

## **Chapter 1**

### **General Introduction**

Sheep and cattle that are grown and maintained under grazing systems undergo large and continual fluctuations in liveweight, and in body reserves of fat and protein in response to the significant seasonal variations in feed availability and quality. The mechanisms that enable these animals to adapt to the fluctuating nutrient supply include alterations to the metabolic capacity and the energetic efficiency of maintenance of body tissues and specific priorities for tissue mobilisation and deposition. Through evolution some of these adaptive processes to a variable environment where feed supply has become limiting have become endogenous biological rhythms that exist independent of feeding levels.

Our present meat production systems are faced with the challenge that the primary goal for a successful producer has been changed by environmental pressures from a traditional approach of maximising output, to a situation where the efficiency of conversion of inputs to outputs is paramount. This focus on inputs to outputs is consistent with a ultimate goal of remaining viable and sustainable through time. As a result selection emphasis in recent times has included efficiency traits such as residual feed intake or net conversion efficiency into indices that previously contained growth rate, mature size and fertility. Producers have also been recently introduced to a market situation that demands consumer acceptability of the final product. Thus any improvements in feed efficiency have to be concurrent with maintaining other desirable traits such as fertility, maternal performance and carcass quality.

One of the most significant ways in which feed requirements can be reduced in a meat producing enterprise is to reduce the maintenance requirements of the individual animal and in particular the requirements of the mature breeding female (Thompson and Barlow, 1986). Several techniques for estimating maintenance requirements that have been developed rely on either measuring the heat production associated with essential

metabolic processes, by partial regressions of changes in energy in the body to energy consumed, or from long term relationships between equilibrium weight and feed intake (Webster, 1978; Turner and Taylor, 1983, Baldwin and Bywater, 1984). These techniques have shown that considerable variation in the maintenance requirements per unit of body weight exist between species (Brody, 1945, Klieber, 1975), within species and between breeds (Ferrell and Jenkins, 1985b; DiContanzo *et al.*, 1990; Birkelo *et al.*, 1991a; Jenkins and Ferrell, 1994), and between individuals within breeds (Taylor *et al.*, 1981; Carstens *et al.*, 1989; Jopson *et al.*, 1994; Arthur *et al.*, 1996).

The techniques used have also identified a number of factors that contribute to the variation that exists between animals. Differences in the proportions of fat and lean tissues within the body was one of these factors. Animals that were leaner as a result of selection for lean growth had higher maintenance requirements than animals that were proportionally fatter (Oltoff and Dickerson, 1989a,b; Rao and McCracken, 1991; Jopson *et al.*, 1994), which is primarily due to the higher energetic requirements of maintaining protein as compared to adipose tissue (Pullar and Webster, 1977). Although Ferrell and Jenkins (1995) stated that variation in body composition accounted for little of the variation in efficiency that was observed between growing steers. Recently Ball *et al.* (1995) and Kolstad and Vangen (1995) showed that adjustment for differences in the body composition removed a significant proportion of the variation that existed in maintenance requirements between animals. By adequately assessing the relationship between body components and energy expenditure, selection for “true” maintenance requirements will be possible (Enting, 1990).

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, 1985b; Burrin *et al.*, 1990; Freetly, 1995). A 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). A

metabolic lag in the reduction in the energy requirements, initially as a result of lower visceral organ weights, that occurs when animals are refed is thought to promote the acceleration of tissue deposition that is known as compensatory growth (O'Donovan, 1984; Ryan, 1990). Another important component of variation in energy expenditure are differences in thermoregulation and activity. Verstegen *et al.* (1982) indicated that differences in activity contributed to differences in energy requirements of feed restricted and normally fed pigs, whilst Luiting *et al.* (1994) showed that activity levels contributed to differences in residual feed intakes of laying hens.

A number of studies that are summarised in reviews of O'Donovan, (1984), Ryan, (1990) and Carstens, (1995) have examined the changes occur in animals that experience periods of interrupted growth followed by compensatory growth. These studies show that the severity of the restriction, the length of the restriction and the stage of maturity at which the restriction is enforced all contribute to differences in the final body composition of animals as they near either slaughter or mature weights. Butler-Hogg (1984) indicated that the body composition of the animal after a restriction will effect the proportion of tissues deposited during the compensatory phase. Palsson (1955) from a review of the data that described differences in body components in relationship to nutritional history concluded that for "*animals kept on a sub-maintenance ration, the different tissues and body regions that are utilised for the supply of energy and protein for the maintenance of life is the reverse order of their maturity i.e. fat followed by muscle and bone*"., although several studies have shown that sex, maturity and level of the restriction will effect the proportions of components lost (Black, 1974; Thorton, *et al.*, 1979). Clearly the priorities for tissue mobilisation during weight loss and tissue regain during realimentation need to be investigated within individual animals so that growth path manipulation may be optimised for carcass specifications and production efficiency.

This thesis examines the changes in body components that occur in mature sheep of two sexes from lines selected for differences in body composition during a period of weight loss in order to characterise the priorities for tissue mobilisation within individual animals when subjected to different levels of feed restriction. The thesis describes the

changes in body components that occur when sheep are fed at original levels for maintenance after the restriction in order to outline the true priorities that exist for tissue regain after weight loss by removing variations that are observed with *ad libitum* feeding in the compensatory phase. Implications on total body energetics as affected by sex and initial body energy reserves during weight loss and weight regain are discussed with particular emphasis placed on the requirements for maintenance and the concept of maintenance efficiency.

After identification of differences between sexes and severity of restriction in the first component of the thesis, attention was directed towards an understanding of the implications of differences in changes in body components between immature and mature sheep that are forced into an energy deficit during restricted feeding on total body energetics and the ability to recover when feeding levels are returned to that for original liveweight maintenance. The second component of the thesis examined the implications of increasing and decreasing feeding levels on equilibrium maintenance requirements to expand the concept of Taylor's diagonal (Parks, 1982) to production situations where feeding levels fluctuate rather than continually increasing for immature animals.

## Chapter 2

### Literature Review

#### 2.1 Maintenance efficiency

##### 2.1.1 Definition

Maintenance in the mature animal has been defined as the feed energy required for zero body weight change, or a zero body energy change (Turner and Taylor, 1983; Ferrell and Jenkins, 1985b). Whilst this is a relatively simple concept, it remains somewhat idealistic. Previous attempts to measure maintenance efficiency have been unable to reliably remove the confounding effects of changes in body composition and prior feeding levels (Taylor *et al.*, 1981; Ferrell and Jenkins, 1985b). It is inappropriate to apply the principal of maintenance at zero change in body weight and energy, to situations that are confounded by changes in body composition and weight associated with stage of maturity, physiological state, feeding levels and environment (Turner and Taylor, 1983; Koong *et al.*, 1985; Shuey *et al.*, 1993). These changes result in difficulties in partitioning energy requirements between “true” maintenance costs and those processes associated with production such as growth, pregnancy and lactation.

Regardless of the difficulties that are associated with measuring maintenance efficiency, indirect calculation of  $Me_m$  has widely occurred in an attempt to characterise those requirements associated with non-growth. Several studies have shown that those requirements for maintenance that have been estimated, contribute significantly to the overall costs in most ruminant production systems (Webster, 1979; Thompson and Barlow, 1986; Ferrell, 1988).

All systems that utilise metabolisable or net energy as the basic unit for the assessment of nutritional requirements for maintenance (ARC, 1980; SCA, 1990), are dependent on the basic assumption that a increment in energy intake is either transformed into the heat resulting from metabolic processes associated with vital functions or work, or

stored within body tissues or body products (Baldwin and Bywater, 1984). This partitioning of feed energy as described above is shown in Figure 2.1. The assumption that  $\Delta\text{MEI} = \Delta\text{RE} + \Delta\text{HE}$  where MEI is metabolisable energy intake, RE is retained energy and HE is heat energy, is robust and absolute. That is, energy received by the animal must either be retained within the tissues, or converted into heat energy by essential metabolic activities (Baldwin, 1995). However inaccuracies that exist in the measurement of both RE and HE results in error in assigning biological significance to the physiological and metabolic processes that underpin estimates for maintenance and growth (Baldwin and Bywater, 1984).

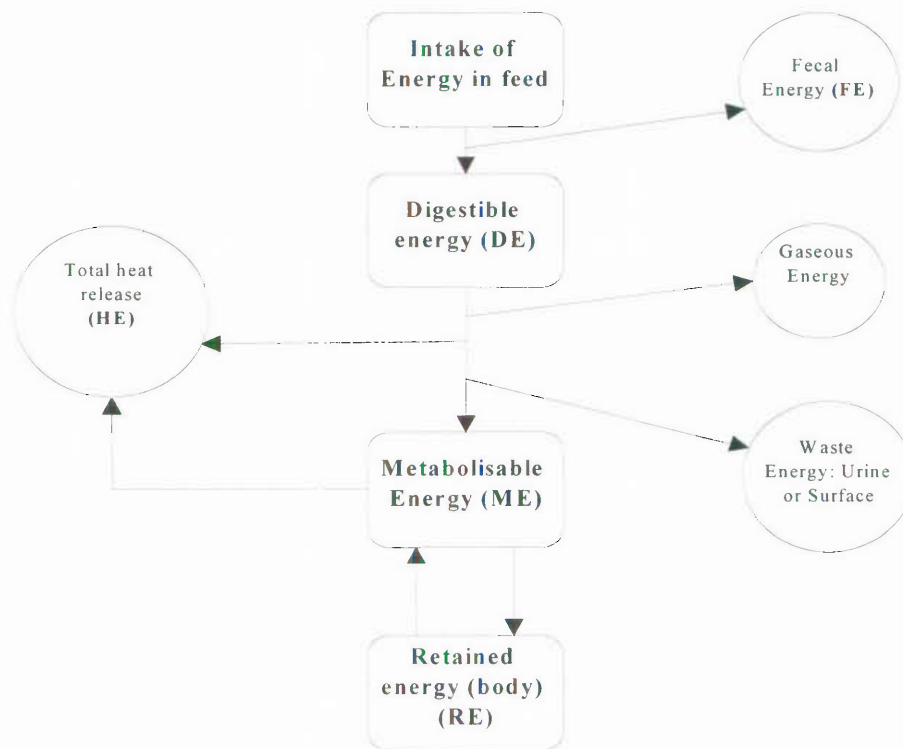


Figure 2.1 Partition of Feed energy in animals.

Source Baldwin and Bywater (1984).

### 2.1.2 Measurement of Maintenance Efficiency

There have been a variety of techniques used to estimate the component of total energy expenditure which is related to maintaining the body in an equilibrium state. These techniques include:-

- 1) estimates of fasting metabolism (or basal metabolic rate),
- 2) statistical regressions of fasting heat production, liveweight, body weight and body components on feed intake,
- 3) partitioning of energy consumption with assumptions on efficiency, partitioning and metabolic interactions, and
- 4) feed intake at a equilibrium weight (Webster, 1978; Turner and Taylor, 1983).

#### 2.1.2.1 Fasting heat production/ Basal Metabolic rate.

The heat produced when an animal is fasted represents the energy expenditure due to essential metabolic processes as well as that due to the gradual catabolism of body tissues (Blaxter, 1962; Graham, 1974). Although fasting heat production (FHP) is not strictly constant in the fasting animal. its value has been widely interpreted as a reference point for basal metabolism in human subjects as well as animal species (Webster, 1974; Blaxter, 1989; Cammell *et al.*, 1993). Blaxter (1962) and Graham (1966) indicated that basal metabolic rate (BMR) can be measured adequately in ruminants (sheep) given that the animal:

- 1) *was in a thermoneutral environment.*
- 2) *was adapted or accustomed to the physical environment in which it was measured,*
- 3) *remained in a rested state for the majority of the measurement period and*
- 4) *was in a post-adsorptive phase: this usually involves feeding the animal at near maintenance prior to the fasting period with the measurement period commencing 3-4 days after the final meal.*

The estimate of fasting metabolism includes FHP measured in calorimeters during this period as well as the gross energy of the urine excreted during the period (SCA, 1990).

As the net value for urinary energy loss during the measurement of FHP can be estimated, BMR is most often predicted as  $0.96-1.08 \times \text{FHP}$  (SCA, 1990; Emmans, 1994).

The net energy required for maintenance ( $Ne_m$ ) can be calculated in energy terms from the summation of the functions for which energy is required, which includes basal or fasting metabolism as well as endogenous and metabolic losses in both urine, manure and the exterior surface of the animal together with heat losses associated with activity (Lofgreen and Garrett, 1968). The metabolisable energy requirements for maintenance ( $Me_m$ ) can then be estimated by the function

$$Me_m = \frac{Ne_m}{km}$$

where  $Me_m$  is the net energy required from feed to maintain energy balance

$Ne_m$  is the net energy requirements

$km$  is the efficiency of utilisation of ME for maintenance

As estimates of fasting heat production and consequently basal metabolism require expensive indirect calorimetric techniques, several attempts have been made to predict this parameter. Both Brody (1945) and Kleiber (1975) noted that heat production for mature animals can be estimated from its allometry with body weight such that

$$y (\text{basal heat production}) = a \times x(\text{body weight})^b$$

where the term  $a$  is a coefficient that has the units of energy (calories or joules)/day  $\times$  BW<sup>b</sup>

The early work of Brody (1945), and later by Kleiber (1975), noted that an allometric coefficient between 0.73 and 0.75 best described the relationship between heat production and body weight across species. A value of 0.75, or metabolic weight, for this exponent has been widely accepted within all equations that attempt to estimate basal metabolism for sheep, even though later work has shown that the component within species can vary between 0.4-0.84 (Thonney *et al.*, 1976; Turner and Taylor, 1983). Freetly *et al.* (1995) also showed that there were breed differences in the relationship between heat production and body weight. He suggested that the differences were a function of stage of maturity rather than breed differences in metabolic rate. Blaxter and Wainman (1966) and later the ARC (1980) and Heusner (1982) indicated that a coefficient



of 0.66 might be more appropriate for growing animals, although subsequent studies showed that the difference between this coefficient and that of 0.75 was not significant (Baldwin and Bywater, 1984). Therefore the coefficient for 0.75 was retained for cattle and sheep by both the SCA (1990) and the NRC (1996). This is despite the results from Carstens *et al.* (1989) who indicated that the exponent of the allometric relationship between FHP and BW in 20 month old cattle was 1.095, and this was significantly greater than 0.75.

By accepting a common allometric coefficient, Baldwin and Bywater (1984) suggested that there was a tendency to under estimate BMR in immature animals and over estimate BMR in mature animals. They also noted that the wide use of 0.75 in those experiments that examined the relationship between BMR and BW resulted in all the variance being attributed to the coefficient “a”. This results in wide condemnation of the use of the allometric relationship (Turner and Taylor, 1983) because of the variance of “a” arising from differences such as plane of nutrition, physiological state, age, sex, season and level of productivity. Freetly *et al.* (1995b) indicated that the use of metabolic weight resulted in heat production of lightweight animals being underestimated, whilst heat production of heavier weight animals was over predicted.

Whatever the exponent used in the relationship between FHP and body weight the underlying assumption is that heat production is solely a function of body size (Koong *et al.*, 1985). As there are several confounding effects that influence estimates of FHP, outside of the body size relationship, there has been an attempt in recent studies to correct the basic relationship for other parameters. Koong *et al.* (1985), attempted to correct the exponent of body weight for the variation that exists in average daily gain of growing animals. They stated that the equation

$$\text{FHP} = 106 W^{0.686 + 0.165\text{ADG}}$$

no longer was restricted to the underlying assumption that FHP is a sole function of metabolic body size and that a change in metabolic activity due to a change in the level of production is also considered. More recently, Freetly *et al.*(1995b), proposed that FHP should be related to body size as a function of both the current weight of the growing

animal as well as mature weight, arguing that the inclusion of mature size resulted in a more robust predictor than the traditional allometric equation.

Both Webster (1978) and Turner and Taylor (1983) in their respective reviews, noted that fasting metabolism has several shortcomings when trying to estimate the true maintenance requirements of an animal. Turner and Taylor (1983) concluded that fasting metabolism overestimated the true basal metabolic rate as it represents the level of metabolism prior to the fast and as such is confounded by the nutritional history of the animal prior to the fasting period (Graham, 1974). As the animal is in a post-adsorptive state during the fasting period and is sustained by the mobilisation of substrates from body stores, the level of these stores prior to the fast will also affect the measurement of BMR.

Turner and Taylor (1983) further questioned the validity of fasting metabolism as an indicator of maintenance requirements as the time taken for metabolism to reach an equilibrium state is much longer than the three-four day period of fasting that is used conventionally before estimating FHP (Blaxter, 1962). They suggested that fasting metabolism has no unique utility over metabolism estimates from fed animals, or ME intake in relation to body weight.

Webster *et al.* (1974) and Webster (1978) described measurements of fasting metabolism as being irrelevant in growing animals forced into a sudden shortage of food. Metabolic estimates made on these animals, are confounded by varying adaptive responses to the feed restriction, and with carry over effects of previous intake, growth rates and stages of maturity. Baldwin (1995) stated that fasting an animal that is either growing, lactating, pregnant or otherwise producing at varying rates, perturbs metabolism and productivity such that heat production estimates are not representative of the normal fed state. Even scaling body weight and metabolisable intake to the power  $^{0.75}$  (Brody, 1945; Kleiber, 1975) was considered inappropriate (Turner and Taylor, 1983). This has led to the conclusion that maintenance derived from physiologically stable animals is of limited use to systems that attempt to predict the response to nutrient intake in actively growing, fattening or reproductively active ruminants (Cammell *et al.*, 1993).

The inability to accurately measure fasting heat production in growing animals resulted in an alternative approach of *Predicted Basal Metabolism* ( $F'$ ; Webster *et al.*, 1974; Webster, 1978). Webster *et al.* (1974) accepted the relationships between ME,  $k_m$  (efficiency of ME use for maintenance) and  $k_f$  (efficiency of use of ME for growth) as proposed by the ARC (1965). From a plot of retained energy (R) against ME intake, Webster extrapolated along the slope  $k_f$  to a level of zero energy storage and then along the slope  $k_m$  to the intercept at zero intake which he defined as  $F'$  (Turner and Taylor, 1983). The point  $F'$  can be described by the formula

$$F' = k_m \left( ME - \frac{R}{k_f} \right)$$

This procedure has an advantage over estimating FHP directly for immature animals as the prediction can be made without altering normal physiological relationships that would occur when feed intake is reduced to maintenance levels (Webster, 1978). However as the estimate  $F'$  is clearly dependent on the assumed values for the slopes of  $k_f$  and  $k_m$ , errors in  $F'$  are proportional to the errors for  $k_m$  and inversely proportional to the errors of  $k_f$  (Armstrong and Blaxter, 1984). Furthermore, Turner and Taylor (1983) noted that the values obtained for  $F'$  as a function of body weight are dependent on feeding levels and the physiological condition of the animal and hence the relationship between  $F'$  and W must not be assumed and must be calculated for each type of animal (Webster, 1978).

### 2.1.2.2 Equilibrium weight

The definition of equilibrium maintenance requirements is the metabolisable energy intake (ME) when an animal is in an equilibrium state (Taylor and Young, 1968). The work of Taylor and Young (1968) and Taylor *et al.* (1981) in feeding animals to a constant level over a prolonged period of time, provided the basis for estimates of equilibrium maintenance efficiency. This estimate recorded at a steady state condition where body weight does not change, in essence, is the literal meaning of maintenance (Turner and Taylor, 1983). Evidence presented by Taylor *et al.* (1981) shows that equilibrium maintenance requirements are strongly dependent on body weight within and also between animals, that is, weight maintained is dependent on food intake and is

constant across a wide range of weights and stages of maturity. As a result of this consistent relationship between body weight and feed intake, equilibrium maintenance requirement is a desirable trait to measure, as it is highly repeatable over an animals lifetime.

Parks (1982) used the results of Taylor and Young (1968) who showed that there was a consistency between  $A$  (equilibrium weight) and  $q$  (equilibrium feed intake) to further develop the concept of  $T_0$  or the efficiency of maintenance of equilibrium weight (refer figure 2), or as Parks (1982) defined this as the *Taylor Diagonal* such that  $T_0 = A/C$ . He further showed that the Taylor diagonal divided the growth phase plan into regions of controlled growth and partial starvation (figure 2.2). From this Parks developed the differential growth equation under controlled feeding situations to include estimates of  $A$ ,  $C$  and  $T_0$  such that

$$dw/dt + gW = hq(t) \quad (1)$$

became

$$dw/dt + [(AB)/T_0]W = (AB)q(t) \quad (2)$$

which can be integrated to estimate weight at time (t) in a controlled feeding situation as a function of AB (the efficiency of growth free of the maintenance component),  $T_0$  and the previous estimate of weight at t-1.

$$W_t = (T_0 f_t - W_{t-1}) (1 - e^{-(AB)/T_0}) + W_{t-1} \quad (3)$$

where:

$W_t$  = body weight at age t or at time t after the beginning of the experiment

$f_t$  = cumulative food intake at age t or time t since the beginning of the experiment

(kg)

$T_0$  = efficiency of maintenance equilibrium weight (week)

AB = growth efficiency factor (kg BW / kg food intake)

$W_{t-1}$  = body weight at age or time t-1

The parameters of both AB and  $T_0$  are independent of the mode of feeding. From equation (3) estimates for the efficiency of feed utilisation and the efficiency of maintenance of equilibrium weight can be obtained from liveweight changes in animals that have been controlled fed (Parks, 1982).

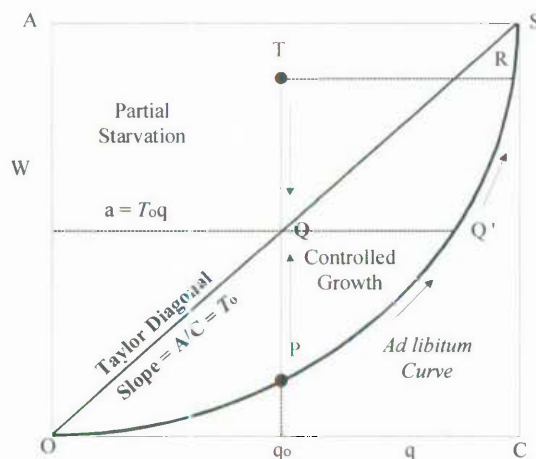


Figure 2.2 The Taylor Diagonal OS divides Parks Growth phase plan into regions of controlled growth and partial starvation. With a constant food intake  $q_0$ , an animal at P grows towards Q. An animal at T when restricted to  $q_0$  loses weight towards Q. Source Parks (1982)

However, Taylor *et al.* (1981) stated that there still remains variation in equilibrium requirements that are independent of mature weight and systematic components, a concept further refined in the review of Turner and Taylor (1983). They noted that body composition interacted with the stage at which the equilibrium point was applied. Immature animals became progressively leaner over time, which was also evident in the work of Frish and Vercoe (1977). Towards maturity the cows used in the experiment of Taylor and Turner (1968) became progressively fatter as they approached their equilibrium weight.

Tess *et al.* (1984), questioned the validity of the use of stabilising intakes for estimates of equilibrium maintenance efficiency in immature animals. They argued that the impact of enforcing a period of “stability” on growing animals will disrupt the normal patterns of metabolism and may provide unrealistic estimates of the true maintenance requirements of those animals. Importantly it must be recognised that the equilibrium state is different to the productive state in a variety of metabolic and physiological parameters.

As a result the maintenance requirements of a productive animal is quantitatively different to that at equilibrium maintenance as productive requirements cannot be partitioned from vital functions when estimates are made on the one dynamic pool of energy utilisation. Recently Luiting *et al.* (1995) showed that pigs that have the lowest metabolic rate when growing seemed to have the highest metabolic rate when fed at maintenance. They suggested that the lower maintenance requirements were not a result of lower maintenance costs, but were a result of higher efficiencies of both fat and lean accretion. From this result, it appears as though the reservations of Tess *et al.* (1984) are validated.

### 2.1.2.3 Partial regressions

In growing animals maintenance energy expenditure can be defined as the difference between total metabolisable energy intake and the energy required for growth. A number of experiments have used this relationship in regression procedures to estimate maintenance expenditure from

$$Me_m = \text{Energy intake (MEI)} - \text{retained energy (RE)} \quad (\text{ARC, 1980})$$

where, energy intake is measured in units of metabolisable energy from the metabolisable energy density of the diet supplied (MJ/kg) and retained energy represents some function of the rates of change in liveweight, body weight or in the components of fat and protein multiplied by energy content of the tissue (Lofgreen and Garrett, 1968; Ferrell *et al.*, 1976; Garrett, 1980; Roux *et al.*, 1982; Olthoff *et al.*, 1989; Tess and Greer, 1990).

There have been a number of studies that have examined the effects on growth rate, physiological state, sex on the relationship between changes in liveweight or body weight and the retained energy in that respective change (Webster, 1978; Geay, 1984; Hicks *et al.*, 1990; Murphy and Loerch, 1994). Obviously the most desirable method is to accurately measure the changes in protein (lean) and fat using direct methods of serial slaughter or indirectly by techniques such as specific gravity, ultrasonics or isotope dilution techniques (Panaretto, 1964; Graham, 1967; Russel and Wright, 1982; Kempster, *et al.*, 1982). Using estimates for the changes in protein and fat tissue, equations of the basic form

$$MEI = b_0 + b_p RE_p - b_f RE_f \quad (\text{Olthoff } et al., 1989)$$

where

MEI is the metabolisable energy intake

$b_0$  is metabolisable energy requirements

$RE_p$  and  $RE_f$  are measures of retained energy in protein and fat tissues (including wool)

$b_p$  and  $b_f$  are partial regression coefficients for fat and protein respectively.

The inverse of these coefficients is equal to the efficiency of energy utilisation for protein and fat respectively. Combining the terms of  $RE_f$  and  $RE_p$  yields the value for energy of growth  $Re_g$  and its efficiency term  $b_g$ .

This method of estimating maintenance requirements considers energy deposition to be a linear function of protein and fat gain (Bishop, 1992). Constraining the partial efficiencies of growth components to linear terms will result in biased estimates for  $Me_m$ , as Marias *et al.* (1991b) showed that there was an effect of stage of maturity (body mass) which resulted in the partial efficiency of protein deposition increasing with mass and the partial efficiency of fat declining slightly with mass in growing sheep. Marias *et al.* (1991b) also showed that there was a sex effect on the partial efficiencies of both fat and protein at any given mass, and that the differences due to sex changed in a differential manner as body mass increased. In order to account for a non-linear change in body components with growth, Bishop (1992), used allometric equations to describe changes in the weights of body fat and protein during growth. Although the predictions for mean value of maintenance did change with this technique, correlations between this method and the one previously described, were equal to 1 for several parameters examined.

The ability to accurately measure changes in body components of live animals using CAT-scanning techniques (Enting, *et al.*, 1990; Thompson and Kinghorn, 1992; Kolstad and Vangen, 1995) removes some of the drawbacks of obtaining only one reliable measurement per animal (Webster, 1978). However as Tess and Greer (1990) indicated,

the ability to construct and utilise the results from within animals multiple regression techniques still relies on three key points that:

- 1) the model is correctly and completely specified,*
- 2) values of independent variables are completely uncorrelated and,*
- 3) autocorrelation among variables are accounted for correctly.*

Obviously the correlation among the variables of fat and protein is not independent and could be different for each animal dependent on the animals inherent ability for partitioning nutrients, given that there will be different interactions with nutrition and management for each individual animal. This makes identification of the underlying autocorrelation between variables difficult to predict and account for appropriately. Overall there will be bias and inaccuracies that are introduced into measurements of maintenance and growth efficiency within individual animal through having correlation's between estimates of energy gained in fat and protein. However, these estimates will be more reliable than those obtained from serial slaughter or indirect estimate techniques, although caution must be exercised in interpreting the biological significance of efficiencies obtained from partial regression procedures (Garrett, 1980).

Recently Baldwin (1995) concluded that the statistical approach of using partial efficiency regression models described the experimental data from the majority of the studies with a high level of accuracy. The results obtained from this approach can be satisfactorily used in empirical equations that estimate feed requirements such as those of the ARC (1980), SCA (1990) and NRC (1996). The problem, as discussed by Webster (1981), Roux *et al.* (1982), Tess and Greer (1990) and Baldwin (1995), exists when attempts have been made to assign biological meaning to the coefficients of  $b_o$ ,  $b_f$  and  $b_p$  ( $b_g$ ). In light of high level of variation that exists in estimates for maintenance and growth efficiencies which occur in part through differences in sex, age, feeding level, environment and collinearity between other variables, Baldwin (1995) stated that the concept of maintenance is inadequate and should be replaced with more explicit considerations of the physiological and metabolic functions that contribute to energy expenditure.



#### 2.1.2.4 Residual Feed Intake

Production levels in livestock have been increased considerably by selection for gross feed efficiency (Webster, 1989; Luiting *et al.*, 1994). However as improvements in efficiency in meat production are generally correlated with increases in mature size or growth rate (Bishop, 1992; Veerkamp and Emmans, 1995), this has led to a corresponding increase in maintenance, costs particularly with respect to the mature breeding female (Luiting, *et al.*, 1994). Koch *et al.* (1963) first proposed the use of residual feed intake (RFI) as an alternative method for estimating efficiency in beef cattle. Residual feed intake is defined as  $RFI = (\text{actual ME intake}) - (\text{the estimated ME requirement})$ , and has the advantage that the variation in feed consumption is adjusted for differences in production levels and liveweight through the use of multiple regression procedures (Luiting *et al.*, 1994). In essence the value for RFI reflects the difference in the utilisation of energy of an animal when compared to a population mean.

Veerkamp and Emmans (1995), examined several alternative methods for estimating efficiency in dairy cattle, suggested that RFI has a key misgiving that correction of feed intake by phenotypic regression did not account sufficiently for the genetic correlation between liveweight and feed intake. This resulted in no genetic variation in RFI, after accounting for the genetic variations in liveweight and feed intake. Kennedy *et al.* (1993) showed that an index containing feed intake and production traits lead to identical responses as selection for residual feed intake. They stated that residual feed intake adds no new genetic information. Fan *et al.* (1996) stated that measurement of RFI is difficult, heritabilities are low and that estimates depend on the method of calculating estimated requirements.

Archer and Pitchford (1996), showed that the correlation between maintenance requirements and RFI in immature mice was low, indicating that RFI estimates in the growing animal is unlikely to be a reliable predictor of maintenance efficiency in the mature animal. This result suggests that selection for RFI in immature animals may result in no improvement in maintenance efficiency of the breeding female, where maximal improvements in efficiency can be achieved (Thompson and Barlow, 1986). Luiting *et al.*

(1994) also showed that hens selected for low RFI were more susceptible to stress and that meat quality was reduced in pigs selected for a lower RFI. Thus improvements in efficiency may come at the cost of a reduction in animal fitness and product acceptability.

### 2.1.3 Physiological effects on maintenance efficiency.

#### 2.1.3.1 Growth and maturity

Maintenance requirements can contribute up to 50% of the total energy costs of an individual animal during growth (Geay, 1984). As such techniques that attempt to estimate this component, although often giving variable results, are still considered to be worthwhile for partitioning the variation in energy expenditure that occurs between animals during growth.

Kleiber (1975) originally proposed that fasting heat production was related to metabolic body weight ( $w^{0.73}$ ) in mature animal. However, in growing animals as indicated by a review of the literature (ARC, 1980) a coefficient of 0.66 would be more appropriate, whilst Turner and Taylor (1983) indicated that the relationship was close to unity. From this evidence it is clear that body size does have an impact on maintenance requirements, although the biological basis for this difference remains unclear. Indeed the techniques for measuring maintenance requirements show no accord for an effect of body weight *per se* on estimates for  $Me_m$ . In calorimetric studies, basal metabolism is often related to the body weight raised to a power function. This relationship indicates that the maintenance requirement per unit of body weight declines with increasing weight. This is confirmed by the results of Geay (1984) who showed that for every 100kg increase in weight,  $Me_m$  declined by 3.0 Kcal/ $w^{0.75}$  and 10.5 Kcal/ $w^{0.75}$  in Charolais and Freisian bulls respectively. In contrast, the consistency between equilibrium weight and equilibrium feed intake that has been proposed by Taylor and his colleagues (Taylor and Turner, 1968; Taylor *et al.*, 1981; Turner and Taylor, 1983) indicates that there is no change in the maintenance requirements per unit of body size as size increases. The experimental results of Gettys *et al.* (1987) indicates that in growing males and females, the proportionality between  $Me_m$  and body weight did not differ significantly from 1.0.

Several studies have observed that maintenance requirements is not a constant function in the growing animal and appears to be curvilinear when the animals are fed at above maintenance levels (Taylor, 1970; Webster *et al.*, 1974; Graham, 1974). However, as shown by Turner and Taylor (1983), as animals are restricted in intake towards the point of body weight maintenance, the relationship between heat production (the major component of maintenance) and body weight changes from a curvilinear to a near linear relationship. The change in the relationship between heat production and body weight probably indicates that true equilibrium maintenance efficiency in immature animals, as estimated by a proportionality of  $BW^{1.0}$ , will be lower than estimates for an actively growing animal where the prediction of  $M_m$  is based on a proportionality of  $BW^{0.68-0.75}$  (Webster, 1978).

Graham (1974) proposed that 86% of the variations in FHP were accounted for by body weight. He suggested that only a further 6% of the variation in FHP was accounted for by factors such as age and feeding level. The SCA (1990) indicated that there was an age effect on fasting metabolism although the decrease with age that had been observed was not always consistent. The data of Moe (1981) indicates that FMR declined by approximately one half in dairy heifers in the first two years and thereafter the decline was minimal. In the equations that estimate maintenance requirements as proposed by the SCA (1990), the coefficient that is used for weight is scaled by  $e^{(-0.03A)}$ , where A is age measured in years. Thus for every one year increase in age the scaling reduces  $Me_m$  by approximately 3%. Loblely (1990) in a review of the effects of age, nutrition and hormonal status on energy metabolism in the muscle, reported that the reduction in basal metabolic rate that was associated with age was matched by declines in both muscle oxygen consumption, muscle protein synthesis and  $Na^+/K^+$  ATPase activity.

Early work of Graham (1967) indicated that age did not have an effect on  $Me_m$ , if  $Me_m$  was expressed as a function of lean body weight. As a consequence the “age effect” might represent a slight change in  $Me_m$  resulting from differences in body composition (Birkelo, 1995). More recently, Freetly *et al.* (1995a) showed that FHP did decline with

age in both Suffolk and Texel ewes, although the exponent of the relationship varied between -0.066 for the Suffolks and -0.019 for the Texels. This variation suggests that the maturity pattern of each individual breed type might have an effect on the coefficients of the relationships between heat production and age.

### **2.1.3.2 Sex**

In most of the equations and models that have been developed to estimate feed requirements for maintenance for both cattle and sheep, correction factors for sex are included (ARC, 1980; SCA, 1990). In early experiments conducted by Graham (1968) the fasting heat production in rams was shown to be higher than that for ewes when corrected to the same empty body weight. Ferrell *et al.* (1979) showed that the requirements for body weight maintenance of immature rams was higher than that for ewes. Ferrell and Jenkins (1985a) also showed that bulls have higher maintenance requirements and lower efficiency of gain than females. In contrast Bull *et al.* (1970) showed that there was no difference in the  $Me_m$  requirement for rams and ewes and that differences only existed in the net utilisation of ME for energy gain. The higher proportion of fat in the gain of ewes being responsible for overall higher efficiency of energy gain. Whilst the efficiency of body weight gain did not differ between the rams and ewes in that experiment, the results of Ferrell *et al.* (1979) and Ferrell and Jenkins (1985a) suggests that males may be more efficient than females in terms of the efficiency of body weight gain due to the greater proportion of water and protein (muscle) in the gain.

More recently, Ball *et al.* (1995) showed that in mature sheep, rams had a 19% higher requirement for feed to maintain empty body weight than ewes and when corrected to the same body composition rams still had an 11% greater requirement. They suggested that higher turnover rates in the muscle of the rams was responsible for the increased feed requirements. Although, Freetly (1995) estimated that protein synthesis in the skeletal muscle represented only 12% of total body energy expenditure. Accepting that this is an underestimate of the true contribution to energy expenditure of carcass muscle, as costs of degradation are not included, this questions the conclusions made by Ball *et al.* (1995). The results of Ball *et al.* (1995) also contrast with the results of Graham (1967) who

showed that  $Me_m$  as a function of lean body mass did not differ between rams and ewes. Furthermore, Gettys *et al.* (1987) suggested that in growing cattle, males had lower maintenance requirements than females and indicated that there may be an inverse relationship between lean body mass and maintenance intake. Afonso, (1992) also showed that the feed required to maintain weight was proportionally lower in ram lambs when compared to ewe lambs. Stephens (1991) showed that maintenance requirements were lower in female mice compared to male mice, although Archer and Pitchford (1996) observed that the maintenance requirements of mature female mice was higher than that for male mice.

In those experiments where castrated males have been compared to either sex, maintenance requirements of the castrate appear to be lower than those for males (Webster *et al.*, 1982; Webster, 1989) with no significant difference to entire females (Garrett, 1982). Graham, (1964) did note that there was a difference in the relationship of FHP to BW between wethers and ewes, although in later studies this result was not repeated. Similarly Sainz *et al.* (1990) indicated that wethers have higher maintenance requirements than ewe lambs. Carstens *et al.* (1989) showed that the sex difference in energy expenditures between castrates and females changed with age, with  $Me_m$  being higher in heifers than steers at 9 months of age, whilst the reverse occurred at 20 months of age. Adeola *et al.* (1990) reported that the total respiration rates were lower in castrates when compared to females for growing pigs. They suggested that differences in the levels of  $Na^+ - K^+$  ATPase was the major component of lower respiration costs of the castrates.

### 2.1.3.3 Feeding level

Marston, (1948) showed that the prior level of nutrition affected the value for fasting metabolism, principally through the lag adaptation of the body's metabolism to a new feeding level (Turner and Taylor, 1983). Since then there has been a multitude of studies that have shown that as the level of intake at which the estimate of  $Me_m$  is increased, the actual estimate for  $Me_m$  also increases (Webster *et al.*, 1974, Corbett, 1985; Olthoff *et al.*, 1989; Birkelo, *et al.*, 1991). In the latter study,  $Me_m$  increased by 13.6% per multiple of maintenance intake. Of the increase only 6.8% was due to an elevation in FHP,

which suggests that the efficiency of energy use for maintenance ( $k_m$ ) declines as feed intake increases or that  $k_m$  improves as animals are restricted (Graham and Searle, 1975).

Olthoff *et al.* (1989) compared estimates of  $Me_m$  obtained at two feeding levels of *ad libitum* and maintenance and concluded that the lower requirements of sheep fed at maintenance per unit of body weight resulted from a reduction in activity rather than a decline in FHP. In contrast, Koong, *et al.* (1982) showed that in both pigs and sheep FHP was significantly higher (20-40%) in *ad libitum* fed animals when compared to animals fed at maintenance. Koong *et al.* (1982) suggested that as the weights of the metabolically active visceral tissues were directly proportional to the measurements of FHP, then changes in  $Me_m$  resulting from differences in prior feeding levels, are probably linked to differences in the weights of the metabolically active tissues.

Interestingly, Ortigues *et al.* (1993) showed that there was no effect of the level of feeding on  $Me_m$  in mature Charolais cows and that FHP reached a nadir within 10 days of a change in feeding level. They noted that an absence in hormonal differences in mature animals that may contribute to differences in responses observed between mature and immature animals. Loblely (1990) indicated that the effects of energy intake of hind limb metabolism of adult ruminants is likely to be small, resulting in little effect on overall energy metabolism. Thus the true effects of feeding levels on FHP and its derivative of  $Me_m$  remains unequivocal in the literature.

An interesting situation exists when animals are fed at feed levels to maintain liveweight. Graham and Searle (1975), Foot and Tulloh (1977), Ledger and Sayers (1977), Burrin *et al.* (1990), all showed that the feed requirements to maintain liveweight decreased with time although the feed requirements stabilised after a period of 15 weeks. Ledger and Sayers (1977) indicated that the decline in feed requirements with time represented an adaptation of the animal to the weight restriction. Both Graham (1974) and Koong and Nienaber (1985), showed that FHP did decline with time in animals held at weight maintenance, supporting the conclusion of Ledger and Sayers (1977). More recently, Cammell (1993) also showed that metabolisable energy requirements for weight

maintenance declined during the first 21 days when calves were restricted, although after this point there were no systematic changes in either metabolisable energy intake or heat production at weight maintenance.

The work of Taylor and his colleagues (Taylor and Young, 1968; Taylor *et al.*, 1981; Turner and Taylor, 1983) shows that  $Me_m$  is constant when animals were held at equilibrium weights after they had stabilised. Turner and Taylor (1983) indicated that the final estimates of  $Me_m$  for steers of Ledger and Sayer (1977) ranged from between 31 and 70% of their initial estimates for  $Me_m$ . This clearly illustrates that estimates of  $Me_m$  must allow sufficient lag time for animals to adapt to weight maintenance before reliable estimates can be obtained. The results of Ledger and Sayer (1977) highlights the importance of the interaction between maturity and the lag time for metabolic stability. They showed that the proportional reduction in the initial estimate for  $Me_m$  over time, was greater in immature animals than for animals near maturity. This indicates that the marked reduction in the metabolic activity of body tissues when food is restricted was more severe in younger animals (Armstrong and Blaxter, 1984).

In pigs, two recent studies show the difference between feeding to maintain liveweight and feeding at a constant level estimated to be maintenance. In the study that fed pigs to maintain liveweight, Kolstad and Vangen (1995) showed that there was a decline in the feed required to maintain liveweight, whilst in the second study Luiting *et al.* (1995) showed that pigs fed at a constant level suffered a slight decline in body weight and thereafter there was no change. In both studies the changes in body components during the maintenance feeding period were similar, that is a decline in carcass fat and an increase in carcass lean, so it is unclear why this difference exists.

The review of Armstrong and Blaxter (1984), cited the work of Fuller (1968), who indicated that the feeding levels for weight maintenance were highly dependent on the protein content of the feed. Pigs fed on the low protein diet increased body energy content through fat deposition, whilst pigs fed at high protein levels decreased body energy content through fat mobilisation. The difference being that the feeding level for weight

maintenance was 2-3 times higher for low protein diets than for high protein diets. In ruminants, Drouillard *et al.* (1991a) has also shown that if protein levels in the diet were sufficient then fat is mobilised at a time where lean tissue can be deposited. A key point is that, at energy balance, nitrogen balance is still positive which would favour the deposition of protein whilst fat reserves are mobilised (Fattat *et al.*, 1984). This evidence suggests that the level of protein within the diet can effect the level at which animals need to be fed for maintenance.

#### **2.1.3.4 Body composition**

Webster (1980) reported the energy cost of maintaining a unit weight of protein is higher than that for fat, which has led to the concept that maintenance may be more closely related to lean body mass (Ferrell *et al.*, 1979; Tess, 1984; Olthoff and Dickerson 1989; McCracken, 1992), rather than simply as a function of metabolic body size (Brody 1945; Taylor *et al.*, 1981). In support of this Graham, (1967) noted that if FHP was described as a function of lean body mass then the exponent of the function is 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. Animals that are comparatively leaner have been shown to have a higher maintenance energy requirement in a number of species including mice (Stephens, 1991), pigs (Tess, 1984; Rao and McCracken, 1991), sheep (Jopson *et al.*, 1994, Ball *et al.*, 1995) and cattle (Klosterman, 1968; Solis *et al.*, 1988; DiContanzo *et al.*, 1991). Ortigues *et al.* (1993) indicated that a distinction exists between animals, that comparatively leaner than their contemporaries, who have higher maintenance requirements and animals, that are leaner as a result of a period of weight loss from feed restriction, who have lower maintenance requirements due to a metabolic adaptation to the lower feeding level (Marston, 1948).

Many experiments have shown that considerable variation in maintenance requirements exists between individual animals from within strains, within breeds and between breeds (Frish and Vercoe 1977, Taylor *et al.*, 1981; Jopson *et al.*, 1994). Differences in body composition have been implicated as contributing to the differences in the maintenance requirements that exist between dairy and beef genotypes (Jenkins and



Ferrell, 1994). Ferrell and Jenkins (1985b) indicated that cows from dairy breeds have a greater proportion of lean and a lower proportion of fat at any given weight when compared to beef breeds. Solis *et al.* (1988) indicated that there were significant differences in the efficiency of energy used for tissue exchange in beef breeds (subcutaneous fat, carcass lean) as opposed to high body lean mass, visceral organ mass and internal fat in dairy breeds. From these experiments it would appear that body composition and exchange within specific tissues could partially explain the higher maintenance requirements of the dairy breeds.

Within breeds, Lemenager *et al.* (1980), Thompson *et al.* (1983) and Byers and Carstens (1991) have shown that cattle that have higher body condition scores have lower maintenance requirements, suggesting that fatter animals are more efficient when compared on a weight basis (Ferrell and Jenkins, 1985b). Herd (1995), showed that in lines of Angus cattle that had been selected for growth rate at weaning, differences that occur in  $Me_m$  of mature cows between the lines are removed, after adjusting to the same body condition score. DiCostanzo *et al.* (1991) showed that cows that were characterised as having low maintenance efficiency deposited more lean and less fat over a test period than high efficiency cows. This indicates that the proportion of lean:fat in the estimate of retained energy can influence the estimates for maintenance requirements. Recently Nielsan (1995) indicated that mouse lines that had been selected for lower heat loss in males, had lower feed intakes per unit of metabolic weight and were proportionally fatter than control and high heat loss lines.

The difference in body composition between males and females also has been suggested as contributing to the greater  $Me_m$  of the entire male (Webster, 1989, Ferrell and Jenkins, 1985b). Adjusting for body composition has been shown to account for a significant proportion of the difference (Carpenter *et al.*, 1995; Ball *et al.*, 1995), although females were still more efficient than males. Solis *et al.* (1988) suggested that rather than absolute fat weight, the site of fat deposition or storage had a substantial impact on the energy requirements for maintenance. Sites for protein deposition and storage in either carcass or visceral components may also influence maintenance requirements (Ortigue,

1993), as rates of protein turnover and metabolism vary between skeletal muscle and visceral organs (Freetly, 1995).

In contrast to the direct effects that body composition *per se* has on estimates of maintenance requirements, Ferrell and his colleagues have shown that FHP was not related to either body composition or the composition of retained energy in both growing lambs (Ferrell *et al.*, 1986) and growing steers (Ferrell and Jenkins, 1996a,b). This has lead this group to conclude that estimates of maintenance requirements are independent of body composition, or the composition of gain. However the technique that was used by Ferrell and Jenkins (1996a) which scaled estimates of both FHP and retained energy for metabolic weight may have compromised their ability to detect differences between breeds that have known body compositional differences.

The NRC (1996) 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 between a condition score of 0.8 to 1.2 normal ( where normal, or average condition score was 5). As Ferrell (1995), stated the equation used 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.

Birkelo (1995) summarised the importance of the visceral tissues by stating that they contribute between 40-50% of the total body energy expenditure although only occupying 10% of total body mass. Ferrell and his co-workers (Ferrell *et al.*, 1983, Ferrell and Jenkins, 1985b; Koong *et al.*, 1985; Burr n *et al.*, 1990), in a number of studies that have examined the effects of growth paths on maintenance requirements, have clearly shown that the response in  $Me_m$  to levels of feeding prior to the estimates, are mirrored by a direct response in the mass of visceral organs. Growing lambs that were fed at high levels then low levels of intake had lower maintenance requirements than lambs of the

same weight that had been fed at low levels followed by high levels. The LH lambs had higher weights of visceral organs (Ferrell *et al.*, 1983; Ferrell, 1988). Comparison of maintenance requirements of growing steers following similar growth paths are basically the same as those for lambs (Sainz *et al.*, 1995).

Both the liver and the gut tissue have the highest energy demands of the visceral organs (Freetly *et al.*, 1995b) and thus these tissues have been more comprehensively studied. Ferrell (1988) and Ortigues and Visseiche (1995) indicated that the liver, although being only between 1-2.5% of total body mass, consumes between 17-31% of total energy expenditure in ruminants. Thus alterations to the mass of this organ will contribute significantly to a change in maintenance requirements. Several studies that have recorded changes in maintenance requirements during weight loss, have also recorded significant reductions in liver weights (Koong *et al.*, 1985; Johnson *et al.*, 1990). Dicostanzo *et al.* (1991) also showed that high efficiency cows had lower liver weight when compared to low efficiency cows.

Therefore changes in body components, even whilst in an apparent steady state, obviously would be expected to have an important impact on the maintenance requirements for an individual animal. For these reasons it is difficult to reconcile with the conclusion of Turner and Taylor (1983) and more recently Ferrell and Jenkins (1995), that maintenance requirements are dependent on body weight and independent of body composition. This implies that an animal will always exhibit the same requirement per unit of body weight regardless of its body composition, pattern of energy metabolism or absolute body size.

Refinements in techniques to estimate body composition *in vivo* such as the use of a CAT-scanner (Thompson and Kinghorn, 1992), will enable an approach that defines maintenance in terms of the "energy" cost of maintaining a certain weight of lean, fat or bone tissue for individual animals when adjusted for differences in maturity, physiological stage or feeding level. This approach may be far more beneficial to programs designed to improve the efficiency in either the breeding herd or feedlot. If progress is to be made

towards an understanding of maintenance of a specific body composition rather than live weight, then the underlying biological mechanisms that are associated with differences in body composition that contribute to individual variation in the maintenance efficiency trait need to be better understood.

#### **2.1.3.5 Compensatory growth**

One of the key elements of compensatory growth is the persistence, during the early phase of realimentation, of a reduction in estimates for maintenance requirements that occurs when animals are restricted below normal growth. Several 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). Animals that have been restricted to maintenance have also shown a significant decline in maintenance requirements (Graham and Searle, 1975; Ledger and Sayers, 1977; Yambayamba *et al.*, 1996a). Furthermore it has also been shown that sheep that have been restricted below maintenance have significantly lower maintenance requirements (Graham and Searle, 1979; Gingens *et al.*, 1980, Ryan *et al.*, 1993a). However Ortigues and Durand (1995), showed that the maintenance requirements of mature ewes that were fed at half that required for maintenance also decreased although the energetic efficiency when expressed on a metabolic liveweight basis was the same as estimates at maintenance.

The majority of these studies showed that the proportion of metabolically active tissues of the total body was lower in the restricted animals when compared to the control animals (Ferrell, 1988). Keenan *et al.* (1969) showed that a 32% reduction in maintenance efficiency between control and previously restricted mature sheep was closely correlated with a 35% decrease in the mean weight of liver rather than a 14% difference in the mean metabolic weight of the two groups. These results indicate that visceral organ energy expenditure is reduced during the restriction period which increases maintenance efficiency. Wester *et al.* (1995) showed that oxygen consumption increased per gram of liver tissue during weight loss, but 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, 1995a). In complete opposition to the previous results, Drouillard *et al.* (1991a) indicated that the activity of visceral tissues was not responsible for the occurrence of 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.

Shetty (1990), proposed that the reduction in maintenance requirements in response to a restricted feed intake would occur in two stages. The first response would occur due to decreased metabolic activity of body tissue (2-3 weeks) and the second long-term response would result from the loss in mass occurring from mobilisation of the metabolically active tissues to partially meet some of the energy deficit during the feed restriction. Ortigues and Durand (1995), suggested that there may be a further reduction in the metabolic activity of muscle in long-term feed restricted mature animals.

When the feed restriction ceases there is a significant time lag before metabolism responds to the change in feeding levels (Turner and Taylor, 1983). The lag time required for a change in animal expenditure following feed restriction has been estimated to be of the order of 6-21 days (Clapperton and Blaxter, 1965; Turner and Taylor, 1983). This delayed response results in comparatively more energy that is available for growth (Ryan, 1990), when control and re-fed animals are compared at the same feed level. In contrast, Schnyder *et al.* (1982) indicated that there was a rapid increase in FHP that occurred with increased feeding level in compensating steers, with levels remaining below that for normally grown animals for only five days. However they suggested that this may reflect the inability of FHP to accurately measure changes in  $Me_m$  in compensating steers.

Recent evidence from Sainz *et al.* (1995), suggests that the type of feed fed during the restriction affects  $Me_m$  during the subsequent realimentation period. Steers that were fed 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. Sainz *et al.* (1995) showed

that proportional differences in visceral organ weights mirrored the differences in maintenance requirements, suggesting that 28% heavier visceral weights of the FA steers was a forage diet effect that prompted higher  $Me_m$  in these steers during the compensation period.

#### **2.1.3.6 Seasonality**

Seasonality in body growth and composition appears to exist independently of feed intake levels. Forbes *et al.* (1981), Petitclerc *et al.* (1984) and Zinn *et al.* (1986) showed that growing animals exposed to long-daylength stimulated non-fat tissue deposition at the expense of fat. In contrast, Laurenz *et al.* (1992) found that in mature cows, from two breeds, carcass protein was mobilised and fat tissue was deposited in summer, whilst carcass protein was increased in winter and spring. Despite this conflict, it seems that maintenance requirements may differ with season due to changes in body composition and tissue exchange (Laurenz *et al.*, 1992).

The study of Blaxter and Boyne (1982) showed that in sheep fed to maintain body weight, heat production corrected to zero energy retention and zero feed intake was sinusoidal with time, with an amplitude of 14%. The phase of the sine function indicated that minimal metabolism occurred in mid winter and maximal metabolism in midsummer and was independent of feed intake or quality of the diet. As basal metabolic rate is an indicator of maintenance, and seasonal changes in body composition (Petitclerc *et al.*, 1984) appear to be linked to the oscillations in BMR recorded by Blaxter and Boyne (1982). Walker *et al.* (1991) also showed similar patterns in the metabolic rates of mature ewes that were subjected to different photoperiods. However they held feed intake constant, which accounted for one of the confounding effects that had previously confounded the results of Blaxter and Boyne (1982). The higher metabolic rates occurred in the same season as higher lean growth and lower metabolic rates occurred when there were increasing proportions of fat tissue deposition. These apparent relationships are consistent with general relationships that exist between body protein, fat and maintenance requirements that have been identified in growing sheep (Ball *et al.*, 1996) and in mature cows (Laurenz *et al.*, 1991) and deer (Weber and Thompson, 1995). As a result it remains

to be determined which is the cause and the effect in the relationship between the oscillations in metabolic rate and changes in body composition.

### 2.3.1.7 Endocrine

Manipulation of maintenance requirements through a modification of the endocrine environment of an animal relies on the ability to understand the interaction between specific hormones and a specific component of energy expenditure. In many cases the exact assignment of the source of variation in either the maintenance component or to the deposition of nutrients is difficult (Sainz, 1995b).

The difference in maintenance requirements between the sexes provided a clear hypothesis that the addition of exogenous anabolic steroids would alter energy requirements of growing animals. Hunter *et al.* (1993) indicated that a reduction in maintenance energy requirements could be achieved by reducing the rate of protein turnover and the associated processes of either a reduction in degradation rates or increase in synthesis rates. From a series of experiments, they concluded that the implant of the anabolic steroid “Trenbolone acetate” reduced FMR in steers by 10%. It is significant that the live weight loss that was experienced by steers fed at below maintenance was reduced for the anabolic steroid treatment, indicating a sustained effect on overall energy requirements, principally as a result of a reduction in the rate of protein degradation. Hunter (1989) showed that an implant of testosterone did not alter the FHP, or the relationship between LW change and MEI in steers. This contrasts with the review of Sainz *et al.* (1995b) who indicated that heat production was reduced by 16% though the use of an anabolic steroid.

Freetly and Nienaber (1994) showed that splanchnic tissues of ewes treated with oestradiol have an increased oxygen consumption, which suggests that maintenance requirements would also increase. Solis *et al.* (1988) showed that steers treated with oestradiol had marginally higher maintenance requirements (5%) than control animals.

Fox *et al.* (1974) and Murphy and Loerch (1994) have shown that thyroid hormone levels in feed restricted cattle are lower than those in controls and that there is a direct correlation between thyroid hormones (T3 and T4) and maintenance requirements. Thyroid hormones regulate oxygen consumption and have indirect effects on the Na<sup>+</sup>-K<sup>+</sup> ATPase and hence cellular energy expenditure (Milligan and McBride, 1985). However it is still unclear whether a reduction in serum T3 concentrations is a cause or an indicator of a reduction in maintenance requirements.

Collier *et al.* (1992) showed that in both ruminants and swine treated with Somatotrophin, or growth hormone, had higher maintenance requirements due to increased lean growth rate. However as lean growth rate increases, relative maintenance costs are reduced due to the dilution of maintenance costs when expressed as a proportion of maintenance plus lean gain. In contrast, McBride *et al.* (1992) showed that Somatotropin had no effect on elevating respiration of the skeletal muscle or the partitioning of maintenance energy requirements within the skeletal muscle. Both Ferrell *et al.* (1979) and Johnson *et al.* (1985), reported that treatment with Somatotrophin increased visceral lean gain, with little effect on carcass lean gain. The increase in visceral lean gain would be expected to increase overall maintenance requirements, due to the proportionally high influence these tissues have on overall energy expenditure (Ferrell, 1988).

Although Somatotrophin has an indirect effect on maintenance requirements by altering the lean accretion rates, Brockman and Laarveld (1986), suggested that growth hormone does not appear to be involved in the minute to minute regulation of metabolism in ruminants. However administration of growth hormone does appear to have a small effect on resting metabolic rate in human studies (Shetty, 1990).

Brockman and Laarveld (1986) indicated that metabolism in the resting animal is under the primary control of insulin and as a result modifications to normal insulin levels will cause changes to the animals metabolic demands. Shetty (1990) stated that insulin can increase energy expenditure in several ways, the most prominent is the direct stimulation of the Na<sup>+</sup>-K<sup>+</sup> pump across the membrane, as insulin modulates thermogenesis of the body



by stimulating glucose transfer across the cell membrane. Brockman and Laarveld (1986) showed that the metabolic adaptation of energy metabolism to a fasting situation through mobilisation of body energy stores is primarily under the hormonal regulation of insulin. This leads to the hypothesis that the energetic demands in the fasting animal may be modified by changes to insulin levels (Shetty, 1990).

Hunter *et al.* (1993), showed that a continuous intravenous injection of a  $\alpha$ -agonist (Guanfacin) decreased FMR by 20%. Whilst MacRae *et al.* (1988) and Kim and Sainz (1992) have both showed that heat production and overall maintenance requirements increased in wether lambs treated with the  $\beta$ -agonists Clenbuterol and Cimaterol respectively. Recently Moloney *et al.* (1995) have shown that the treatment of wether lambs with  $\beta$ -agonists increased maintenance requirements and suggested that the majority of this increase was due to increased protein deposition rates.

#### **2.1.4 Selecting for Maintenance efficiency**

Thompson and Barlow (1986) indicated that reducing the maintenance cost of the breeding female would be one of the most desirable methods of improving the overall efficiency of beef cattle production. Variations that exist in maintenance requirements ( $Me_m$ ), after correcting for differences in retained energy and the efficiencies of retaining energy in both fat and lean, must be confined to either differences in energy requirements for metabolic processes (FHP or equilibrium requirements) or to the efficiency of ME use for maintenance ( $K_m$ ). Both Taylor *et al.* (1986) and Carstens *et al.* (1989) indicated that variations in  $K_m$  was the major determinant for variations in  $Me_m$ . In contrast Rompala *et al.* (1991) and Shuey *et al.* (1993) showed that FHP was responsible for variations in  $Me_m$  in lambs selected for efficiency and reproductively active heifers respectively. Shuey *et al.* (1993) further suggested that provided feed intake was limited, although sufficient enough to maintain both maintenance and production, then indicators of fasting metabolism would be an appropriate criteria for selection for improved maintenance efficiency.

Several studies have shown that the phenotypic coefficient of variation for maintenance efficiency ranges from between 5% to 40% (Taylor *et al.*, 1981; Solis *et al.*,

1988; Montaña-Bermudez *et al.*, 1990). DiCostanzo *et al.* (1990) indicated that there is sufficient divergence within breeds to directly select for improved maintenance efficiency. Carstens *et al.* (1989) reported a high heritability of 71% in 9 month old beef cows and 49% at 20 months of age, whilst Hotovy *et al.* (1991) also reported a high heritability of 34% for maintenance efficiency in beef cows. Bishop (1992) showed that the heritability of maintenance requirements was moderately heritable (20%), although after adjusting maintenance for metabolic weight the trait was weakly heritable at 11%. Bishop (1992) stated that there is no doubt that genetic variation exists in maintenance requirements, although surprising little is known about the degree to which they are genetically determined, with further work required to identify those components that are more strongly inherited. However the work of Birkelo *et al.* (1991) indicated that an improvement in efficiency will not have a major effect on overall production efficiency.

Stephens (1991) showed that selection for decreased maintenance requirements at maturity, in mice, resulted in increased improvements in reproductive and maternal traits, principally resulting in increased litter size, weight and milk production. In his experiment there were no correlated changes in growth or the weights of either the carcass components or internal depots except for an opposing result of the low efficiency line being fatter at maturity. From these results Stephens (1991) indicated that it is unlikely that there will be deleterious effects of selection for maintenance requirements on production traits. However, caution must be exercised if selection for a highly efficient animals is undertaken in larger species. Shuey *et al.* (1993) indicated that high efficiency breeds may be at a disadvantage due to a less adaptable maintenance requirement. Luiting *et al.* (1995) also showed that high efficiency pigs might be more prone to stress resulting from a less than desirable environment. Webster, (1989) suggested that traits that favour efficiency in the breeding female, such as small size, increased fat deposition etc. may be diametrically opposed to those traits that are ideal for efficient meat production such as high growth and a greater lean content in the progeny, which contrasts with the earlier conclusions of Stephens (1991).

Selection for growth and lean content of the carcass has had dramatic effects on maintenance efficiency. Selection for growth has been shown to improve the efficiency of energy utilisation for growth, although the maintenance costs of the breeding herd will increase due to the larger mature size of the breeding female. (Webster, 1989; Veerkamp and Emmans, 1994). As selection for growth is a function of voluntary food intake, then efficiency increases, as the proportion of energy that is utilised for non-productive maintenance costs become comparatively smaller with respect to the costs associated with gain. However, Herd (1995) showed that feed costs of maintenance per unit of liveweight was lower in high growth rate cows than in a line selected for low growth rate, indicating that the efficiency of feed utilisation of the larger mature size breed is improved. In contrast the equivalent comparison of lines selected for weaning weight in sheep showed no difference in the feed requirements for maintenance when expressed per kilogram of liveweight (Herd *et al.*, 1993). Owens *et al.* (1993) indicated that selection for an index of growth rate scaled for mature weight might enhance metabolic efficiency at other stages of growth and should avoid the bias associated with higher lean mass at a given weight with the greater mature body size. Recently Fan *et al.* (1996) indicated that cows with higher body weights were more efficient for fetal growth, consumed slightly more energy and had desirably lower residual feed intakes than cows with lighter body weights.

Selection for an increase in lean has been predicted to decrease maintenance efficiency due to the higher costs of maintaining lean than fat (Olthoff and Dickerson, 1989a). In comparisons of lines selected for lean growth compared to controls, the lean animals do have higher maintenance costs per unit of liveweight (Hofstetter and Wenk, 1985; Rao and McCracken, 1991; Ball *et al.*, 1995; Cameron *et al.*, 1995). However as shown by Ball and Thompson (1995). the reduction in maintenance efficiency that occurs through selection for lean growth was compensated for by improvements in growth efficiency and salable lean product resulting in no overall loss in terms of biological efficiency for a meat producing enterprise. Surprisingly, Bishop (1992) showed that lean food conversion ratio (LFCR) was strongly correlated with estimates for  $Me_m$  (scaled for metabolic size), indicating that selection for LFCR might have a beneficial effect of reducing maintenance requirements in growing bulls.

Recently Arthur *et al.* (1996) indicated that significant variation existed between individuals and sire progeny groups for postweaning net feed intake. They suggested from phenotypic correlations with production traits, that selection for NFI was associated with lower feed intake, better feed conversion and lesser deposition of subcutaneous fat during the test period. Fan *et al.* (1996) indicated that although selection may change residual feed intake, the trait was sensitive to methods of adjustment for weight change and involves considerable difficulties in measurement. However Genand *et al.* (1996) showed that progeny from bulls selected for superior NFI had higher growth rates, greater weights of muscle and lower weights of total body fat when compared to the progeny from bulls that had inferior NFI. They suggested that selection for growth rate and residual feed intake may be an index that allows producers to discriminate bulls on their efficiency and muscular growth.

Overall, Veerkamp and Emmans (1995), indicated that there is no strong evidence to allow us to assume that there are genetic differences in either the partial efficiencies for maintenance or growth or in residual feed intake. Further evidence needs to be collected to determine whether there is true genetic variation in maintenance or growth efficiency. They concluded that high genetic merit animals are more efficient because they partition more of the available energy towards production and not because the processes used to transform consumed feed into a desirable product, is more efficient in these animals.

### **2.1.5 Conclusions**

It is clearly apparent that the present empirical feeding systems in use by nutritionists throughout the world relies on estimates of the energy costs of those metabolic and physiological processes that are apparently associated with “maintenance”. Whilst there have been numerous studies and statistical approaches that have described and removed variations in the estimates of maintenance requirements, there still remains significant variation in maintenance requirements that cannot be accounted for by present methods. In the future as experimental and analytical techniques continue to develop, precise mathematical descriptions of the underlying processes will enable the construction

of models that describe maintenance and production as robust continuous functions rather than as static discrete variables which have limited biological application. This concept of a superior model for describing energy utilisation in production systems may not occur for a considerable time period, however research that develops mechanistic descriptions of the elements of “maintenance” will contribute to a substantial reduction of that time period.

## **2.2 Tissue mobilisation and accretion patterns during natural and enforced periods of feed restriction: Aspects of Compensatory growth.**

### **2.2.1 Introduction**

Sheep and cattle maintained in most Australian production systems are subjected to a wide seasonal variation in both pasture supply and quality that can lead to periods of restricted growth involving either reduced growth, weight stasis, or in severe situations, weight loss. When feed supply becomes non-limiting after a period of restricted growth there is a phase of growth referred to as compensatory gain or growth (O'Donovan, 1984; Ryan, 1990; Broekhuizen *et al.*, 1994). This phenomena has generally been thought of as a product of reduction in maintenance requirements, a decrease in the energy value of body mass gains, an increase in feed intake (appetite) and in some cases an improvement in the utilisation of energy above maintenance requirements for growth (O'Donovan, 1984; Greef *et al.*, 1986a; Ryan, 1990). The ability to predict and then manipulate the effects of compensatory growth depends on an understanding of the mechanisms that are involved, and outcomes during the restriction and realimentation.

The real value for the producer and the industry, is a knowledge of how to use compensatory growth to control and then manipulate both feed efficiency and body composition of the animal in order to meet the carcass specifications of various markets. For this reason, quantifying and then predicting the changes in body components, both with respect to time and weight, during both the feed restriction and realimentation period is critical for the optimal practical use of compensatory growth.

### **2.2.2 *Ad libitum* or Normal growth**

The accumulation of body tissues in animals when fed *ad libitum* is often defined as "normal growth" and it is these tissue accretion patterns against which most comparisons of the component changes that occur during compensatory growth are made. Tulloh, (1963) indicated that the effects of nutrition and age on the carcass composition of

normally grown animals were minimal when compared to the influence of body weight. He also suggested that the most variable component was body fat. The changes in individual components during normal growth have been quantified with respect to weight by the allometric function (Huxley, 1932; Tulloh, 1963; Fourie *et al.*, 1970). In general, as body weight increases the proportion of fat increases (allometric coefficient ranges from 1.5 to 2.0), the proportion of muscle decreases slightly, or remains constant (allometric coefficient ranges from 0.9 to 1.0) and the proportion of bone decreases (allometric coefficient ranges from 0.6 to 0.8). A similar pattern is observed for the chemical components of fat, protein and ash.

The rate at which tissues are deposited relative to empty body weight during normal growth differ for sexes. Relative to rate of maturing for the total body, fat in entire males is earlier maturing than in females, whilst muscle and bone is later maturing in males than in females for both sheep and cattle (Berg and Butterfield, 1976; Butterfield, 1988). Thompson (1983) showed that there was a crossover point for body component development of rams and ewes which occurred at near 50% of maturity. He showed that ewes contained more muscle and less fat prior to 50% of maturity, where near equal with rams at 50% of maturity, and contained significantly lower proportions of muscle and higher proportions of dissectible fat at maturity. Thompson (1983) showed that there was a major difference in fat partitioning between the sexes, with ewes partitioning more of their fat into the subcutaneous depots and less into intermuscular fat at maturity. However Butterfield (1988) highlighted that, due to differences in maturity patterns of the different fat depots, at slaughter weights of sheep there is little difference in fat partitioning between the two sexes.

Castrated animals are usually slightly leaner than females at any stage of maturity (Kellaway, 1973; Butterfield, 1988). When compared to entire males, castrates have lower proportions of muscle and bone and higher proportions of fat. Castration changes the proportion of fat within each depot, with higher proportions of subcutaneous fat and lower proportions of intermuscular and internal fat being recorded in the castrate (Butterfield, 1988). The maturity type of the breed also affects the proportions of tissues when

expressed on a weight basis. Earlier maturing breeds will have more fat and less lean tissue if compared at the same weight (Searle *et al.*, 1972, Berg and Butterfield, 1976; Butterfield, 1988). However at maturity the relative proportions of each tissue will be similar for large and small frame animals.

### **2.2.3 Response of Animals to a period of feed restriction**

One of the most important components of compensatory growth is the relative changes in tissue weights that occur during the periods of feed restriction prior to this growth (Butler-Hogg, 1984; Iason *et al.*, 1992). Clearly the severity and duration of the feed restriction will influence the patterns of tissue mobilisation. Other factors however, including sex and stage of maturity, must be considered. In general, the consequence of a period of feed restriction on body components can be categorised into situations where growth is reduced but is positive, liveweight is maintained, or where weight loss occurs.

#### **2.2.3.1 Restricted positive growth**

Several studies have examined the effects of restricted feed intake on the composition of growth. Most studies have showed that composition at any point in time is primarily dependent on the empty body weight of the animal and less so on age, or previous feed restriction (Burton and Reid, 1969). Although restricted animals require longer to reach a given weight and thus are usually older when compared to *ad libitum* fed animals (Greef *et al.*, 1986a). At this stage it remains unequivocal on whether plane of nutrition has an effect on the carcass composition of restricted versus *ad libitum* fed animals. Black (1974), Turgeon *et al.* (1986), Bass *et al.* (1990), Marias *et al.* (1991a) and Wright and Russel (1991) have all reported that when compared at the same liveweight, animals that had been restricted below *ad libitum* had lower proportions of fat and higher proportions of lean than unrestricted animals (although the effect diminished as animals approached mature size; Black, 1974). It appears that restricting the energy that is supplied above that for maintenance results in a decline in rate of fat accretion, whilst maximal rates of lean deposition are maintained (Bass *et al.*, 1990). This is supported by the results of Marias *et al.* (1991a) and Murphy and Loerch (1994) who showed



respectively, that lambs and steers restricted to 80% of ad libitum had lower daily fat accretion rates, although daily accretion rates of protein and water were unaffected.

Steen (1995), showed that feed restriction had a greater effect on carcass lean growth in entire males compared to castrates and females. He suggested that the effect of the feed restriction will have the greatest effect on that tissue which is undergoing the greatest change at the time which the restriction is enforced. Butler-Hogg and Johnsson (1986) showed that there was virtually no effect on growth path on the weight of carcass muscle in growing ewe lambs. This contrast between the sexes may represent a difference in the priority for tissue deposition, with fat deposition being earlier in the female and therefore more prone to an effect of nutrition.

However there are experimental results that show that plane of nutrition has no effect on the body composition of growing animals (Kellaway, 1973, Drennan, 1979). Whilst others show 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, although the proportions of protein to energy in the experimental rations used, will alter the relative rates of fat to protein deposited (Black, 1974; Butler-Hogg and Johnsson, 1986; VanHouten, 1991) which may explain some of the differences observed. The stage of maturity at which the restriction is enforced and the point in time where the restricted versus ad libitum fed animals are compared will also contribute to the variation (Carstens *et al.*, 1991).

In contrast to the effects on the carcass, there appears to be little effect of mild feed restriction on the development rates of the non-carcass components (O'Donovan, 1984). However there are a few exceptions to this, the most notable being the effect on the liver. Liver weight was higher in restricted bulls (Leeche, 1973), whilst both the kidneys and liver were lighter in restricted steers when compared to *ad libitum* fed steers (Wright and Russel, 1991). However, Sainz (1995a) stated that liver weights were not closely related to changes in energy expenditure in restricted steers and may not be a reliable indicator of total visceral organ mass.

As mildly restricted animals are older when compared at the same weight, it is expected that carcass bone weight and the weight of both head and feet would be heavier in these animals (Wright and Russel, 1991). This observation agrees with the conclusion of Murray *et al.* (1974) that any phase of restricted growth that lengthens the time taken for animals to mature will increase the proportion of bone at a given weight or age prior to maturity. Murray *et al.* (1974) indicated that low growth rates in steers (0.4 kg/day) increased the relative proportion of the connective tissue associated with the skeleton at the same carcass weight when compared to steers grown at a faster (0.8kg/day) growth rate.

Fat partitioning is influenced by restricted levels of positive growth. Ledger and Sayers (1977) observed higher levels of subcutaneous fat as opposed to intermuscular fat in steers fed a higher plane of nutrition. A similar result was observed by Wright and Russel (1991), who found higher weights of subcutaneous fat weight in high versus low plane fed steers with only minor differences in the other fat depots. Hodge and Star (1984) recorded differences in fat depths and internal fat weights between low and high plane fed lambs, the higher plane fed lambs had greater depth and weight, respectively. Butler-Hogg and Johnsson (1986) showed that the greatest relative change in fat tissues when ewe lambs were restricted occurred in the carcass fat depots when compared to internal fat depots. In contrast Murray *et al.* (1974) showed that nutritional restriction had a greater effect on the internal fat of growing steers. In general a period of feed restriction will affect the fat depots that are undergoing the most change at the time at which the restriction is placed. In the majority of experiments, restriction occurred during the finishing phase and consequently the greatest effect is on the later maturing carcass fat depots.

### **2.2.3.2 Weight stasis**

Imposing a period of weight stasis during growth forces the animal to alter metabolic activities and priorities for tissue deposition and mobilisation (Tess *et al.*, 1984) and thus there is likely to be significant changes in body composition during weight stasis that will affect the animals ability to compensate during realimentation. A decline in the

weight and proportion of visceral organs, particularly the liver and the digestive tract, is the most notable change in body composition that occurs in animals that are maintaining liveweight (Foot and Tulloh, 1977, Murray and Slezacek, 1988b, Ryan and Williams, 1990; 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 (Foot and Tulloh, 1977; Ledger and Sayers, 1977; Turner and Taylor 1983; Afonso, 1992).

Liveweight is maintained 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, 1990). This results in an increase in fat as a proportion of the both the carcass and of the empty body weight. The results from Fox *et al.* (1972), however indicated that initial body composition prior to the period of weight stasis might influence the changes that do occur in body components. They showed that fatter animals tend to gain body fat during weight maintenance whilst leaner animals mobilised body fat. In contrast there appears to 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 Afonso (1992) showed that lambs maintaining weight increased both total body fat and carcass lean, to compensate for a decline in visceral organ weights. Afonso (1992) also showed that the proportion of subcutaneous fat declined relative to proportions of intermuscular and internal fat. 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.

Warrington *et al.* (1988) showed that in pregnant heifers fed to maintain maternal weight, carcass lean increased at the expense of carcass fat. Afonso (1992) also showed a

similar pattern in pregnant ewes fed to maintain maternal weight. Thus it appears that pregnancy can alter the priorities for tissue conservation whilst an animal maintains weight.

In pigs, the effects on body components of imposing a period of weight stasis on immature animals appears to be the reverse pattern to ruminants. Pekas (1993), Luiting *et al.* (1995) and Kolstad and Vangen (1995), showed that carcass lean weight increased at the expense of carcass and internal fat reserves. There was no decline in visceral weights, as recorded for ruminants, in either of the latter studies, although the study of Pekas (1993) indicated that there was significant catabolism of the visceral organs and this enabled accretion of the lean tissue in the carcass to be continued.

The seasonal effect on priorities for tissue mobilisation and deposition must be considered when quantifying the changes in body composition that occur when animals are forced to maintain weight. A seasonal effect on body components when adjusted to the same empty body weight, has been shown in sheep (Ball *et al.*, 1996), mature cows (Laurenz *et al.*, 1992) and mature fallow deer does (Weber and Thompson, 1995). All studies showed that body fatness increased in summer and decreased in winter. It may be that the increase in body fatness and decline in lean that has been observed for animals experiencing weight stasis may be a reflection of seasonal influence (Greef *et al.*, 1986b; Nicol and Kitessa, 1994).

The impact of experimental design also must be taken into account when evaluating an animal's response to weight stasis. Black (1974) suggested that if the level and frequency of feeding is such, that there is a period of starvation then infrequent feeding, such as once a day, results in fatter animals. Most experiments where changes in body composition at weight maintenance have been measured have used once daily feeding, which may indicate that the changes observed are simply a function of frequency of feeding.

Black (1974), indicated using simulated data that at maintenance energy intakes there would be a gain in body protein and a loss in body fat. This opposes the majority of experimental results and suggests that the pattern of nutrient uptake will also influence body composition at weight stasis. Importantly, during maintenance pigs showed an increase in protein and a decrease in fat within the carcass (Enting *et al.*, 1990; Pekas, 1993), suggesting that the pattern of nutrients forthcoming from the rumen influences body composition during weight stasis. Both Meyer and Clawson (1964) and Phillipson (1955) recognised the importance of considering the effect of a long term restricted feed intake on rumen microbe populations, although to date there is no experimental evidence that relates the changes that occur in rumen microbe populations to body composition changes during feed restriction periods.

### **2.2.3.3 Weight loss**

The mobilisation of body components to meet a net energy deficit during weight loss has received considerable attention (for reviews see O'Donovan, 1984, Ryan, 1990). 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 the mobilisation of lean tissue that results in a loss of both protein and water from the body. This occurs primarily from a reduction in the size of the visceral organs (heart and liver) and of the digestive tract and is followed by a loss of muscle tissue from the carcass (Meyer and Clawson, 1964; Drew and Reid, 1975a, Winter *et al.*, 1976; Thorton *et al.*, 1979; Searle *et al.*, 1979; Butler-Hogg, 1984, Ryan *et al.*, 1993b). The weight of the skin is also reduced during the early phase of weight loss as shown by Little and Sandland (1975), who noted that protein contained within the skin tissue is highly labile. There is a reduction in some fat, primarily from the carcass fat depots (Berg and Butterfield, 1976), although this varies with physiological state and the sex of the animal.

As weight loss progresses the rate at which lean in both the carcass and the viscera declines and the rate at which fat from the carcass depots is mobilised increases (Drew and Reid, 1975a; Aziz *et al.*, 1992). It appears there is selective depletion of fat from the subcutaneous depot to meet the energy deficit during weight loss, whilst the weight of

internal depots remains relatively unaffected (Robinson, 1948; Butterfield, 1966; Seebeck, 1967; Russel *et al.*, 1968; Little and Sandland, 1975). However Seebeck and Tulloh (1968) showed that if weight loss occurred at low body weight, there was a lower proportion of kidney and channel fat in the carcass at the end of the weight loss phase, whilst weight loss at higher weights resulted in a greater proportion of kidney and channel fat in the carcass at the end of the weight loss phase. From these results it is clear that if animals are compared with controls during the earlier phase of weight loss they will be comparatively fatter, whereas animals that have been in a weight loss phase for a longer time period will be assessed as leaner than controls (Butler Hogg, 1984; Aziz *et al.*, 1992)

The rate of weight loss has a significant effect on the proportions of lean and fat that are mobilised. The model proposed by Black (1974) showed that a high rate of weight loss would result in a higher rate of lean mobilisation and that a lower rate of weight loss would result in a higher rate of fat mobilisation. The predictions from Black's model were confirmed by results (Searle and Graham, 1972; Butler-Hogg, 1984) that showed that sheep which have lost weight rapidly are proportionally fatter and sheep that have lost weight slowly are proportionally leaner, when compared at the same weight to animals that have been unrestricted. Both Black (1974) and Searle *et al.* (1979) suggested, that given time to equilibrate at a new lower weight, animals will return to a body composition similar to that of the unrestricted animal.

The results of both Thorton *et al.* (1979) and Butler-Hogg and Tulloh (1982) indicate that there is a differential response to weight loss in mature versus immature animals. Immature animals mobilise higher proportions of lean during weight loss when compared to mature animals, whereas mature animals mobilise a higher percentage of fat, particularly from the internal depots, although there is an increase in body fatness as a proportion. Seebeck (1967) indicated that there was a differential effect of stage of maturity on the relative losses of internal organs during weight loss. He showed that as animals matured, they retained proportionally more liver, kidney and gut tissue. Seebeck (1967) indicated that the visceral organs may be less affected by weight loss in animals of higher weight as they contain proportionally less labile protein. The inability of immature

animals to conserve lean components may be a reflection of their lower proportions of body fat (Hogg, 1977), as more fat becomes available in the carcass for mobilisation to support body energy needs as the animal matures (Seebeck, 1967; 1973).

However a lack of mobilisation of fat reserves in mature animals has also been observed (Panaretto, 1964; Hight and Barton 1965), where ewes subjected to severe feed restriction maintained carcass fat depot weights. In both experiments animals died whilst still having significant amounts of fat, particularly in the subcutaneous depot. There is some evidence to suggest that animals that go through periods of weight cycling involving both loss and gain, as would be the case for reproductively active mature ewes, lose the ability to regulate fat mobilisation resulting in obesity (Rozen *et al.*, 1994).

Dissections of mature ewes have shown that a low plane of nutrition does not significantly reduce the weight of bone (Robinson, 1948; Hight and Barton, 1965), although, as a proportion of the total body, ash weight has been shown to increase as a result of severe depletion of both body fat and protein (Rattray *et al.*, 1974). Seebeck and Tulloh (1968) showed that the combined weights of bone and connective tissue remained relatively constant during body weight loss in immature steers. But indicated that the stage of maturity at which the restriction is imposed influenced bone weight and not connective tissue weight. In lighter steers bone weight was reduced during weight loss, whilst in heavier steers bone weight increased.

Consideration of 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 observed during weight loss. In most experiments, weight loss has been achieved by restricting the supply of a high quality diet. However 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, and 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 this experiment and that of Fattet *et al.* (1984), energy restricted lambs mobilised carcass fat as well as 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. Recently work by Chowdhury *et al.* (1995) has shown 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.

In association with a period of weight loss, there are a number of metabolic and endocrine changes that enable the animal to prioritise the patterns of tissue mobilisation that have been observed. The reduction in the visceral organs, as discussed previously, is seen as a mechanism whereby animals can rapidly reduce their maintenance requirements (Ferrell *et al.*, 1986; Ferrell, 1988; Ryan, 1990). The results of Graham and Searle (1979), who showed that BMR declined in lambs that were losing liveweight, and Ledger and Sayers (1977), who showed a decline in maintenance requirements in steers undergoing weight loss, support this conclusion.

Robinson (1948) and McManus *et al.* (1972) showed that the digestibility of feed in animals undergoing weight loss was higher than that of control animals. Interestingly, Grimaud and Doreau (1995) indicated that the protozoa populations declined during feeding in cows fed below maintenance. Evidence from experiments conducted on sheep and cattle suggests that there is an increased protein supply from the rumen in animals that have been defaunated (Leng, 1988; Bird, 1988). It is possible that an increased level of protein may reduce the level of protein loss in animals during weight loss. Grimaud and Doreau (1995) also showed that a reduction in feed intake lead to an increase in N<sub>2</sub> utilisation through a reduction in the endogenous urinary losses. Yambayamba *et al.* (1996a) showed that nitrogen utilisation was improved in heifers that were feed restricted, although there was no recorded difference in steers or bulls. In contrast Iason and Manetcom (1993), showed that there was no effect on growth path on the digestibility of feed offered to growing lambs.



Hart *et al.* (1992) showed that during liveweight loss, there is a significant reduction in plasma insulin, glucose and urea and increased non esterified fatty acids (NEFA). They suggested that these characteristic changes in endocrine and metabolic adjustments are necessary for the animal to preserve protein whilst mobilising fat. Both Hayden *et al.* (1993) and Yambayamba *et al.* (1996a) showed that GH increased during weight loss, whilst insulin like growth factor-1 (IGF-1) decreased, which Beermann *et al.* (1990) suggested favoured the retention of protein at the expense of fat. Yambayamba *et al.* (1996a) indicated that compensatory growth could be described as a function of the persistence of the changes to the GH / IGF-1 / Insulin axis which promotes protein accretion when feeding levels are returned to normal.

#### **2.2.4 Compensatory growth or Realimentation**

The classic response of animals showing compensatory growth is an acceleration in liveweight gain as feed availability increases and the period of restricted growth ends (O'Donovan, 1984; Ryan, 1990). From the literature it is clear that compensatory gain occurs in two phases (Fox *et al.*, 1972; Turgeon *et al.*, 1986, Wright and Russel, 1991; Ryan *et al.*, 1993a,b), with the phases being the reverse pattern of weight loss. The initial phase of compensatory gain has a high rate of lean deposition that primarily reflects the replenishment of the visceral organs and the digestive tract. (Butterfield, 1966, Butler-Hogg, 1984; Greef *et al.*, 1986b; Ryan, 1990; Drouillard *et al.*, 1991a,b; Iason and Mantecom, 1993).

The most notable experimental result that demonstrated the first phase was that of Drew and Reid (1975a), who showed that the first five kilograms of gain was due primarily to an increase in visceral mass of organs and the digestive tract in lambs that had previously lost body weight. In that experiment it is interesting to note that fat continued to be mobilised whilst this period of protein deposition occurred. Searle and Graham (1975) and Kabbali *et al.* (1992a) both showed that in compensating lambs the early phase was dominated by protein deposition with the later phase showing a similar composition of gain as that for normally grown animals. In cattle Fox *et al.* (1972), Rompala *et al.* (1985)

and Wright and Russel (1991) showed that steers deposited more protein during the initial stage of compensation. Therefore in the earlier stages of compensatory growth of cattle (<350kg), compensating animals will be leaner than *ad libitum* fed animals. In all three experiments fat deposition in cattle increased in the latter part of compensatory growth such that by 450-500kg there was no difference between previously restricted and control animals. Mosoni *et al.* (1996) has concluded from studies in fasted and refed rats, that the opposing controls of ribosome number that coordinates responses in liver and muscle protein synthesis, allows muscle proteins to be spared during fasting at the expense of liver proteins and hence facilitates the rapid recovery of liver protein during refeeding

It has long been suggested that a change in the protein synthesis and degradation rates allows the animal to sustain the increase in lean deposition (Ryan, 1990). Indeed, during realimentation, animals that have been previously restricted show an increase in the rate of both lean and protein deposition (Greef *et al.*, 1986b; Marias *et al.*, 1991a). Recent evidence from rats (Kreienbring *et al.*, 1994) indicates that the increase in lean accretion that occurs in compensating animals results from an increase in protein synthesis, whilst the rate of protein degradation is almost unaffected. This contrasts with recent studies that have indicated that elevated IGF-1 plays a role in the compensatory gain effect (Hays *et al.*, 1995; Wester *et al.*, 1995). This recent work suggests that as IGF-1 reduces the rate of degradation, this provides a mechanism that increases accretion rates during the compensatory phase. Growth hormone levels also remain at an elevated level during the early phase of compensatory growth, which enables protein accretion to be favoured by reducing fat accretion through inhibiting glucose utilisation for lipogenesis (Claus and Weiler, 1994). As GH levels return to normal during realimentation this inhibition of fat synthesis diminishes allowing fat accretion to proceed in the latter phase of compensation.

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. The type of feed restriction also influences the response during early realimentation. Drouillard *et al.* (1991) showed that lambs previously restricted in protein were able to regain a large proportion of lost protein in the first 2 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 2 weeks of realimentation. McLennan (1994) presented a clear argument for the need to consider the effect of protein to energy ratios in the diet when explaining the observed response or, in some experiments, lack of response, in compensating cattle.

As Ryan *et al.* (1993b) suggested, replenishment of both liver and digestive tract is the major priority for compensating animals, with the majority of experiments that have examined compensatory growth showing no differences in the weights of the non-carcass component between compensatory and normally grown animals (O'Donovan, 1984; Ryan, 1990). 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). This 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 that this phase of fat development during the latter part of compensatory growth that enables animals to obtain a similar body composition as animals that have not been restricted. Hayden *et al.* (1993) showed that there was a differential effect on fat partitioning of compensatory growth with compensating steers still having lower internal fat weights at a final endpoint. They suggested that a period of feed restriction will have a greater effect on the internal depots when compared to the later maturing subcutaneous and intramuscular fat depots, which will respond to lipid accumulation during the latter stages of compensatory growth.

Black (1974) indicated that a higher level of energy supplied at the tissue level would cause an increase in the rate of fat:protein deposition. Given that restricted animals during realimentation have lower maintenance requirements than unrestricted animals, when compared at the same liveweight, (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, 1991a), 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 is not solely a function of a higher feed intake of compensating animals as suggested by Ryan *et al.* (1993a,b). However, Thorton *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, and as a result it is still possible that the deposition of fat may be due to maturity rather than as an associated effect of compensatory gain.

The severity of the restriction plays an important role in the response of animals during compensatory growth. This has been discussed in the review of O'Donovan (1984) and shown in the results of Greef *et al.* (1986b), where a higher degree of restriction led to a higher rate of realimentation in cattle and sheep. There is however an important case to consider for severely restricted animals. Animals near, or at, maturity that experience a period of severe feed restriction, may not compensate fully, if compensation is expressed on a liveweight basis, even when offered *ad libitum* feed (Ryan, 1990). Both 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, loses its ability to compensate and thus there is an alteration in both endocrine control of, and substrate supply for, tissue accretion in the carcass. As Broekhuizen *et al.* (1994) identified, physiological modifications, such as reduced maintenance requirements after feed restriction or increased assimilation efficiency during realimentation, must act at some long-term cost to tissue turnover and repair. As a result, in severe cases of weight loss, such disruptions may cause animals to

effectively arrive at a new equilibrium weight and composition after the period of realimentation.

Collectively, there appears to be no difference in body composition between restricted and continuously grown animals, given that the period of compensation is of sufficient time 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, 1991; Ryan *et al.*, 1993a,b). The longer the recovery period before the effects of compensatory growth are determined, the greater the possibility that animals, when compared at the same weight, will show no difference in body composition (Bass *et al.*, 1990). Thus it is possible that results from Burton *et al.* (1974), Drew and Reid (1975a), Little and Sandland (1975), and Foot and Tulloh (1977), who showed that restricted animals were leaner than *ad libitum* fed animals, may be due to the fact that comparisons were made before animals had finished compensatory growth. Although, Kabbali *et al.* (1992a) 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. From the previous observations, it is also important that comparisons between compensating and control animals be made at live weights that are of commercial significance (market specified weights), as the weight at which animals are slaughtered during compensation can greatly affect the conclusions of compensatory growth studies (Turgeon *et al.*, 1986).

In contrast, there are a number of studies which suggest that the stage of maturity at where the restriction is imposed will affect the ultimate carcass composition of the animal as it nears maturity (Carstens, 1995). If restriction is imposed at a very early stage of maturity, it appears as though the protein deposition curve of the animal can be altered such that compensatory growth animals at near maturity are fatter than control animals (Thorton *et al.*, 1979; Tudor *et al.*, 1980). However Carstens (1995), using a growth simulation model of Keele *et al.* (1992), showed that imposing a restriction on cattle at three months of age will have little effect on total body fat at maturity. At about 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 will have little effect on the ultimate body composition of the animal.

As an animal nears maturity, the composition of growth is more likely to be leaner during the compensatory period resulting in leaner animals (Thorton *et al.*, 1979; Wright and Russel, 1991, Carstens *et al.*, 1991). The differences may be that a high proportion of fat was mobilised during the restriction period in mature animals as opposed to immature animals where proportionally more lean is lost (Thorton *et al.*, 1979). At maturity, Hight and Barton (1965) showed that ewes that had lost 10% and 19% of their body weight during a 21 and 42 day restriction period did not compensate and had no gain in body weight after the restriction, even though feeding was *ad libitum* during a 40 day realimentation period. Collectively these results show that there is an ability to obtain a specific market required body composition at slaughter weights through nutritional manipulation at differing levels of maturity

Hormonal regulation of compensatory growth has been implicated but not directly shown (Bass, 1994). Ellenberger *et al.* (1989) and Hayden *et al.* (1993) showed that plasma IGF-1 levels were significantly higher at the same liveweight in realimentating steers when compared to *ad libitum* fed control steers. Higher levels of IGF-1 also occurred in lambs during the realimentation phase (Wester *et al.*, 1995). Bass (1994) suggested that IGF-1 plays an important role in enhancing the animals ability to grow following the nutritional restriction. Although growth hormone levels decline during the compensatory growth phase, it appears as though there is a sufficient lag-phase before the levels return to that of normally grown animals (McManus *et al.*, 1972; Bass, 1994). As elevated growth hormone levels favour lean accretion (Pullar *et al.*, 1986; Collier *et al.*, 1992), it is possible that the high levels of protein deposition that occurs in the early phase of compensation. Johnson *et al.* (1985) showed that treatment with growth hormone stimulated the development of the non-carcass visceral lean components and had little effect on the carcass muscle, which may indicate why there is the preferential repletion of visceral organs at the expense of carcass muscle and fat tissues (Ryan, 1990).

### **2.2.5 Conclusions**

Changes in maintenance requirements, efficiency of growth, feed intake and the energy content of differential tissue depletion and deposition all affect body composition during periods of feed restriction and realimentation in both sheep and cattle. As such, the influence of compensatory growth on body composition must be considered when supplying carcasses at particular market weights. Animals that are restricted, but maintain positive growth have been shown to be proportionally leaner, proportionally fatter or not different from unrestricted animals, with the type of restriction influencing the observed result. Animals deplete non-carcass tissue and increase carcass weight, particularly fat, when forced to maintain weight. Animals that lose weight do so in two phases, the initial period involving mobilisation of non-carcass lean tissue, followed by carcass muscle. As the period of weight loss continues an increase in the rate of mobilisation of fat occurs, whilst the rate of lean mobilisation decreases.

The pattern of body tissue deposition that occurs in animals that have been previously restricted also occurs in two phases. Replacement of non-carcass tissue is a priority during the early stage of compensatory growth. As the period of realimentation increases and the proportion of non-carcass tissue achieves that of unrestricted animals, the rate of fat deposition increases. Consequently previously restricted animals will be proportionally leaner during the early phase of compensatory growth, but when compared in the latter stage there will be only minor differences between realimentating and unrestricted animals. Only in severely restricted animals does there appear to be a permanent effect of feed restriction on body composition as animals approach maturity during realimentation.

Compensatory growth is of vital importance in those Australian environments where pastoral animals experience a period of feed restriction such that growth is below that of normal unrestricted animals. The phases of compensation that have been identified during realimentation indicate, that through the use of compensatory growth, there will be critical weights at which animals may be slaughtered to meet specific fatness/weight specifications for both domestic and export markets. However as the data provided from

numerous experiments indicates, prior periods of feed restriction does not grossly affect carcass composition of compensating animals at empty body weights near maturity. As a result the biological and economic constraints and efficiencies of balancing feed surpluses and deficits may ultimately control the utilisation of compensatory growth in grazing situations.