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CHAPTER 7. ADAPTATION TO GRAIN FEEDING

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Introduction

The efficiency of grain feeding is limited by the rate of adaptation to both the feed and feeding system. The speed of introduction to grain in supplementary feeding situations and intensive feedlots is influenced by several factors. The animal must adjust physiologically to the new diet and depending on the grain used there may be a high risk of acidosis during the adjustment phase. Sheep have to adapt to the novel aspects of the feeding situation such as feeding equipment, diet format and possibly the type of grain. Finally, there will be altered patterns of social interaction, especially in a confined feeding system.

Acidosis can occur when sheep are introduced to a high starch diet without an adequate introductory period. The risk of acidosis is high during confinement feeding due to the level of feeding and availability of grain, but it can also occur during introduction to grain in supplementary feeding situations. Acidosis has long been recognised as a significant impediment to successful grain feeding (Bigham and McManus 1975; Ikin and Pearce 1978) and continues to be identified as the primary health problem in feedlots despite the management and intervention strategies that have been developed (Langman and Ashton 2000; Seymour 2000). Advisers from Primary Industries and Resources South Australia carried out a survey of farmers who were lot feeding sheep in drought conditions and reported that 19 per cent of the farmers identified acidosis as the main cause of deaths in their feedlot (Langman and Ashton 2000).

Social or behavioural adaptation to grain feeding is equal in importance to physiological adaptation. Social interaction and animal dominance can cause variation in intake between animals, contributing to variation in growth rate. At the extreme, there will be a proportion of animals that do not adapt at all to supplementary feeding and these animals are referred to as 'shy-feeders'. The incidence of shy-feeders is increased by the intensity of the feeding system and it is usual to budget for at least 5 per cent shy-feeders in a feedlot operation (Bell *et al.* 2003). However, the amount eaten of a new food can vary by as much as four- to five-fold between sheep within a similar age group (Juwarini *et al.* 1981). Clearly, the rate of adaptation to diets continues to impact on grain finishing systems and this is an area that requires further investigation.

Physiological adaptation to grain feeding

Acidosis (lactic acidosis)

By definition, acidosis is 'a pathological condition resulting from accumulation of acid or depletion of the alkaline reserve (bicarbonate content) in the blood and body tissues and characterised by increase in hydrogen ion concentration (decrease in pH)' (Blood and Studdert 1990). When applied to ruminants, the term acidosis more specifically encompasses a range of metabolic disturbances that arise from the excess production of lactate and other acids by bacteria in the rumen or hindgut. Acidosis can be separated into two main categories, acute or subclinical (chronic). Acute acidosis presents as an overt illness following excessive consumption of highly fermentable carbohydrates and may lead to death. In contrast, chronic acidosis may not be associated with obvious clinical signs but commonly causes a reduction in feed intake and an accompanying decrease in performance.

Subclinical acidosis is perhaps more economically important for large feedlot operations, but acute acidosis can be a significant problem during introduction to high-grain diets.

The common cause of acidosis in ruminants is the production and absorption of large quantities of fixed acid such as lactic acid and the excess loss of the bicarbonate ion during acute carbohydrate engorgement (Blood *et al.* 1983). The introduction of highly fermentable carbohydrates to the rumen leads to rapid production of volatile fatty acids, including lactate. Lactate removal from the rumen is slow and when the rate of production exceeds the rate of removal, the pH may fall below 6.0. This favours the rapid growth of lactic acid-producing bacteria including *Streptococcus bovis* and *Lactobacillus* spp. The pH continues to fall, exacerbating the imbalance between lactate-producing and lactate-using bacteria by allowing *Lactobacillus* spp. to proliferate (Al-Jassim and Rowe 1999). Ruminal pH of 5.2 and 5.6 have been suggested as benchmarks for clinical diagnosis of acute and subclinical acidosis (Owens *et al.* 1998).

Acidosis can also occur in the hindgut (caecum and colon) as a result of starch passing through to the small intestine without complete digestion. During a grain engorgement challenge, the pH of digesta in the caecum and colon decreases to levels similar to or lower than those seen in the rumen (Godfrey *et al.* 1993a; Lee 1977). Godfrey *et al.* (1993a) suggested that post-ruminal changes in pH and digesta dry matter are important in the development of clinical signs of acidosis, especially diarrhoea (scouring).

Strategies to control acidosis predominantly rely on management practices or feed additives (Figure 7.1). Management strategies such as choice of grain and method of feeding reduce the level of fermentation substrates entering the rumen and thereby decrease the risk of acidosis. Intervention strategies within the rumen aim to control lactate accumulation either by decreasing production or increasing utilisation. Acidosis is initiated by the proliferation of lactate-producing bacteria; therefore a logical strategy for controlling acidosis is to prevent lactate production through use of selective antibiotics or vaccines. Other investigations have focussed on methods of promoting lactate utilisation by inoculation with rumen fluid or bacterial cultures, dosing with probiotics and dicarboxylic acids. The addition of buffering salts is aimed at maintaining a more favourable pH in the rumen to control the clinical signs of acidosis.

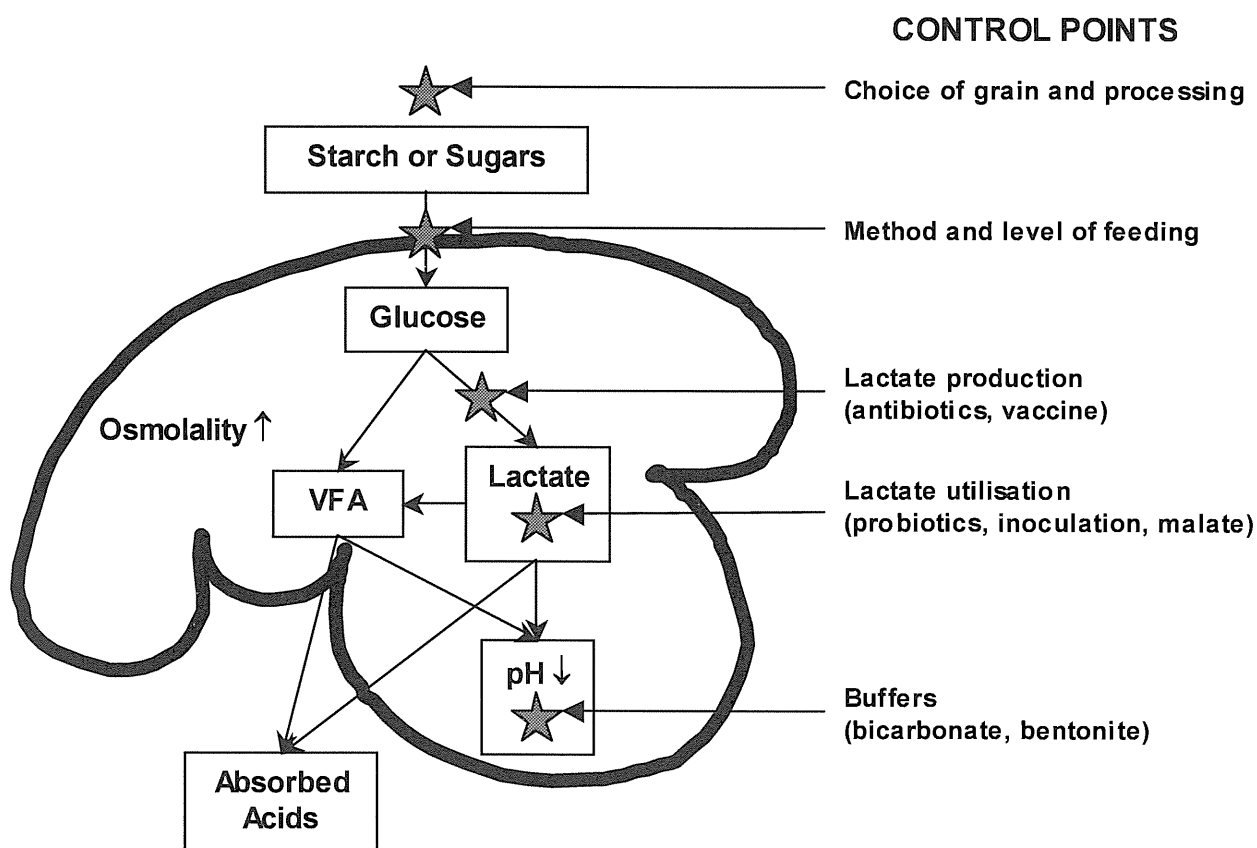


Figure 7.1. Principal reactions and control points for managing acidosis (Owens *et al.* 1998; Rowe *et al.* 2002).

Rumen modifying antibiotics

Antibiotic compounds that have selected activity against gram-positive bacteria are useful for controlling the accumulation of lactic acid, because many lactate-producing bacteria are gram-positive, while lactate users are gram-negative. Several antibiotic compounds have been investigated for their efficacy in preventing acidosis in ruminants. The compound that has been most thoroughly investigated under Australian conditions is virginiamycin.

There has been limited registration of antibiotics for use as feed additives for sheep in Australia. Sheep production systems are predominantly extensive so there has been relatively little demand or funding for development of feed additives for sheep compared to other livestock (e.g. pigs, poultry and cattle). The ionophore lasalocid is registered for use as a feed additive in sheep (and cattle) rations for reduction of gram-positive bacteria in the rumen and faecal shedding of coccidia and virginiamycin¹ is registered for use in ruminant rations to reduce the risk of acidosis when feeding grains.

¹ As of 1 January 2004 all veterinary chemicals containing virginiamycin became Schedule 4 Poisons (Prescription Animal Remedies) and must be supplied or prescribed by a Veterinarian. The change in scheduling relates to the view that the continued unrestricted use of this product poses an unacceptable risk to humans from the development and transfer of resistance to this class of antibiotics. Draft review report available at [WWW document]. URL <http://www.apvma.gov.au/chemrev/virginiamycin.pdf> (accessed 31/3/04).

Non-ionophore antibiotics

Over the last four decades a number of antibiotics have undergone *in vitro* or *in vivo* evaluation for potential to prevent lactate accumulation and the development of acidosis in ruminants. Early evaluations of antibiotics including tetracycline, penicillin, capreomycin disulfate, oxamycin and thiopeptin were reviewed by Nagaraja *et al.* (1981). These authors concluded that tetracycline and penicillin had limited usefulness due to existing resistance to these antibiotics and their negative effects on production of volatile fatty acids. In addition, penicillin has been shown to suppress lactate fermentation for less than 16 h, so has limited effectiveness at preventing acidosis (Muir *et al.* 1980b).

During the late 1970s and early 1980s, there was some interest in thiopeptin, a sulfur-containing peptide antibiotic with high specificity for *S. bovis*. It was shown to be highly active against *S. bovis* in an *in vitro* system and effective at preventing acidosis during an acute challenge (Kezar and Church 1979; Muir and Barreto 1979; Muir *et al.* 1980b). Inclusion of 11 ppm or more of thiopeptin in the ration improved feed intake and growth rate of lambs during an 8-week finishing period where a high starch diet was abruptly introduced (Muir *et al.* 1980a). Muir *et al.* (1980a) also demonstrated that lower doses of thiopeptin were able to prevent death although there was no improvement in performance compared to controls, suggesting that at least 11 ppm of thiopeptin was required to prevent subclinical acidosis. Other thiopeptin-like antibiotics were similarly successful at preventing acidosis without inhibiting normal volatile fatty acid production (Muir *et al.* 1980b). The available literature suggests that thiopeptin and related compounds are suitable for prevention of acidosis but there has been no commercial development of these products for use in sheep.

The gram-positive spectrum glycopeptide antibiotics, avoparcin and flavomycin (bambermycin; flavophospholipol) have been examined for their potential to prevent acidosis. Preliminary *in vivo* investigation showed that flavomycin did not prevent lactate accumulation during an acute grain challenge (Aitchison *et al.* 1987; McDonald *et al.* 1987). McDonald *et al.* (1987) and Aitchison *et al.* (1987) reported that lactate concentration was reduced by dosing with avoparcin prior to, or during an acute grain challenge. However, avoparcin was less effective for controlling lactate production *in vitro* than other antimicrobial compounds (Nagaraja *et al.* 1987). Subsequently, Butler *et al.* (1992) reported that avoparcin depressed feed intake and liveweight change rather than provided a beneficial effect on ruminal fermentation. Avoparcin and flavomycin do not appear to be effective for use in alleviating acidosis. In addition, avoparcin is no longer considered suitable for use as an animal feed additive as it is closely related to antibiotics used in human medicine (APVMA 2001; JETACAR 1999).

The antibiotic that has been most thoroughly investigated in Australia for the mitigation of acidosis in ruminants is the streptogramin antibiotic, virginiamycin. Virginiamycin is highly effective at reducing lactate concentration and acidity during *in vitro* fermentation of rumen fluid and during an acute grain challenge *in vivo* (Godfrey *et al.* 1995; Nagaraja *et al.* 1987). Godfrey *et al.* (1995) simulated abrupt introduction to grain supplementation by offering 2.1 kg wheat either with or without virginiamycin to sheep maintained on 300 g/day chaff for the previous 9 days. In support of *in vitro* results, rumen L-lactate concentration and hydrogen ion concentrations were lower in sheep offered wheat with virginiamycin compared to sheep fed wheat only. During simulation of long-term grain supplementation under grazing conditions, Godfrey *et al.* (1993b) demonstrated that inclusion of virginiamycin with barley resulted in higher liveweight gains, higher chaff intake and a reduction in the incidence of diarrhoea compared to a diet of barley alone. These results suggest that inclusion of virginiamycin controls acute acidosis during grain introduction and subclinical acidosis during intermittent grain supplementation.

In grazing situations where animals are harvesting residual grain from stubbles or failed crops it is not possible to include antibiotics with the grain. Preliminary investigations have been conducted to examine the feasibility of treating the animal directly with virginiamycin for

the prevention of acidosis during grain feeding. Pre-dosing sheep with virginiamycin prior to a single acute grain challenge was successful in maintaining a higher pH in the rumen (Thorniley *et al.* 1996) and preventing lactate accumulation in the caecum and colon (Godfrey *et al.* 1993a). To be successful under commercial feeding conditions, treatment with virginiamycin must give protection against the accumulation of lactic acid while the rumen population adapts to a high-grain diet. Thorniley *et al.* (1998) demonstrated that a single drench treatment with at least 80 mg virginiamycin reduced rumen acidity and consequently increased rumen pH of sheep with no prior introduction to grain when they were offered wheat for 14 days. The sheep treated with virginiamycin resumed eating more rapidly than untreated animals following inappetence caused by overeating when grain was first offered. Interestingly, animals drenched with virginiamycin did not overeat to the same degree as untreated animals, so the severity of acidosis may have been reduced simply because intake of starch was lower. Thorniley *et al.* (1998) suggest that this may be an important mechanism of action of virginiamycin that complements the direct antibiotic activity. It would be valuable to isolate the magnitude of effects of restricted intake and direct antibiotic activity in preventing acidosis during abrupt introduction to grain.

The development of virginiamycin for use in sheep has focussed mainly on extensive grazing situations where grain supplements are used. There are fewer studies investigating inclusion of virginiamycin in complete grain-based rations. McDonald *et al.* (1994) showed that inclusion of virginiamycin in a barley-based shipping pellet increased the number of sheep that began feeding during a simulated export assembly period. In contrast, Murray *et al.* (1992) reported decreased feed intake by sheep when virginiamycin was included in grain-based pelleted diets. Unpublished studies summarised in the APVMA review of virginiamycin failed to show any production benefits when virginiamycin was included in pelleted diets (APVMA 2003). However the production situations and experimental detail were not clear from the summaries so it is not possible to determine whether this conclusion is relevant to intensive feeding for meat production. Other evidence suggests that virginiamycin may have a role in preventing subclinical acidosis in production feeding situations. Where grain has been introduced gradually to prevent acute acidosis, inclusion of virginiamycin in beef feedlot diets has been shown to improve weight gain and feed conversion efficiency and reduce the development of liver abscesses (unpublished data APVMA 2003). There may be some scope to clarify the efficacy of virginiamycin for the prevention of subclinical acidosis during confined production feeding; however alternative ionophore antibiotics may be more suitable for this purpose.

In the future, the use of antibiotics may be restricted or potential applications altered and therefore avenues for strategic use or alternative acidosis controlling strategies should be investigated. The report produced by the Joint Expert Technical Advisory Committee on Antibiotic Resistance (JETACAR 1999) recommended a review of the use of virginiamycin for animal treatment due to concerns that its use may impair the efficacy of related therapeutic antibiotics for humans through the development of resistant strains of organisms. The resulting draft review of the Australian Pesticides and Veterinary Medicines Authority recommended the following changes to the registration of virginiamycin for use in sheep production (Table 7.1, APVMA 2003).

The recommended label changes indicate that the long-term use of virginiamycin within feeding regimes will be restricted. Presently there is no recommendation for period of in-feed inclusion of virginiamycin placed on labels but some producers rely on use for the duration of the grain feeding program. The proposed label amendments mean that virginiamycin will no longer be approved for prophylactic use in feedlot diets; however, it will still be available as a management strategy for extensive grain feeding.

Table 7.1. An extract of the draft recommendations for the use of virginiamycin when grain feeding sheep (APVMA 2003) [For current schedule refer footnote 1].

Product	49111 Eskalin wettable powder spray-on feed premix.
Active ingredient	virginiamycin 400 g/kg (individual sachets of 20 g).
Poison schedule classification	Schedule 5.
Registrant	Phibro Animal Health.
Claims on APVMA approved label	For use in cattle and sheep rations to reduce the risk of acidosis when feeding grain.
Recommendations	Label changes required. Schedule currently under consideration by NDPSC.
Proposed label amendments	Drought fed sheep and cattle: For use to reduce the risk of acidosis in sheep and cattle fed grain on a weekly or twice weekly basis.
Regulatory decision	Vary conditions of label approval. Affirm registrations.

Virginiamycin has never been approved for prophylactic or therapeutic use for sheep in the European Union, New Zealand or the United States (APVMA 2003). In 1998, the authorisation for use of virginiamycin as a growth promotant for pigs and poultry was withdrawn by the European Union, bringing this antibiotic and the issue of antibiotic resistance to the attention of consumers. Consumer pressure from both domestic and international markets is likely to have as much influence on use of virginiamycin within the sheep industry as any regulatory controls. Identification of alternatives for adaptation of livestock to grain-based diets will be an important priority for the sheep industry.

Ionophores

Ionophores are a class of antibiotics named for their ability to form complexes with particular cations and facilitate their transport across biological membranes (Nagaraja 1995). Carboxylic polyether ionophores have the ability to beneficially modify rumen fermentation through selective activity against gram-positive bacteria and those with a gram-positive cell wall structure (Bergen and Bates 1984; Nagaraja 1995). Following the discovery of the efficacy of monensin in 1976, a range of ionophores were developed or are under investigation for use as growth promotants for ruminants (Nagaraja 1995; Raun *et al.* 1976). In general, ionophores improve feed efficiency, but can have a variable influence on feed intake and weight gain (Table 7.2). Ionophores fed with diets that are high in readily fermentable carbohydrates (grain-based diets) generally lead to a reduction in feed intake with improvements in feed conversion ratio (Schelling 1984). On the other hand, when used in roughage diets that contain β -linked carbohydrates ionophores may not depress feed intake, but the weight gain of the animal is generally improved (Bergen and Bates 1984). The chemical and physical properties of different fibre sources can also influence the digestibility and intake response when fed with ionophores.

Table 7.2. The general response of beef cattle to ionophore antibiotics (↑ increase; ↓ decrease; 0 no change) (Nagaraja *et al.* 1997).

Ionophore	Grain fed			Pasture fed
	Intake	Gain	Efficiency	Gain
Monensin	↓	0	↑	↑
Lasalocid	0.↑	↑	↑	↑
Laidlomycin	0.↑	↑	↑	N/A
Lysocellin	↓	0.↑	↑	↑
Narasin	↓	0	↑	N/A
Salinomycin	0.↓	0.↑	↑	↑
Tetronasin	↓	0.↑	↑	↑

Bergen and Bates (1984) identified three main areas of metabolism that are affected by ionophores that may account for the improvement in feed efficiency in ruminants:

1. Improved efficiency of energy metabolism.
2. Improved nitrogen metabolism.
3. Shift in rumen fermentation away from lactate production and reduction in froth formation, resulting in a reduction in lactic acidosis and bloat.

It is outside the scope of this review to consider the effect of ionophores on energy and nitrogen metabolism. These effects have been well characterised by others, especially in cattle (reviews Bergen and Bates 1984; Nagaraja 1995). It is generally agreed that ionophores produce a consistent improvement in feed efficiency in cattle, but results are more variable for sheep (Daugherty *et al.* 1986; Horton and Stockdale 1981; Muwalla *et al.* 1998; Nagaraja 1995; Spears 1990). Spears (1990) summarised a number of studies and concluded that on average, there was no increase in energy digestibility for sheep fed either lasalocid or monensin.

The potential of ionophores to reduce the prevalence of feedlot disorders such as acidosis has been demonstrated in specific investigations. In contrast to narrow-spectrum antibiotics that are primarily active against gram-positive bacteria, e.g. *S. bovis*, lasalocid and monensin were shown to inhibit a wide range of lactate-producing bacteria *in vitro*, e.g. *Lactobacillus*, *Butyrivibrio*, *Ruminococcus*, *Eubacterium* and *Lachnospira* (Dennis *et al.* 1981b). Studies have also shown that ionophore antibiotics are effective in preventing the accumulation of lactate in rumen fluid *in vitro* (Dennis *et al.* 1981a; Newbold and Wallace 1988). Ionophores have been examined for their efficacy *in vivo* by simulating acute (grain or glucose challenge) and subclinical acidosis in cattle (Burrin and Britton 1986; Nagaraja *et al.* 1981, 1982). Nagaraja *et al.* (1981) reported that acute acidosis was prevented by treating cattle with lasalocid or monensin for 7 days prior to a grain challenge. Monensin alleviated the rumen pH decline during subclinical acidosis induced by an abrupt change from forage to a concentrate ration in steers (Burrin and Britton 1986) but was not effective when administered with the diet or as a controlled release capsule to dairy cows with experimentally induced subclinical acidosis (Mutsvangwa *et al.* 2002).

The ionophores lasalocid and monensin were more effective in the prevention of rumen pH decline in cattle challenged with glucose than the sulfur-containing peptide antibiotic, thiopeptin (Nagaraja *et al.* 1982). This is not surprising considering that the ionophores have a broader spectrum than thiopeptin. Lasalocid and tetronasin were shown to be more effective than monensin at inhibiting lactate production during *in vitro* incubation with rumen fluid from cattle (Dennis *et al.* 1981a; Newbold and Wallace 1988). Nagaraja *et al.* (1987) screened a range of antimicrobial feed additives and found that incubation of rumen fluid

from cattle with narasin or salinomycin resulted in higher final pH than incubation with other ionophores.

Improvements in feed efficiency are reported more consistently in cattle than sheep indicating that the inhibitory effects of ionophores exert subtly different pressure on the rumen bacteria populations of each of the two species (Spears 1990). This suggests that it is not appropriate to assume that the mitigation of acidosis by ionophores observed in cattle will be apparent in sheep. There is only one study on the efficacy of ionophores for preventing acidosis in sheep. Rowe (1988) hypothesised that the improved performance of sheep receiving lasalocid during a simulated shipping assembly period was due to alleviation of acidosis. Further investigation is required to determine whether ionophores influence rumen fermentation sufficiently for sheep to avoid acidosis when challenged with high grain diets during production feeding.

Inoculants and probiotics

There is potential to reduce the susceptibility of sheep to acidosis through the introduction of naturally occurring organisms (probiotics) to the rumen (Mackie and McSweeney 2002). The two main approaches to probiotic prevention of acidosis in ruminants have been inoculation with lactate utilising bacteria and inclusion of yeasts in the diet.

Amylolytic, lactate-producing bacteria proliferate when sheep are introduced to grain. If the introduction occurs gradually, lactate-utilising bacteria such as *Megasphaera elsdenii* respond to the increase in their primary substrate and multiply concurrently to prevent lactate accumulation. Several authors have demonstrated that this process can be accelerated by inoculating unadapted animals with crude rumen fluid from animals that are already adapted to grain (Allison *et al.* 1964; Godfrey *et al.* 1993a; Huber 1974). This approach has been refined by targeting the predominant lactate-utilising bacteria in the rumen of animals adapted to a high grain diet. Kung and Hession (1995) reported that *in vitro* inoculation with *M. elsdenii* prevented accumulation of lactate when rumen fluid from cattle was incubated with rapidly fermentable carbohydrates. This finding is supported by *in vivo* investigations in sheep. Wiryawan and Brooker (1995) demonstrated that inoculation of the rumen with *Sel. ruminantium* in combination with *M. elsdenii* prior to acute grain feeding of animals prevented the accumulation of lactate and stabilised ruminal pH for 4 days. Although *Anaerovibrio* spp. have been identified as one of the primary lactate utilising bacteria in the rumen of grain-adapted sheep (Mackie *et al.* 1978), there has been no investigation of their efficacy as an inoculant for the prevention of acidosis. Determining the right combination of probiotics to be included in a feeding regime may help during the initial period of adaptation to grain.

There is interest in microbial feed additives, most commonly based on *Saccharomyces cerevisiae* and *Aspergillus oryzae*, as an alternative to hormonal and antibiotic growth promotants. The production responses to these products reported for ruminants are variable, but generally positive (Newbold 1995). Although the mode of action of fungi and yeasts is unclear, the most common effect is an increase in bacterial numbers, including lactate utilising bacteria (Wallace 1996). *S. cerevisiae* was shown to prevent the accumulation of lactate in the rumen during fermentation of starch (Williams and Newbold 1990), possibly through a stimulatory effect on *M. elsdenii* and *Sel. ruminantium* (Chaucheyras *et al.* 1996; Nisbet and Martin 1991). These findings suggest that microbial feed additives may be suitable for the prevention of acidosis in sheep; however *in vivo* investigations have not supported this hypothesis. Chademana and Offer (1990) reported no effect on rumen pH when *S. cerevisiae* was included in the diet and pre-dosing sheep with *S. cerevisiae* prior to a grain challenge did not appear to cause any changes in the pattern of rumen fermentation and digestion compared to untreated animals (Godfrey *et al.* 1993a).

It has been proposed that the stimulatory effect of *S. cerevisiae* on lactate utilisation by rumen bacteria is mediated through its high dicarboxylic acid content (Nisbet and Martin 1991, 1994). In support of this hypothesis, Martin (1998) demonstrated that the addition of malate increased final pH during *in vitro* fermentation of starch in rumen fluid. Martin (1998)

concluded that there is potential for dicarboxylic acids to be utilised *in vivo* to alleviate acidosis. Further work is required to investigate this hypothesis.

Vaccines

The use of vaccinations to reduce the incidence of lactic acidosis in ruminants may be a long-term option to facilitate rapid adaptation to high grain diets. Brown *et al.* (2002) demonstrated an antibody response in sheep immunised with bacterial isolates of *S. bovis*, *Sel. ruminantium*, *S. equis* and *L. vitulinus* suggesting that it may be possible for protective immunity to be conferred via vaccination against a range of lactate-producing bacteria. In support of this hypothesis, immunisation against *S. bovis* was shown to attenuate clinical signs of acidosis when sheep were challenged by an abrupt change to a high grain diet (Gill *et al.* 2000). While Gill *et al.* (2000) were able to demonstrate the effectiveness of the vaccine, the regime used involved three booster immunisations over a period of 56 days. The authors acknowledged that this may not be a practical solution to prevention of acidosis during grain finishing and further investigation of this management strategy is required before it can be applied commercially.

Sodium bicarbonate and bentonite

It is common to include sodium bicarbonate or bentonite in high grain diets to alleviate acidosis. During introduction to grain, the addition of sodium bicarbonate has been shown to result in higher rumen pH (Ha *et al.* 1983; Kezar and Church 1979); however, following the initial adaptation period, the benefits are less apparent (Ha *et al.* 1983; Huntington *et al.* 1977). Interestingly, Phy and Provenza (1998a, 1998b) demonstrated that sheep show a preference for feeds that contain sodium bicarbonate when they are consuming feeds that are likely to promote acidosis.

High concentrate diets are associated with decreased salivary output due to reduced mastication and rumination of feed. This results in a reduction in the amount of bicarbonate entering the rumen in saliva and lowers the buffering capacity of the rumen. Attempts to alleviate this problem have focussed on the addition of exogenous bicarbonate, however Hibberd *et al.* (1995) took a novel approach and investigated the feasibility of increasing saliva flow. They demonstrated that the administration of slaframine, a parasympathomimetic compound, increased salivary output and ruminal pH in steers during a subacute acidosis challenge.

It is generally assumed that the effectiveness of sodium bicarbonate is due to increased buffering in the rumen (Matrone *et al.* 1959), but an alternative hypothesis has been proposed (Russell and Chow 1993). Russell and Chow (1993) suggest that dietary addition of carbonate is unlikely to provide buffering capacity because rumen fluid is already saturated with CO₂ so there is limited opportunity for the equilibrium to shift in favour of decreased hydrogen ions. They postulate that the actions of buffering salts are more likely due to a cascade of events initiated by increased water intake which leads to increased rumen dilution rate causing more rapid passage of starch from the rumen and decreased production of propionate (Russell and Chow 1993). This hypothesis is supported by the observation that pH change in the rumen in response to buffering salts is often negligible and a positive production effect may be apparent without a pH change (Clayton *et al.* 1999).

It may be appropriate to extrapolate the hypothesis proposed by Russell and Chow (1993) to other buffering compounds such as bentonite and limestone that have been observed to have a small effect on rumen pH, but that tend to alleviate acidosis during introduction to high concentrate diets (Ha *et al.* 1983).

Conclusions

Many intervention strategies have been assessed for their potential to reduce the impact of acute and subclinical acidosis. Appropriate introductory feeding to allow microbial populations to adapt to diet change remains one of the most effective tools for limiting the risk of acidosis. Antibiotic feed additives that selectively control gram-positive bacteria efficaciously control acidosis and there is scope for further work to investigate the targeted use of antibiotics during introduction to grain feeding in confined feeding systems. In light of consumer concerns about antibiotic growth promotants, it may be more appropriate to focus research efforts on ionophore compounds rather than non-ionophore antibiotics. The effectiveness of ionophores against subclinical acidosis in sheep has not been thoroughly investigated.

There has been limited investigation into the commercial feasibility of specific vaccination against lactic acid-producing bacteria or inoculation strategies to increase the prevalence of lactic acid using bacteria. Further investigation to develop these strategies is warranted.

Social and behavioural adaptation to grain feeding

The profitability of supplementary or lot feeding is linked to the speed at which animals adapt to the feeding system and reach maximum intake. Livestock quite often display neophobia (i.e. fear of the new) when first exposed to a novel feed (Juwarini *et al.* 1981; Lynch *et al.* 1983), feed delivery device (Chapple *et al.* 1987a; Holst *et al.* 1994) or indeed feeding environment (Burritt and Provenza 1997). Typically when exposed to a new feed, animals sample the feed cautiously before accepting it and it can take a number of days to reach a stable intake pattern. Consequently, within contemporary groups there can be considerable variation in the rate of acceptance of a novel feed (Bowman and Sowell 1997; Juwarini *et al.* 1981). Furthermore, a three- to five-fold variation in feed intake between animals may still prevail even after the initial feed acceptance period (Lynch *et al.* 1992). Several environmental and animal factors underpin this observed variation and these have been reviewed by Bowman and Sowell (1997).

Environmental factors such as the feed delivery method, trough space, and feed formulation and allowance have all been shown to influence feed intake variability (Bowman and Sowell 1997). Often the first hurdle in becoming accustomed to a novel feed such as grain, is overcoming the fear of the feed delivery method (Chapple *et al.* 1987a). For example, Holst *et al.* (1994) reported much higher variation in supplement intake between individuals when the supplement was offered in a self-feeder rather than being offered in a more familiar context such as being trail fed on the ground. Furthermore, a change to the animals' environment is likely to elicit some latency in food acceptance even when the animals are familiar with the feed (Burritt and Provenza 1997). Clearly, when ruminants are placed in a feedlot it represents a significant change in their feeding environment. At this point, apart from ensuring that trough space and feed allowance are optimised, there is very little that can be done to enhance the rate of acceptance of the feed or indeed minimise the level of variation between animals in feed intake.

The prominent attributes of the animal that can influence the variation in the acceptability and intake of a novel feed include social order and prior experience. Whilst social order or dominance hierarchies are not as obvious in sheep as they are in other genera, they are evident particularly in competitive situations (Lynch *et al.* 1992). However, there is little published data examining the effect of social order on feeding behaviour in sheep (Arnold and Maller 1974; Lobato and Beilharz 1979) which is in stark contrast to the extensive literature in cattle, in particular dairy cattle (e.g. Corkum *et al.* 1994; Hasegawa *et al.* 1997; Leaver and Yarrow 1980; Olofsson 1999; Reynolds and Campling 1981). For cattle under intensive feeding conditions or during the provision of supplements, the results indicate that dominant animals can influence the feeding behaviour of subordinates. This was manifest through increased displacements from the feed/feed station and as a consequence,

subordinates fed less frequently, spent more time during a feeding bout but often not at the preferred daily times of the individual (Hasegawa *et al.* 1997; Leaver and Yarrow 1980; Olofsson 1999). These changes in feeding behaviour are likely to be exacerbated during increased competition for the feed (e.g. reduced trough or bunk space) (Arnold and Maller 1974; Hasegawa *et al.* 1997; Olofsson 1999). Whilst there is general agreement that behaviour is affected in group feeding situations, the results are not conclusive as to whether feed intake is adversely affected. Leaver and Yarrow (1980) concluded that dominance value was positively correlated with silage intake under restricted access conditions. In contrast, others have shown either no change (Reynolds and Campling 1981) or indeed an increase in feed intake (Olofsson 1999) when competition for the feed resource was increased through reduction of feed access. In the one ovine study where intake was measured, dominance value was positively correlated with the mean intake of oats and hay supplements when provided at pasture (Lobato and Beilharz 1979). Although no firm conclusions can be drawn here with respect to feed intake, there are sufficient grounds in the context of managing group feeding situations and maximising productivity to minimise the impact of social dominance (Phillips and Rind 2002). To that end, the most practical, but not always effective solution would be to ensure that grouped animals are similar in age and body size. Dominance has been shown to be positively correlated with these two variables (Lobato and Beilharz 1979; Lynch *et al.* 1992).

Prior experience with a novel feed has been shown to expedite the acceptability of that food later in life (Bowman and Sowell 1997). For example, Green *et al.* (1984) demonstrated that lambs exposed to wheat at a young age more readily accepted the grain in later life compared to the control group. However, the decrease in food neophobia was dramatically improved if the initial exposure was undertaken in the presence of experienced social partners (Chapple *et al.* 1987b; Green *et al.* 1984; Lynch *et al.* 1983; Thorhallsdottir *et al.* 1990). The study of Green *et al.* (1984) perhaps highlights this effect best. Merino lambs were given access to wheat for 1 h/day for periods varying from 5 to 20 days in the presence or absence of their mothers. After weaning the lambs were exposed to wheat again at 3, 6, 12, 24 and 34 months of age. The lambs given wheat in the presence of their mothers pre-weaning, consumed significantly more at these time points compared to those exposed to wheat in the absence of their mothers or controls. Another compelling result was the proportion of animals consuming wheat after one day, whereby 92 per cent of the lambs from the group exposed to the grain with their mothers, were eating. This is in stark contrast to the results for the group exposed without their mothers (20%) or control group (5%). Even by day 5, there were still large differences between the groups. In a separate study reported by Lynch and Bell (1987), grain-experienced ewes and their naïve lambs were offered grain on three occasions, one day apart. By the third day, most of the lambs were eating the grain. When tested 2 years later (with no other grain feeding since), all the sheep exposed as lambs readily ate offered grain, whereas almost none of their control cohorts from the same farms ate the grain.

It is important to recognise that whilst the social transmission of feeding behaviour is effective; its efficacy can be influenced by the quality of the relationship between the two animals (Veissier *et al.* 1998). In this instance, the maternal influence is certainly stronger than the effect of a non-maternal social partner. This was particularly evident in the study of Thorhallsdottir *et al.* (1990) where the lambs that consumed a novel food in the presence of their mother (pre-weaning) ate twice as much after weaning compared to the lambs exposed in the presence of a dry ewe.

The above results highlight the strength of social models in the transmission of feeding behaviour and food acceptance and also suggest that socially acquired information was more efficient than trial and error learning in the development of feeding behaviour and food acceptance (Veissier *et al.* 1998). In the context of either supplementary feeding or intensive finishing of sheep, it appears that the introduction of pre-weaning exposure of lambs to a novel feed/supplement, together with their experienced dams, in order to expedite the acceptance of such feeds later in life, has considerable practical and economic merits. However, there are several key issues requiring further research. The most obvious is

whether the benefit is maintained when the feed type is varied. For example, if lambs are given wheat pre-weaning, will they still readily consume an alternative grain (e.g. sorghum) or novel feed/supplement? Another issue is the duration of exposure, and although there is some evidence to suggest that this may not be important (J.J. Lynch 2003, pers. comm.), research to identify the minimum necessary duration or number of exposures would be valuable.

Conclusions

Rapid adaptation to grain feeding will maximise intake and reduce the variation in intake between individual animals. In comparison to cattle, the period of time on feed for sheep in intensive finishing systems is very short, so rapid acceptance of grain is especially important. The impact of social interaction on variation in feed intake can be addressed by adopting appropriate management strategies to reduce competition. There are existing recommendations for trough spacing, introduction to novel feeds and managing shy-feeders but there may be an opportunity to further investigate management strategies to enhance behavioural adaptation to intensive grain feeding. To that end, further investigation of the usefulness of social transmission of feeding behaviour early in life would appear to offer most promise.

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