10 Nutrition during Lactation

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Introduction

In the majority of sheep production systems, sheep are kept for meat or wool production and ewes rear their lambs until weaning, at 3 or 4 months of age. During this period, lamb growth is largely determined by milk intake. Early lactation is the period of highest nutrient requirements in the ewe's whole productive cycle, and failure of management at this time has a major impact on lamb growth. This generally affects the profitability of the system and, in lambs retained as flock replacements, can reduce lifetime performance.

In a number of countries, mainly in Asia and Europe, ewes' milk is an important direct source of animal protein in the human diet. In Afghanistan, Greece, Iraq, Somalia and Syria, more than 30% of the total production of milk, from cows, buffalo, sheep and goats, comes from ewes. In France, Greece, Italy and Spain, large numbers of dairy sheep are kept to produce milk for high-quality, expensive cheeses. In dairy systems, ewes generally rear their lambs before milking is started. The length of both suckling and milking periods varies widely, from 1 month of suckling and 5 or 6 months of milking, in the traditional Mediterranean system, to 3 months suckling and a month of milking in, for example, central Europe. The various dairy systems are discussed in Treacher (1987).

Composition of Ewes' Milk

Typical figures for the mean composition of ewes' milk (g kg^{-1} liquid milk) are: fat 71, protein 57, lactose 48, ash 9 and solids-not-fat 115 (Ashton *et al.*, 1964). At the start of lactation, the contents of fat and protein are high. They decrease to the peak of lactation and then increase through the remainder of lactation, as yield decreases. Lactose content shows little variation, as the amount of lactose synthesized determines milk yield. The negative relationship between yield and the contents of fat and protein is more general and applies also when differences in yield arise from genotype, individual variation or selection within a breed (see review by Bencini and Pulina, 1997). Change in composition during lactation has a large effect on the gross energy of milk, which may vary from 3.8 to 5.5 MJ kg^{-1} (Brett *et al.*, 1972). Equation (1) (Brett *et al.*, 1972), based on data from 92 samples taken from Merino (mean fat 72 g kg^{-1}) and Border Leicester (mean fat 105 g kg^{-1}) ewes, predicts gross energy, E (MJ kg^{-1}), from fat, F (g kg^{-1}), and day of lactation, D:

$$E = 0.0328F + 0.0025D + 2.20 \qquad \text{RSD} = \pm 0.14 \qquad (1)$$

Milk fat consists almost entirely of triglycerides, with most of the fatty acids being monounsaturated and containing even numbers of carbon atoms in the range 14 to 18. However, about 22% of the lipid consists of fatty acids in the C4 to C10 range (Yousef and Ashton, 1967). The major constituent of milk protein is casein in a number of variant forms, all of which are characterized by a high content of proline and are present in complexes with calcium and phosphate. In addition, milk protein contains β-lactoglobulin and α-lactalbumin and traces of immunoglobulins. Colostrum, secreted in the first day or two of lactation, contains high concentrations of lipid and protein – in particular, immunoglobulins. These are absorbed directly through the gut of the young lamb and are crucial to its survival, giving it passive immunity to diseases to which the ewe has immunity. They also provide protection against gut infections.

The mean metabolizability of the gross energy (GE) in ewe's milk is 0.94 and the efficiency of use of the resultant metabolizable energy (ME) is 0.85 for the maintenance of the lamb and 0.7 for growth (ARC, 1980). If the GE of the milk were 4.5 MJ kg^{-1}, then a daily intake of 1 kg in excess of the lamb's maintenance requirement would sustain a daily growth rate of between 330 g and 270 g as the energy value of the live weight gain increased, with the lamb's growth, from 9 MJ kg^{-1} to 11 MJ kg^{-1}.

The Mammary Gland

Milk is secreted from alveoli laid down in the fat pad of the udder in the period between mid-pregnancy and just after parturition, under the control of a large number of hormones. These include oestrogen, progesterone, adrenal corticoids, somatotrophin, prolactin, placental lactogen, insulin and thyroid hormones, and, in addition, there are numerous growth factors produced by the fat pad itself. Each alveolus is spherical, with a central lumen that is lined with a single layer of secretory cells. The bases of these cells are covered by a layer of myoepithelial cells and a basement membrane. A capillary network supplies each alveolus with the milk precursors. The alveoli discharge into fine ducts leading to larger ducts and the gland cistern. Full milk secretion starts when progesterone secretion falls at parturition. The milk is ejected from the alveoli when the myoepithelial cells contract in response to the release into the bloodstream of oxytocin from the posterior pituitary gland. At weaning, the secretory tissue undergoes involution through cell death, leaving only the myoepithelial layer.

Synthesis of Milk

The main pathway for the synthesis of the fatty acids in milk fat is through the condensation of 2-carbon units (molecules of malonyl-coenzyme A (CoA)) originating from the microbial breakdown of carbohydrate to acetate in the rumen. Fatty acids are also derived directly from the diet or from the breakdown of adipose tissue. The esters of the fatty acids are incorporated into triglycerides, the glycerol being derived either from the hydrolysis of plasma lipids or by glycolysis. The milk fat is released from the epithelial cells as globules, each enclosed in a membrane.

Lactose, a carbohydrate found only in milk, is synthesized from glucose, via galactose. The secondary stage, the combination of glucose and galactose to form the disaccharide, is facilitated by the milk protein α-lactalbumin. β-Lactoglobulin, α-lactalbumin and the milk caseins are synthesized from circulating amino acids, whereas the immunoglobulins are transferred directly into the epithelial cells from the bloodstream. Milk protein and lactose move together through the secretory cells in micelles and the osmotic pressure exerted by lactose draws water into the secretion, which, at the surface of the cell, is discharged into the duct, together with the mineral components of the milk. For greater detail on the synthesis of milk in the ewe, refer to Thomas and Rook (1983).

Estimation of Milk Production

Accurate estimates of milk production (by the ewe) or intake (by the lamb) are difficult, as all methods interfere to some extent with the natural behaviour of ewes and lambs. Three methods have been used to measure yield directly: weighing before and after suckling; measuring milk secretion rate; or tracer-based techniques. In addition, milk production in early lactation can be estimated indirectly, with reasonable accuracy, from the growth rate of lambs. Although the gross efficiency of conversion of milk to liveweight gain increases as intake increases above maintenance, the curvilinearity is not great over the first few weeks and a linear relationship can be assumed. Published relationships of this kind (e.g. Dove and Freer, 1979; Dove, 1988) indicate that lambs consuming only milk gain 160–170 g day^{-1} per kg of liquid milk, which is equivalent to about 6.0 kg of milk kg^{-1} of gain or about 1 kg gain kg^{-1} milk dry matter (DM) consumed. Beyond 4–6 weeks of age in most management systems, the slope of relationships between liveweight gain and milk intake declines markedly, indicating the intake of nutrients from herbage.

Estimating milk intake by weighing before and after suckling

This method is very laborious, as the lambs are weighed before and after suckling on four to six occasions in 24 h (e.g. Wallace, 1948) or, less commonly, on three occasions in 12 h. Between sucklings, the lambs are separated from their mothers or the udder is covered. The daily yield is the total of the weight increments of the ewe's offspring during suckling. Errors can arise from disturbance affecting suckling behaviour or milk ejection, the incomplete emptying of the udder by single lambs, the difficulty of measuring small weight increments as the lambs get larger and defecation or urination between the first and second weighings.

Estimating milk production rate using oxytocin

Milk production can be estimated by milking the ewe until the udder is empty, after an intravenous injection of approximately 2 iu of oxytocin to achieve ejection of the milk. This procedure is done at the beginning and end of a period of approximately 4 h, during which the lambs are prevented from sucking. Production rate is calculated as the weight of milk at the second milking divided by the exact time in minutes between the two milkings and then extrapolated to a daily milk production (e.g. Doney *et al.*, 1979). This method can lead to overestimates of milk intake if the degree of emptying of the udder by milking is greater than would be achieved by the lambs. Doney *et al.* (1979) found that this method gave higher estimates of yield than the lamb-weighing method in the first week of lactation, especially in ewes with single lambs, but, by the third week of lactation, the differences between the two methods were not significant and were unaffected by the number of lambs suckled or by ewe genotype.

Tracer-based methods

The third approach to measuring milk intake is to estimate the dilution, by a component of the milk consumed by the lamb, of a marker or tracer introduced into a known body pool. Most commonly, the body-water pool is labelled by the administration to the lamb of either tritiated water (TOH) (Dove and Freer, 1979) or deuterium oxide (D_2O) (Dove, 1988). The turnover of the tracer is monitored in water extracted from blood samples taken 4–7 days apart, during which period the animals are left undisturbed. The procedure is based on two assumptions: that milk is the only source of water for the lamb and that the amount of water in the lamb does not change over the period of measurement. Before peak lactation in the ewe, lambs consume negligible amounts of drinking water and solid food and single markers have been used successfully to estimate milk intake (e.g. Dove and Freer, 1979). The second assumption is clearly not met, because weight gain in the lamb contains at least 65% water and estimates of milk intake have to be corrected for the increase in body-water content (Dove and Freer, 1979).

In older lambs, the overestimation of milk intake resulting from the ingestion of drinking water or solid food, especially herbage, is overcome by using a ‘double-isotope’ procedure, in which D_2O is injected into the lamb to estimate its total water turnover, while the proportion of this coming from milk is estimated by injecting the ewe with TOH and monitoring the transfer of TOH to the offspring (Dove, 1988).

The major disadvantages of the tracer-based methods are the possible environmental and regulatory consequences of administering radioisotopes (TOH) to animals and the difficulty and cost of D_2O analysis. Nevertheless, these methods are the most accurate for estimating milk intake and have a further advantage in nutritional studies in that changes in the protein and fat content of both ewe and lamb can be estimated from their body-water contents.

Factors Affecting Milk Production

Effect of genotype of ewe

Variation in milk yield between and within breeds is very wide. In meat breeds selected for lamb production, yield at the peak of lactation varies between 2.0 and 4.0 kg day^{-1}, with total yields in 3 months of lactation varying from 150 to 200 kg in ewes with twin lambs and from 90 to 160 kg in ewes with singles. In small local breeds and some wool breeds, notably Merinos, yields are lower. Differences between dairy breeds are larger. Unselected local breeds may produce less than 100 kg during 6 months of milking, after rearing a lamb for about 1 month, while highly selected breeds, such as the East Friesland and Assaf, which are milked throughout a longer lactation, have yields of 600–1000 kg. Between these extremes are a number of European dairy breeds, including Lacaune, Manchega, Churra, Latxa, Manech and Sarde, which now have significant numbers of ewes in selection schemes and have yields, after rearing a lamb for a month, of 150–250 kg in approximately 200 days of milking.

Nutrition in pregnancy

Almost all the development of secretory tissue in the ewe’s udder occurs in the last third of pregnancy, with a very small amount – approximately 5% – occurring in the first month of lactation. Severe undernutrition in the last weeks of pregnancy results in a small udder, which has little colostrum present at lambing, and a delay of several hours in the initiation of full lactation. This may have a major effect on lamb survival, especially as the lambs are likely to be small and lacking body reserves at birth. Experiments in which underfeeding was severe (reduction of 17–32% in twin birth weight) found reductions of 7–35% in milk yield over the whole lactation (Wallace, 1948; Treacher, 1970).

Nutrition earlier in pregnancy (see Robinson *et al.*, Chapter 9, this volume), before the period of mammary development, may affect milk production via placental size and secretion of placental lactogen. Growth of the placenta, which is completed by 90 days of pregnancy, can be affected by severe underfeeding. If nutrition in late pregnancy is good, this does not lead to a reduction in lamb birth weight, but Davis *et al.* (1980) and Dove *et al.* (1988) found effects of mid-pregnancy feeding on milk yield and lamb growth, even when birth weight was not reduced. This may be related to nutritional effects on placental size and hence placental lactogen concentrations. In sheep, plasma lactogen concentrations increase until close to the end of pregnancy and are affected by placenta size and by the number of fetuses carried.

If there is underfeeding in early lactation, milk production may be affected by the amount of body reserves available for utilization after lambing. Although undernutrition in pregnancy increases the utilization of body reserves before lambing, the level of reserves is also affected by deposition and utilization of fat occurring before mating and in early and mid-pregnancy. The effects of body reserves at lambing on feed intake and on the level and efficiency of milk production are discussed below.

Effect of number of lambs suckled

Ewes suckling twins generally produce 40% more milk than ewes with singles at the same level of nutrition (Treacher, 1983). Differences reported in the literature range from negligible to increases of 70%, with the majority in the range of 30–50%. In ewes with twins, the peak of lactation is not only higher but is reached sooner – in the second or third week of lactation, compared with the third to fifth week in ewes with singles (Wallace, 1948). Yield decreases slightly more rapidly in ewes with twins and, by week 12 of lactation, the difference in yield between ewes with twins and singles is negligible (Fig. 10.1).

The small amount of information on yields from ewes suckling larger litters of three or four lambs shows wide differences, which may, in part, reflect the small numbers of ewes studied. Differences between ewes suckling triplets and those suckling twins range from negligible (Wallace, 1948) to increases of 30% (Loerch *et al.*,1985). This occurs almost entirely in the first month of lactation, with little difference, or even slightly lower yields, in mid- and late lactation (Peart *et al.*, 1975), possibly related to problems with sore teats and lamb rejection (Gallo and Davies, 1988).

Increases in milk production in ewes suckling twins or larger litters result mainly from the number of lambs suckled. This reflects the increased stimulus resulting from the increased frequency and duration of suckling by two or more lambs. It is not affected by the number of fetuses carried in pregnancy. For example, Loerch *et al.* (1985) found that ewes suckling triplets produced 28% more milk than ewes allowed to suckle only two lambs after carrying triplets in pregnancy. The potential milk yield of ewes suckling singles is not expressed and their production

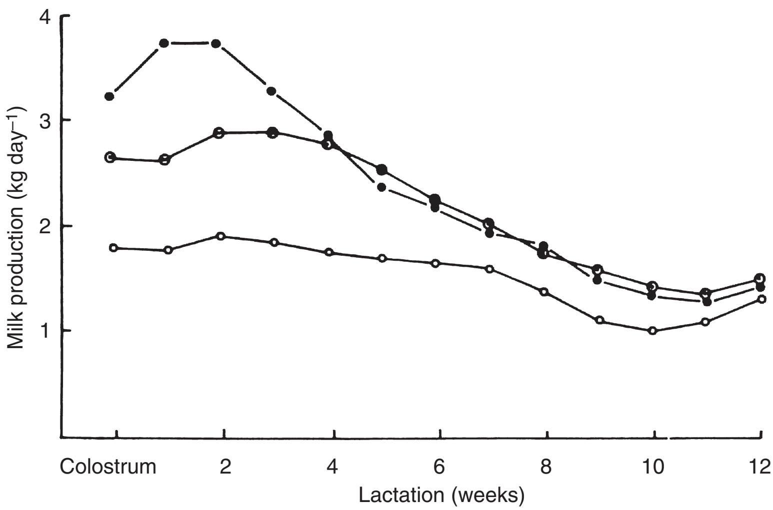

Fig. 10.1. Mean lactation curves of ewes: ●, triplet-suckled; ⊖, twin-suckled; ○, single-suckled (reproduced from Peart *et al.*, 1975, by courtesy of the editor and publishers, *Journal of Agricultural Science, Cambridge*).

reflects the voluntary intake of milk by the lamb. This is supported by differences in yields in ewes suckling lambs of different genotypes, as a result of mating with different breeds of ram or of cross-fostering of lambs at birth between ewes of different breeds. This response may be mediated through initial differences in lamb birth weight (e.g. Moore, 1966), but, in other cases (e.g. Peart *et al.*, 1975), the increase appears to result from differences in appetite between lamb genotypes. Although Slen *et al.* (1963) suggested that the yield of ewes suckling twins reflected their potential, increases in yield in ewes suckling triplets show that the potential may be slightly greater.

All the information discussed above relates to management systems where lambs have continuous access to ewes, except when this is altered during measurements of milk yield. In dairy systems, management during the suckling period, before milking is started at about 1 month after lambing, may be different, with lambs separated from the ewes for some part of the day. Gargouri *et al.* (1993) found a reduction of 20% in yield in the first month of lactation when suckling was restricted to two periods of 15 min compared with unrestricted access (see Fig. 10.2). The restricted suckling regime also reduced fat content and increased crude protein content of the milk.

Effect of milking

In dairy systems, the start of milking at the end of approximately 1 month of suckling results in a dramatic reduction in milk yield, which persists for the remainder of the lactation (Labussière and Pétrequin, 1969). Figure 10.2 shows reductions of 55% and 29% between the fourth week of suckling and the first week of milking in ewes with previously unrestricted and restricted access of lambs, respectively. In the period of machine milking, yields in both groups were almost identical.

Pattern and Level of Intake in Lactating Ewes

Voluntary intake of feed by ewes normally increases rapidly at the start of lactation and then continues to rise for several weeks. Foot and Russel (1979) measured intakes of a high-quality chopped, dried grass (DM digestibility (DMD) 70%) over the full cycle of pregnancy, lactation and dry periods. Intake in the first week of lactation was 10% higher than the intake 2 weeks before lambing. Intake increased rapidly in weeks 2 and 3 of lactation and then continued to rise at a slower rate to a maximum in week 8, approximately 4 weeks after the peak of lactation. In ewes suckling twins and singles, maximum daily intakes were 3.0 and 2.5 kg DM, respectively (44 and 37 g DM kg^{-1} of weight post-lambing, respectively), 85% and 47% above their intakes in week 1 of lactation. Thereafter intake decreased slowly until weaning, after which it declined by 20%.

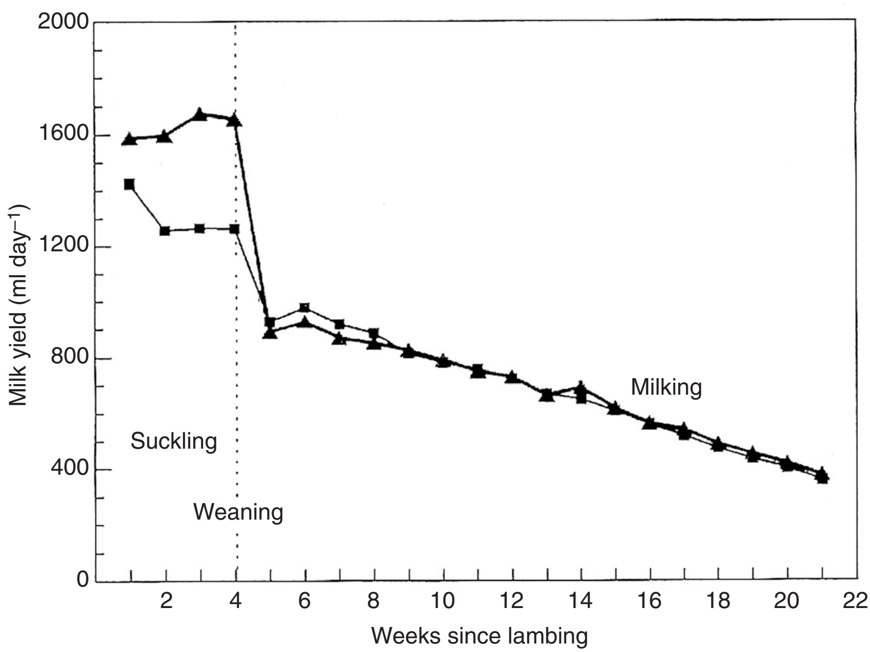

Fig. 10.2. Effects of extent of access by lambs to the ewe: ▲, unrestricted access; ■, access restricted to two 15 min periods per day, on the milk yield of Manchega ewes during suckling and subsequent machine milking (adapted from Gargouri *et al.*, 1993).

These large increases in intake in early lactation, as a result of the great increase in metabolic demand for milk production, are accompanied by major effects on the digestive system. The weight, size, nitrogen content and enzyme activity of reticulorumen, abomasum and small intestine increase. The small intestines reach a maximum weight 30 days after lambing and the rumen and abomasum later, at about 50 days. These changes enable the lactating ewe to maintain the same diet digestiblity in spite of large increases in intake. If food intake is restricted in early lactation, these changes to the digestive tract are reduced.

While the pattern of intake described above is typical of ewes offered high-quality long forage, it is clear that on other diets and at pasture different patterns and levels of intake may occur. On a low-quality forage, intake rises slowly and may not peak before weaning occurs 3 or 4 months after lambing (Hadjipieris and Holmes, 1966). At pasture, grazing pressure, availability of herbage and changes in pasture digestibility and sward structure, which are often rapid, all affect the level and pattern of intake. Generally, peak intakes by lactating ewes at pasture in spring occur within 4 weeks of lambing, unless herbage availability is very restricted by either poor pasture growth or high grazing pressures. Gibb *et al.* (1981), for example, found that a peak daily intake of 3.75 kg organic matter (OM) (44 g OM kg^{-1} live-weight (LW) post-lambing) occurred in week 3 of lactation in ewes suckling twins and grazed at a daily herbage allowance of 60 g DM kg^{-1} LW of ewe, while at an allowance of 30 g DM kg^{-1} LW a lower peak intake of 2.30 kg OM (27g OM kg^{-1} LW) was delayed to week 5 (see Plate 10.1).

Plate 10.1. Border Leicester × Scottish Blackface ewes and their lambs grazing perennial ryegrass pastures in Lanarkshire, central Scotland. The ewe on the left is carrying equipment that allows the estimation of the intake and nutritive value of the pasture in relation to the nutrient requirements for lactation.

Penning *et al.* (1991) and Morris *et al.* (1994) found that lactating ewes grazing swards with surface height in the optimum range (4.5–12 cm) for maintaining near-maximal intakes reached peak intakes of 2.6–3.0 kg OM (38–46 g kg^{-1} LW) in week 4 of lactation, approximately 20% higher than the intake in the first week of lactation. On shorter swards, the patterns of intake varied from a peak at 8 weeks to an almost constant intake over this period.

Body condition at lambing does not have a major effect on absolute intake by lactating ewes. Peart (1970), Foot and Russel (1979) and Gibb and Treacher (1980) found that non-significant differences in intake occurred in ewes differing in live weight at lambing by 10–15 kg or by 1.0–2.0 units of body-condition score (on a scale of 1–5).

Requirements in Lactation

Responses to intake of energy and protein

The model described by Robinson (1980) provides a useful starting-point for considering responses in milk production by the ewe to intake of energy and protein and hence nutrient requirements of the ewe during early lactation. Figure 10.3 demonstrates three important principles relating to the response to variation in intake of ME and metabolizable protein (MP):

1. For a particular level of ME intake there is a critical protein intake, below which milk yield will decrease.
2. The minimum ratio of crude protein (CP) to ME increases with increasing level of milk yield.

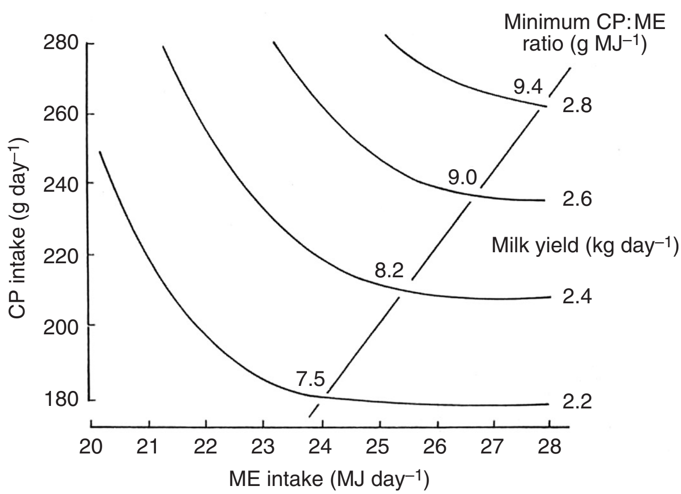

Fig. 10.3. Response in milk yield to alterations in dietary CP and ME for 70 kg ewes suckling twin lambs (reproduced with permission from Treacher, 1983).

3. An increase in MP intake without a change in ME intake will result in an increase in milk production and mobilization of body reserves, if the ewe has not reached her potential yield.

This model demonstrates that, in early lactation, when energy requirements are high and voluntary intake has not reached its peak, protein intake is likely to have a critical effect on milk production. The extent of the response to protein intake, however, depends on the level of body reserves in the ewe in early lactation. This is discussed further below.

Although this model was derived from data from a single experiment, there are many experiments that confirm its principles. Figure 10.4 from Robinson (1990) shows responses of milk yield in a series of experiments in which increasing amounts of soybean meal and fish meal were added to low-protein basal diets while maintaining a constant intake of energy. At each energy level, the addition of protein to the basal diet increased milk production. At an ME intake of 18.3 MJ day^{-1}, the maximum response occurred with an intake of CP of 300 g day^{-1} and was not increased by a greater intake of protein. At intakes of 22.5, 25.0 and 28.3 MJ ME day^{-1}, the maximum response occurred at protein intakes of 350, 450 and 450 g CP day^{-1}, respectively.

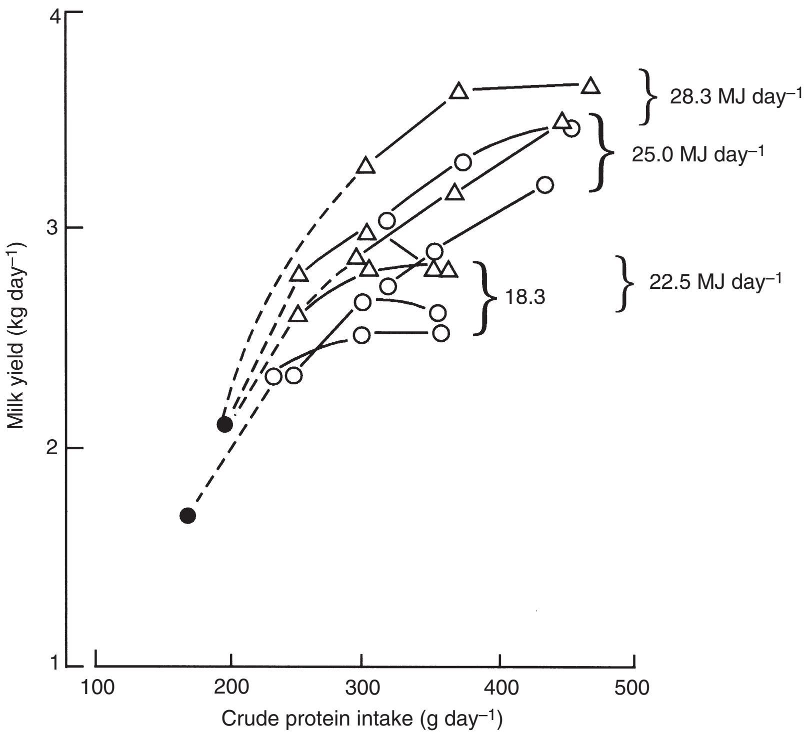

Fig. 10.4. The effect of metabolizable energy intake (18.3, 22.5, 25.0 and 28.3 MJ day^{-1}) and protein sources on the milk yield of Finn Dorset ewes in early lactation: ●, basal diet of hay and barley; ○, basal diet with different proportions of barley replaced by soybean meal; △, basal diet with different proportions of barley replaced by fish meal. (Adapted from Robinson, 1990.)

Requirements for lactating ewes

The Agricultural and Food Research Council (AFRC, 1993) system uses the following procedures for calculating the ME and MP requirements for lactating ewes. Systems in other countries (e.g. SCA, 1990) generally follow a similar process.

Metabolizable energy

The requirement for adult ewes, ME_{mp} (MJ) is derived from Equation (2), which sums the requirements for maintenance of a ewe of weight W kg, producing Y kg day^{-1} of milk with a GE content of V MJ kg^{-1} and changing in weight by G kg day^{-1}. For each fraction, the net energy (NE) requirement, E, is divided by the efficiency, k, with which ME is used; each of the appropriate k values is a function of the quality of the diet, calculated either as q_m (NE/GE) or M/D (ME kg^{-1} DM). The total is adjusted, C, for the level of feeding (for an alternative approach to this adjustment, as used in the Australian system (SCA, 1990), see Corbett and Ball, Chapter 7, this volume). In the examples shown in Table 10.1, a 5% safety margin has been included.

$$ME_{mp} = C(E_m/k_m + E_l/k_l + E_g/k_g) \qquad (2)$$

where:

$$C = 1 + 0.018((ME_{mp}/ME_m) - 1)$$
$$E_m = 0.23(W/1.08)^{0.75} + E_a$$
$$k_m = 0.35q_m + 0.503$$
$$E_l = VY$$
$$k_l = 0.35q_m + 0.420$$
$$E_g = \begin{cases} (26.0G/1.09) & \text{for weight gain} \\ -(26.0G/1.09)0.84 & \text{for weight loss} \end{cases}$$
$$k_g = 0.95k_l$$

Table 10.1. Daily requirements based on AFRC (1993) for metabolizable energy (MJ ME) and metabolizable protein (g MP) for housed[a] lactating ewes, weighing 70 kg, producing 5 g clean wool per day, yielding 1, 2 or 3 kg of milk per day and either maintaining weight or losing 100 g per day when fed a diet with an energy concentration of 11.5 MJ ME kg^{-1} DM (q_m = 0.61).

Weight change (g per day)	Milk yield (kg per day) 1		2		3	
	ME	MP	ME	MP	ME	MP
0	16.6	152	24.6	228	33.0	303
–100	13.0	140	21.1	215	29.5	291

[a]For ewes on lowland and on hill pasture, ME requirements are increased by 0.35 and 1.30 MJ day^{-1}, respectively.

In Equation (2), the activity allowance, E_a, depends on the distance walked and the steepness of the terrain and may range from 0.0096*W* MJ for housed ewes to 0.024*W* MJ for ewes grazing hills. The energy content of milk may be adjusted to suit a specific analysis.

Metabolizable protein

In a similar way, the requirement for MP (Table 10.1) is calculated as the sum of the requirements for maintenance (MP_m), wool growth (MP_w), lactation (MP_l) and weight change (MP_g). The efficiency of utilization of absorbed amino acids for these four purposes is 1.0, 0.26, 0.68 and 1.0, respectively, so the total requirement for a ewe of weight *W* kg, producing *F* g wool and *Y* kg milk (containing 48.9 g true protein kg^{-1}) and retaining *P* kg protein as body tissue is as shown in Equation (3).

$$MP = 2.1875W^{0.75} + F/0.26 + 48.9Y/0.68 + P \quad (3)$$

The ewe's requirement for MP is met from the digestible fractions of the microbial CP synthesized in the rumen in proportion to ME intake and the dietary CP that escapes degradation in the rumen (see Annison *et al.*, Chapter 5, this volume). Calculations of MP supply, using the AFRC (1993) system are shown in Table 10.2 for one of the feeding situations set out in Table 10.1. It should be noted that, although microbial protein provides by far the largest part of the MP requirements, the effective rumen degradability of dietary protein (ERDP) may be critical in determining whether the MP needs of the lactating ewe are met by a particular diet.

Table 10.2. The supply of metabolizable protein (AFRC, 1993) from a diet with an energy concentration of 11.5 MJ ME kg^{-1} DM and a crude protein content of 200 g kg^{-1}, at two levels of protein degradability in the rumen, when used to maintain the weight of a 70 kg housed lactating ewe that is producing 5 g wool and 2 kg milk day^{-1} and is estimated to require 228 g MP day^{-1} (see Table 10.1).

Intake of dry matter (DMI) (kg)		2.14	
Intake of ME (MJ)		24.6	
Intake of crude protein (CPI) (g)	200 × DMI	428	
Fermentable ME (FME)[a] (MJ)	10.8 × DMI	23.1	
Microbial crude protein (MCP) (g)	11 × FME	254	
Effective rumen degradability of protein (ERDP)[b]		0.75	0.85
Undegraded dietary protein (UDP) (g)	CPI(1-ERDP)	107	64
Digested undegraded protein (DUP)[c] (g)	0.7 × UDP	75	45
Metabolizable protein (g)	0.6375 × MCP + DUP	237	207

[a]FME = ME intake (MEI) – (ME in fat and silage acids; here assumed to total 0.7 MJ kg^{-1} DM).
[b]ERDP is a measure, expressed as a decimal proportion, of rumen degradability weighted for the speed of degradation and adjusted for rumen outflow rate (AFRC, 1993).
[c]Digestibility of the undegraded protein is predicted from the content of acid-detergent insoluble protein and is here assumed to be 70%.

Efficiency of use of body reserves for milk production

Energy requirements in early lactation are high and, because of the slow increase in voluntary intake following parturition (see above), are unlikely to be met from the ewe's diet. As a result, ewes generally utilize body reserves in the first weeks of lactation, even when offered feed *ad libitum* (Cowan *et al.*, 1980) or when grazing at high herbage allowances (e.g. Gibb and Treacher, 1980). Although energy allowances for ewes in early lactation include adjustments for the energy derived from mobilization of fat reserves, they are calculated, as discussed above, assuming constant values for both the energy content of liveweight loss and the efficiency of its use for milk production. Both these assumptions are simplifications, as both the energy value of weight change and the efficiency of its use for milk production vary.

Cowan *et al.* (1980, 1981) and Geenty and Sykes (1986) found that the apparent energy content of weight change in the first 6 weeks of lactation varied widely, from 24 to 90 and from 43 to 100 MJ kg^{-1} of liveweight loss, in pen-fed and grazing ewes, respectively. These large differences in the energy values of weight change arise from the effect of two processes: an increase in body water, as fat is mobilized, and an increase in the weight of digesta and of the alimentary tract, which accompanies the increase in voluntary intake in early lactation. Both these processes lead to an underestimation of the energy content of live weight lost in early lactation.

Estimates of the efficiency of use of energy derived from body reserves for milk production vary widely but decline as the rate of loss of reserves from the body increases (Robinson, 1987). The reserves utilized in early lactation are mainly fat, as the labile reserve of protein in the body is small. Cowan *et al.* (1979) found that a loss of fat of 6.9 kg between days 12 and 41 of lactation was accompanied by a non-significant reduction in protein of only 0.4 kg, approximately 14 g day^{-1}. Energy from the fat was sufficient to produce approximately 50 kg of milk, while the body protein contributed protein for synthesis of approximately 6 kg of milk. Bocquier *et al.* (1987) suggested that the maximum rate of mobilization of protein from body reserves is 25 g day^{-1} in lactating ewes. Geenty and Sykes (1986) comment that, although the mobilization of protein in early lactation is small, it may have an important metabolic effect in ewes that are well fed in late pregnancy. In their study, there was a positive relationship between efficiency of milk production and body protein, which contributed between 2 and 10% of the total energy mobilized in the first 6 weeks of lactation.

The extent of losses of reserves in early lactation is affected not only by nutrient intake, but also by the level of body reserves. Thin ewes with poor reserves mobilize less energy and produce less milk than fatter ewes subjected to the same level of undernutrition. Figure 10.5, from Robinson (1990), shows the response of yield in 70 kg ewes with 5, 10, 15 or 20 kg of body fat, equivalent to body-condition scores in the range 1.0–3.5, to intakes of 20, 25 and 30 MJ ME day^{-1}. The highest intake supplied the energy requirements with all ewes producing 3.5 kg milk day^{-1} and almost main-

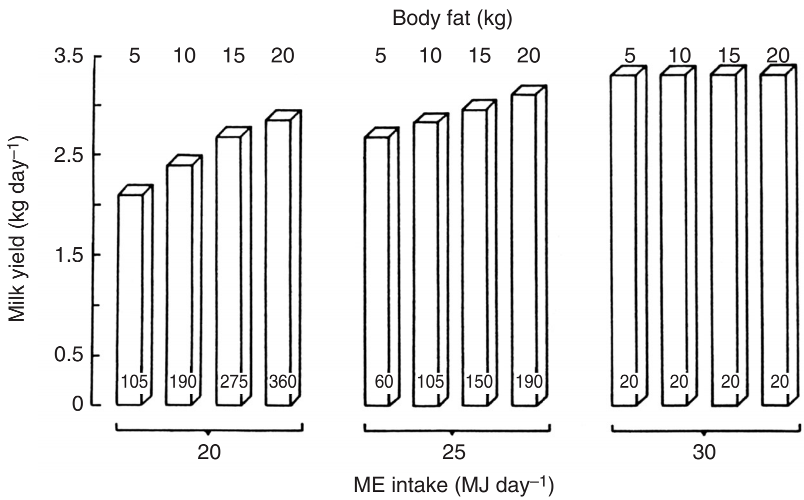

Fig. 10.5. The effect on milk production in twin-suckling ewes of 70 kg body weight of metabolizable energy (ME) intake (20, 25 or 30 MJ day^{-1}) and body fatness (5, 10, 15 or 20 kg of body fat equal to body-condition scores ranging from 1 to 3.5). The values in each histogram are the rates of fat loss (g day^{-1}) from the body. (Reproduced with permission from Robinson, 1990.)

taining weight (20 g day^{-1} loss). At lower intakes, yield was reduced to a greater extent in the ewes with lower reserves, as ewes with larger reserves mobilized more fat and produced more milk, although they were unable to compensate in full for the reduction in energy intake. Ewes with 20 kg of fat reserves and daily intakes of 20 and 25 MJ ME produced 2.9 and 3.0 kg of milk day^{-1} and lost 360 and 190 g LW, respectively. At the same intakes, the thinnest ewes, with 5 kg of fat, produced 2.1 and 2.8 kg of milk and lost 105 and 60 g LW, respectively. This model demonstrates that intakes below requirements inevitably lead to some reduction in milk yield. In the case of ewes in good body condition, however, the reduction is small.

Protein requirements and periparturient rise in faecal egg counts

Recent work in New Zealand suggests that protein requirements derived by the factorial method outlined above may underestimate the requirements for lactating ewes exposed to nematode parasite infection. This is because the immune system has a relatively low priority for nutrients, compared with other physiological requirements, and may need additional protein. The periparturient rise in worm burdens and faecal egg counts is attributed to a temporary relaxation of the immune response of the ewe to nematode parasites (see Coop and Sykes, Chapter 14, this volume). Donaldson *et al.* (2001) showed that, in lactating ewes fed just below their full requirements for ME, worm burdens were inversely related to protein intake in the range 85–145% of AFRC (1993) requirements for MP. The reduction in the parasite burden was caused by an increase in the ability of the ewes to reject ingested larvae. The authors suggest that a daily intake of MP of approximately 350 g, 20% above the AFRC (1993) requirement, is necessary to maintain maximum immunity against nematode parasites in ewes with milk yields of more than 3.0 kg day^{-1} rearing rapidly growing twins.

Effects of poor nutrition in early lactation

Restricted nutrition for periods of 7–14 days in early lactation has little lasting effect on milk yield, which returns to a normal level within a few days of feeding being increased. If, however, low-plane feeding is continued for 28 days, there is either no response to an increase in feeding (Peart, 1970) or only a slow return to a normal level of yield over a period of 2 weeks.

Mineral nutrition

The most important mineral disorders in lactating ewes are hypomagnesaemia and, to a lesser extent, hypocalcaemia.

Hypomagnesaemia

The incidence of hypomagnesaemia (grass tetany or staggers) is generally low in sheep, but can be a problem in individual flocks at pasture at the peak of lactation, in the first 4–6 weeks after lambing. It is more common in older ewes rearing twin lambs, particularly if the ewes are underfed, as is the case with grass tetany in beef cattle. It is most likely to occur in spring on heavily fertilized, improved pastures, especially where fertilizers containing high levels of potassium have been applied in early spring. High levels of potassium in herbage reduce the absorption and utilization of magnesium by the animal.

Onset of hypomagnesaemia is generally very rapid and will result in death unless treated. An outbreak usually starts with the death of a ewe that appeared normal a few hours earlier. Before tetany occurs, ewes appear nervous or excited, with trembling, particularly in the facial muscles. These symptoms may be induced by transportation, exercise, rapid diet change or the presence of strange dogs or people.

Underwood and Suttle (1999) suggest that a mean serum magnesium concentration below 0.60 mmol l^{-1} indicates that a flock will probably respond to supplementation with magnesium. Response to supplementation may possibly occur at serum levels in the range 0.60–0.75 mmol l^{-1}. The disorder can be diagnosed in dead animals by analysing the vitreous humour of the eye, where values below 0.75 mmol l^{-1} indicate hypomagnesaemia. Dietary requirements for magnesium specified by Underwood and Suttle (1999) for lactating ewes are given in Table 10.3.

Ewes in the early stages of hypomagnesaemia can be treated by intravenous injection with magnesium hypophosphite. This is always given with calcium, as 50 ml of a 250 g l^{-1} solution of calcium borogluconate contain-

Table 10.3. Dietary requirements for magnesium for lactating ewes weighing 75 kg (Underwood and Suttle, 1999).

Milk yield ($kg\ day^{-1}$)	Dry-matter intake[a] ($kg\ day^{-1}$)	Dietary requirement ($g\ kg^{-1}$ DM)	
		At pasture	Indoors
1	1.5	1.4	0.70
2	2.2	1.3	0.65
3	2.9	1.3	0.65

[a]Energy concentration of diet (q) = 0.6.

ing 25 g of magnesium hypophosphite. Although ewes often show a rapid response to injection and may resume grazing within minutes, relapses are frequent. In intensive systems, treated ewes may be moved indoors and fed hay and concentrates. No additional magnesium is required in the diets of housed ewes but supplementation may be needed for lactating ewes at pasture in early spring. This is normally given as calcined magnesite in concentrates or in free-access mineral blocks or feed blocks. Individual intakes of blocks, however, vary widely (see Dove, Chapter 6, this volume) and a significant proportion of ewes may be inadequately supplemented (Underwood and Suttle, 1999).

Hypocalcaemia

Hypocalcaemia is not common in lactating ewes. It is more likely to occur in late pregnancy, when the highest requirements for calcium are found in twin-bearing ewes. In pregnancy, hypocalcaemia may be associated with pregnancy toxaemia resulting from low feed intake or a sudden change in feed. Hypocalcaemia itself generally results from the poor mobilization of Ca from bone, rather than from low Ca intake. Excess phosphorus in the diet, relative to its Ca content, reduces bone resorption and is a predisposing factor. The Ca : P ratio of the diet should, if possible, be maintained in the range 1.4 : 1.0 to 1.0 : 1.0. Inadequate protein intake in early lactation also affects Ca metabolism. Chrisp *et al.* (1989) found that a dietary protein supplement increased milk yield, with the resulting increase in Ca demand being met by increased absorption from the alimentary tract, rather than from increased bone resorption.

The symptoms of hypocalcaemia are uncoordinated movement, tremors and rapid breathing. The animal falls, rapidly becomes paralysed, with the head and legs extended, and finally goes into a coma. Death is not generally as rapid as in hypomagnesaemia and the ewe may survive for 4–48 h.

The Ca requirements in Table 10.4 were derived using a coefficient of absorption of 0.68 (AFRC, 1991). As skeletal mobilization occurs and dietary requirements do not have to be met each day, Underwood and Suttle (1999) suggest that a diet with an average concentration of 3 g Ca kg^{-1} DM throughout the year is unlikely to reduce performance.

Table 10.4. Dietary requirements for calcium for lactating ewes weighing 75 kg (AFRC, 1991).

Physiological state	Diet quality	Dry-matter intake (kg day^{-1})	Weight change	Dietary requirement (g kg^{-1} DM)
End of pregnancy	L	2.4		3.2
	H	1.6		4.3
Lactation	L	2.8–3.7	M	2.8
	L	2.3–3.2	N	3.1
	H	1.8–2.4	M	3.8
	H	1.5–2.1	N	4.3

L, poorly digestible diet (q = 0.5); H, highly digestible diet (q = 0.7); M, maintenance; N, weight loss of 0.1 kg day^{-1}.

In the early stages of hypocalcaemia, treatment by intravenous injection of calcium borogluconate is generally effective and ewes will stand and eat within about an hour of treatment. Calcium intake in late pregnancy should be restricted to a level close to requirement, as high intake of Ca reduces the ability of the ewe to maintain Ca levels in the blood by mobilizing bone Ca in early lactation.

Nutritional Management for Lactation

Management at pasture

Management in lactation is critical. Within the constraints of other management operations, lambing is usually timed to coincide with the start of herbage growth, so that the peak of herbage production coincides, as far as possible, with the period of greatest feed requirements of the flock.

In many northern-hemisphere temperate pasture areas, spring lambing is constrained quite narrowly by winter cold. In intensively grazed systems, operations aimed at achieving particular sward heights have been shown to form a sound basis for management, in concert with supplementation, N fertilization and herbage conservation (Treacher, 1990). The use of decision rules based on sward height results from studies on grazed swards showing that, although gross herbage production is lower on short swards, greater amounts of leaf are harvested and less dies. Key guidelines relate to the use of supplementation in early spring, until the sward maintains a target height of 3–4 cm. Thereafter, until the flowering season ends, in about mid-June, grazing pressure may be increased by closing areas for conservation in order to maintain sward height at below 6 cm, and nearer to 4 cm on mixed-grass swards. This prevents deterioration in sward structure and a decline in herbage digestibility.

In many southern-hemisphere temperate pasture areas, winters are milder but pastures senesce in late spring and there is often a pressing need to minimize supplementary feeding. In such areas, lambing in winter rather than spring may be more appropriate. This allows sufficient time for lambs to be marketed or to reach a survival weight before the end of the pasture season, although it may reduce early growth rates in the lambs. Management based on sward height is less common in these systems and management is concerned, rather, with selecting a year-round stocking rate that strikes the best balance between individual ewe nutrition, especially at lambing, and profit per hectare of pasture.

Diet composition

Concentrate : forage ratio

A low proportion of long forage in the diet of lactating ewes results in a reduction in the fat content of the milk, as it does in dairy cows. Goodchild *et al.* (1999) found that, from day 60 to 120 of lactation, when milk yields were low (*c.* 420 g day^{-1}), feeding a diet with a concentrate to straw ratio of 92 : 8 and an acid-detergent fibre (ADF) content of 170 g kg^{-1} DM, compared with a diet with a ratio of 47 : 53 and 385 g ADF kg^{-1} DM, decreased the fat content (73 vs. 65 g kg^{-1}) but did not affect the milk yield. This problem of low fat is common in some intensive dairy systems in Mediterranean countries, where forages are expensive and it is economic to feed high levels of concentrates. It can be overcome, at least partially, by feeding buffers in high-concentrate diets to correct the rumen pH.

Protected fat

In experiments with dairy ewes, the inclusion in the diet of calcium soaps of long-chain fatty acids (CSFA), which are protected from hydrolysis in the rumen, did not affect milk yield or weight change of the ewes (e.g. Casals *et al.*, 1999). Fat content, however, increased, particularly in early lactation, while protein content declined throughout lactation. The few experiments on suckling ewes generally show that, although milk composition was altered, lamb growth rates did not increase.

The increase in milk fat is accompanied by changes in the proportions of fatty acids, which could potentially affect the organoleptic characteristics of cheese made from the milk. In general, the proportion of short- and medium-chain fatty acids (C4:0–C14:1) is reduced and that of palmitic (C16:0) and oleic (C18:1) acids is increased, but initial studies in Spain have shown little difference in the quality of cheese at the end of the maturation period. These results suggest that supplementation with concentrates containing CSFA may be used to increase milk fat in early lactation, where penalties are imposed by cheese manufacturers for milk with a low fat content.

Protein sources and protected protein sources

In general, supplementing diets of lactating ewes with protein sources of low degradability in the rumen has given variable results. Responses are most likely in early lactation, when voluntary intake is low and the ewes are in negative energy balance. Figure 10.6 from Robinson (1983) shows that the responses of milk yield to supplements of approximately 70 g day^{-1} of groundnut, soybean, meat and bone, linseed, fish and blood meal are broadly related to the degradability of the protein in the rumen. Urea, a non-protein nitrogen source that is completely degraded in the rumen, had a negligible effect on milk production. In the case of the less degradable protein sources of fish and blood meal, but not linseed, there was a response to feeding an additional increment of approximately 60 g day^{-1} of supplement. Although 75–80% of the variation in yield resulted from differences in the amount of amino acid nitrogen reaching the abomasum, the remaining variation probably results from differences in the amino acid composition of the protein. Dove *et al.* (1985) supplemented ewes

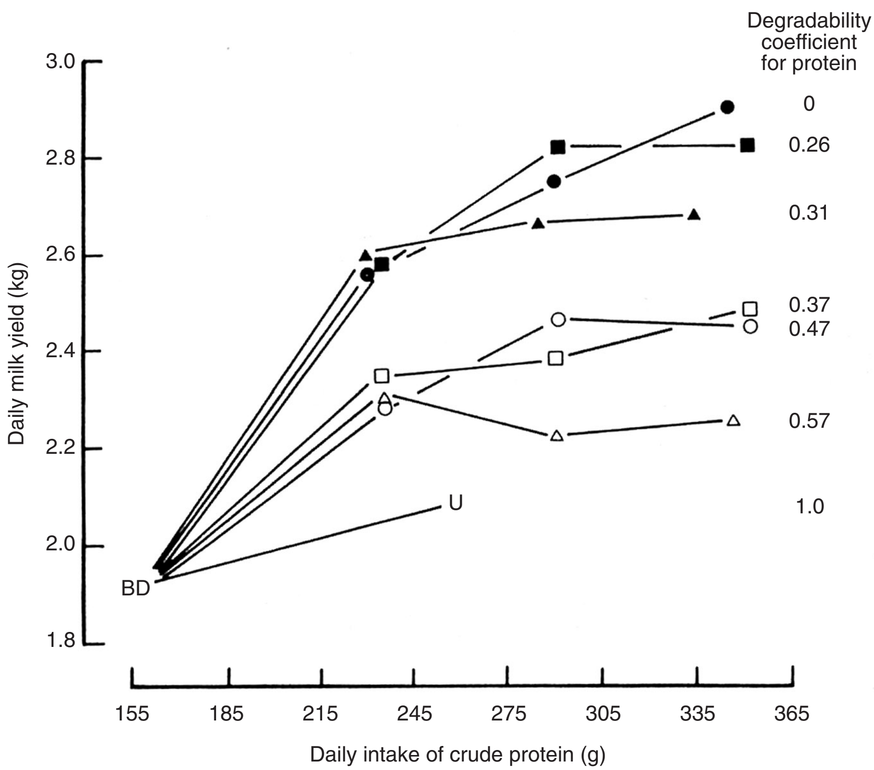

Fig. 10.6. The effect of supplementing a basal diet (BD) of hay and barley with: urea (U); groundnut meal (△); soybean meal (○); meat and bone meal (□); linseed meal (▲); fish meal (■) or blood meal (●), together with the degradability coefficient for each protein source. (Reproduced with permission from Robinson, 1983.)

grazing short pasture with an energy source, with or without formaldehyde-treated soybean meal, and the presence of the protected protein increased milk yield by 33%. Bocquier *et al.* (1994) increased the protein content of milk by feeding 3 or 6 g day^{-1} of protected methionine to dairy ewes already fed more than their energy and protein requirements. Lynch *et al.* (1991) and Baldwin *et al.* (1993), however, found no significant response in either yield or protein content to feeding protected lysine and/or methionine.

These and other similar results must be seen within the context of the overall protein requirements of the ewe; a partially protected protein supplement may be satisfying a need for ERDP. For example, Wilkinson *et al.* (2000) found that supplements differing in digestible undegradable protein content had no effect on the yield of dairy ewes at pasture. The ratio of ERDP to fermentable ME (FME) was, however, below the optimum for rumen function and milk yield increased in response to an increased intake of ERDP resulting from feeding urea.

Conclusion

Ewe milk production has a major impact on the performance and profitability of many sheep systems. The slow increase in voluntary intake in early lactation, when nutrient requirements are at their peak, means that ewes are invariably in negative balance for a few weeks after lambing, although weight change may conceal the energy loss, due to tissue hydration. In the absence of supplementary feeding, this will result in a reduction in milk yield unless the ewe had sufficient body reserves at lambing. The main areas of doubt with current recommendations on nutrient requirements are the energy value of body reserves utilized during lactation and the minimum energy intakes required in early lactation to prevent reduction in milk production throughout the remainder of the lactation.

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