

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 affects 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and sheep-meat production systems are faced with the challenge that the traditional goal of **maximising** output has been replaced by a goal of optimising utilisation of inputs and maximising efficiency.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.

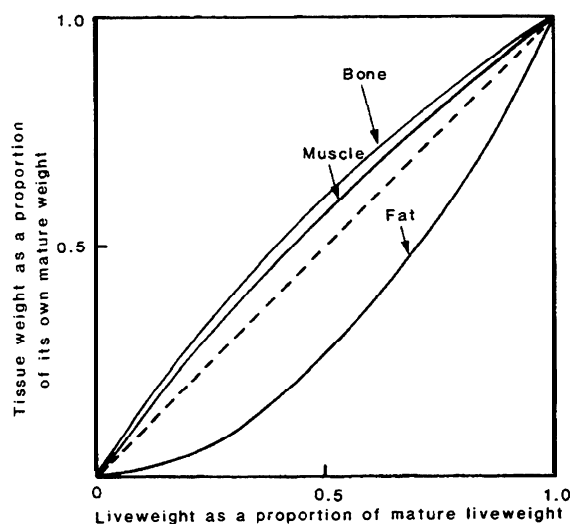


Figure 1 Tissue deposition patterns as a function of maturity. (Source: Butterfield, 1988).

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 animals’ 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).

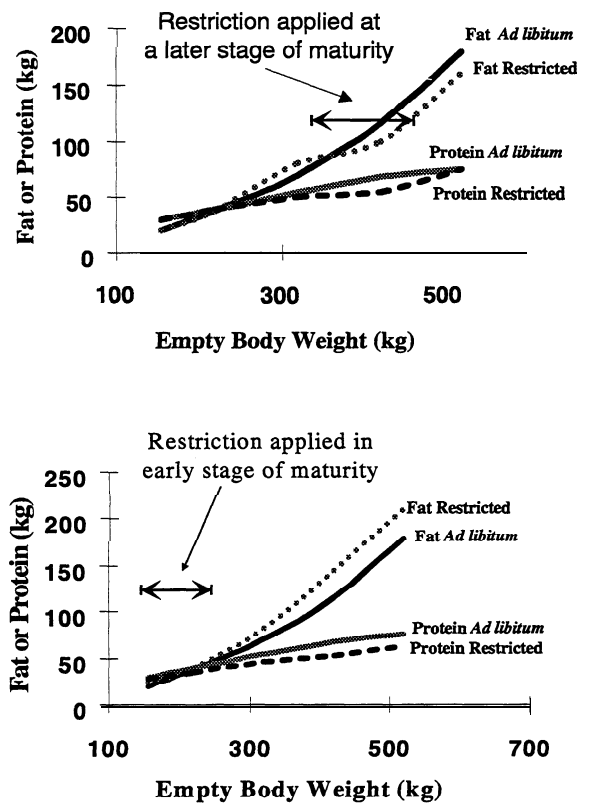


Figure 2 Interaction between feed restriction and stage of maturity on body composition. Restriction at an early stage of maturity will result in animals being assessed as fatter at slaughter. Restriction at a later stage of maturity will result in animals being assessed as leaner at slaughter (Source: Oddy 1997a).

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 Ørskov, 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 than well grown control animals (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 stasis

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 Slezacek, 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 effects 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.

Weight loss

A number of studies have examined the potential of a short term weight loss period as a mechanism of reducing fat prior to slaughter (Hodge and Star, 1984; Kirton *et al.* 1995). There appears to be two phases of tissue mobilisation for immature animals that are forced to lose weight due to a severe feed restriction. The initial phase of weight loss involves mobilisation of lean tissue, initially from a reduction in the size of the visceral organs and the digestive tract, and subsequently a loss of muscle tissue from the carcass (Meyer and Clawson, 1964; Drew and Reid, 1975; Winter *et al.* 1976; Thorton *et al.* 1979; Searle *et al.* 1979; Butler-Hogg, 1984; Ryan *et al.* 1993b). There is a reduction in carcass fat (Berg and Butterfield, 1976), although the extent of this loss varies with the physiological state and the sex of the animal. Pregnancy increases the rate of carcass fat loss (Pettersson *et al.* 1994) and males tend to lose at a faster rate than females (Ball, 1996).

As weight loss progresses through the second stage, the rate of loss of lean from the viscera and carcass declines and the rate at which fat from the carcass depots is mobilised increases (Drew and Reid, 1975; Aziz *et al.* 1992). During this phase there is a

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; Greef *et al.* 1986b; Ryan, 1990; Drouillard *et al.* 199 1 a,b; Iason and Mantecom, 1993).

Fox *et al.* (1972), Rompalaet *al.* (1985) and Wright and Russel (199 1) 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 visceral 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 Kiteessa, 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 Greef *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 Slezacek, 1976; Butler-Hogg, 1984; Wright and Russel, 199 1; 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; Freetly, 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 Tyrrell, 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_d 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 realimentation 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 (ME_m)

There is a clear response of estimates for ME_m 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 liveweight 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

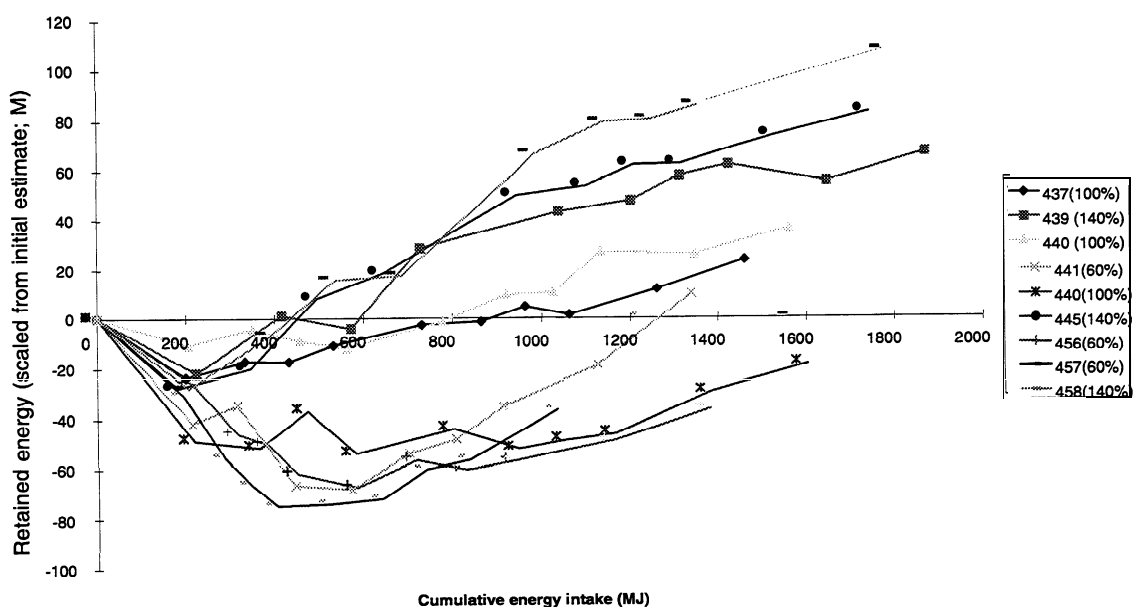


Figure 3 Retained energy as a function of cumulative energy intake for immature ewes of three growth paths, being 140%, 100% and 60% of maintenance. The individual animal responses are identified (Source Ball, 1996).

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 (Brody 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_m 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;

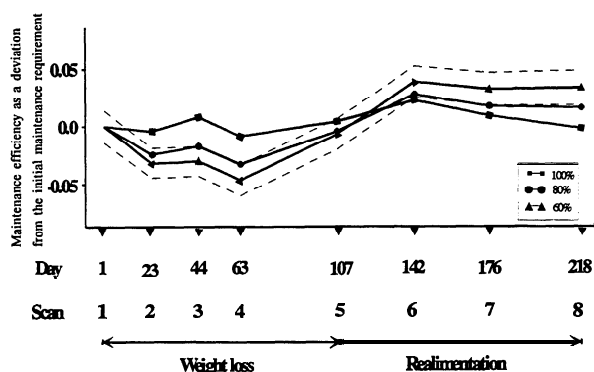


Figure 4 Changes in maintenance efficiency relative to the initial estimate obtained at the end of a six week maintenance feeding period (MJ ME required to maintain a kg of empty body weight per day, ME/kg) as a function of time for 60, 80 and 100% of maintenance during the restriction and realimentation 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; Gingsens *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 (k_m) 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.

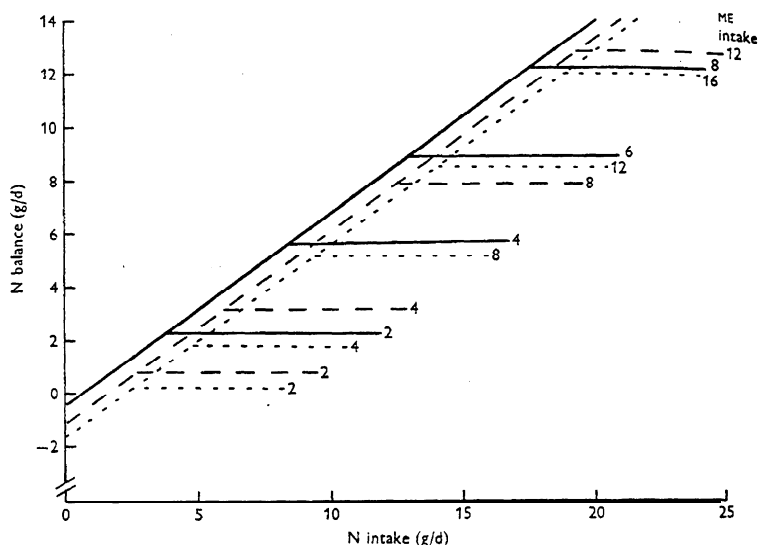


Figure 5 Fitted relationship between nitrogen balance and N intake for liquid-fed lambs differing in liveweight. (— 5 kg, -- 15 kg and -·-·- 25 kg) and metabolisable energy intake (ME; MJ/day). [Source: Black and Griffiths, 1975].

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

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).

Fat Depot	Control	Calcium OH	Oil	Oil+CalciumOH	SE
Number	29	30	30	30	
12/13 th Rib (mm; change in finishing period)	6.0	4.7	5.0	6.0	0.57
L.Dorsi Fat% (wet basis)	4.5	4.0	4.6	4.4	0.23

Control : Feedlot diet containing 10% milled roughage, 75% rolled barley grain, 8% molasses / mineral vitamin mix, 5% Cottonseed meal and 1.2% CaCO₃

Calcium OH: Control diet, with CaCO₃ replaced by Ca(OH)₂

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

Oil + Calcium OH: Oil diet with CaCO₃ replaced by Ca(OH)₂

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 **overfat** 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

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 Pethick 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 diffusable at least into muscle (see Pethick 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 (Ørskov *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.* (1991 a) tested the effect of a reduction in the both the quality and quantity of feed on compensatory growth. They showed that lambs that had restricted protein intake lost considerable amounts of carcass muscle, whilst lambs that had restricted energy intake, but had adequate amounts of dietary protein, were able to maintain carcass muscle. In that experiment, and that of Fattet *et al.* (1984), energy-restricted lambs mobilised carcass 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.* (1991 b) 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_m during the subsequent realimentation period. Steers that were fed a concentrate diet at restricted levels (CL) had a 7% lower ME_m 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_m 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_m 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.* 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'Donovan, 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 Schadereit *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

- Abdalla, H. O., Fox, D. G and Thonney, M. L. (1988). Compensatory gain by Holstein calves after underfeeding protein. *Journal of Animal Science* **66**, 2687-2695.
- Afonso, J.J. and Thompson, J.M. (1996). Changes in body composition of sheep selected for high and low **backfat** thickness during periods of *ad libitum* and maintenance feeding. *Animal Science* **63**, 395-406.
- Andrews, R.P and Ørskov, E.R. (1970). The nutrition of the early weaned lamb. 2. The effect of dietary protein concentration, feeding level and sex on body composition at *two* live weights. *Journal of Agricultural Science (Cambridge)* **75**, 19-26.
- Aziz, N. N. and Murray, D. M. (1987). The effect of weight stasis on the chemical composition of Merino **wethers**. In: *Herbivore Nutrition Research*, Ed. M. Rose *Australasian Association of Animal Production* pp. 155-156
- Aziz, N. N., Murray, D. M. and Ball, R. O. (1992). The effect of live weight gain and live weight loss on body composition of merino **wethers**: Dissected muscle, fat and bone. *Journal of Animal Science* **70**, 18 19-1828.
- Baker, R. D., Young, N. E. and Laws, J. A. (1985). Changes in the body composition of cattle exhibiting compensatory growth and the modifying effects of grazing management. *Animal Production* **41**, 309-321.
- Baldwin, R. L. (1995). *Modeling ruminant digestion and metabolism*, 1st Edition. Chapman and Hall: London. pp. 577.
- Ball, A. J. and Thompson, J. M. (1995). The effect of selection for differences in ultrasonic **backfat** depth on the feed utilization for maintenance and biological efficiency in sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* **11**, 403-407.
- Ball, A.J. (1996). Changes in body composition and maintenance efficiency during periods of restricted and maintenance feeding in immature and mature sheep. Ph.D. Thesis. University of New England: Armidale. pp 233.
- Ball, A.J., Thompson, J.M. Alston, C.L. Blakely, A.R. and Hinch, GN. (1997). Changes in maintenance efficiency of mature sheep fed at different levels of feed intake. *Livestock Production Science (in press)*.
- Ball, A.J., Thompson, J.M. and Pleasants, A.B. (1996). Seasonal changes in body composition of growing Merino sheep. *Livestock Production Science*. **46**, 173-180.
- Bass, J. J., Butler-Hogg, B. W. and Kirton, A. H. (1990). Practical methods of controlling fatness in farm animals. In: *Reducing fat in farm animals*. (Eds. J. D. Wood and A. V. Fisher). Elsevier Applied Science: Amsterdam.
- Bell, A.K. and Bower, S.M. (1990). Effect of a cottonseed meal and barley straw diet on the carcass quality of prime lambs. *Proceedings of the Australian Society of Animal Production* **18**, 455.

- Berg, R. T. and Butterfield, R. M. (1976). *New concepts in cattle growth*. Sydney University Press: Sydney. pp. 240.
- Birkelo, C. P. (1995). Specification of energy requirements to optimise production efficiency in beef cattle: Factors affecting energy utilisation. In: *Beef Cattle Energetics Workshop*. Denver WRCC-92. pp. 1-26.
- Black, J. L. (1974). Manipulation of body composition through nutrition. *Proceedings of the Australian Society Animal Production* **10**, 2 1 1-2 18.
- Black, J.L. and Griffiths, D.A. (1975). Effects of live weight and energy intake on nitrogen balance and total N requirement of lambs. *British Journal of Nutrition* **33**, 399-413.
- Black, J.L., Gill, M., Beever, D.E., Thomley, J.H.M. and Oldham, J.D. (1987). Simulation of the metabolism of absorbed energy-yielding nutrients in young sheep: efficiency of utilisation of acetate. *Journal of Nutrition*. **117**, 105-1 15.
- Blaxter, K.L. (1962). *The energy metabolism of ruminants*. Hutchinson and Company Ltd.: London.
- Boleman, S.L., Boleman, S.J., Bidner, T.D. Southern, L.L. Ward, T.L., Pontif, J.E. and Pike, M.M. (1995). Effect of Chromium picolinate on growth, body composition and tissue accretion rates in pigs. *Journal of Animal Science*. **73**, 2033-2042.
- Brody, S. (1945). *Bioenergetics and growth: With special reference to the efficiency complex in domestic animals*. Hafner Press: New York. pp. 1023.
- Burrin, D. G., Ferrell, C. L., Britton, R. A. and Bauer, M. (1990). Level of nutrition and visceral organ size and metabolic activity in sheep. *British Journal of Nutrition* **64**, 439-448.
- Burton, J. H., Anderson, M. and Reid, J. T. (1974). Some biological aspects of partial starvation. The effect of weight loss and regrowth on body composition in sheep. *British Journal of Nutrition* **32** 5 15.
- Butler-Hogg, B. W. (1984). Growth patterns in sheep: changes in the chemical composition of the empty body and its constituent parts during weight loss and compensatory growth. *Journal of Agricultural Science Cambridge* **103**, 17-24.
- Butler-Hogg, B. W. and Johnsson, I. D. (1986). Fat partitioning and tissue distribution in cross-bred ewes following different growth paths. *Animal Production* **42**, 65-72.
- Butler-Hogg, B. W. and Tulloh, N. M. (1982). Growth patterns in sheep: the effects of weight losses on compensatory growth and feed intake in Corridale sheep. *Journal of Agricultural Science* **99**, 64 1-649.
- Butterfield, R. M. (1966). The effect on nutritional stress and recovery on body composition of cattle. *Research in Veterinary Science* **7**, 168-179.
- Butterfield, R.M. (1988). *New concepts of sheep growth*. Griffin Press Limited: South Australia
- Campbell, R.G., Taverner, M.R. & Curic, D.M. (1985) The influence of feeding level on the protein requirement of pigs between 20 and 45 kg liveweight. *Animal Production* **40**, 489-496.
- Carstens, G. E. (1995). Compensatory growth in beef cattle. In: *Intake by feedlot cattle*. Oklahoma State University. pp. 942-970.
- Carstens, G. E., Johnson, D. E. and Ellenberger, M. A. (1989). Energy metabolism and composition of gain in beef steers exhibiting normal and compensatory growth. In: *Energy metabolism of farm animals*, pp. 13 1-134 (Eds. Y. V. D. Honing and W. H. Close Lunteren), Wageningen: Purdoc, Netherlands.
- Carstens, G. E., Johnson, D. E., Ellenberger, M. A. and Tatum, J. D. (199 1). Physical and chemical components of the empty body during compensatory growth in beef steers. *Journal of Animal Science* **69**, 325 1-3264.
- Chowdhury, S. A., Hovell, F. D. D., Orskov, E. R., Scaife, J. R., Mollison, G. and Bogoro, S. (1995). Protein utilisation during energy undernutrition in sheep sustained on intragastric infusion: effect of changing energy supply on protein utilisation. *Small Ruminant Research* **18**, 2 19-226.
- Cook, L.J. and Scott, T. W. (1970). Protection of dietary poly-unsaturated fatty acids from ruminal microbiological hydrogenation. *Proceedings of the Australian Biochemical Society* **3**, 93.
- DiCostanzo, A., Meiske, J. C. and Plegge, S. D. (1991). Characterisation of energetically efficient and inefficient beef cows. *Journal of Animal Science* **69**, 1337-1348.
- Dove, H. Pearce, G.R. and Tribe, D.E. (1977 a) Utilization of amino acids by preruminant lambs. I The effect of alterations in total essential amino acid intake at constant nitrogen intake. *Australian Journal of Agricultural Research*. **28**, 9 17-32.
- Dove, H. Pearce, GR. and Tribe, D.E. (1977 b) Utilization of amino acids by preruminant lambs. II. The effects of independent alteration in total nitrogen and total essential amino acid intake. *Australian Journal of Agricultural Research* **28**, 933-946.
- Drennan, M.J. (1979). Compensatory growth in cattle. Influence of feeding level during the first winter (9-14 months) on subsequent performance and carcass composition. *Irish Journal of Agriculture* **18**, 13 1-143.
- Drew, K. R and Reid, J. T. (1975). Compensatory growth in immature sheep. I The effects of weight loss and realimentation on the whole body composition. *Journal of Agricultural Science* **85**, 193-204.
- Drouillard, J. S., Ferrell, C. L., Klopfenstein, T. J. and Britton, R. A. (199 1b). Compensatory growth following metabolisable protein or energy restrictions in beef steers. *Journal of Animal Science* **69**, 811-818.

- Drouillard, J. S., Klopfenstein, T. J., Britton, R. A., Bauer, M. L., Gramlich, S. M., Wester, T. J. and Ferrell, C. L. (1991a). Growth, body composition, and visceral organ mass and metabolism in lambs during and after metabolizable protein or net energy restrictions. *Journal of Animal Science* **69**, 3357–3375.
- Dunkin, A. C., Black, J. L. & James, K. J. (1984). Relationship between energy intake and nitrogen retention in the finisher pig. Proceedings of the Australian Society Animal Production. 15: 672.
- Edwards, S. R., Neutze, S. A., Oddy, V. H., Warren, H. M. and Nandra, K. S. (1989a). Escape protein supplementation of lambs. 1. Differential response in gastrointestinal tract and contents. *Proceedings of the Nutrition Society of Australia* **14**, 13 7.
- Edwards, S. R., Oddy, V. H., Neutze, S. A., Riley, K. D. and Jones, A. W. (1989b). Escape protein supplementation of lambs. 2. Differential response in organ weight. *Proceedings of the Nutrition Society of Australia* **14**, 138.
- Edwards, S. R., Oddy, V. H., Speck, P. A., Warren, H. M. and Riley, K. D. (1990). Nutrient supply and endocrine control of muscle growth in lambs. *Proceedings of the Australian Society of Animal Production*. **18**, 474.
- Fattet, I., Hovell, F. D. D., Orskov, E. R., Kyle, D. J., Pennie, K. and Smart, R. I. (1984). Undernutrition in sheep. The effect of supplementation with protein on protein accretion. *British Journal of Nutrition* **52**, 561-574.
- Ferguson, K. A., Hemsley, J. A. & Reis, P. J. (1967). *Australian Journal of Science*. **30**, 2 15.
- Ferrell, C. L. (1988). Contribution of visceral organs to animal energy expenditure. *Journal of Animal Science* **66**(Suppl 3), 23-34.
- Ferrell, C. L. (1995). Some limitations to current approaches to predict energy requirements of feedlot cattle and beef cows. In: *Positionpapers for workshop on Beef cattle energetics*. Denver Colorado WRCC-92 pp. 27-36.
- Ferrell, C. L. and Jenkins, T. G. (1985). Cow type and the nutritional environment: Nutritional aspects. *Journal of Animal Science* **61**, 725–74 1.
- Ferrell, C. L., Crouse, J. D., Field, R. A. and Chant, J. L. (1979). Effects of sex, diet and stage of growth upon energy utilisation by lambs. *Journal of Animal Science* **49**(3), 790–80 1.
- Ferrell, C. L., Nienabar, J. A. and Koong, L. J. (1983). Effects of previous nutrition on maintenance requirements and efficiency of feed utilisation of growing lambs. *Journal of Animal Science* **57** (Suppl 1), 431–432.
- Fluharty, E. L. and McClure, K. E. (1997). Effects of dietary energy intake and protein concentration on performance and visceral organ mass in lambs. *Journal of Animal Science* **75**, 604–610.
- Foot, J. Z. and Tulloh, N. M. (1977). Effects of two paths of live weight change on the efficiency of feed use and on body composition of Angus steers. *Journal of Agricultural Science* **88**, 135–142.
- Fourie, P. D., Kirton, A. H. and Jury, K. E. (1970). Growth and development of sheep. II Effect of breed and sex on the growth and carcass composition of the Southdown and Romney and their crosses. *New Zealand Journal of Agricultural Research* **13**, 75370.
- Fox, D. G., Johnson, R. R., Preston, R. L., Dockerty, T. R. and Klosterman, E. W. (1972). Protein and energy utilisation during compensatory growth in beef cattle. *Journal of Animal Science* **34**, 3 1 O-3 17.
- Garlick, P. J. and Grant, I. (1988). Amino acid infusion increases the sensitivity of muscle protein synthesis in-vivo to insulin. *Biochemistry Journal*. **254**, 579-584
- Gerritts, W. J. J., Tolman, G. H., Schrama, J. W., Tamminga, S., Bosch, M. W. and Versteegen, M. W. A. (1996). Effect of protein and protein-free energy intake on protein and fat deposition rates in preruminant calves at 80 and 240 kg liveweight. *Journal of Animal Science*. **74**, 2129–2139
- Gingens, M., Bickel, H. and Schurch, A. (1980). Efficiency of energy utilisation in undernourished and realimentated sheep. *Livestock Production Science* **7**, 465–471.
- Girard, J. (1996). Nutrient regulation of gene expression. *Proceedings of the American Society of Animal Science and Western Section meeting*. South Dakota.
- Greff, J. C., Meissner, H. H., Roux, C. Z. and Rensburg, R. J. J. v. (1986b). The effect of compensatory growth on body composition in sheep. *South African Journal of Animal Science* **16**(4), 162-168.
- Greff, J. C., Meissner, H. H., Roux, C. Z. and Rensburg, R. J. J. v. (1986a). The effect of compensatory growth on feed intake, growth rate and efficiency of feed utilisation in sheep. *South African Journal of Animal Science* **16**, 155-1 6 1.
- Hayden, J. M., J. E. and Collier, R. J. (1993). Plasma growth hormone, insulin-like growth factor, insulin and thyroid hormone association with body protein and fat accretion in steers undergoing compensatory gain after dietary energy restriction. *Journal of Animal Science* **71**, 3327–3338.
- Hays, C. L., Davenport, G. M., Osborn, T. G. and Mulvaney, D. R. (1995). Effect of dietary protein and Estradiol-17B on growth and insulin-like growth factor 1 in cattle during realimentation. *Journal of Animal Science* **73**, 589–597.
- Hegarty, R. S., Oddy, V. H., Smith R. L. and Neutze, S. A. (1994). Growth path affects the carcass composition of lambs. *Proceedings of the Australian Society of Animal Production* **20**, 360
- Hicks, R. B., Owens, F. N., Gill, D. R., Martin, J. J. and Strasia, C. A. (1990). Effects of controlled feed intake on performance and carcass characteristics of feedlot steers and heifers. *Journal of Animal Science* **68**, 233-244.
- Hodge, R. W. and Star, M. (1984). Comparison of the fat status of lambs during continuous growth and following nutritional restriction and subsequent re-alimentation. *Australian Journal of Experimental Agriculture and Animal Husbandry* **24**, 150–155.

- Huxley, J. S. (1932). Problems of relative growth. 1st Edition *Methuen* London.
- Iason, G. R. and Mantecom, A. R. (1993). The effects of dietary protein level during food restriction on carcass and non carcass components, digestibility and subsequent compensatory growth in lambs. *Animal Production* **56**, 93–100.
- Johnson, C. L., Johnson, D. E. and Rumpler, W. V. (1985). Source and level of alimention effects on visceral organ mass of fat steers. In: *Energy metabolism of farm animals*, Eds. P. W. Moe, H. F. Tyrrell and P. J. Reynolds *Airlie, Virginia Rowman and Littlefield* pp. 50–53
- Johnson, D. E., Johnson, K. A. and Baldwin, R. L. (1990). Changes in liver and gastrointestinal tract energy demands in response to physiological workload in ruminants. *Journal of Nutrition* **120**, 649–655.
- Johnsson, I. D., Hart, I. C. and Butler-Hogg, B. W. (1985). The effects of exogenous bovine growth hormone and bromocriptine on growth, body development, fleece weight and plasma concentrations of growth hormone, insulin and prolactin in female lambs. *Animal Production* **41**, 207–217.
- Jopson, N. B., Kolstad, K. and Vangen, O. (1994). In search of genetic variation in biological components of efficiency: Examples from various species. *Proceedings of the European Association of Animal Production*. p. 8
- Kabbali, A., Johnson, W. L., Johnson, D. W., Goodrich, R. D. and Allen, C. E. (1992). Effects of compensatory growth on some body component weights and on carcass and noncarcass composition of growing lambs. *Journal of Animal Science* **70**, 2852–2858.
- Keenan, D. M., McManus, W. R. and Freer, M. (1969). Changes in the body composition and efficiency of mature sheep during loss and regain of liveweight. *Journal of Agricultural Science* **72**, 139–147.
- Kellaway, R. C. (1973). The effects of plane of nutrition, genotype and sex on growth, body composition and wool production in grazing sheep. *Journal of Agricultural Science* **80**, 17–27.
- Kempton, T.J. (1979) Protein to energy ratio of absorbed nutrients in relation to wool growth. In: *Physiological & environmental limitations to wool growth* (Eds. J.L. Black and P.J. Reis) University of New England Publishing Unit: Armidale, Australia.
- Kirton, A. H., Bennett, G. L., Dobbie, J. L., Mercer, G. J. K. and Duganzich, D. M. (1995). Effect of sire breed (Southdown, Suffolk), sex and growth path on carcass composition of crossbred lambs. *New Zealand Journal of Agricultural Research* **38**, 105–114.
- Kitchalong, L., Fernandez, J.M., Bunting, L.D. Southern, J.L. and Bidner, T.D. (1995). Influence of Chromium tripicolinate on glucose metabolism and nutrient partitioning in lambs. *Journal of Animal Science* **73**, 2694–2705.
- Klosterman, E. W., Sanford, L. G. and Parker, C. F. (1968). Effect of cow size and condition and ration protein content upon maintenance requirements in mature beef cows. *Journal of Animal Science* **27**, 242–246.
- Koong, L. J., Ferrell, C. L. and Nienaber, J. A. (1982). Effects of plane of nutrition on organ size and fasting heat production in swine and sheep. In: *Energy metabolism of farm animals*, (Eds. A. Ekem and F. Sundstol). Lillehammer: The Agricultural University of Norway pp. 244–249.
- Koong, L. J., Ferrell, C. L. and Nienaber, J. A. (1985). Assessment of the interrelationships among levels of intake and production, organ size and fasting heat production in growing animals. *Journal of Nutrition* **115**, 1383–1390.
- Kouakou, B. Goetsch, A.L. Patil, A.R. Galloway, D.L. and Park, K.K. (1997). Visceral organ mass in wethers consuming diets with different forages and grain levels. *Livestock Production Science*. **47**, 125–137.
- Ledger, H. P. and Sayers, A. R. (1977). The utilization of dietary energy by steers during periods of restricted food intake and subsequent realimentation. 1. The effect of time on the maintenance requirements of steers held at constant live weights. *Journal of Agricultural Science* **88**, 11–26.
- Lines, E.W. and Peirce, A. W. (1931). The basal (standard) metabolism of the Australia merino sheep. CSIRO Bulletin. No 55.
- Little, D. A. and Sandland, R. L. (1975). Studies on the distribution of body fat in sheep during continuous growth and following nutritional restriction and rehabilitation. *Australian Journal of Agricultural Research* **26**, 363–374.
- Marais, P. G., Merwe, H. J. v. d. and Toit, J. E. J. d. (1991). The effect of compensatory growth on feed intake, growth rate, body composition and efficiency of feed utilisation in Dorper sheep. *South African Journal of Animal Science* **21**(2), 80–88.
- Marston, H. R. (1948). Energy transactions in sheep. 1. The basal heat production and heat increment. *Australian Journal of Scientific Research*. **1**, 93–129.
- Mathison, G. W. and Engstrom, D. F. (1995). *Ad libitum* versus restricted feeding of barley and corn based feedlot diets. *Canadian Journal of Animal Science* **75**, 637–640.
- McCracken, K. J. (1992). Merits of empirical and mechanistic approaches to the study of energy metabolism. *Proceedings of the Nutrition Society* **51**, 125–133.
- Meyer, J. H. and Clawson, W. J. (1964). Undernutrition and subsequent realimentation in rats and sheep. *Journal of Animal Science* **23**, 214–224.
- Mooney, K.W. and Cromwell, G.L. (1995). Effects of dietary Chromium picolinate supplementation on growth, carcass characteristics and accretion rates of carcass tissues in growing-finishing swine. *Journal of Animal Science*. **73**, 3351–3357.
- Morgan, J. A. and Owen, J. B. (1973). The nutrition of artificially reared lambs. 3. The effect of sex on the performance and carcass composition of lambs subjected to different nutritional regimes. *Animal Production* **16**, 49–57.

- Muir, P.D. Smith, N.B. and McCall, D.G. (1997). Live weight gains and feed intake of **Angus** and Simmental steers when undergoing compensatory growth at heavy weights. (In this volume).
- Murphy, T. A. and Loerch, S. C. (1994). Effects of restricted feeding of growing steers on performance, carcass characteristics and composition. *Journal of Animal Science*. **72**, 2497–2507.
- Murray, D. M. and Slezacek, O. (1976). Growth rate and its effect on empty body weight, carcass weight and dissected carcass composition of sheep. *Journal of Agricultural Science Cambridge* **87**, 171–179.
- Murray, D. M. and Slezacek, O. (1988a). The effect of weight stasis on the dissected carcass composition of crossbred sheep. *Australian Journal of Agricultural Research*. **39**, 645–5 1.
- Murray, D. M. and Slezacek, O. (1988b). The effect of weight stasis on the non-carcass components of crossbred sheep. *Australian Journal of Agricultural Research* **39**, 653–658.
- Murray, D. M., Tulloh, N. M. and Winter, W. H. (1974). Effects of three different growth rates on empty body weight, carcass weight and dissected carcass composition of cattle. *Journal of Agricultural Science* **82**, 535–547.
- Newsholme, E.A. and Start, C. (1973). Regulation in metabolism. John Wiley and Sons: London.
- Nicol, A. and Kitessa, S. (1994). Influence of compensatory growth on production systems in New Zealand. In: *Growth and Development Workshop*, Armidale Meat Quality CRC.
- Norton, B.W. Jagusch, K.T. and Walker, D.M. (1970). Body composition studies with milk fed lambs. 3. The effect of protein and energy intake on the composition of the liveweight gain. *Journal of Agricultural Science* **75**, 297–292.
- Notter, D. R., Ferrell, C. L. and Field, R. A. (1983). Effects of breed and intake level on allometric growth patterns in ram lambs. *Journal of Animal Science* **56**(2), 380-39 1.
- NRC (1996). *Nutrient requirements of beef cattle*. Seventh revised edition. 7th National Academy of Sciences: Washington D.C. pp. 242.
- Oddy, V.H. (1997a). The impact of growth in early life on subsequent growth and body composition of cattle. *Proceedings of the Armidale Feeder Steer School*. **27-32**
- Oddy, V.H. (1997b). Efficiency and compensatory growth. The Growth and Development Workshop. Meat Quality CRC. University of New England
- Oddy, V.H., Ball, A.J. and Pleasants, A.B. (1997a). Understanding body composition and efficiency in ruminants – a non-linear approach. (These proceedings).
- Oddy, V.H., Edwards, S.R., Warren, H.M., Speck, P.A., Nicholls, P. J. and Neutze, S.A. (1997b). Interrelationships between amino acid and glucose metabolism in lambs of different dietary history supplemented with rumen escape protein. *Journal of Agricultural Science Cambridge*. **128**: 105–1 16
- Oddy, V.H., Hegarty, R.S. Smith, R.L. and Neutze, S.A. (1994). Effects of growth path, feed intake and rumen escape protein on the rates of gain of carcass components in lambs. *Proceedings of the Australian Society of Animal Production*. **20**, 36 1
- O'Donovan, P. B. (1984). Compensatory gain in cattle and sheep. *Nutrition Abstracts and Reviews. Series B*. **54**: 390–410.
- Olthoff, J. C. and Dickerson, G. E. (1989). Relationship between fasting heat production, body composition and tissue distribution, in mature ewes from seven breeds. *Journal of Animal Science* **67**: 2576-2588.
- Ørskov, E.R. Grubb, D.A., Smith, J.S. Webster, A.S.F. and Corrigan, W. (1979). Efficiency of utilization of volatile fatty acids for maintenance and energy retention in sheep. *British Journal of Nutrition*. **41**: 1429-1435
- Ørskov, E.R. McDonald, I., Grubb, D.A. and Pennie, K. (1976). The nutrition of the early weaned lamb. 4. Effects on growth rate, food utilisation and body composition of changing from low to high protein diet. *Journal of Agricultural Science*. Cambridge **86**: 411–423
- Ortigue, I. and Durand, D. (1995). Adaptation of energy metabolism to undernutrition in ewes. Contribution of portal-drained viscera, liver and hindquarters. *British Journal of Nutrition* **73**: 209-222.
- Ortigue, I., Petit, M. and Agabriel, J. (1993). Influence of body composition on maintenance energy requirements of Charolais cows. *Animal Production* **57**: 47-53.
- Owens, F. N., Dubeski, P. and Hanson, C. F. (1993). Factors that alter the growth and development of ruminants. *Journal of Animal Science* **71**: 3 138-3 150.
- Palmquist, D.L. and Jenkins, T.C. (1982). Calcium soaps as a fat supplement in dairy cattle feeding. In *Proceedings of the 12th World Congress on diseases of cattle*. Eds M.H. Lucas, C. Richardson and S.R. Bicknell. Utrecht. Pp 477–481
- Pethick, D.W. and Lindsay, D.B. (1982). Acetate metabolism in lactating sheep. *British Journal of Nutrition*. **48**: 3 19-328
- Pethick, D.W. and Veman, B. (1984). The effect of acetate on the utilisation of glucose by skeletal muscle of the sheep hind limb. *Canadian Journal of Animal Science* (Suppl) **64**: 291-292
- Petterson, J.A., Slepetic, R. Ehrhardt, R.A., Dunshea, F.R. and Bell, A. W. (1994). Pregnancy but not moderate undernutrition attenuates insulin suppression of fat mobilisation in sheep. *Journal of Nutrition*. **124**: 243 1-2436

- Reynolds, C.K. and Tyrrell, H.F. (1991). Effects of diet composition and intake on visceral insulin and glucagon metabolism in cattle. In: *Energy Metabolism of Farm Animals*. Eds. C. Wenk and M. Boessinger. Pp 12-15 EAAP. Zurich Switzerland.
- Robinson, P. (1948). The effect of supermaintenance and submaintenance diets on mature Border Leicester-Cheviot Ewes. *Journal of Agricultural Science*. :**38**, 345-353.
- Rompala, R. E., Jones, S. D. M., Buchanan-Smith, J. G and Bayley, H. S. (1985). Feedlot performance and the composition of gain in late-maturing steers exhibiting normal and compensatory growth. *Journal of Animal Science* **61**(3): 637-646.
- Russel, A. J. F., Gunn, R. G and Doney, J. M. (1968). Components of weight loss in pregnant hill ewes during winter. *Animal Production* **10**(1): 43-5 1.
- Ryan, W. J. (1990). Compensatory growth in cattle and sheep. *Nutrition Abstracts and Reviews*. **19**: 653-664.
- Ryan, W. J. and Williams, I. H. (1989). Changes in the body composition of sheep fed a maintenance level. In: *Proceedings of the Australian Society of Animal Production*, 435-347.
- Ryan, W. J., Williams, I. H. and Moir, R. J. (1993a). Compensatory growth in sheep and cattle. I Growth pattern and feed intake. *Australian Journal of Agricultural Research*. **44**: 1609-1 62 1.
- Ryan, W. J., Williams, I. H. and Moir, R. J. (1993b). Compensatory growth in sheep and cattle. II. Changes in body composition and tissue weights. *Australian Journal of Agricultural Research*. **44**: 1623-1633.
- Sainz, R. D. (1995a). Why does feed restriction improve efficiency. In: *Intake by feedlot cattle.*, Ed. F. Owens Oklahoma Agricultural Experimental Station Oklahoma State University pp. 175-180
- Sainz, R. D., Torre, F. D. I. and Oltjen, J. W. (1995). Compensatory growth and carcass quality in growth-restricted and refed beef steers. *Journal of Animal Science* **73**: 2971-2979.
- Schadereit, R., Klein, M., Rehfeldt, C., Krienbring, F. and Krawielitzki, K. (1995). Influence of nutrient restriction and realimentation on protein and energy metabolism, organ weights, and muscle structure in growing rats. *Journal of American Physiology and Animal Nutrition* **74**: 253-268.
- Searle, T. W. and Graham, N. M. (1975). Studies of weaner sheep during and after a period of weight stasis. II Body composition. *Australian Journal of Agricultural Research*. **26**, 355-361.
- Searle, T. W., Graham, N. M. and E. Smith (1979). Studies of weaned lambs before, during and after a period of weight loss. II Body composition. *Australian Journal of Agricultural Research* **30**, 525-53 1.
- Seebeck, R. M. (1967). Developmental growth and body weight loss of cattle. 1. Experimental design, body weight growth, and the effects of developmental growth and body weight loss on dressed carcass and offal. *Australian Journal of Agricultural Research* **18**, 1015-1031.
- Seebeck, R. M. and Tulloh, N. M. (1968). Developmental growth and body weight loss of cattle. II. Dissected components of the commercially dressed and jointed carcass. *Australian Journal of Agricultural Research*. **19**.
- Solis, J. C., F.M.Byers, G.T.Schelling, Long, C. R. and Greene, L. W. (1988). Maintenance requirements and energetic efficiency of cows of different breed types. *Journal of Animal Science* **66**, 764-773.
- Standing Committee on Agriculture (1990). Feeding standards for Australian livestock. In: *Ruminants*. (Eds. GE. Robards and J.C. Radcliffe), Australian Agricultural Council Ruminants Sub-committee. CSIRO.
- Taylor, S. C. S., Turner, H. G and Young, G. B. (1981). Genetic control of equilibrium maintenance efficiency in cattle. *Animal Production* **33**, 179-194.
- Tess, M. W., Dickerson, G. E., Nienaber, J. A. and Ferrell, C. L. (1984). The effects of body composition on fasting heat production in pigs. *Journal of Animal Science* **58**(1), 99-1 10.
- Thompson, J. M., Butterfield, R. M. and Perry, D. (1985b). Food intake, growth and body composition in Australian Merino sheep selected for high and low weaning weight. 2. Chemical and dissectible body composition. *Animal Production* **40**, 7 1-84.
- Thornton, R. F., Hood, R. L., Jones, P. N. and Re, V. M. (1979). Compensatory growth in sheep. *Australian Journal of Agricultural Research*. **30**, 13 5-1 5 1.
- Tudor, G.D. and O'Rourke, P.F. (1980). The effect of pre and post natal nutrition on the growth of beef cattle. 2. The effect of severe restriction in early post natal life on growth and feed efficiency during recovery. *Australian Journal of Agricultural Research*. **3 1**, 179-189.
- Tulloh, N. M. (1963). The carcass compositions of sheep, cattle and pigs as functions of body weight. In: *Carcass composition and appraisal of meat animals*, (Ed. D. E. Tribe), CSIRO: Melbourne Australia.
- Turgeon, O. A., Brink, D. R., Bartle, S. J., Klopfenstein, T. J. and Ferrell, C. L. (1986). Effects of growth rate and compensatory growth on body composition in lambs. *Journal of Animal Science* **63**, 770780.
- Turner, H. G and Taylor, C. S. (1983). Dynamic factors in models of energy utilisation with particular reference to maintenance requirement of cattle. *World Review of Nutrition and Dietetics* **42**, 135-190.
- Van Houtert, M. (1991). Nutritional manipulation of tissue growth in roughage-fed lambs. Ph.D Thesis University of New England: Armidale, Australia pp. 143.
- Vipond, J.E., King, M.E., Ørskov, E.R. and Wetherill, G.Z. (1989). Effects of fish-meal supplementation on performance of overfat lambs fed on barley straw to reduce carcass fatness. *Animal Production*. **48**, 131-138
- Webster, A. J. F. (1980). The energetic efficiency of growth. *Livestock Production Science* **7**, 243-252.

- Wester, T. J., Britton, R. A., Klopfenstein, T. J., Ham, G. A., Hickok, D. T. and Krehbiel, C. R. (1995). Differential effects of plane of protein and energy nutrition on visceral organs and hormones in lambs. *Journal of Animal Science* **73**, 1674–1688.
- Winter, W. H. (1971). A study of weight loss and compensatory growth in sheep. Ph.D Thesis University of Melbourne.
- Winter, W. H., Tulloh, N. M. and Murray, D. M. (1976). The effect of compensatory growth in sheep on empty body weight, carcass weight and the weights of some **offals**. *Journal of Agricultural Science* **87**, 433-441.
- Wright, I. A. and Russel, A. J. F. (1991). Changes in the body composition of beef cattle during compensatory growth. *Animal Production* **52**, 105-113.
- Yambayamba**, E. S. K., Price, M. A. and **Foxcroft**, G. R. (1996). Hormonal status, metabolic changes and resting metabolic rate in beef heifers undergoing compensatory growth. *Journal of Animal Science* **74**, 57-69.
- Zinn**, R.A. and Shen, Y. (1996). Interaction of dietary calcium and supplemental fat on digestive function and growth performance in **feedlot** steers. *Journal of Animal Science*. **74**, 2303–2309.