaced.

5.2. Protein transactions

Protein storage in the animal has traditionally been measured in terms of nitrogen balance, that is, as with energy balance, the difference between intake and that excreted in faeces, urine, and sweat together with nitrogen in milk and wool or hair. However these studies do not fully explain the mechanisms by which protein is catabolised and anabolised in the animal .by both the rumen microbes and the host animal. In the rumen, bacteria produce ammonia by the deamination of protein and non-protein nitrogen. Ammonia is then incorporated into bacterial protein using as energy sources the high-energy phosphates that are released during the production of short chain fatty acids. The amount of protein that leaves the stomach may be less than intake if the rate of uptake of ammonia by rumen bacteria is less than ammonia release from the diet. If ammonia accumulates in the rumen, some will be lost by absorption, whereas at the opposite extreme, a deficit in ammonia from the diet can be partially compensated by using ammonia released from urea entering the rumen from the blood, both across the rumen wall and in saliva. In that situation, the amount of crude protein leaving the rumen would be greater than intake. From knowledge of the amounts of digestible organic matter and crude protein eaten, it is possible to predict the quantity of microbial protein that passes to the small intestine. To this is added an estimated amount of dietary protein that passes through the rumen unfermented. Studies have shown that, of the mixture of nitrogenous compounds that pass into the small intestine, about 80% are amino acids, of which about 80% are absorbed from the intestine, so approximately two thirds of the organic nitrogen that leaves the stomach (that is 80% x 80%) is absorbed as amino acids from the small intestine. The proportions of individual essential amino acids are regarded as nutritionally well balanced.

As indicated previously, the efficient use of feed requires levels of ammonia in the rumen adequate for rumen microbes, together with a supply of essential amino acids to the tissues to match the energy derived from the feed. Forage plants with crude protein levels less than about 50g/kg are unlikely to provide adequate ammonia or amino acids for ruminants, and it is estimated that the welfare of the animal may be threatened if the level of ammonia falls below 50mg N/L (Satter & Slyter, 1974). With low protein forages, feed intake may increase in response to supplementary non-protein nitrogen in forms such as urea. It can increase still further by the addition to the diet of protein that in part at least escapes microbial attack in the rumen and subsequently supplies additional amino acids to the animal following digestion in the small intestine. In the study by Lindsay *et al.* (1982), the intake of spear grass (*Heteropogon contortus*) providing 25 g/kg crude protein by cows in the last trimester of pregnancy was increased from (kg/d) 4.1 to 6.2 by providing urea and sulphur and then to 8.1 by the further addition of protein meal. The benefits to animal welfare were obvious. With the basal diet being offered at a time in pregnancy when the contents of the uterus and the mammary glands would be developing rapidly, the body weight loss (850 g/d) clearly masked a much greater loss of maternal tissues, but supplementary feeding first reduced this loss and then reversed it. The benefits were also demonstrated in calf birth weights, which increased from 22 kg with the basal diet to a normal 30-32 kg with supplementary feeding. Survival of the light-weight calf would have been in doubt in many environments, whereas there was a better chance of survival of calves born to dams receiving supplements. In addition to effects on calf survival, protein malnutrition may also have effects on social activity, recorded in other mammalian species, but not yet in ruminants (Chamove, 1980; Gallo *et al*., 1980).

6. Feed Intake and Animal Welfare

As well as feed composition, the welfare of the animal may be threatened by inadequate feed intake. The control of feed intake in ruminants involves many plant, environmental and animal factors (see reviews by Weston, 2002; Forbes, 2003). Plant factors involved include the type, accessibility, maturity, and chemical composition, including various forms of toxic substances of available pasture.

Feed intake may be undesirably low if the pasture is too short or if density is too low, leading to intake restrictions due to the small size of the bites (Phillips & Leaver, 1986, although the animal attempts to compensate by grazing for long periods, between 13 and 15 hours/day (Weston, 1996). However, ruminants are also affected by behaviour of conspecifics, and when grazing efficiency for individual animals is interrupted, such as by predators or biting insects, the amount of lost grazing time will be reflected by correspondingly reduced feed intake. There is limited information on the effects on feed intake of plant palatability (Weston, 1996).

A major factor affecting feed intake, particularly under extensive grazing conditions, is plant maturity. Immature plants contain relatively low levels of fibre and are thoroughly and rapidly fermented in the rumen. Grazing ruminants preferentially select a diet composed mainly of leaf, and in areas with a suitable climate, the farmers manipulate grazing systems to provide plant leaf for the animals for as much of the year as possible. However in most areas conditions for grass growth are seasonally dependent, and plants become increasingly mature over the main growth season. Outside this season, the animal depletes plants of green leaves and the diet contains a high proportion of brown leaves and stem. Selective grazing of this nature depends on the ruminant species, with cattle and their broad dental arcade being less selective than narrow-mouthed sheep and goats. With advancing plant maturity the herbage becomes more fibrous and highly lignified and therefore less fermentable, and nutritional value is further depressed by declining levels of protein and minerals. Finally at senescence, the diet consists almost entirely of highly lignified stem that is depleted of protein and minerals and is only slowly fermentable. With this type of diet, intake by ruminants may fall to the extent that welfare is threatened.

Environmental factors affecting animal feed intake include temperature, frost, rain precipitation, the presence of ecto- and endo-parasites, distances walked to obtain feed and water and quality of and availability of drinking water. The latter is particularly important when salt-based mineral blocks provided to correct mineral deficiencies in animal diets are placed at a distance from drinking water. In such situations, supplements provided to improve animal welfare can, through excessive salt intake, occasionally cause fatal increases in plasma osmolarity.

Animal factors affecting feed intake include animal genotype and environment interaction, mobility, grazing or browsing ability, social interactions, physiological state and the capacity of the digestive and metabolic systems to function effectively with feed of varying composition. The grazing industries have by selection and cross-breeding developed animals best adapted to their environment and hence most tolerant to the factors limiting production, whether they are temperature, distance to be walked or internal and external parasites. Within each genotype, the animal's ability to harvest and process feed depends on walking ability and the possession of sound teeth. The development of sound limbs in the young growing animal can be threatened by inadequate or imbalanced supplies of calcium and phosphorus, which cause a lameness called "pegleg". Lame animals and those stressed by the presence of predators, including insects, lose grazing time, while struggling to maintain contact with their companions. Social synchronisation of behaviour dictates that very few sheep or cattle continue to graze individually when the remainder of the flock is resting so an animal distracted from grazing will suffer a reduced feed intake. This situation is exacerbated when the availability of pasture is low and even healthy animals have to spend long periods grazing to satisfy their feed intake demands. Sensitivity to the supply of dietary calcium and phosphorus also occurs during the development of permanent teeth. The "milk teeth" with which the young animal is born are gradually replaced by permanent incisor and molar teeth. This process is at a critical stage of development at 3 to 6 months of age in sheep and requires a suitably balanced supply of calcium and phosphorus. Lambs weaned onto a diet of wheat grain deficient in calcium compared with phosphorus failed to develop a full set of sound teeth, either incisors or molars, and showed depressed productivity throughout their adult lives (Franklin, 1950). Abnormal bone and dental development cannot be cured by subsequent dietary manipulation. Feed intake is also reduced in animals with damaged incisor teeth. Ruminants hold herbage between the incisor teeth in the lower jaw and a hard dental pad in the upper jaw and tear it off by upward movement of the head. This type of harvesting places strain on the insertion of incisors into the gums and can lead to periodontal disease and the loss of incisors. Damage to the incisors also occurs through chewing tree bark and timber during drought and through ingestion of soil during drought and on wet, boggy pastures

(Healy & Ludwig, 1965). When one or more of the eight incisors in the adult is lost, feed intake is reduced because of the difficulty of achieving effective apposition between damaged and irregularly shaped or spaced incisors and the dental pad.

Herbage intake is strongly influenced by the rate of movement of feed through the rumen, and this is largely a function of the rate of reduction of feed particles to a size and specific gravity that permits passage through the stomach. Particle reduction is brought about mainly through chewing, in part during eating but mainly during rumination, especially when plant fibre has been weakened by microbial fermentation. Chewing is rendered much less effective by damage to the molars and by reduction in the rate of fermentation of plant fibre that might follow a malnutrition-induced reduction in particular microbial populations.

The delay to feed particles leaving the rumen may vary from a few hours with immature pastures to 48 or more hours with very mature forage. In consequence the weight of dry matter in the rumen may vary from about one half to twice the daily dry matter intake. Muscular contraction of the reticulo-rumen constantly mixes the digesta, moves the fermentation gases, carbon dioxide and methane to the base of the oesophagus for eructation, returns digesta to the mouth via the oesophagus for further chewing between the molars during rumination, and regularly passes some digesta through and past the third compartment, the omasum to the fourth, the abomasum. The efficient functioning of all these processes is essential to the animal's welfare. Inadequate grinding of feed through ineffective rumination associated with defective molars, for instance, may delay the comminution of feed particles to sizes sufficiently small to pass onwards from the rumen and hence reduce feed intake. Failure to eructate gases leads to the development of bloat, a condition observed in some feed lots (Cheng *et al.*, 1998) and some rapidly fermented pastures in which the build up of gas pressure leads to the death of the animal (Phillips *et al.*, 1996). Maintaining an adequate mineral balance in the herbage, if necessary by applying fertilizers, will minimize the risk of bloat (Phillips *et al.*, 2001). The stoppage of rumen movements, as can occur following the ingestion of some plant toxins (McSweeney & Pass, 1983), not only prevents the flow of digesta onwards, but facilitates toxin absorption by delaying expulsion from the digestive tract and hence jeopardizes the life of the animal.

The effective functioning of the abomasum and small intestine is challenged by various helminths. Some, such as the Haemonchus species that are found in the abomasa especially of young animals, cause anaemia by extracting blood from the host. Others such as *Trichostrongylus* spp inhabit the small intestine and damage the epithelium, causing the loss of protein from endogenous sources (Van Houtert & Sykes, 1996). Acute infection can cause death especially in young animals, but many adult animals develop partial immunity and tolerate low worm burdens. Although with such chronic infections, the helminths act as stressors on the animal and reduce productivity, the main effect may be an associated depression in feed intake. In a study of the effect of Trichostrongylus, 85% of the depression of wool growth was ascribed to reduced feed intake (Symons & Jones, 1975).

6.1. Fermentation in the rumen

When forage arrives in the rumen, part of the bacterial population initially attacks soluble carbohydrate and nitrogenous components. Microbes need energy, which is mostly released as high-energy phosphates during carbohydrate fermentation. For efficient protein synthesis, energy supply should match the release of ammonia from sources of nitrogen. If it doesn't, for example during cold, dull weather when the concentration of soluble carbohydrates in the plant tends to be low and that of soluble nitrogen high, ammonia accumulates in the rumen and is largely wasted, with some energy required to recycle surplus ammonia. During the initial phase of fermentation, bacteria become closely associated with particulate material, and after a delay of a few hours commence enzymatic attack on plant fibre. This process is aided by anaerobic fungi, the motile zoospores of which attach to the ends of plant material or pass through the stomata and on germination produce hyphae that begin to digest plant structures.

Any depression in rumen pH caused by the accumulation of short chain fatty acids is controlled by the inflow of well-balanced alkaline saliva. Control of pH by salivary buffers can be difficult if the animal ingests large quantities of starch, which is rapidly fermented to permit the development of a bacterial population dominated by Lactobacilli and the production of lactic acid. Part of the dietary protein escapes attack in the rumen, but most is extensively hydrolysed and, while some released amino acids are taken up by microbes, most are deaminated resulting in the accumulation of ammonia in the rumen. Little if any amino acid appears to pass across the wall of the rumen. The microbes also release ammonia from urea that reaches the rumen by recycling from the blood either directly across the rumen wall or in saliva, a process consuming scarce energy, as referred to above. The subsequent fate of ammonia is critical to the protein metabolism of the animal. Some travels across the rumen wall and passes via the portal venous system to the liver for conversion to urea, and some passes onward with digesta through the omasum, but the main part is taken up by microbes for the synthesis of microbial protein. In some situations the total amount of protein leaving the rumen may be less than that consumed, whereas with mature, low protein forges, the conversion of recycled urea to microbial protein can result in a significant gain. This capacity to convert recycled urea to high quality protein confers on ruminants significant advantages over non-ruminant herbivores and greatly aids their welfare when the only feed available is mature, low protein forage.

The needs of cellulolytic bacteria are met by an ammonia concentration of 50 mg N/L (Satter & Slyter, 1974), but the intake of feed by cattle has responded positively to ammonia levels as high as 200 mg N/l (Boniface *et al.*, 1986). Apart from nitrogen, bacterial cells require adequate amounts of minerals such as sulphur and phosphorus, deficiencies of which reduce the size and thus the fermentation capacity of the rumen microbial population and impact directly on animal welfare. It has been suggested (Komisarczuk-Bony & Durand, 1991) that the ratios of nitrogen to sulphur and phosphorus respectively should be 16/1 and 6/1.

6.2 Hunger

From an adaptive perspective, it would be expected that persistent hunger exists to alert the animal to the continued threat of an inadequate food supply or composition, whilst not continuously activating the two neuro-endocrine response systems, the sympatho-adrenalmedullary and the hypothalamic-pituitary-adrenal axes. Thus, the stress of inadequate or unsuitable food supply is unlikely to evoke the same responses as those stresses from which the animal has to flee. During prolonged hunger the animal is faced with a dilemma, a greater investment in food searching will utilize scarce energy resources, whilst conserving energy by invoking lethargy will inevitably reduce the chance of restoring nutrition to its required level.

Motivation to feed in cattle, and hence probably hunger, increases with the length of a period of feed restriction, up to 9 hours (Schutz *et al.*, 2006). Temporary restriction of access to food and water for 6-12 hours before livestock travel has been popular in recent years in Australia, in order to restrict excreta building up on the vehicles (Hogan *et al.*, 2007). Livestock may experience stress as a result of this restriction, and depletion of glycogen reserves is more likely before slaughter, potentially leading to more dark, firm, dry meat. Food absence in the early stages is associated with activation of the sympathetic nervous system and production of cortisol (Moberg & Mench, 2000).

The impact of food and water deprivation in the longer term is unclear. As outlined above, lethargy is induced, which whilst obviously adaptive in terms of energy conservation, may also relate to depression, with associated downward position of the head and eyes half closed. Furthermore, fasting in humans is advocated in many religions as a means to obtain a higher level of purity, which may refer to the attainment of a semisomnambulent state (Pewzner-Apeloig, 1998).

Food intake restrictions are possible when ruminant livestock are provided with adequate food of suitable quality. Such inappetence is experienced by a small proportion of sheep on long distance shipments from Australia to the Middle East, a journey of 10-14 days and it seems possible that it is a similar syndrome to the anorexia nervosa in humans, which is associated with the negative affects, depression and anxiety.

In the foetus, the negative emotion of hunger in the long gestation, precocial ruminant livestock species is unlikely, given that the foetus exists in a ‘narcolepsy-like’ state (Dickinson *et al.*, 2008). Orexins, which are implicated in hunger mechanisms immediately after birth, are present in the sheep foetus brain, whereas they are not in the foetuses of altricial animals, in which much brain development occurs in the early postnatal stage (Dickinson *et al.*, 2008). However, they are believed to prime the lamb’s brain to have a fully functional hunger mechanism at birth. The main risk factor for neonatal lambs is light birth weight (Dwyer, 2007).

7. The Rumen - Always a Friend?

Many plants produce chemicals to protect against attack by bacteria, fungi or insects. These include compounds containing cyanide, fluoroacetate, tannins, isoflavones and alkaloids (*e.g.* James *et al.*, 1992; D'Mello, 2000). In addition fungi may produce alkaloids either within the growing plant after infecting the seed or saprophytically on dead plant material. Some chemicals become toxic following enzymatic attack in the rumen. When this occurs, the extent of harm done to the animal depends on the amount released, the availability of enzymes to catabolize further the harmful metabolite and, finally, the capacity of the liver to aid detoxication, The types and quantities of enzyme available for toxin release and detoxication purposes in the rumen depend on the nature and abundance of particular microbes, whose numerical importance in the population is strongly influenced by the diet provided to them. For example, cyanide is present as the non-toxic cyanogenetic glycoside in plants such as the Brazilian *Cnidosculos phyllacanthus* and *Anadenanthera (Piptadenia*) *macrocarpa*. Microbial enzymes hydrolyse the glycoside and release hydrogen cyanide. This metabolite can be fatal unless sufficient sulphide and appropriate enzymes are present to permit the conversion of cyanide to thiocyanate. In other words, microbes in the rumen can create a problem, which may require other microbes to solve. Frequently, appropriate bacteria are present in the rumen or are soon acquired and simply need time to develop in sufficient numbers to be effective. However animals exposed to novel substrates may not be able to develop microbes capable of catabolizing those substrates, as has been observed with oxalate (Dodson, 1959) and with mimosine, a potentially harmful amino acid found in *Leucaena leucocephala* (Jones & Megarrity, 1986). Even when suitable microbes are present in the rumen, several days may be needed to build up a population to a size sufficient to catabolize a toxin. This happens to sheep which initially show oestrogenic effects of the isoflavone biochanin A when fed on *Trifolium subterraneum c v Clare*, but within a few days oestrogenic activity ceases as the molecule is converted to p-ethyl phenol. This protection may be adequate if the chemical is of low toxicity. However, more toxic substances like fluoroacetate, found in *Palicourea aeneofusca*, may cause the death of the animal before a suitable microbial population can develop.

Little is known of the extent of detoxication of alkaloids, whether of plant or fungal origin. Alkaloids exert their effects initially on the liver but the symptoms may occur elsewhere. The pyrrolizidine alkaloid found in *Heliotropium europaeum* (Bull *et al.*, 1956) impairs the ability of the liver to form and discharge copper thiomolybdate and the animal succumbs to chronic copper poisoning, sometimes months after the initial exposure. Similarly Sporidesmin, produced by the saprophytic fungus *Pithomyces chartarum*, causes liver damage that diverts bile and the chlorophyll derivative phylloerythrin to the bloodstream. The affected animal becomes jaundiced and photosensitive and the face exposed to sunlight erupts in scabby sores referred to as facial eczema. Several endophyte fungi produce tremors or a staggering gait in ruminants. In locoweed (*Astragalus spp)* such symptoms are associated with the presence of indolizidine alkaloids.

Although the balance between microbial release of toxins and detoxication in rumen fermentation generally favours the protection of the animal from deleterious substances, outbreaks of toxicity indicate that this does not always occur. An example is the conversion of the non-oestrogenic isoflavone formononetin to the potent oestrogen, equol, observed with some varieties of subterranean clover. In addition, there are situations in which homeostatic mechanisms controlling the maintenance of rumen pH within a desirable range are overcome by exposure of rumen microbes to excessive amounts of readily fermented substrate. For instance, the rapid release of short chain fatty acid following the fermentation of large amounts of starch in grain or sucrose in molasses may depress rumen pH to such an extent that lactic acid producing bacteria begin to dominate the microbial population. The subsequent release of lactic acid may cause acidaemia with fatal consequences. Similarly, the ingestion of urea, which is frequently added to low protein diets as a source of ammonia for rumen bacteria, can in excess give rise to high levels of ammonia. The subsequent rise in rumen pH favours the rapid transfer of ammonia from the rumen to the liver in amounts that exceed the detoxifying capacity of that organ and ammonia can reach lethal levels in the peripheral circulation. Nitrate, present at low concentration in most plants, may reach levels toxic to ruminants in crops heavily fertilized with nitrogen fertilizers or in some pasture plants growing under cold, dull weather conditions. In the rumen, nitrate is reduced to nitrite, which, if transferred to the blood in sufficient quantities, can cause the conversion of haemoglobin to lethal levels of methaemoglobin. The welfare of animals is best protected by introducing such rapidly fermented feeds gradually and preferably combined with appreciable proportions of roughage to permit the animal to maintain homeostasis in the rumen and to develop a microbial population capable of fermenting the substrate in a controlled way.

A largely ignored aspect of the fermentation system is the protective role exerted by the bacterial population against invasion by pathogenic organisms. Protection depends on the maintenance of an active fermentation, possibly through the direct effects of released short chain fatty acids on the pathogens (Wallace *et al.*, 1989), but possibly in consequence of competition for high energy phosphates released during fatty acid production. Regardless of the mechanism, protection is reduced when the feeding pattern is interrupted (Brownlie & Grau, 1967), permitting the establishment of infection by Salmonella species in the intestine. Such interruptions occur in consequence of feed and water deprivation during transport from breeding property to sale yard or abattoir and appear to be most severe in effect when animals are removed from lush pastures (see review by Hogan *et al.*, 2007). There is evidence, too, of the establishment of colonies of the Shiga toxin- producing *Escherichia coli* Strain 0157 H7, following interruption of feed intake by animals offered diets rich in starch. Protection from this organism in humans is thought to be afforded by the acid conditions indicated by pH levels of about 1.5 in the stomach, but such protection is probably reduced in the ruminant glandular stomach compartment, the abomasums, where pH is generally about 2.5. These enteropathogenic organisms not only pose problems for the welfare of animals, but can contaminate meat derived from them and thus threaten the health of humans.

8. Management and Welfare

Grazing animals live in ecosystems influenced by soil, plant, animal and climatic factors but ultimately regulated by management decisions. Overgrazing can lead to the removal of highly palatable and nutritious plant species leaving behind bare soil subject to loss of fertility from wind and water erosion with eventual colonization by plant species of lower nutritional value. In addition, management decisions to introduce to one location, animals bred in another, carry the risk of introduction in animal faeces of seed of toxic plants that may remain viable in the digestive tract several days after ingestion (Alomar *et al.*, 1994). Factors such as these add to the difficulty for the animal husbandryperson in maintaining pastures capable of meeting the nutritional needs of the animal at all times of the year. The most vulnerable animals are the reproducing females which may become pregnant following ovulation at a time of year when the pasture is of high nutritional value but which have to meet the demands of late pregnancy and lactation many months later when the nutritional value of available pasture may be much lower. The situation becomes even more complicated if for instance, the female sheep becomes grossly obese early in pregnancy, but then faces a submaintenance supply of energy late in gestation with the metabolic consequences discussed earlier. In the production cycle of one pregnancy per year, ewes with a five-month gestation have time to restore weight lost during parturition and lactation before becoming pregnant again. This is not true for cattle. Cows attempting to produce a calf each year must become pregnant within three months of calving. If the calf is not weaned for five or six months, the cow must make good the body weight lost following calving to ensure first the resumption of ovulation and then the increasing nutritional demands of pregnancy. Some breeds of cattle do not recommence ovulation until a suitable weight has been attained. Others, however, become pregnant regardless of body condition and risk damage especially in the skeleton from the depletion of calcium and phosphorus during lactation.

Despite at times consuming minerals in ingested soil and in drinking water, the animal relies for its mineral intake mainly on forage. The concentration of minerals in plants generally reflects the levels in the soil in which they are growing. Plants take up minerals in early growth and distribute those minerals through the developing plant. If photosynthesis is extensive, the concentration of mineral per kg DM may be lower than in a plant showing less growth. This is particularly relevant for senescent or dead pasture, the mineral concentration of which may be lower after a highly productive growing season than after a less productive period. Rain falling on dead pasture may exacerbate any deficiency by leaching out minerals. Low levels in the soil of minerals such as potassium, essential for plant growth may retard the growth of a plant, but the concentration in plant DM should be adequate to meet the modest requirements of the ruminant for this mineral. Conversely the development of a pasture plant is not likely to be retarded by lack of sodium in the soil, and plants growing under such conditions may not be able to accumulate sufficient sodium to meet the relatively high demands of the animal. A similar consideration applies to chloride, iodine, cobalt, selenium and sulphur. A deficiency of these minerals affects the animal in different ways. Sodium deficiency, for instance, results in the transfer of potassium from intracellular fluid with consequences for acid-base balance and decline in productivity. Cobalt and sulphur first affect rumen microbes, the former being required by bacteria responsible for the synthesis of Vitamin B-12, the latter for many microbes requiring sulphide and especially the anaerobic fungi. A prominent feature of iodine deficiency is the grossly enlarged thyroid glands in newborn calves.

A third type of interaction occurs with phosphorus for which both plant and animal have similar requirements. When grown on phosphorus deficient soils, plants may show only limited growth, and the concentration of phosphorus in the plant may also be low. Further, the provision of additional phosphorus to the soil as fertilizer may increase plant growth but not necessarily increase the concentration of phosphorus in the plant. There are differences, too, in the interaction of plants and heavy metals. There is rarely excessive accumulation of such metals as As, I, Be, Ni and Zn, so little danger exists of toxicity. By contrast, some plants accumulate Se, Cd and Mo, all of which are potentially toxic. Surface lead pollution is now much less common following the removal of lead as an antiknock agent from petrol (Wilkinson et al., 2003). Nevertheless lead is still widely used in industry. Cattle show initial dislike of grazing contaminated pastures, but they quickly adapt and adverse effects of the lead on rumen function become evident (Phillips & Strojan, 2002). Cadmium is a contaminant of phosphorus fertilizer and sewage sludge and can reach concentrations in pasture that increase liver and kidney concentrations to the legal maximum (Prankel *et al.*, 2004, 2005). Absorption is increased if the metal is organically bound, as it is in pasture plants. High concentrations have now become evident in deer in central Europe (see review by Phillips & Prankel, in press).

9. Resolving Animal Welfare Issues

The ruminant industries are commercial enterprises and as, in general, they aim to maximize profit in a sustainable manner, economic considerations such as financial returns per hectare, financial risk, proximity to markets, availability of labour, and costs play a part in deciding the nature of the livestock venture. In any region, climatic and nutritional limitations coupled with assessment of the effects of global warming may first force decisions on the nature of the enterprise. For instance decisions that impinge not only on commercial considerations, but also on animal welfare, could include choosing buffaloes or camels instead of cattle, or sheep instead of goats, or, within a sheep venture, meat production instead of wool. The length of the pasture growing season could decide that a region was better suited for meat production rather than milk production or for breeding rather than fattening purposes or even for wool growing with castrate male sheep rather than breeding from females. When that has been established, further decisions need to be made on the most productive breeds of animals for that region. For example, some breeds are better adapted or better adaptable to hot, dry conditions with infrequent access to water. Conversely, some breeds or strains within breeds, exhibit greater capacity to remain productive under cold, wet conditions or show the benefits of greater tolerance to internal or external parasites, especially in hot, humid conditions.

Regardless of the system, grazing animals are likely to encounter one or more of the welfare problems already described. Techniques are available to diagnose the often multiple reasons for poor performance of animals in a particular region, and to recommend ways in which the problem can be solved. Strategic supplementary feeding can be used to cure or prevent mineral deficiencies. When animals face deficiencies of energy, the owner has to decide how much weight loss is tolerable, and to devise feeding strategies to maintain the animals at about the desired weight by use of cheapest available sources of energy. Treatment of protein deficiency generally involves the use of urea with additions of sulphur and a source of energy for the rumen microbes. The strategic use of protein meal may also assist in maximizing the energy derived from mature forage. The presence of organic toxins presents difficulties.

In extreme situations it may be necessary to exclude animals from affected areas, combined with efforts to eradicate the noxious plants. With less severe problems, rationing of time spent grazing the affected plants may be effective. A similar situation may prevail with mineral toxicities. Some such toxicities are imposed on the animal receiving mineral supplements, *e.g.* if a phosphate supplement is contaminated with cadmium. This type of problem can be solved by seeking other sources of phosphorus. Problems with land contaminated with heavy metals or radioactive material probably require total exclusion or soil remediation or removal. Regardless of the nutritional problem, the owner and manager are responsible for the welfare of the animals in their care. Hence there is a moral obligation to follow established Recommended Codes of Practice relating to the care and nutrition of animals, and the current trend is to give such Codes greater legal standing.

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11. About the Author

Jim Hogan graduated with honours in Agricultural Science from Sydney University. His subsequent studies for a PhD degree at the University of Aberdeen, Scotland, were supervised by Professor A T Phillipson. Hogan joined the Commonwealth Scientific and Industrial Research Organization and pioneered the development of methods to estimate the extent of digestion in the stomach and intestines of sheep and cattle. He has published extensively in that area. Relationships developed between organic matter fermentation and microbial protein synthesis form the basis for the evaluation of protein adequacy in ruminant diets in Australia and Britain. He has been involved in environmental issues and in the welfare of sheep and cattle undergoing transport He is a Fellow of the Australian Society of Animal Production.

Clive Phillips studied agriculture at Reading University and obtained a PhD in dairy cattle nutrition and behaviour from the University of Glasgow in 1983. He spent the next 11 years at the University of Wales, Bangor, researching dairy cow responses to changes in their environment, as well as investigating toxic and nutritive minerals for ruminants. From 1995 to 2003 he studied models of toxic mineral pathways in the human food chain at the University of Cambridge's veterinary school. In 2003, he became the inaugural holder of Australia's only Chair in Animal Welfare, at the University of Queensland, and established the Centre for Animal Welfare and Ethics there. The Centre currently has approximately 20 researchers studying topics on a wide range of animals, including companion, farm and zoo animals, and many welfare issues. He is a member of the Animal Welfare Committee of the National Health and Medical Research Council and has been involved in the planning and implementation of the Australian governments' Animal Welfare Strategy. He has published approximately 150 papers on animal welfare and management in scientific journals and is the author/editor of eight books, including *Principles of Cattle Production* and *The Behaviour and Welfare of Cattle*. He also edits a series of books, published by Springer, on the welfare of animals, and has just written the latest in the series, entitled *The Welfare of Animals; the Silent Majority*.