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CHAPTER 2. NUTRITIONAL REQUIREMENTS OF GROWING LAMBS: PROTEIN AND ENERGY REQUIREMENTS

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Introduction
The quantity and array of nutrients required by tissues is a function of the stage of growth of the animal, its nutritional history and its genetic capacity for growth. How animals metabolise absorbed nutrients will be modified by the supply of these and other nutrients in relation to tissue requirements at that time. The greatest demand by the tissues of the growing animal is for energy, specifically metabolisable energy (ME), to fuel protein synthesis from amino acids. Measurements of animal growth have provided the basis for defining the energy and protein requirements of animals used in global feeding standards. This review of the principles underlying the protein and energy requirements of lambs, explains how and why these requirements change through the life of a lamb and how genotype and growth path can modify tissue deposition. The protein and energy content of cereal grains is considered relative to the nutrient requirements of the microorganisms in the rumen and of the metabolic requirements of a finishing lamb.

The physiological basis for energy and protein requirements

Energy
The synthetic processes in lambs, as in all mammals, require adenosine triphosphate (ATP) to fuel the reaction and this ATP results from oxidation of high-energy substrates. In ruminants the principal energy substrates for ATP synthesis are the volatile fatty acids (VFA) arising from microbial fermentation of dietary carbohydrates in the rumen (Ørskov and Ryle 1990). Acetate is quantitatively the most important substrate, but propionate also plays an essential role as a glycogenic precursor to ensure the energy requirements of the neural system are met (Blaxter 1962). Feeding of grains such as sorghum and maize, which resist rumen fermentation, may also provide glucose for direct absorption from the small intestine. While extremely high levels of grain have been associated with soft fats (Duncan \textit{et al.} 1972), feeding of less degradable cereal grains is now being considered as a way of stimulating the ATP citrate lyase pathway by providing glucose to the intestine, increasing the synthesis of intracellular lipid associated with marbling in meat (Pethick \textit{et al.} 1995; Rowe and Pethick 1994).

Protein
There is no single figure that can adequately describe the percentage of crude protein that finishing lambs require in their diet. When considering the protein requirements of lambs, it is critical to partition the requirement for amino acids and other nitrogenous compounds into that required by the rumen microorganisms (in order to grow and ferment feedstuffs) and that required by the host animal (the lamb) for deposition and endogenous losses. Figure 2.1 illustrates this division between the true amino acid requirement of the ruminant which is met through the combination of undegraded dietary protein (UDP) and microbial protein. In contrast, the rumen microbial requirement for protein precursors is met through rumen degradable protein (RDP).
Rumen degradable protein (RDP) requirements

Due to the differing yield of energy that rumen microbes obtain from production of the individual VFAs, the quantity of microbial growth and so protein produced varies with the VFA pattern, which is in turn determined by the nature of the carbohydrates being fermented. The type of diet determines the microbial cell yield and so the quantity of RDP required per MJ of ME. For high quality diets, this is typically 11 g RDP per MJ of ME available, decreasing to 8.4 and 6.1 for less digestible forages and silages respectively (SCA 1990). This yield will also vary with the time of year and level of intake but for high-grain diets, the RDP requirement is assumed to be approximately 10 g RDP per MJ of ME in practical formulations. Considering protein in cereal grains is typically 80 per cent rumen degradable (Neutze 1991), a crude protein content of 12.5 g/MJ of ME may be required to meet the ruminal requirement for unrestricted microbial growth. If the RDP:ME ratio is less than this, voluntary feed intake will be below the potential intake of the lamb.

Amino acid requirements

Amino acids reaching the intestine of growing lambs are inevitably partitioned into wool, organ accretion and endogenous urinary and faecal losses. The balance of these is dependent upon the genotype of the animal as well as stage of maturity, energy intake, the intake and characteristics of the protein itself (e.g. intestinal degradability, amino acid profile). Protein deposition in muscle, which is the desired outcome of feeding prime lambs, is intimately reliant upon the supply of energy (ATP) to support anabolism. Unlike RDP requirements however, there is no near-constant relationship by which the balance of energy and amino acids required by the lamb can be simply calculated. A description of the development pattern of lambs is provided below for the purpose of demonstrating why and how the amino acid requirement of lambs changes during growth. On the basis of these principles, it should be apparent when and why, a response to extra amino acids should be expected for a given lamb on a given diet.
Stage of growth effects on energy and protein requirements

The general allometric pattern of maturation of tissues in sheep was well defined by Brody (1945) and more thoroughly by Butterfield (1988). Associated with this pattern of development is an average pattern of accretion of fat, muscle and ash (or minerals) in the body, with bone maturing first, then muscle and finally fat (Figure 2.2).

![Graph showing the relationship between weight and carcass weight for muscle, fat, and bone.]

**Figure 2.2.** Pattern of allometric growth of bone muscle and fat (after Sainz and Cubbage 1997).

![Graph showing the relationship between weight and liveweight for fat.]

**Figure 2.3.** Accretion of total body fat and protein in lambs (after Searle and Graham 1970).

In sheep the rapid development of fat is initiated between 35 and 40 kg liveweight, immediately prior to the time when lambs typically commence on grain-based finishing rations (Figure 2.3). Implicit in this developmental pattern is the fact that as lambs mature postnatally, the quantity of protein (23.6 MJ/kg) in every kilogram of body gain decreases while the proportion of fat (39.3 MJ/kg) increases, meaning every successive kilogram of liveweight contains more energy than the one before (Figure 2.4). This pattern of increasing energy content in gain as lambs mature was confirmed by Searle and Graham (1970) with crossbred lambs from 5 kg (6.3 MJ/kg) to 50 kg (27.6 MJ/kg).

![Bar chart showing the proportion of protein, water, and fat in fasted liveweight for lambs.]

**Figure 2.4.** Proportion of protein (spots), water (lines) and fat (grid) in each additional kilogram of fasted liveweight for lambs (Standard reference weight = 60 kg) indicating that composition of gain changes as lambs approach maturity. Calculations based on equations 1.32 and 1.34, SCA (1990).
Associated with a change in the protein and energy content of deposited tissues with maturity is a change in the balance of energy and amino acids required for growth. Simulations in GrazFeed™ (ver. 4.1.5) were run to estimate the daily feed intake of crossbred lambs consuming a grain:lycine pellet (80:20; M/D [Megajoules of ME/kg DM] = 12.8) sufficient to sustain approximately 240 g/day liveweight gain as they matured from 20 to 60 kg liveweight (Figure 2.5). The lamb requirements for protein (UDP and RDP) and energy (ME for maintenance and for growth) were obtained either directly from the GrazFeed™ results or from equations in SCA. GrazFeed™ assessed a RDP requirement of 8.9 g RDP/MJ MEI [Maintenance energy intake].

![Figure 2.5a. Increase in energy requirements for maintenance (●) and gain (○) of crossbred lambs sustaining a growth rate of 240 g/day as they mature.](image)

![Figure 2.5b. Change in requirements for rumen degradable protein (●) and protein to the intestine (○) by crossbred lambs sustaining a growth rate of 240 g/day as they mature.](image)

Figure 2.5a demonstrates that while maintenance energy requirements rise with liveweight, energy available for gain does not correspondingly increase as voluntary feed intake approaches the biological limit. Considering the energy content of liveweight gain is also increasing (Figure 2.3), it is not surprising that growth rates of 400 g/day, which are readily seen in unweaned lambs, are uncommon for lambs in feedlots, even when grain-based energy dense diets are fed.

Figure 2.5b demonstrates that while the daily requirement for RDP increases to enable greater microbial activity to ferment the increasing intake of energy, the protein requirement to the intestine (for tissue synthesis and endogenous losses) hardly changes. The implications of this are that efficient feedlot finishing of lambs to heavy weights will need to focus primarily on ensuring the RDP supply is sufficient to match the ME intake and support uninhibited rumen fermentation. Provision of additional proteins (protected, bypass or undegraded) will be unnecessary in grain finishing diets, since the microbial protein synthesised from supplying adequate RDP will be more than sufficient to meet tissue requirements of the host animal.
Setting the allometric pattern of growth

The general principles of how growth, feed intake and body composition interact to continuously change the nutritional requirement of lambs on a gram/day and gram/kilogram feed basis are consistent across all types of lamb. Between lambs however, the pattern of development (Figure 2.2) will deviate in accordance with the genetic and physiological attributes of the lamb as described below.

Breed and genetics

Genotypes that are heavier at maturity generally grow faster and are leaner when compared at the same weight (Black 1983; Searle and Griffiths 1976b; Tatum et al. 1998; Theriez et al. 1981). It is generally accepted that recognised meat breeds or crossbreds tend to grow faster than Merinos (Gardner et al. 1999; Wiese et al. 2003; Wynn and Thwaites 1981) and second-cross lambs have been reported to grow faster than first-cross lambs due to greater hybrid vigour (Atkins and Thompson 1979; Holst et al. 1998; Hopkins et al. 1996) but these principles are not always supported (Davidson et al. 2000; Gardner et al. 1999). When comparisons are made at the same liveweight, tissue depth at the GR site is generally lower in Merinos followed by first- then second-cross lambs (Atkins and Thompson 1979; Searle and Griffiths 1976b; Shands et al. 2002).

The choice of mating system (e.g. first- vs second-cross), or breed selection, may not be based purely on maximising growth rate and feed conversion efficiency. It can be influenced by many factors including local environmental conditions and the relative importance of the lamb enterprise in the whole farming system. Regardless of the production system, the benefits of selecting sires with high estimated breeding values for growth and leanness have been clearly demonstrated (Fogarty et al. 1997; Hall et al. 2002; Hegarty 2002; Wiese 2000).

Age, body weight and sex

Body composition is linked closely with body weight but there is no inherent relationship between age and body composition (Black 1983). As animals reach physiological maturity there is a transition from lean growth toward an increasing rate of fat deposition. This transition occurs earlier in ewes than rams (Searle and Griffiths 1976a). When animals are slaughtered prior to the transition to increased fat deposition, there may not be a difference in tissue depth at the GR site, but when slaughtered at heavy weights there tends to be an increase in GR depth or fatness according to sex; rams < cryptorchids < wethers < ewes (Andrews and Ørskov 1970b; Atkins and Thompson 1979; Lee 1986a).

Growth rate tends to be influenced by sex, being faster in rams than cryptorchids, followed by wethers, then ewes. The difference in growth rate between sexes can be of the order of that created by different nutritional treatments (Andrews and Ørskov 1970a; Arnold and Meyer 1988; Atkins and Thompson 1979; Holst et al. 1997; Jackson et al. 1990; Lee 1986a; Van Vleck et al. 2000; Wynn and Thwaites 1981). Interestingly, the difference in growth rate between sexes is primarily related to differences in feed intake so may not be expressed when nutrition is limiting (Lee 1986a, 1986b).
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Breaking the allometric pattern of growth (more muscle and less fat)

Once lambs are of an appropriate weight to be grain finished (> 30 kg liveweight), there appears to be little scope to modify body composition simply by providing amino acids in excess of those required for allometric growth (Hegarty et al. 1999). A low rumen degradable nitrogen (RDN) intake simply limits voluntary food intake (Hegarty et al. 2001). Any scope to modify the composition of gain for an individual lamb to achieve greater muscle and reduced fat deposition through finishing is dependent upon conditioning the lamb through its prior nutritional history, be it prenatal, preweaning or postweaning.

Prenatal

Foetal undernutrition can reduce mature size of sheep (Bell 1992; Schinckel and Short 1961) although post-natal growth rate at least to 20 kg liveweight is not compromised by foetal undernutrition (Greenwood et al. 1995). The composition of postnatal growth however is modified by foetal undernutrition, with less bone, less muscle and more fat making up the gain (Greenwood et al. 1998, 2000; Greenwood and Bell 2003). There does not appear to be any mechanism for manipulation of foetal nutrition to stimulate the more desirable aberration of enhancing muscle growth while suppressing fat accretion once lambs are born.

Postnatal

The priority for energy utilisation in growth is to fuel protein deposition, which is typically limited by amino acid availability, with residual energy deposited as fat (Oltjen et al. 1986). Nutritional restriction of young ruminants (< 40% maturity) can have long-term suppressive effects on muscle and bone growth capacities, so subsequent refeeding will cause them to deposit additional fat (Oddy and Sainz 2002). When growth is nutritionally restricted in more mature lambs, it is likely to lead to a more marked reduction in fat accretion than muscle accretion, leading to lambs being typically leaner after a period of slow continuous growth (Ball and Thompson 1997; Thatcher and Gaunt 1992). Lambs that have been grown slowly due to inadequate nutrition will therefore be leaner at commencement of grain feeding and be likely to exhibit compensatory growth, which will further accelerate growth rate and the lean content of that growth (Table 2.1). It is likely that this will increase the tissue amino acid requirement (UDP) as the rate of protein synthesis increases during realimentation (Kreienbring et al. 1994).

Table 2.1. Effect of nutritionally induced slow growth (LOW) or unimpeded rapid growth (HIGH) prior to finishing on the rates of fat and protein gain in the carcase of crossbred lambs during finishing. Lambs were provided with 0 (P_0) or 90 (P_90) g of cottonseed meal supplement daily during finishing on a diet providing 10 MJ of ME/kg (after Hegarty et al. 1999).

<table>
<thead>
<tr>
<th></th>
<th>LOW</th>
<th></th>
<th>HIGH</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P_0</td>
<td>P_90</td>
<td>P_0</td>
<td>P_90</td>
</tr>
<tr>
<td>Starting liveweight</td>
<td>36.55</td>
<td>36.55</td>
<td>51.66</td>
<td>51.66</td>
</tr>
<tr>
<td>Starting fat mass (kg)</td>
<td>4.35</td>
<td>4.35</td>
<td>8.02</td>
<td>8.02</td>
</tr>
<tr>
<td>LWG during finishing (g/day)</td>
<td>188.00</td>
<td>200.00</td>
<td>133.00</td>
<td>131.00</td>
</tr>
<tr>
<td>Carcase protein gain (g/day)</td>
<td>14.10</td>
<td>13.70</td>
<td>6.60</td>
<td>7.10</td>
</tr>
<tr>
<td>Carcase fat gain (g/day)</td>
<td>19.20</td>
<td>30.60</td>
<td>39.10</td>
<td>40.00</td>
</tr>
</tbody>
</table>
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**Grain as a protein and energy source**

Cereal grains are one of the most energy dense feedstuffs available for ruminants and so there is a high requirement for RDN to ensure maximum fermentation of grain carbohydrates. While protein requirement of the lamb changes with maturity, the RDN:ME requirements of the rumen microbes do not change as the lamb grows and a ratio of approximately 10 g RDP per MJ of ME consumed is required to optimise rumen fermentation and feed intake. In the Metabolisable Protein Feeding Standards developed in the United Kingdom (AFRC 1993), a comparable ratio of approximately 10 g of effectively degradable rumen protein (ERDP) to fermentable metabolisable energy (FME) ratio is sought. Protein in cereal grains is readily degraded in the rumen and approximately 80 per cent of the crude protein in grain can be considered rumen degradable. A brief overview of the energy to protein ratio in feed grains indicates most cereal grains have a slight deficiency in RDN relative to the energy they contain (Table 2.2).

<table>
<thead>
<tr>
<th>Grain</th>
<th>ME (MJ/kg)</th>
<th>CP (%)</th>
<th>Degradability (%)</th>
<th>RDP (g/kg)</th>
<th>RDP:ME (g/MJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorghum</td>
<td>12.4</td>
<td>10</td>
<td>45</td>
<td>45</td>
<td>3.3</td>
</tr>
<tr>
<td>Maize</td>
<td>13.5</td>
<td>10</td>
<td>45</td>
<td>45</td>
<td>3.6</td>
</tr>
<tr>
<td>Oats</td>
<td>10.5</td>
<td>11</td>
<td>70</td>
<td>77</td>
<td>7.4</td>
</tr>
<tr>
<td>Barley</td>
<td>11.6</td>
<td>12</td>
<td>75</td>
<td>92</td>
<td>7.9</td>
</tr>
<tr>
<td>Lupin</td>
<td>11.3</td>
<td>31</td>
<td>72</td>
<td>221</td>
<td>19.6</td>
</tr>
</tbody>
</table>

**Conclusions**

The ruminant lamb has two distinct spheres of nutritional requirement, being the requirements of the rumen microbes and the requirements of the animal tissues themselves. A tendency to describe these requirements using a single term such as crude protein is naive and restricts practical nutritional management. First in digestive/fermentation sequence and in importance are the requirements of the rumen microbial population. Rumen fermentation requires a synchronised supply of fermentable energy and rumen degradable nitrogen, either in a protein or non-protein form. RDP should be provided in a ratio of approximately 10 g RDP/MJ of ME intake. While the protein in cereal grains is highly degradable in the rumen, most grains have less than this optimal RDP relative to energy, and inclusion of a secondary source of RDN in the ration is required to maximise voluntary feed intake. While the RDN requirements of the rumin can be considered fixed in relation to energy intake, the amino acid and energy requirements of the lamb itself change dramatically over time.

The standard pattern of sequential growth (bone, muscle, fat) occurs in lambs but the level and timing of growth and its components are influenced by mature size, other aspects of genotype and growth history. During early life, lambs have a high daily requirement for amino acids but are constrained by a low potential feed intake. Maximum liveweight gain by small lambs is reliant upon optimising RDN intake, to ensure feed intake and microbial protein production is maximised, but additional UDP will be required to ensure the tissue requirements for amino acids are met. As lambs mature, their voluntary intake increases while the daily requirement for amino acids is little changed. Consequently, microbial protein synthesised from RDN can meet the amino acid requirement for tissue and for obligatory losses in finishing lambs, so no growth benefit is likely to result from providing UDP in grain-based finishing systems.
Importantly, animals require certain quantities of nutrients per day (g, mole, MJ); they do not require an absolute percentage of nutrients in the diet. It is the voluntary intake of the animal and the level of other diluents in the diet that are important in translating a daily requirement for a quantity of nutrient into an estimated concentration of nutrient that must be present in the feedstuff.

Efforts to use high levels of amino acid supply to enhance muscle growth in finishing lambs have proved unsuccessful and nutritional modification of body composition is best effected by management of growth rate and comparative growth in preparation for finishing.

References


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