Nutritional manipulation of body composition and efficiency in ruminants

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Summary

Future meat production systems will focus on maximizing efficiency and optimizing utilization of inputs. There will be large penalties for product that fails to comply with market specifications, particularly carcass yield and meat quality traits. This paper reviews nutritional options for manipulation of body composition and their associated effects on carcass composition and quality and the efficiency of energy utilization for growth.

Key elements that dictate the response of ruminants to feed restriction are the severity and timing of the restriction with respect to maturity. Variation in either of these elements results in differential affects on gross composition, fat partitioning and the efficiency of feed use for gain. The efficiency with which the animal uses energy to maintain the body and the ability of the animal to exhibit compensatory gain is coupled to the metabolic state of the visceral organs. Strategic manipulation of the energy yielding nutrients relative to protein content of feed and the specific addition of dietary constituents (for example, rumen escape amino acids, starch and oil) can also affect body composition and the efficiency of energy utilization for growth and maintenance. To capture the benefits of these effects and devise new and novel management procedures to manipulate body composition, a model which incorporates the interaction between nutrient supply and body composition is being developed.

Introduction

Cattle and sheep-meat production systems are faced with the challenge that the traditional goal of maximizing output has been replaced by a goal of optimising utilisation of inputs and maximising efficiency. Increasing pressure is placed on the product (that is the carcass) to meet graded criteria that include weight, yield, fatness and consumer acceptability. Failure of carcasses to meet market specifications will result in immediate financial penalties followed by a longer-term loss of market access. Reducing fatness to an optimum level (accepting that there are specialist beef markets where intramuscular fat is desirable) and increasing lean content are seen as necessities for increased production efficiency and consumer acceptability of red meat. Whilst genetic selection for carcass and efficiency traits are possible, changes achieved are long-term, often have a high initial cost of implementation, occur in a fixed direction and are inflexible in the short term. Immediate, short term, often lower cost and flexible changes in both carcass composition and efficiency can be achieved through manipulation of nutrition. Some of the options for nutritional manipulation of body composition and their associated affects on carcass quality and efficiency will be discussed.
Effect of nutrient supply on body composition

Carcass composition and feed efficiency can be manipulated through varying the quantity of feed provided or by altering the constituents of diet. Some knowledge of the accumulation of body tissues in animals when fed ad libitum throughout their life (often defined as “normal growth”) is required for comparisons of the component changes induced through nutritional manipulation. In general changes in individual components that occur relative to each other during normal growth are best quantified with respect to weight by non-linear functions such as the allometric or quadratic growth equations (Huxley, 1932; Tulloh, 1963; Fourie et al. 1970; Butterfield, 1988). As body weight increases towards an animal's mature weight the proportion of fat increases, the proportion of muscle decreases slightly, or remains constant and the proportion of bone decreases. The differential maturing pattern for carcass traits are shown in Figure 1.

Growth path or rate of growth at specific periods of development has historically been used, albeit in many cases unknowingly, as a method of altering carcass composition. The critical nutritional factors that affect responses in body composition during growth path are the timing and severity of the nutritional intervention, and nutrition subsequent to the point of intervention. The severity and duration of the feed restriction influences the patterns of tissue mobilisation, but other factors including sex and stage of maturity affect the magnitude and direction of the response. In general, a feed restriction which leads to altered body composition can be classified into situations where growth during restriction relative to normal growth is reduced, is held at maintenance or no-growth, or involves weight loss. Recovery from these different situations is called compensatory growth or realimentation, although the rate and composition of recovery may differ depending on the nature of the restriction, and the feed quality and quantity available during refeeding. In the examples discussed below the responses reported are to variation in nutrient intake, irrespective of quality and quantity of feed available i.e. nutrient intake is considered as the product of quantity and quality (i.e. nutrient density) of feed.

Restricted positive growth

Restricting feed supply, and hence growth rate, in the finishing phase of ruminants has received considerable attention with regard to manipulating efficiency of feed use and limiting fatness (Owens et al. 1993; Murphy and Loerch, 1994; Sainz et al. 1995; Mathison and Engstrom, 1996). Restricting energy supplied above that for maintenance results in a decline in the rate of fat accretion, whilst proportionately higher or maximal rates of lean deposition are maintained (Bass et al. 1990).

This was consistent with the observations of Marias et al. (1991) and Murphy and Loerch (1994) who showed that lambs and steers, respectively, restricted to 80% of ad libitum had lower daily fat accretion rates, although daily accretion rates of protein and water were unaffected. As a result when compared at the same live weight, animals that had been restricted below ad libitum have lower proportions of fat and higher proportions of lean than unrestricted animals (Turgeon et al. 1986; Bass et al. 1990; Marias et al. 1991; Wright and Russel, 1991). However, the proportional decrease in fat due to restriction diminished as animals approached mature size (Andrews and Orskov, 1970 Black 1974).

Although the above response to nutrition is most commonly reported it is by no means universal. Kellaway (1973) and Drennan (1979) reported that plane of nutrition had no effect on the body composition of growing animals, whilst others have shown that restricted animals have higher proportions of fat and
lower proportions of lean (Baker et al. 1985; Butler-Hogg and Johnsson, 1986; Greef et al. 1986b). It is difficult to reconcile these differences through a single mechanism. From a dietary perspective, the proportions of protein to energy in the rations used will alter the relative rates of fat to protein deposited (Black, 1974; Butler-Hogg and Johnsson, 1986; Van Houtert, 1991). Stage of maturity at which the restriction is imposed and the difference in length of time and magnitude of restriction relative to ad libitum fed animals will also contribute to the variation (Carstens et al. 1991; Carstens, 1995).

A hypothesis to explain the response of carcass composition to restriction at increasing levels of maturity was proposed by Oddy (1997a) (Figure 2). If restriction is imposed at a very early stage of maturity (prior to weaning), subsequent protein deposition may be reduced so that near maturity regrown animals are fatter (weaning), subsequent protein deposition may be reduced so that near maturity regrown animals are fatter (Thorton et al. 1979; Tudor et al. 1980). Carstens (1995) showed that imposing a restriction on cattle at eight months of age will have little effect on total body fat at maturity. He suggested that at approximately 40% of maturity the impetus for fat deposition is low and the ability of the animal to adjust protein deposition rates appears high (Ryan, 1990). This suggests that restriction at this stage of maturity may have little effect on the body composition of the animal at normal carcass weights.

Partitioning of fat is influenced by growth rate. In general, high rates of gain result in relatively more subcutaneous than intermuscular fat (Murray and Slezacek, 1976; Ledger and Sayers, 1977; Wright and Russel, 1991). Fat deposition is favoured in the carcass depots compared to the internal fat depots as the rate of live weight gain increases (Hodge and Star, 1984; Butler-Hogg and Johnsson, 1986). Feed restriction has the greatest effect on those fat depots that are undergoing the most change at the time at which the restriction is imposed. The majority of experiments have implemented restricted feeding during the finishing phase, consequently the greatest change that has been observed is a difference in weights of the later maturing carcass fat depots.

**Weight loss**

The most notable change in body composition that occurs in the short term for animals that are maintaining liveweight, is a decline in the weight and proportion of visceral organs, particularly the liver and the digestive tract (Foot and Tulloh, 1977; Murray and Slezachek, 1988b; Ryan and Williams, 1989; Iason and Mantecom, 1993). This results in a reduction in maintenance requirements of animals in weight stasis by reducing the size of those organs that have a high metabolic activity (Keenan et al. 1969; Kellaway, 1973; Koong et al. 1985; Ferrell, 1988; Iason and Mantecom, 1993). This reduction probably accounts for the relative decline in the amount of feed required to maintain liveweight in animals exhibiting positive growth at the time when the restriction is imposed (Lines and Pierce, 1933; Foot and Tulloh, 1977; Ledger and Sayers, 1977; Turner and Taylor 1983; Afonso and Thompson, 1996).

As weight stasis results in a decline in visceral weight, this decline must be matched by an increase in carcass weight, particularly that of the carcass fat depots (Keenan et al. 1969; Winter, 1971; Foot and Tulloh, 1977; Notter et al. 1983; Aziz and Murray, 1987; Murray and Slezacek, 1988a; Ryan and Williams, 1989). However, there may be additional affects due to initial body composition. Fox et al. (1972) showed that fatter animals tend to gain body fat during weight maintenance, whilst leaner animals mobilised body fat. There may be no effect on the weight of carcass muscle during a period of weight stasis for immature cattle or sheep (Murray et al. 1974; Murray and Slezacek, 1988a). However, this may not always be the case in immature sheep, as Afonso and Thompson (1996) showed that ewe and ram lambs maintaining weight, increased both total body fat and carcass lean to compensate for a decline in visceral organ weights. These authors also showed that the proportion of subcutaneous fat declined relative to proportions of intermuscular and internal fat, thus subcutaneous fat was more responsive to nutrition. In contrast, Murray et al. (1974) showed that carcass fat was not utilised to any great extent during a period of maintenance feeding of steers, whilst kidney and channel fat was significantly reduced during the period of maintenance. In summary animals that have experienced a period of weight stasis have higher proportions of carcass fat and lower proportions of viscera and internal fat. Carcass muscle is relatively unaffected by weight stasis.
selective depletion of fat from the subcutaneous depot, whilst the weight of internal depots remains relatively unaffected (Robinson, 1948; Butterfield, 1966; Seebeck, 1967; Russel et al., 1968; Little and Sandland, 1975). An exception to this pattern occurs at low body weight, where kidney and channel fat may be lost more quickly than carcass fat (Seebeck and Tulloh, 1968). In summary, if animals are compared with controls during the early phase of weight loss (less than one month) they will be comparatively fatter, whereas animals that have been in a weight loss phase for a longer time period (greater than one month) will be leaner than controls (Butler Hogg, 1984; Aziz et al., 1992).

The rate of body weight loss effects the proportions of lean and fat that are mobilised. Searle and Graham (1972) showed that a high rate of weight loss results in a higher rate of lean mobilisation and a lower rate of weight loss results in a higher rate of fat mobilisation. These results were incorporated into a conceptual model by Black (1974), and subsequently confirmed by Butler-Hogg (1984). However Black (1974) and Searle et al. (1979) suggested, that given time to equilibrate at a new lower weight, animals will have a body composition similar to that of the unrestricted animal.

Realimentation and compensatory growth

Compensatory growth is the most widely acknowledged form of growth path manipulation. Fox et al. (1972), Turgeon et al. (1986), Wright and Russel. (1991) and Ryan et al. (1993a,b) have all proposed that there are several distinct phases to live weight compensation. The initial phase of compensatory gain has a high rate of lean deposition that primarily reflects the growth of the visceral organs including the digestive tract. (Butler-Hogg, 1984; Greet et al. 1986b; Ryan, 1990; Drouillard et al. 1991 a,b; Iason and Mantecom, 1993).

Fox et al. (1972), Rompalaet al. (1985) and Wright and Russel (1991) showed that steers deposited more protein during the initial stage of compensation. Searle and Graham (1975) and Kabbali et al. (1992) also observed higher rates of protein (muscle) deposition in the early phases of realimentation in compensating lambs. Therefore in the initial stages of compensatory growth or realimentation, compensating animals will be leaner than ad libitum fed animals. The second phase of realimentation is characterised by a higher proportion of fat deposition that occurs once visceral organs have been replenished (Hayden et al. 1993; Ryan et al. 1993b; Henricks et al. 1994). Fox et al. (1972), Butler-Hogg, (1984), Turgeon et al. (1986), and Wright and Russel, (1991), have shown that it is this phase of fat development during the latter part of compensatory growth that enables animals to achieve a similar body composition to those that have not been restricted. Hayden et al. (1993) showed that compensatory growth had differential effect on fat partitioning, with compensating steers still having lower internal fat weights at a final endpoint. They suggested that a period of feed restriction had a greater effect on the internal depots, compared to the later maturing subcutaneous and visual intramuscular (marbling) depots, which respond to lipid accumulation during the latter stages of compensatory growth.

The longer the recovery the greater is the possibility that animals, when compared at the same weight, will show no difference in body composition (Bass et al. 1990). However before that time, compensating animals may be leaner or fatter depending on the nature and length of the previous restriction period. As a result the discrepancies in the literature reporting that animals can either be leaner or not different after compensatory growth, appear to be related to the length of time that animals are in the second phase of compensatory growth (Nicol and Kitessa, 1994). Results from Burton et al. (1974), Drew and Reid (1975), Little and Sandland (1975) and Foot and Tulloh (1977), show that restricted animals were leaner than ad libitum fed animals. However these results can be explained by the fact that comparisons were made before animals had finished compensatory growth. Kabbali et al. (1992) suggested that compensating lambs were leaner due to the inability of internal fat depots to recover. This may explain the results from experiments that have used chemical analysis of the whole body to compare compensating and normally grown animals.

A special case exists for animals near or at maturity that experience a period of severe feed restriction; they may not compensate fully if compensation is expressed on a live weight basis, even when offered ad libitum feed (Taylor et al. 1981; Ryan 1990). Meyer and Clawson (1964) and Greet et al. (1986a,b) indicated that there is a shift in metabolic pathways in severely restricted sheep such that fat deposition is enhanced. For these severely restricted animals the shift towards fat deposition was maintained during realimentation resulting in fatter animals. A possible explanation is that under severe restriction the viscera, and in particular the liver, does not compensate fully and thus there is an alteration in both endocrine control of, and substrate supply for, tissue accretion in the carcass.

Our conclusion is that there appears to be no difference in ultimate body composition between restricted and continuously grown animals, provided that the period of compensation is of sufficient length to enable the latter phase of compensatory growth to occur (Fox et al. 1972, Kellaway, 1973; Murray and Slezachek, 1976; Butler-Hogg, 1984; Wright and Russel, 1991; Ryan et al. 1993a,b). From the previous observations, it is important that comparisons between compensating and control animals are made at live weights which are of commercial significance (market specified weights), because the weight at which animals are slaughtered during compensation can greatly affect the conclusions of compensatory growth studies (Turgeon et al. 1986).
Role of visceral organs on efficiency and composition

Variation in the mass of the visceral organs, specifically the liver, is seen as a major contributor to variation in energy expenditure. This occurs through the disproportionately high energy requirements with respect to mass of the metabolically active visceral organs (Baldwin and Bywater, 1984; Ferrell and Jenkins, 1985; Burrin et al., 1990; Freethy, 1995). Birkelo (1995) summarised the importance of the visceral tissues in total animal energetics by stating that they contribute between 40–50% of the total body energy expenditure although only occupying 10% of total body mass. More importantly, approximately 70% of energy use above maintenance is used by the liver and gut (Johnson et al., 1990; Ortigues and Doreau, 1995). As a result the reduction in the mass of the visceral tissues is the one of the most notable events that occurs in animals that are forced to lose weight when subjected to a period of feed restriction (O’Donovan, 1984; Ryan, 1990; Carstens, 1995; Wester et al., 1995). The metabolic lag in the reduction in the energy requirements, initially as a result of lower visceral organ weights, that occurs when animals are re-fed is thought to promote the acceleration of tissue deposition that is known as compensatory growth (O’Donovan, 1984; Ryan 1990).

Effects on composition

Clearly any nutritional manipulation that effects the relative proportion of viscera with respect to the total body will alter the effective energy that is available for muscle and fat accretion. The results of Oddy (1997b) emphasize the importance of the contribution of visceral organs to total body energetics in compensating and normally grown animals. He showed that although the gross efficiency of carcass gain per unit of metabolisable energy intake was apparently higher in compensating lambs, there was no difference in the energy gain in the carcass per unit of metabolisable energy available for gain. This was after adjusting for energy use of the visceral organs for the compensating and normal lambs. Differences in the rate and composition of gain between cattle that have been fed at forage diet and those fed on a concentrate diet (at an equal metabolisable energy intake), can also be accounted for by differences in the heat production from the portal drained viscera (Reynolds and Tyrell, 1991; Oddy et al., 1997a).

Ryan et al. (1993b) suggested that replenishment of visceral organs is the major priority for compensating animals. This conclusion is supported by the results of numerous experiments that have examined compensatory growth where there are no differences in the weights of the non-carcass component between compensatory and normally grown animals despite differences in the weights of the carcass tissues (O’Donovan, 1984; Ryan, 1990; Carstens, 1995). The concept of priority may be misleading as this suggests cause and effect. Our interpretation differs in that we believe that the rapid response in visceral organ size during realimentation (as reflected in higher rates of deposition; Butler-Hogg, 1994) occurs through a capacity of the viscera to replenish. There is a clear functional relationship between the size of the digestive organs (rumen, small intestine, etc) and feed intake that indicates that as feed intake increases the weights of these tissues must increase (Koong et al., 1985; Johnson et al., 1985; Fluharty and McClure, 1996; Kouakou et al., 1997). In addition as the rate of turnover in the viscera is high (K, ca. 60%/day liver, 50–60% small intestine and 30–40%/day rumen), being approximately 5 times that of muscle turnover, the capacity to deposit tissue is greater. A similar logic can be extended as an explanation of the high rate of visceral lean loss during feed restriction.

The capacity of the viscera to respond to nutritional supply results in clear differences in body composition, particularly if comparisons between treatment groups are based on chemical composition. Short-term recovery of visceral lean during refeeding usually is consistent with animals being assessed as leaner relative to controls. As a result of this high rate of visceral organ hypertrophy the ratio of lean:fat in accreted tissue is higher, resulting in the efficiency of retained energy being greatly increased in animals that exhibit compensatory growth (Johnsson et al., 1985; Carstens et al., 1989).

Studies on perturbed growth on viscera mass have predominately concentrated on the mean difference between treatment groups. However of greater importance may be the increase in the variation of visceral organ weights that has been observed within restricted feeding groups (Morgan and Owen, 1993; Hicks et al. 1990). We believe that an increase in the variation of visceral organ mass leads to a greater increase in the variation in muscle and fat deposition. Failure to describe adequately an increase in the variance within a treatment group may have contributed to the confusion about the effects of nutritional manipulation on body composition.

Maintenance requirement (MEₙₙ)

There is a clear response of estimates for MEₙₙ to prior levels of feeding (Ball, 1996). This is mirrored by a direct response in the mass of visceral organs (Ferrell et al., 1983, Ferrell and Jenkins, 1985; Koong et al., 1985; Burrin et al., 1990). As an example, growing lambs that were fed at high levels and then at low levels of intake (HL) had lower maintenance requirements than lambs of the same weight that had been fed at low levels followed by high levels (LH). The LH lambs had higher weights of visceral organs (Ferrell et al., 1983; Ferrell, 1988). A similar difference existed in maintenance requirements of growing steers following similar growth paths (Sainz et al., 1995).
It was shown that the proportion of metabolically active tissues of the total body was lower in the previously restricted animals when compared to the control animals (for review see Ferrell, 1988). Keenan et al. (1969) showed that a 32% reduction in energy requirements per kilogram of live weight between control and previously restricted mature sheep was closely correlated with a 35% decrease in the mean weight of liver, rather than the 14% difference in the mean metabolic weight of the two groups. Their results indicate that visceral organ energy expenditure was reduced during the restriction period, which concurrently increased maintenance efficiency. Wester et al. (1995) showed that although oxygen consumption increased per gram of liver tissue during weight loss, total liver oxygen consumption declined as a result of a reduction in the mass of the tissue. Thus there is evidence that metabolic activity, as a function of mass, is not constant in animals losing weight and that liver weight per se may not be a reliable indicator of changes in energy expenditure within the visceral organs during weight loss and weight gain (Sainz, 1995). However in complete contrast, Drouillard et al. (1991a) indicated that the activity of visceral tissues was not responsible for the improved efficiency during compensatory growth in previously restricted lambs. In that study although visceral organ size was reduced during the restriction, there was no apparent compensatory growth in the lambs when feeding levels were increased to ad libitum.

Effect of restriction on efficiency

Efficiency of use of feed for gain

Sainz (1995) indicated that moderate feed restriction improves feed efficiency by about 0.6% for each percentage unit in restriction relative to ad libitum, the optimum being between 12–15%, about 80–85% of ad libitum. He stated that the improvement in the efficiency of growth arises from multiple mechanisms whose specific contribution to the magnitude of improvement in efficiency changes with the degree of restriction. Improvements in digestibility and the ME content of the feed occur with feed restriction, although these effects are minor. Sainz (1995) noting that Webster 1980 indicated that the cost of lean gain was 23.7 MJ/kg and the cost of fat was 38.6 MJ/kg, stated that changes in the lean:fat ratio of the gain and lower maintenance requirements probably accounted for the majority of the increase in feed efficiency.

Muir et al. (1997) indicated that when compared at the same live weight, steers from an ad libitum growth path were 10% more efficient than compensating steers, but Butler-Hogg and Tulloh (1982) indicated that growth path did not effect overall efficiency of growth, if animals were compared at the same cumulative feed intake. In our own experiment (Ball, 1996), immature sheep were fed at either 140, 100 or 60% of maintenance (SCA, 1990) for 15 weeks and then at maintenance for a further 21 weeks. When retained energy was expressed relative to cumulative energy intake (Figure 3), the sheep that had

![Figure 3](image-url)  
*Figure 3* Retained energy as a function of cumulative energy intake for immature ewes of three growth paths, being 140%, 100% and 60% of maintenance. The individual animal responses are identified (Source Ball, 1996).
been fed at 140% of maintenance had higher levels of retained energy for the same cumulative energy intake than sheep fed at 60% of maintenance. In this experiment, animals that had been maintained in a positive energy situation had a higher gross efficiency of energy than animals that had experienced an energy deficit at the same level of cumulative feed intake. Thus, in the short term at least, growth path can be used to manipulate growth efficiency at specific slaughter points. These results, however, do not contradict the hypothesis of Butler-Hogg and Tulloh (1982), who suggested that given an adequate length of time there was no difference in the retained energy (measured by body composition) relative to cumulative energy intake of restricted and normally grown sheep. As evident in Figure 3, there is a possibility for responses to treatments to converge with time.

**Efficiency of feed use for maintenance**

Webster (1980) reported the energy cost of maintaining a unit weight of protein was higher than that for fat, leading to the concept that maintenance costs may be more closely related to lean body mass (Ferrell et al. 1979; Tess, 1984; Olthoff and Dickerson 1989; McCracken, 1992), rather than simply to metabolic body size (Brady 1945; Taylor et al. 1981). In support of this Graham (1967), noted that if fasting heat production (FHP) was described as a function of lean body mass then the exponent for body size was not significantly different from unity. This also indicates that FHP, or ME%, is directly proportional to lean mass with no major effect of either fat or bone weights. Sheep (Jopson et al. 1994, Ball et al. 1995) and cattle (Klosterman, 1968; Solis et al. 1988; DiContanzo et al. 1991) that are comparatively leaner have been shown to have a higher maintenance energy requirement. However Ortigues et al. (1993) indicated that a distinction exists between:

1) animals, that are comparatively leaner than their contemporaries and have higher maintenance requirements and 2) animals that are leaner as a result of a period of weight loss from feed restriction and have lower maintenance requirements due to a metabolic adaptation to the lower feeding level (Marston, 1948). This difference may be related to the proportion of lean that is either visceral (high activity) or muscle (lower activity).

An apparently persistent change of use of energy for maintenance (maintenance efficiency) is one of the key effects that manipulating growth path has on production efficiency. There has been a number of studies have compared estimates for maintenance efficiency in animals fed at either low or high levels of feeding (Ferrell et al. 1983; Koong et al. 1985; Ferrell, 1988; Sainz et al. 1995). These studies showed that estimates for maintenance requirements are lower in animals that have been restricted to either maintenance (Graham and Searle, 1975; Ledger and Sayers, 1977; Webster, 1980) and at maintenance feeding period (MJ ME required to maintain a kg of empty body weight per day, ME kg) as a function of time for 60, 80 and 100% of maintenance during the restriction and realimentation phases. The dotted lines represent the 95% confidence limits for sheep fed at 60% of maintenance.

![Figure 4](image-url) Changes in maintenance efficiency relative to the initial estimate obtained at the end of a six week maintenance feeding period (MJ ME required to maintain a kg of empty body weight per day, ME kg) as a function of time for 60, 80 and 100% of maintenance during the restriction and realimentation phases. The dotted lines represent the 95% confidence limits for sheep fed at 60% of maintenance.

Yambayamba et al. 1996; Afonso and Thompson, 1996), or below maintenance feeding levels (Graham and Searle, 1979; Gingens et al. 1980, Ryan et al. 1993a). Ortigues and Durand (1995), showed that there was a decrease in the maintenance requirements of mature ewes that were fed at half the conventional requirements for maintenance, although the energetic efficiency (k₁) when expressed on a metabolic live weight basis was the same as the estimate at maintenance.

As an example the NRC (1996) recently proposed an equation that described changes in maintenance requirements due to prior feeding level as a function of condition score of the animal. The form of the equation used implied that maintenance increases linearly with condition score from 0.8 to 1.2 times the normal (where normal or average condition score was 5). Ferrell (1995), stated that the equation does not address how the animal arrived at that condition score, or for how long it had been at that body composition. The equation also neglects the confounding effects of variations in condition score imposed by seasonal oscillations in body composition or changes in fat partitioning resulting from different physiological states (Ball et al. 1996).

Given this information, our own recent studies have examined the affect that nutritional supply manipulation has on estimates of maintenance efficiency. Ball et al. (1997) fed mature ewes and rams at maintenance or at below maintenance for 15 weeks and then at maintenance for 15 weeks. As shown in Figure 4, sheep that had been fed at 60% of maintenance had higher maintenance requirements per kilogram of empty body weight than sheep fed at maintenance (SCA, 1990). This suggests that nutritional manipulation via feed supply does have an effect on estimates for maintenance requirements.
Nutritional manipulation of body composition

Effect of specific nutrients

Effect of specific nutrients on body composition

The foregoing discussion was based on the assumption that energy supply was the major nutritional influence irrespective of the method by which variation in energy supply was imposed. This would include, as a first approximation, low intake capacity arising from high roughage or low protein feed, or limited availability of feed. In these situations amino acid outflow from the rumen is generally proportional to total intake. It is possible to manipulate relative amounts of amino acids and energy yielding nutrients to ruminants. What happens when the relativity between amino acid and energy supply changes?

Kempton (1979) introduced the concept of an optimal protein (P) to energy (E) ratio (P:E), principally for wool growth response to protein supply. However, for growth of body constituents the idea of a ratio is less useful, principally because amino acid and energy supplies have both dependent and independent effects on nitrogen balance, and hence deposition of protein in body and wool. Black and Griffiths (1975) described the nature of the nitrogen balance response to amino acid and energy supply from a summary of data collected in trials using over 500 lambs over the weight range from 5 to 35 kg. In general, they demonstrated that at a fixed energy intake, N balance increased linearly in response to amino acid supply up to a maximum for that energy supply and the weight of the lamb (Figure 5). This pattern of response has since been shown in pigs (Dunkin et al. 1984; Campbell et al. 1985) and calves (Gerrits et al. 1996). Dove et al. (1977 a,b) demonstrated that balance of essential to non-essential amino acids affected the response, but that with most practical protein sources a gross imbalance of amino acids was unlikely. Accordingly, for the following discussion, it will be assumed that for ruminant diets amino acid imbalance is not a common problem.

Figure 5 implies that where amino acid supply was less than the inflection point for any energy intake, that energy deposition would proceed in the absence of nitrogen deposition i.e. the animal would fatten. Thus the relative amounts of fat and protein in the body could be altered. In that now classic work of Black and Griffiths (1975) body composition change was not measured. However, the implications of protein supply for fat deposition was at that stage in pigs, poultry, pre ruminant (Norton et al. 1970) and young ruminant lambs (Orskov et al. 1976).

An assured supply of supplementary amino acids to ruminants was not readily and quantitatively achievable until Ferguson and colleagues (1967) demonstrated the role of formaldehyde protection of proteins on growth of wool. Effects on body composition were harder to demonstrate, in part because of failure to understand the relationship between amino acids and energy supply, but also because of difficulties in measurement of body composition compared to measurement of wool growth. Although significant live weight responses to a post-ruminal supply of amino acids had been clearly demonstrated, particularly on low quality feeds (Leng, 1975), it was some time before effects of amino acid supply on body composition was seriously studied in

Figure 5. Fitted relationship between nitrogen balance and N intake for liquid-fed lambs differing in liveweight. (---5 kg, ---15 kg and ---25 kg) and metabolisable energy intake (ME; MJ/day). [Source: Black and Griffiths, 1975].
ruminants. Infusion studies of Fattet et al. (1984) demonstrated that at least at low energy intake an increased amino acid supply could prevent weight loss by maintaining muscle mass at the expense of fatty tissue. This suggested a method for reducing fatness in overweight animals (Bell and Bower, 1990; Vipond et al. 1989) which could be applied in practice. There remained the problem that these nutritional strategies when used to reduce fat deposition also restrict growth. Increased amino acid supply relative to energy at low energy intakes has been shown to increase muscle and skin protein deposition (Edwards et al. 1989a,b; Hegarty et al. 1994; Oddy et al. 1994). However, as energy intake increased, rumen escape amino acid supply became less effective in promoting protein deposition and could also lead to increased fat deposition (Van Houtert, 1991; Oddy et al. 1994). We believe that amino acid supply can increase fat deposition because of the increased oxidation of amino acids and thus provision of carbon skeletons (Oddy et al. 1997b).

Manipulating the supply of energy yielding nutrients compared to amino acid supply can increase fat deposition provided there is no reduction in feed intake due to reduced amino acid supply. In practice this does not always happen with high-energy feedlot diets. Our experience and that of others (Zinn and Shen, 1996), indicates that increasing fat in feedlot diets does not result in increased carcass fat, although on high roughage diets supplemental fat (as calcium soaps) can increase fat deposition (Van Houtert, 1991). In high energy feedlot diets the form of fat does not seem to matter. Rumen protection either by formation of calcium soaps (Palmquist and Jenkins, 1982), protective encapsulation (Cook and Scott, 1970), or simply the addition of Ca ion as Ca(OH)$_2$ to a feedlot diet containing fat does not increase carcass or intramuscular fat content of cattle (S. Bird unpublished data, Table 1). Specific nutrients, for example propionate, have been associated with increased fat deposition and increased efficiency of fattening (Blaxter, 1962). However the addition of propionate to roughage diets have shown no effects on fat deposition (Van Houtert, 1991). In part this could be because of homeostatic mechanisms regulating

1. uptake of nutrients by tissues  
2. high rates of inter-organ flux of intermediates / metabolites  
3. alternative energy yielding pathways within tissues.

Control of regulatory processes by nutrients is one way to alter the partitioning between organs, and hence composition of the body. For example, Edwards et al. (1990) suggested that a possible means by which rumen-escape amino acids increased muscle mass in sheep fed low energy diets, was by regulation of plasma IGF-1 and insulin and tissue sensitivity. This was consistent with observations that branched chain amino acids were potent insulin secretagogues and that leucine enhanced insulin sensitivity of muscle (Garlick and Grant, 1988). Trivalent chromium which alters insulin release and tissue sensitivity and thus lean tissue deposition in pigs (Boleman et al. 1995; Mooney and Cromwell, 1995) and lambs (Kitchalong et al. 1995).

These examples illustrate that although substrate, and thus nutrient, regulation of body components is possible, the effects are generally not observed until the nutrients exhibit regulatory effects on pathways outside their normal pattern of mass action (stoichiometry). Those regulatory effects have differential effects across organs.

Indeed consideration of stoichiometry in a whole animal sense is fraught with dangers because of our limited understanding of the complex issues that regulate inter-organ transport and within-organ nutrient utilisation. For example, there are theoretical

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**Table 1**  Means and standard error for the effect of dietary treatments on the fat depot characteristics of feedlot steers (S.H Bird unpublished data).

<table>
<thead>
<tr>
<th>Fat Depot</th>
<th>Control</th>
<th>Calcium OH</th>
<th>Oil</th>
<th>Oil+CalciumOH</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>29</td>
<td>30</td>
<td>30</td>
<td>30</td>
<td>0.57</td>
</tr>
<tr>
<td>12/13th Rib (mm; change in finishing period)</td>
<td>6.0</td>
<td>4.7</td>
<td>5.0</td>
<td>6.0</td>
<td>0.57</td>
</tr>
<tr>
<td>L.Dorsi Fat% (wet basis)</td>
<td>4.5</td>
<td>1.0</td>
<td>4.6</td>
<td>4.1</td>
<td>0.23</td>
</tr>
</tbody>
</table>

Control: Feedlot diet containing 10% milled roughage, 75% rolled barley grain, 8% molasses / mineral vitamin mix, 5%

Cottonseed meal and 1.2% CaCO$_3$

Calcium OH: Control diet, with CaCO$_3$ replaced by Ca(OH)$_2$

Oil: Control diet with 6% grain replaced by Canola oil

Oil + Calcium OH: Oil diet with CaCO$_3$, replaced by Ca(OH)$_2$
reasons why one might think that acetate utilisation is inefficient. Complete oxidation of acetate yields 5 moles ATP per mole C, compared with glucose where complete oxidation yields 6 moles ATP per mole C, or lipid which can yield up to 8 ATP per mole C. These estimates do not allow that acetate oxidation preferentially displaces glucose oxidation in muscle (see Pettick and Vemau, 1984). Moreover, they do not consider the energy cost of glucose transport into the cell, and the regulation of that process, whereas as far as we know acetate is freely diffusible at least into muscle (see Pettick and Lindsay, 1982). Nonetheless, it is possible to perceive schemes that utilise the best available biochemical knowledge and show that substrate supply can affect efficiency of nutrient use (eg. Black et al., 1987; Baldwin 1995), despite experimental evidence that such differences do not occur (Orskov et al., 1979).

There is good evidence that substrates and specific nutrients can regulate processes both within and beyond the metabolic pathways in which they are involved. Allosteric modification of enzyme activity within pathways by feedback, and sometimes feed-forward, from substrates and intermediates is well known (see Newsholme and Start, 1973). It has recently been shown that substrates can regulate gene transcription, and thus alter the expression of regulatory elements within different tissues. For example from birth to suckling a high fat diet regulates expression of Carnityl palmitoyl transferase -1. During the transition from suckling to eating hard food (weaning) in the rat, carbohydrate consumption induces expression of fatty acid synthetase (Girard, 1996). Together these activities demonstrate how pattern of substrate supply might regulate differential development of one tissue with respect to another. However, except for the effect of butyric acid on rumen development, there are no clear examples for ruminants of where specific nutrients might alter tissue development.

Confounding interactions with Feed supply (examples)

There are difficulties (induced partly by statistical limitations and partly by our own thought processes) in interpreting and quantifying the interactions between the level of nutrient supply and the specific pattern of nutrient supply. In this conference Oddy et al. (1997a) presented an alternative conceptual approach that may improve the methodology to describe such interactions. Whilst the interactions are complex and obviously contribute to the variation in responses of both body composition and efficiency to nutrition, they often have been grossly over complicated on the one hand or oversimplified and ignored on the other. We present a few examples to show that the anomalies in published results for nutritional manipulation can be accounted for, by a confounding between nutrient supply and composition of the animal.

The type of restriction that is imposed on the animal in order to create a phase of weight loss is very important when interpreting the different responses. In most experiments, weight loss has been achieved by restricting the supply of a high quality diet. But, feed restrictions that occur in the field are also accompanied by a reduction in the quality (particularly protein content) of the feed. Drouillard et al. (1991a) tested the effect of a reduction in both the quality and quantity of feed on compensatory growth. They showed that lambs that had restricted protein intake lost considerable amounts of carcase muscle, whilst lambs that had restricted energy intake, but had adequate amounts of dietary protein, were able to maintain carcase muscle. In that experiment, and that of Fattet et al. (1984), energy-restricted lambs mobilised carcase fat whilst utilising dietary protein to maintain body lean reserves so that these animals were leaner than both control and protein restricted animals when compared at the same weight. In support of this, Chowdhury et al. (1995) showed that provided protein supply from the diet is adequate, an animal can maintain or even gain lean tissue during weight loss, by fueling energy demands through mobilisation of fat reserves. They suggested that the extent to which lean reserves can be maintained is highly dependent on the body fat reserves of the animal prior to the weight loss period. The conclusion from these studies is that protein supply and the level of fat at the start of the weight loss period interact to affect the proportions of body components that are mobilised in an energy deficit. Clearly the supply of dietary nitrogen in a weight loss situation will be related to the perceived lean content of the carcass.

The composition of the diet during feed restriction also influences the response during early realimentation. Drouillard et al. (1991b) showed that lambs previously restricted in protein were able to regain a large proportion of lost protein in the first two weeks of realimentation. Whereas energy-restricted lambs that had no loss in visceral mass during the restriction, deposited lipid that accounted for 80% of the gain in the first two weeks. Interestingly, there were no differences in tissue deposition between energy and protein restricted lambs after the initial two weeks of realimentation

Recent evidence from Sainz et al. (1995), suggests that the type of feed given during the restriction affects ME_{c} during the subsequent realimentation period. Steers that were fed a concentrate diet at restricted levels (CL) had a 7% lower ME_{c} relative to control fed steers during realimentation, whilst steers that were fed a forage diet (FA) during the restriction phase had a 28% higher ME_{c} relative to the controls. They showed that proportional differences in visceral organ weights mirrored the differences in maintenance requirements, suggesting that the 28% heavier visceral weights of the FA steers was a forage diet effect that prompted higher ME_{c} in those steers during the compensation period.

Quality of the diet has an effect on the magnitude and nature of the gain during compensatory growth, particularly in the early phase of realimentation. Several
experiments have shown that compensating cattle and sheep have higher protein requirements than ad libitum fed animals when compared at the same stage of growth (Fox et al., 1972; Fattet et al., 1984; Hays et al., 1995). In the latter study, additional dietary crude protein in the realimentation diet stimulated an increase in the rate of lean accretion during compensatory growth. There is evidence that suggests that compensating lambs, deposit greater proportions of nitrogen within the body at the same nitrogen intake (Hegarty et al., 1994; Oddy et al., 1997b). This indicates that the efficiency of nitrogen capture may increase in compensating animals, but the dietary requirement for protein may not.

Black (1974) indicated that a higher amount of energy supplied at the tissue level would cause an increase in the rate of fat deposition relative to protein, but only where energy exceeded amino acid supply and the capacity to deposit protein has been met (Black and Griffiths, 1975). Previously restricted animals during realimentation have lower maintenance requirements (O’Donavan, 1984; Koong et al., 1985), and a higher efficiency of energy utilisation above maintenance (Meyer and Clawson, 1964; Fox et al., 1972; Greef et al., 1986a,b; Abdalla et al., 1988; Marias, 1991) when compared to unrestricted animals at the same live weight. As a result the increase in fat accretion observed during the latter phase of compensation may be a function of an increased energy supply at the tissue level. It is also likely from the above results that this phase of fat accretion would occur independently of a higher feed intake (usually observed in compensating animals). However, Thornton et al. (1979) and Schader et al. (1995) suggested that there is a marked transition in fat deposition that occurs as animals increase in maturity. As such it is still possible that the deposition of fat may be due to an increase in maturity, rather than an associated effect of compensatory gain.

Conclusion
This review has shown that nutritional manipulation which encompasses aspects of nutritional supply, specific nutrient composition and their interactions contribute to systematic differences in the final body composition and production efficiency of animals as they near either slaughter or mature weights. Variations in the response of growth path and nutritional manipulations in terms of body composition have often precluded these results being applied to the paddock situation. Clearly we need the methodology that encapsulates the information contained within these systematic effects to devise new and novel management procedures that enables growth path manipulation to be optimised for carcass specifications and production efficiency.

References


