Chapter 5

Body compositional changes in immature Merino rams and ewes during periods of feed restriction and realimentation.

5.1 Introduction

There have been a number of studies that have described changes in body components during weight loss and realimentation for both sheep and cattle (for reviews see O'Donavan 1984, Ryan 1990 and Carstens 1995). However the responses that have been observed are confounded by factors such as severity of the restriction, duration of the restriction and realimentation periods, season and the maturity of the animal at the time the restriction has been enforced. Chapter 3 described changes in body composition of mature sheep that had undergone a period of feed restriction at two levels of severity followed by a period of realimentation. The changes in body composition that occurred during the weight loss and realimentation periods for the mature sheep differed dramatically from the changes in body composition that have been documented for immature sheep (Aziz *et al.*, 1992, 1994; Kabbali *et al.*, 1992b; Kamalzadeh, 1996). The lack of complete compensation of carcass muscle during the realimentation period for the mature sheep that have undergone weight loss was the major difference to previously published results for immature sheep (Drew and Reid, 1975a, Ryan *et al.*, 1993b).

Chapter 3 highlighted the importance of describing changes in body composition within individual animals, suggesting that variation in response between animals may be leading to considerable errors of estimation of treatment effects for those studies that have relied on indirect techniques or serial slaughter. Clearly the precision of estimation of changes in body composition within individuals over time (Afonso, 1992; Thompson and Kinghorn, 1992) will improve the ability to quantify the magnitude of the changes in body composition that occur in immature sheep during weight loss and realimentation. More importantly a description of the relationships between body components within individual animals will enhance models that have been constructed to predict the effect that feeding level has on body tissue development (Baldwin, 1995).

The influence of stage of maturity on the nature of tissue deposition that occurs during compensatory growth may be a response to differences in relative losses of both lean and fat tissues that occur during the restriction period (Butler-Hogg, 1984). Comparisons of immature with mature sheep during feed restriction (Thornton *et al.*, 1979; Butler-Hogg and Tulloh, 1982) indicate a differential response in terms of the rates and proportions of body tissues that are mobilised during weight loss. Immature sheep mobilise higher proportions of carcass lean during weight loss when compared to mature animals, whereas mature animals mobilise a higher percentage of fat, particularly from the internal depots (Thornton *et al.*, 1979). However Butler-Hogg and Tulloh (1982) showed immature ewes mobilised significantly more fat from the carcass than mature ewes who lost more carcass muscle. The greater loss of lean tissue in immature animals may be a reflection of their lower concentrations of body energy (Hogg, 1977), as the greater level of body energy that is stored in the form of adipose tissue as an animal matures would be available for mobilisation to meet an energy deficit (Seebeck,1973).

The work or Fourie *et al.* (1970) and that of Thompson *et al.* (1985b) showed that there were clearly defined differences between rams and ewes in the patterns of tissue deposition relative to body weight during uninterrupted growth. Males deposit bone and muscle at a faster rate, and fat a slower rate relative to empty body weight when compared to females. In contrast, very few studies have attempted to compare the patterns of tissue mobilisation during periods of weight stasis or weight loss and then in a period of compensatory gain in males and females at the same stage of maturity. The results of Notter, *et al.* (1983), Murray and Slezacek (1988a,b), Vangen and Thompson (1992), and Afonso (1992) indicate that the body composition changes in immature males and females when fed to maintain weight are similar. Both rams (Notter *et al.*, 1983; Vangen and Thompson, 1992) and ewes (Murray and Slezachek, 1988a) maintained at a constant body weight showed an increase in carcass fat and a decrease in the visceral organs and gut weight. During weight loss the patterns of tissue loss appear to differ between immature males and females. Kellaway (1973) showed that ewes mobilised fat and lean tissue in similar proportions during a period of weight loss. In contrast Jopson *et al.* (1994) showed that over a three week period of feeding at 70% of maintenance, rams actually increased carcass lean weights, whilst fat was lost primarily from the carcass depots.

Marias *et al.* (1991) showed that sex differences in deposition rates occur during restriction and realimentation phases of compensatory growth. They showed that efficiency of feed utilisation for males improved during feed restriction whilst the efficiency for females declined. This difference lead to a marked sex effect on the deposition of body mass during the realimentation period. The deposition rates of protein and fat for the rams that had been previously restricted was greater than *ad libitum* fed control animals, whilst the deposition rates of protein and fat for previously restricted ewes were unable to match the rates for *ad libiium* fed ewe lambs. Marias *et al.* (1991) concluded that differences due to gender were present after a period of feed restriction and if deposition rates of protein and fat as well as body mass are used as criteria, compensatory growth is only exhibited in rams.

Onischuk and Kennedy (1990) showed that there was a sex effect on the differences that occurred in plasma growth hormone and insulin profiles between compensating and normal growth. They showed that whilst there was little effect of compensatory growth on plasma insulin in ewe lambs, there was a significant depression in plasma insulin for the ram lambs. Growth hormone levels for both sexes were elevated during compensatory growth, although the response in rams was six times higher. From the ratio of insulin : growth hormone, Onischuk and Kennedy (1990) suggested that compensatory growth in rams would be expected to promote high rates of lean growth which is concurrent with a priority for muscle growth required for reproductive success. For ewes the maintenance of insulin levels would promote fat deposition in order to increase reproductive soundness. The hormonal differences between the sexes during compensatory growth suggest that the priorities for tissue deposition will differ, which ultimately may affect the relative proportions of fat and lean that are present at slaughter weights.

Taylor *et al.* (1981) showed that the feed required to maintain liveweight was directly proportional to that equilibrium weight (weight$^{1.0}$) in heifers fed at increasing levels of feed intake. This concept, known as the *Taylor time constant* or T_0 (Parks, 1982; refer to figure 2.2), contrasted with the results of Chapter 3, where the equilibrium weight of mature sheep that had been restricted and then refed differed from the equilibrium weight prior to the restriction period, indicating that T_0 is not appropriate for mature animals. The original design of Taylor and Turner (1968) established the concept of T_0 in animals that were always fed at increasing levels of feed intake, but it was unclear whether T_0 was appropriate for animals that had been fed at a higher level of feed intake and then reduced back to an equilibrium feeding level. Ferrell *et al.* (1986) indicated that the growth path affected both the relative deposition rates of body tissues and the efficiency of deposition of body components. They indicated that lambs that followed a high/low growth path had higher maintenance requirements than lambs from a low/high growth path. However the differences observed were not attributable to differences in body composition. More precise estimates of body compositional changes and feed intake in lambs with different growth paths may alter this conclusion. The present experiment examined the changes in empty body weight and its components in immature sheep fed to gain, maintain or lose weight and then fed to prior levels for liveweight maintenance. As a result the effects of feeding treatments on equilibrium maintenance requirements for immature sheep will be investigated.

5.1.1 Null Hypotheses

The null hypotheses that arise from the comparisons of immature rams and ewes are:-

1) *The differential responses in tissue depletion and deposition due to sex during weight loss and realimentation are not apparent in immature sheep*
2) *The concept of an equilibrium relationship between weight and feed intake (To) is appropriate for immature sheep that are fed to gain or lose weight and then returned to a predetermined equilibrium feeding level*
3) *The relative priorities for tissue retention at a equilibrium feeding level are equal for immature sheep that have been fed at higher or lower feeding levels with respect to the equilibrium point*

5.2 Materials and Methods

This experiment was completed with approval from the ACEC at the University of New England Armidale N.S.W. Australia (PACEC 940061). A total of 18 Merino lambs (immature sheep) were used in the present experiment. The design was a 2x3x3 factorial design with two sexes, three levels of feeding and three replicates. The treatments involved are three feeding levels at 60%, 100% and 140% of maintenance.

5.2.1 Experimental Design

The sheep were shorn, vaccinated with a clostridial vaccine, drenched with Ivomectin® and moved into individual indoor pens (3x3 metres) 5 weeks prior to the start of the experiment. The sheep were weighed after a 24 hour fast and an estimate made of the feed required to maintain liveweight using the same equation as used in chapter 3. The equation predicted metabolisable energy needs as a function of metabolic weight with adjustment terms for both age and sex (SCA, 1990). Adjustments were made to the intake level when a sheep had a deviation of ± 2kg in liveweight when weighed after a 24 hour fast every third day for the first two weeks of the pre-experimental period. At this point feed intakes to maintain liveweight had stabilised for all sheep. This level was defined as 100% of maintenance requirements for each individual. All sheep remained at this level until the start of the experiment (3 weeks) and for the first six weeks of the experiment as shown in table 5.2.1

In week 0, animals were CT-scanned for the determination of full body composition and a dye-band (Durafur-Black R) placed into a mid-side point in all animals. During weeks 0-6 animals were fed daily at levels previously calculated to maintain live weight. In week 6, animals were CT-scanned to define changes in body composition during the period of live weight maintenance. At this point a dye-band was inserted to calculate wool growth at body weight maintenance and to obtain estimates of the relationship between the requirements for wool growth and body maintenance.

In week seven, 6 animals (3 immature rams and 3 immature ewes) were fed at 60% of maintenance intakes to establish a period of weight loss. These animals were fed at this level for 15 weeks during which time each individual was CT-scanned at week 3(week 10 of the experiment), 6(13), 9(16) and 15(22) of the weight loss period At the final two scans in this series a dye-band was inserted so that implications of weight loss on wool growth and wool quality parameters could be assessed. Six control sheep (3 of each sex) were held at live weight maintenance and 6 immature sheep (3 of each sex) were fed at 140% of maintenance to create a period of weight gain followed by restriction. These animals were CT-scanned at the same time as the restricted and dye-bands placed in accordingly. Collectively this series of CT-scans is referred to as the treatment phase (weight loss or gain) of the experiment (Table 5.2.1, Figure 5.2.1).

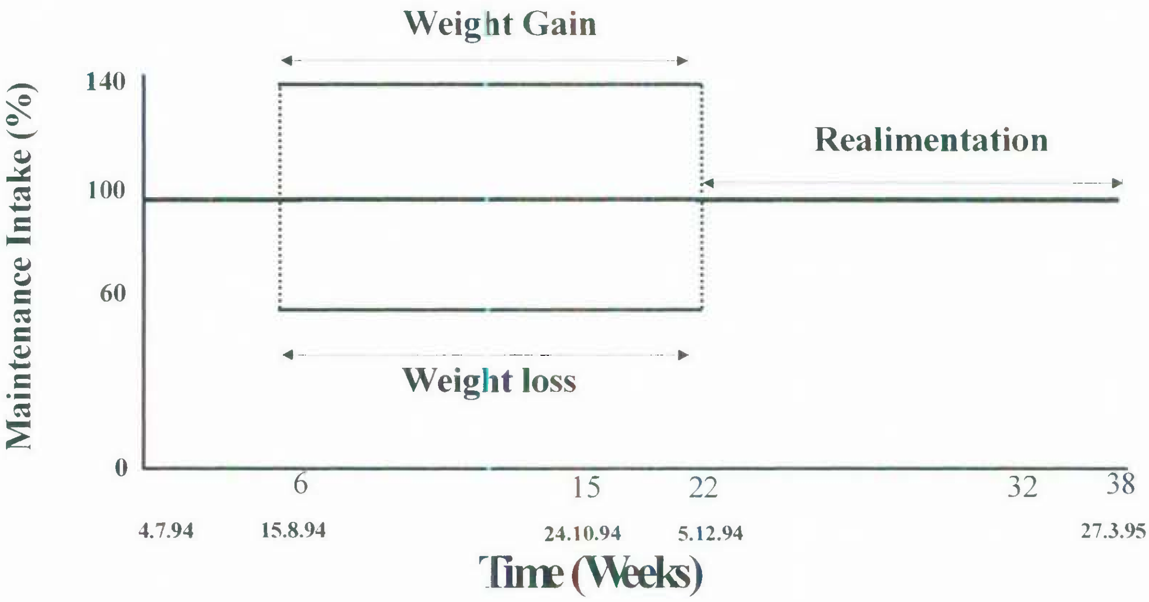


Figure 5.2.1 Experimental design for the timing of the feeding levels for the immature sheep fed at either 60, 100 or 140% of maintenance.

From week 23, all sheep were fed at initial levels estimated to maintain live-weight and then CT-scanned in weeks 3(26), 6(29), 9(32) and 15(38) of the realimentation phase. At the end of this series a dye-band was inserted at each of the last two scans so that wool growth and wool quality could be assessed over the realimentation period. After the scanning phase of the experiment had been completed the sheep were held in the individual pens at maintenance feeding levels for a further 6 weeks to allow sufficient wool growth for the last dye-band to be removed within a mid-side patch. At this point in time a mid-side patch was taken which included all the dye-bands. The area of the mid-side patch was recorded so that the weight of the fleece grown could be calculated in all time periods from the dye-band proportions. At this point the sheep were CT-scanned for a further estimate of body composition. This series of CT-scans is collectively referred to as realimentation phase of the experiment. Live weights were recorded weekly.

Table 5.2.1 Timetable of experimental events.

Week	Date	Event
-5	30.5.94	Sheep moved into shed. Estimation of feeding levels for live weight maintenance.
0	5.7.94	Sheep CT scanned. Dye-band inserted.
6	15.8.94	Sheep CT scanned.
		Treatment
7	22.8.94	Feeding levels reduced to 60% for 6 immature sheep and increased to 140% for 6 immature sheep. Dye-band inserted
10	12.9.94	Sheep CT scanned.
13	3.10.94	Sheep CT scanned.
16	24.10.94	Sheep CT scanned. Dye-band inserted
22	5.12.94	Sheep CT scanned. Sheep bleed. Dye-band inserted.
23	12.12.94	End of weight loss and growth component. Sheep returned to original levels of maintenance.
		Realimentation
26	2.1.95	Sheep CT scanned.
29	23.1.95	Sheep CT-scanned.
32	13.2.95	Sheep CT-scanned Dye-band inserted.
38	27.3.95	Animal CTscanned. Sheep bleed. Dye-band inserted
44	9.5.95	Sheep CT-scanned. End of the experiment.

5.2.2 Animals

Animals in this experiment were Poll Merinos from the same genetic source ("*Lorelmo*" Poll Merino Stud Armidale N.S.W). These sheep were approximately 6 months old at the start of the experiment and had been at pasture at Walcha N.S.W. Australia prior to the start of the experiment. Six weeks prior to being moved into the shed, all sheep were moved to two small paddocks (sheep separated by sex) on the University Property "Kirby", where they were introduced to the pelleted ration through feeding every second day. All sheep were assessed to be in good condition (Condition score 3-4) prior to the experiment.

5.2.3 Feeding and Handling Procedures

The sheep were fed once daily at 8 am. for the entire experimental period with the following exceptions. On the day of weighing, the sheep were bled and weighed prior to feeding, with feeding commencing at 10 am. On scanning days, sheep to be scanned were removed from the shed after weighing for scanning and returned to the shed prior to 5 pm. at which time feeding occurred. Water was provided *ad libitum* from individual self waters in each pen during the experiment. Hooves were regularly trimmed to avoid feet problems.

5.2.4 Diet

The sheep were fed a pelleted ration (Koombi Feeds Pty Ltd, Kootingal, Australia; Table 5.2.2). The feed was weighed into individual buckets in amounts for 4 and 3 days respectively.

Table 5.2.2 Components and dry matter composition of the pelleted feed ration*.

Component	(g/kg)	Dry Matter Component†	(g/kg)
Barley	300	Crude fibre	11.8
Wheat	387.5	Crude protein	17.98
Lucerne meal	150	Metabolisable energy	10.86(MJ/kg)
Cottonseed meal	80		
Powered limestone	17.5		
Sodium bentonite	20		
Urea	5		
Molasses	30		
Salt	8		
Supplement*	2		

* This supplement contained: 0.25% Cobalt sulphate, 2.6% Ferrous sulphate, 2.2% Magnesium oxide, 3.2% Zinc oxide, 0.07% Potassium iodine, 1.5% Sodium Molybdate, 0.5% Selmix, 50% Ammonium chloride, 1.3% Rovimix A, 0.05% Rovimix D3, 2.1% Rovimix E, 36% Polland.

† NSW Department of Agriculture Feed evaluation service.

5.2.5 Animal Health

On the 6th of June 1994, one ewe (437) was diagnosed as having Scabby mouth. Consultation with the previous owner established that all immature sheep had been vaccinated against Scabby mouth, although the procedure had failed. To avoid confounding influences on the results, all sheep were revaccinated with Scabby mouth vaccine and as a precaution with a clostridial vaccine. The start of the scanning was delayed a further 4 weeks at this point to enable sheep to recover. Only one other immature ram (453) showed symptoms of Scabby mouth during this period.

Rams established a clear pattern of aggression during the early phase of the experiment and ewes were observed to have periods of chewing on available wood and metal structures within the pen. A series of stimuli's (including chains, rubber balls and swinging containers) were provided within each pen. This significantly reduced the respective behavioural problems of both rams and ewes over the course of the experiment.

One immature ewe (437) established a pattern of periodically eating a proportion of wool from the hindquarter region (estimated to be a maximum of 10% of the total fleece area). This sheep was further supplemented with mineral mix at 2% of the diet fed, although this did not reduce the wool eating habit.

One immature ram (446) developed an ulcer on the brisket region that was first noticed on the 3rd of January 1995. Treatment was provided to this animal in the form of a intermuscular injection of 2.5ml Norocillin L.A®. and a spray on the wound of an iodine based liquid that contained a fly deterrent. This was repeated at regular intervals until the end of the experiment.

5.2.6 CT-Scanning procedure

On scanning days, the live weights of animals were recorded prior to scanning. All sheep were scanned using a whole body X-ray computer aided tomography system (Hitachi CTW-430 Computed Tomography system) using the procedure outlined in Chapter 3. Briefly, sheep were scanned over a three day period in the weeks of scanning (see Table 5.2.1), with each sheep scanned on the same day (Tuesday, Wednesday or Thursday) respectively. For scanning, animals were transported to the CT scanner-building of the University of New England. Prior to scanning the animals were restrained on a fibreglass bed and sedated with Acepril® (0.1 ml/ 10kg liveweight; Troy laboratories, Australia) when necessary. On average, total actual scan time for each animal was approximately 35 minutes.

From each sheep tomographs were made of the whole body from a randomly positioned point set behind the rump (distal to the proximal hind limb muscles), at distances of 30mm for the immature sheep until the end point of the scanning at the 4th/5th cervical vertebrae. On average 30 scans were taken for the immature sheep.

All images from this experiment were analysed using AUTOCAT (Jopson *et al.*, 1995) The two dimensional images in bitmap format were edited through a commercial image package (Picture Publisher 5.0®), so that two additional images were created. The first image (A) included all body tissues excluding the contents of the rumen, reticulum, omasum, abomasum, caecum, colon and bladder, from this image total fat, total lean and bone areas were calculated. Areas for carcass fat (subcutaneous and intermuscular), and carcass muscle were obtained from a second modified image (B) that contained all tissues from the carcass, by excluding tissues of the internal organs and internal fat depots. By difference, the areas for internal fat and non fat visceral components (NFVC) were obtained.

5.2.7 Statistical methods

This study examined the effects on body tissue development in immature sheep, of feeding at either above or below maintenance for a period of time and then returning the sheep to a previous level for weight maintenance.

The ability to obtain sequential measurements of body composition in all sheep through use of the cat-scanning procedure and the advantages that this procedure provides in terms of fitting repeated measures analysis in a random effects model has been previously discussed in chapter 3. In this study random effects models were fitted as they allowed the effect of treatment and sex on body tissue development to be identified on a within animal basis.

The analysis used data from 18 immature sheep fed at either 140%, 100% or 60% of maintenance for 15 weeks and then returned to initial levels of feeding for weight maintenance. Various components or responses were measured on each animal for a maximum of 11 possible sampling times. As shown in chapter 3, random effects models are the most appropriate method of analysis for CT-data that is in the form of longitudinal settings because the random effects are dominant in the data error structure (Diggle *et al.*, 1994). Variograms (Diggle, 1990) were constructed for the residual correlations against time for all body components that were analysed. These variograms indicated that the random effects due to the between animal variation were dominant in the error structure and that the effect of serial correlation between the repeated measurements were minimal.

The analysis of the present section used ASREML (Gilmour, 1996) to determine the significant random effects that were contained in the models for each body component. Following identification of the random effects, S-plus functions were used to incorporate cubic smoothing splines into a linear mixed model (Cullis *et al.*, 1996). For longitudinal estimates of body tissues from CT-data, the use of the spline techniques was considered preferable to a non-linear method because the experimental design, with an abrupt change in feeding levels, did not easily fit into a parametric setting.

5.2.7.1 Modeling procedure

The first step in the analysis of each component (y) was to fit a saturated model as follows in ASREML (Gilmour, 1996);

$$Y_{ijkl} = \mu + T_i + S_j + TS_{ij} + D_l + F(D_l) + R(D_l) + TD_{il} + T_iF(D_l) + T_iR(D_l) + DS_{jl} + S_jF(D_l) + S_jR(D_l) + DTS_{ijl} + TS_{ij}F(D_l) + TS_{ij}R(D_l) + Animal_{ijk}$$

where

Y_{IJKL} is the response for treatment *i* , sex *j*, maturity *k* and day *l*.

μ is the overall mean

T_i is the ith treatment effect

S_j is the jth sex effect

D_l is the linear time term that was scaled to centred mean by (time-mean(time))/√variance of time

$F(D_l)$ is the non-linear component of the model that is assumed to have the form of a cubic spline

$R(D_l)$ is the random time effect that reflects the lack of fit from the corresponding fitted cubic smoothing spline

Animal_{ijk} is the random animal effect

The variance components (random effects; interactions with either spline time or random time) were tested for significance by successively dropping their terms from the model and assessing the change in the log-likelihood statistic (i.e. $\Delta 2l \sim \chi^2_{(1)}$). After the appropriate variance component model had been selected the significance of the fixed effects was determined using a two-tailed t-test using S-Plus functions (Cullis *et al.*, 1996). The significant effects ($P<0.05$) as well as their non-significant lower order terms were then included in the final model. Treatment was fitted as Helmert contrasts, with corresponding coefficients for the fixed effects of the three treatments of 140, 100 and 60% maintenance recalculated and presented (Chambers and Hastie, 1992). As shown in the model time was fitted as standardised time. Significant time coefficients were rescaled to treatment days by dividing by the standard deviation of time of the experimental period.

The "shape" of the response for each body tissue, rather than the population mean, is of interest when comparing the treatment effects. A combination of the components of the fixed effects and the random terms relevant to the slope ("shape") are shown in graphs as deviations from zero (scaled to the initial overall mean) with respective 95% confidence intervals for each spline calculated as follows

$$\hat{y} = x\hat{\beta} + Z\hat{u}$$

$$\text{var}(\hat{y}) = x\,\text{var}(\hat{\beta})\,x^T + Z\,\text{var}(\hat{u})\,Z^T + 2 * \text{cov}(x\beta + Z\hat{u})$$

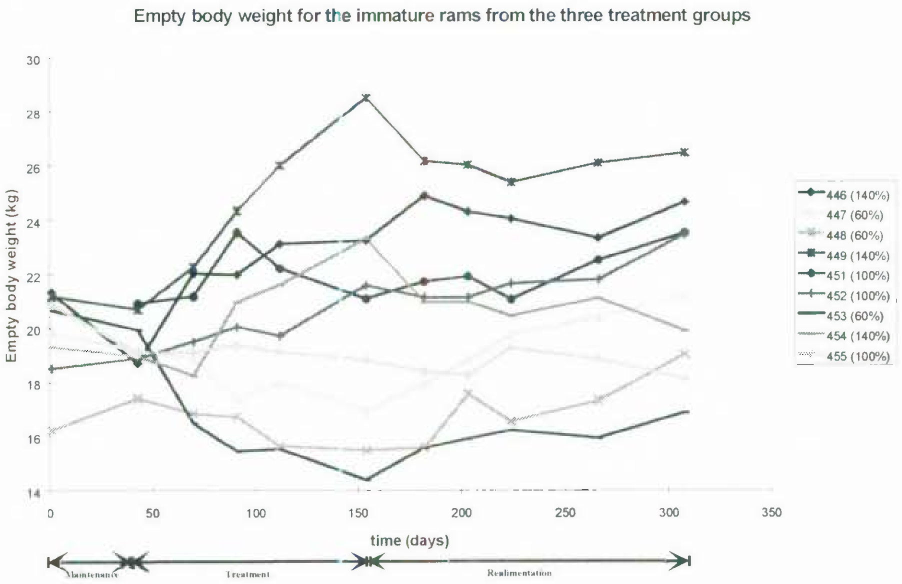
where

x is the design matrix of the fixed effects
Z is the design matrix of the random effects
$\hat{\beta}$ is the estimated fixed effects
$\hat{u}$ is the estimated random effects

5.3 Results

The experimental results presented for the body tissues are in three clear phases, these are the initial maintenance phase; the treatment phase where the treatments of 140%, 100% and 60% of maintenance feeding were applied for 15 weeks; and the realimentation phase where all sheep were returned to the initial maintenance feedings levels (100% maintenance). As shown in figure 5.3. the individual animal response dominated the response in empty body weight for the treatment and sex effects.

The significant random effects for the final models of the body components of empty body weight, carcass muscle, NFVC, total fat, carcass fat, internal fat and bone for the immature sheep subjected to either 140, 100 or 60% of maintenance and then refed at 100% of maintenance are shown in table 5.3.1. There were no random time effects in the final models for any of the body components. The significant fixed effects for the final models for empty body weight, carcass muscle, NFVC, total body fat and bone are given in table 5.3.2. Table 5.3.3 shows the significant fixed effects from the final model for carcass fat and internal fat depots.



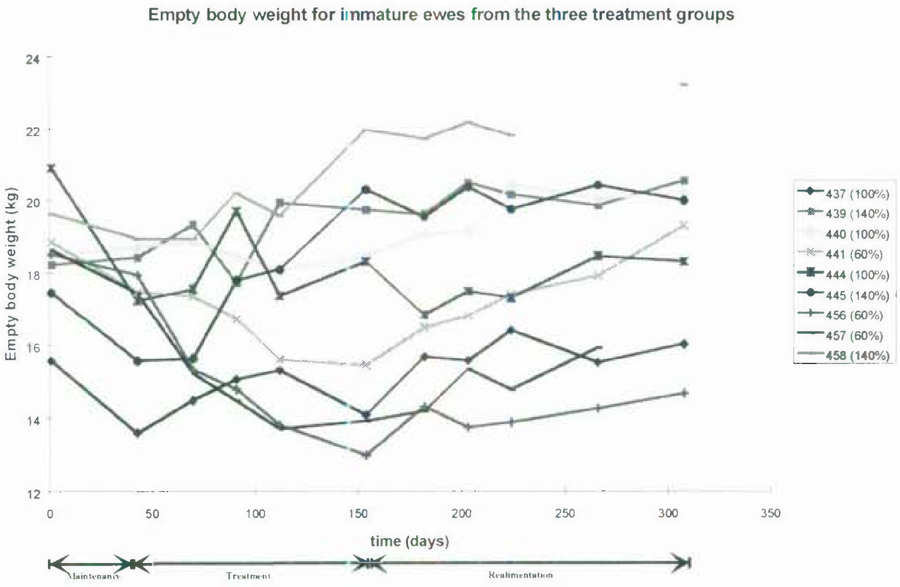


Figure 5.3 Change in empty body weight (EBW; kg) for the individual immature sheep over the maintenance, treatment and realimentation periods.

Table 5.3.1 Significant variance components (Random effects) of the final models for the seven body components for immature sheep from the treatments of either 140, 100 or 60% of maintenance.

Component	EBW	Carcass muscle	NFVC	Total Fat	Carcass Fat	Internal Fat	Bone
Random effects							
Spline time $F(D_l)$	✓	✓	✓	✓	✓	✓	✓
Random time $R(D_l)$							
Treatment * Spline Time $T_iF(D_l)$	✓	✓	✓	✓	✓	✓	✓
Sex * spline time $S_jF(D_l)$							
Treatment * sex *spline time $TS_{ij}F(D_l)$							
Animal	✓	✓	✓	✓	✓	✓	✓
Animal*spline time.				✓	✓	✓	

✓ Indicates significant variance components (random effects) at $P<0.05$

5.3.1 Empty body weight

There were significant treatment* linear time and treatment * spline time effects for the estimate of empty body weight over the experiment. Relative to the initial overall weight (18.9 kg; Table 5.3.2), all immature sheep maintained empty body weight during the initial six weeks of maintenance feeding. During the treatment period, immature sheep fed at 140% of maintenance gained 3.25 kg, or 17% of their initial weight (Figure 5.3.1).

In contrast, as shown in figure 5.3.1, immature sheep fed at 60% of maintenance during the treatment period lost 4 kg, or 21% of their initial weight.

The immature sheep that were previously fed at 140% of maintenance were able to maintain the gain in weight when fed at original levels of maintenance during realimentation period. During the realimentation period the immature sheep that had been fed at 60% of maintenance were able to regain this lost weight, such that by the end of the experiment the weight of these sheep was not significantly different to that at the start. The immature sheep fed at maintenance for the entire experimental period maintained empty body weight, although there was a slight non-significant increase near the end of the realimentation period. At the end of the realimentation period the sheep that had been fed at 140% of maintenance and then returned to their previous maintenance feeding level were significantly heavier than the immature sheep that had been fed at maintenance, or at 60% of maintenance during the realimentation period. There was also a significant difference between the maintenance fed immature sheep and those that had lost and recovered weight, with the maintenance fed immature sheep being heavier as shown in figure 5.3.1.

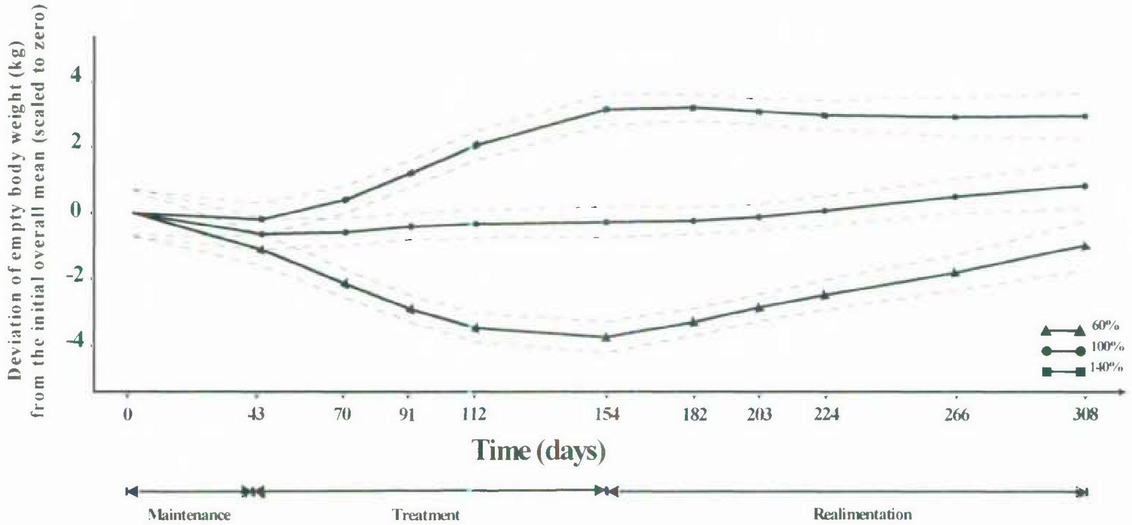


Figure 5.3.1. Deviation for empty body weight (kg) from initial empty body weight (scaled to zero) and the 95% confidence limits (dotted lines) for the three treatment groups during the maintenance, treatment and realimentation periods of the experiment.

5.3.2 Carcass muscle

There were significant treatment*spline time and treatment * linear time effects on the relative changes in carcass muscle weight from the initial weight of 10.072 kg (Table 5.3.2). There was no change in carcass muscle for either sex during the six week maintenance period. As shown in figure 5.3.2. both sexes of immature sheep mobilised carcass muscle when fed at 60% of maintenance during the 15 weeks of the treatment period. However the sex effect influenced the magnitude of the loss, as the loss for the ewes was greater being 1.67 kg or 17% of the initial carcass muscle weight compared to 1.22 kilogram loss, or 12% for the rams. The relative timing of the loss for both sexes was similar with a higher rate of loss observed at the start of the treatment period. Immature sheep fed at 140% of maintenance during the treatment period gained carcass muscle. Sex also influenced the magnitude of the gain as the absolute gain was higher for the rams (1.55 kg, or 16%) relative to the ewes (1.2 kg, or 12%).

The immature rams fed at maintenance for the entire experimental period (100%; Figure 5.3.2) gained carcass muscle so that by the end of the experiment they had 0.95 kg more carcass muscle, or an increase of 9.5% of the initial weight. In contrast there was no change in the carcass muscle weight of the immature ewes fed at maintenance for the entire experimental period. During the realimentation period both sexes that had been fed at 60% of maintenance gained carcass muscle, however the level of gain was sufficient for the rams to recover to the initial weight of carcass muscle, while the ewes did not recover all the carcass muscle that had been lost during the treatment period. Rams fed at 140% of maintenance during the treatment period were able to maintain the increase that had occurred prior to the period where feeding levels were reduced to maintenance. In contrast, the ewes that had been fed at 140% maintenance mobilised carcass muscle when feeding was reduced to maintenance levels.

Table 5.3.2 Significance and t-values for the overall mean (μ (kg)), deviations for fixed effects and deviations for the linear time effects for empty body weight, carcass muscle, non fat visceral components (NFVC) and total fat.

Body Component	Mean (kg)	Fixed effects	Time effects	t-value
Empty body weight				
Mean (μ)	18.964			50.471***
		Treat1		3.290***
		Treat2		4.033***
		Sex		-2.884***
			Time	5.852***
			Treat1*time	3.211***
			Treat2*time	7.144***
Carcass Muscle				
Mean (μ)	10.072			50.456***
		Treat1		2.946***
		Treat2		4.022***
		Sex		-3.649***
			Time	1.761**
			Treat1*time	3.078***
			Treat2*time	3.784***
			Sex * time	-3.647***
NFVC				
Mean(μ)	3.450			43.664***
		Treat1		1.566*
		Treat2		2.675***
		Sex		-4.727***
		Treat1*sex		-1.061
		Treat2*sex		2.264**
			Time	-3.091***
			Treat1*time	-0.494
			Treat2*time	-0.386
			Sex * time	-2.763***
			Treat1*sex*time	1.677**
			Treat2*sex*time	-2.399***
Total Fat				
Mean (μ)	2.976			8.620***
		Treat1		1.638*
		Treat2		0.648
		Sex		-0.577
		Treat1*sex		-0.713
		Treat2*sex		-1.052
			time	14.802***
			Treat1*time	4.714***
			Treat2*time	15.580***
			Sex * time	7.276***
			Treat1*sex*time	0.586
			Treat2*sex*time	6.335***
Bone				
Mean (μ)	2.457			58.797***
		Treat1		1.594*
		Treat2		1.763**
		Sex		-3.861***
			time	12.313***
			Treat1*time	3.325***
			Treat2*time	5.229***
			Sex*time	-4.975***

* P <0.1

** P<0.05
*** P<0.01
Treatment effects of 60, 100 and 140% were fitted as Helmert contrasts of treat1 and treat2.

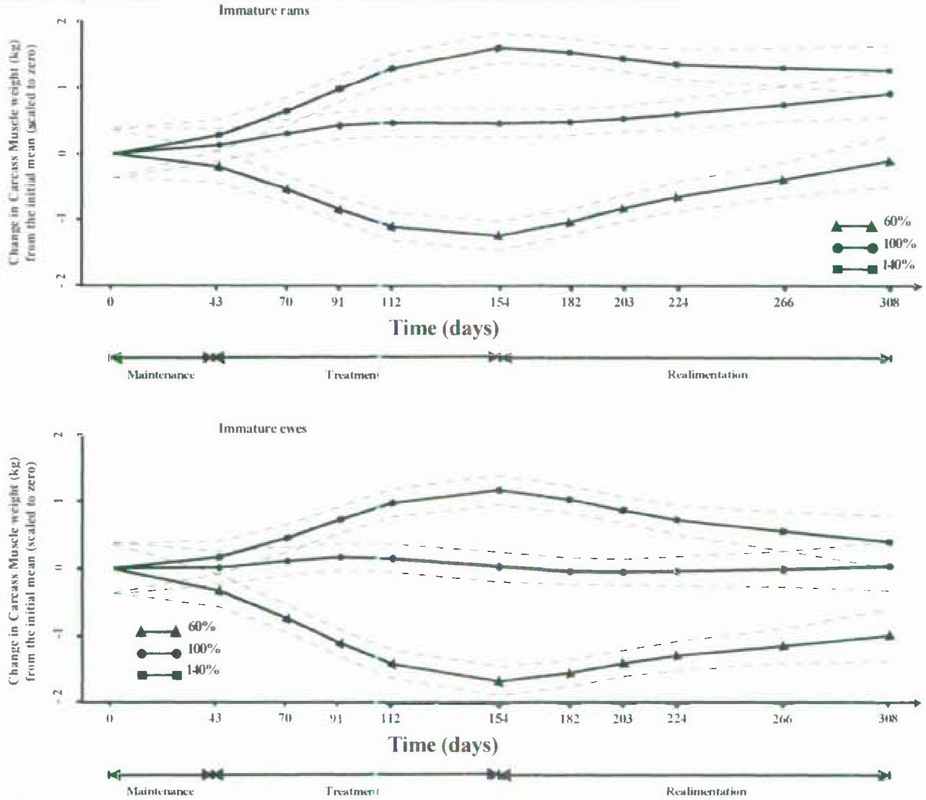


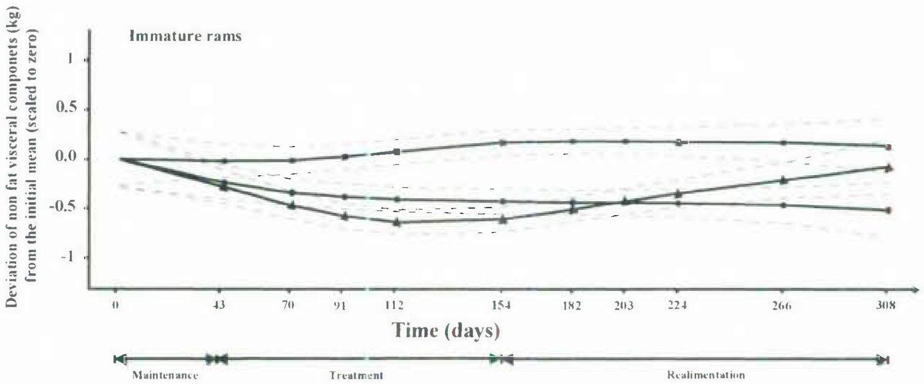
Figure 5.3.2 Deviation for carcass muscle weight (kg) from initial Carcass muscle weight (scaled to zero) and the 95% confidence limits (dotted lines) for the three treatment groups of both sexes during the maintenance, treatment and realimentation periods of the experiment.

At the end of the experimental period, there was no difference in the weights of carcass muscle for the immature sheep that had been fed at either maintenance, or at 140% of maintenance within each sex class. However the immature rams had gained carcass muscle compared to the initial weight. Both sexes that had been fed at 60% of maintenance had significantly less carcass muscle when compared to their respective treatment groups of maintenance and 140% of maintenance.

5.3.3 Non fat visceral components (NFVC)

The final model for NFVC contained significant effects for treatment* spline time and treatment*sex*linear time (Tables 5.3.1; 5.3.2). Compared to the initial weight of 3.450 kg there were no changes in NFVC for either sex during the six weeks of maintenance feeding. Immature ewes fed at 60% of maintenance during the treatment period lost significantly more NFVC (0.9 kg or 27% of the initial weight) than the immature rams fed at 60% of maintenance (0.6 kg or 17% of the initial weight). As with carcass muscle the rate of loss of NFVC was greatest at the start of the treatment period. There were no significant changes in the weight of NFVC for either sex that was fed at maintenance for the entire experimental period (Figure 5.3.3). Immature rams fed at 140% of maintenance showed no respective change in the weight of NFVC during either the treatment or realimentation periods, however at the end of the experiment these rams had more NFVC than rams fed at maintenance. In contrast the ewes fed at 140% of maintenance mobilised NFVC weight during the realimentation period. This resulted in these ewes having less NFVC at the end of the experiment when compared to the ewes fed at maintenance.

Both sexes that had been fed at 60% of maintenance gained NFVC weight when fed at maintenance levels during the realimentation period. Although the rate of compensation was greater for the rams, resulting in rams recovering all of the lost NFVC, whilst the ewes had lower NFVC weights at the end of the experiment. At the end of the experiment the weights of NFVC for immature sheep fed at 60% of maintenance did not differ from those of the immature sheep fed at maintenance.



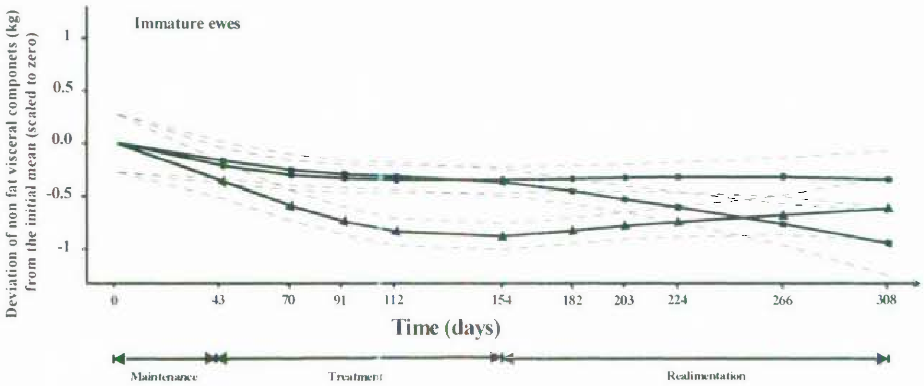


Figure 5.3.3 Deviation for non fat visceral component weight (NFVC; kg) from initial NFVC weight scaled to zero and the 95% confidence limits (dotted lines) for the three treatment groups of both sexes during the maintenance, treatment and realimentation periods of the experiment.

5.3.4 Bone

The final model for bone weight contained significant terms for treatment*spline time, treatment*linear time and sex*linear time. As shown in figure 5.3.4 all immature rams gained total bone weight during the entire experimental period. As expected the relative increase in the rams fed at 140% was highest during the treatment period and declined during the realimentation period. The relative gains for rams fed at maintenance was linear, whilst that for the 60% of maintenance was similar to that of the 140% with a curvilinear gain. At the end of the experiment the increase in bone weight was 0.27, 0.49 and 0.74 kg respectively for the 60, maintenance and 140% of maintenance fed rams.

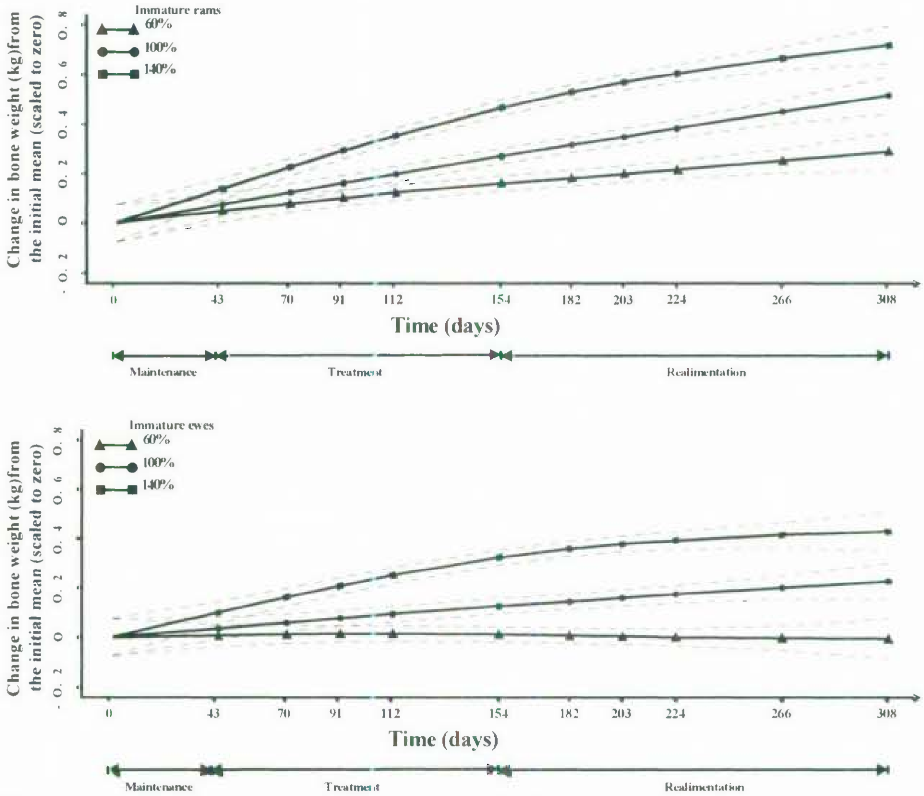


Figure 5.3.4 Deviation for bone weight (kg) from initial bone weight (scaled to zero) and the 95% confidence limits (dotted lines) for the three treatment groups of both sexes during the maintenance, treatment and realimentation periods of the experiment.

As illustrated in figure 5.3.4 immature ewes fed at 140% of maintenance and maintenance increased in bone weight during the experimental period, although the respective gains were much lower than that recorded for the rams. The gains for the ewes from these two treatments were 0.4 and 0.2 kg respectively. In contrast there was no increase in bone weight for the immature ewes fed at 60% of maintenance over the entire experimental period.

5.3.5 Total Fat

As shown in tables 5.3.1. and 5.3.2 there are significant treatment*spline time, animal* spline time and treatment*sex*linear time effects on total fat that indicates that the pattern for fat depletion and deposition over the experimental period was affected by an interaction between feeding level and sex. There was no significant change from the initial total fat weight of 2.98 kg for the immature sheep during the six week maintenance feeding period, although there was a trend for both sexes to mobilise total fat tissue during this period. Both immature rams and ewes mobilised significant amounts of total fat when fed at 60% of maintenance during the treatment period, the relative loss was similar being 1.6 kg (54% of the initial weight) for the rams and 1.5 kg (49% of the initial weight) for the ewes. Figure 5.3.5, shows that sex influenced the absolute gain in total fat during the treatment period. The gain for the ewes (2 kg or 67% of the initial weight) during this period, was greater than the gain for the rams (0.8 kg or 27% of the initial weight).

There was a significant trend for an increase in total fat weight during the time of the treatment and realimentation periods (36 weeks), relative to the weight at the end of the first six week maintenance period for each sex. Both sexes that had been fed at 60% of maintenance deposited total fat tissue during the realimentation period, such that by the end of this period, both sexes had fully compensated in terms of the total fat lost during the preceding treatment period. Immature rams that had been fed at 140% of maintenance were able to maintain the higher weight of total fat when fed at maintenance during the realimentation period. Interestingly the immature ewes continued to gain total fat during the realimentation period, even though feeding levels had been reduced to maintenance. The gain during the realimentation period for this group was 1 kg, which resulted in a total gain of 3 kg or 101% of the initial weight of total fat.

It was apparent from figure 5.3.5, that the weight of total fat for the immature ewes fed at 140% of maintenance was significantly higher than the weights of fat for ewes fed at either maintenance or 60% of maintenance. In contrast the weight of total fat for the rams fed at 140% of maintenance was not significantly different from that of the rams fed at maintenance. The weight of total fat for both sexes fed at 60% of maintenance was significantly lower than the weights of total fat for the immature sheep fed at maintenance.

Table 5.3.3 Significance and t-values for the overall mean (μ (kg)), deviations for fixed effects from the overall mean and deviations for the linear time effects for carcass and internal fat depots.

Fat depot	Mean (kg)	Fixed effects	Time effects	t-value
Carcass Fat				
Mean (μ)	1.810			9.337***
		Treat1		1.849**
		Treat2		0.903
		Sex		-0.664
		Treat1*sex		-0.887
		Treat2*sex		-1.001
			Time	1.412***
			Treat1*time	3.986***
			Treat2*time	15.346***
			Sex*time	5.266***
			Treat1*sex*time	0.801
			Treat2*sex*time	4.200***
Internal Fat				
Mean (μ)	1.166			7.471***
		Treat1		1.312*
		Treat2		0.332
		Sex		-0.395
		Treat1*sex		-0.462
		Treat2*sex		-0.991
			Time	15.083***
			Treat1*time	4.754***
			Treat2*time	13.255***
			Sex*time	8.401***
			Treat1*sex*time	0.290
			Treat2*sex*time	7.738***

* P <0.1
** P<0.05
*** P<0.01
Treatment effects of 60, 100 and 140% were fitted as Helmert contrasts of treat1 and treat2.

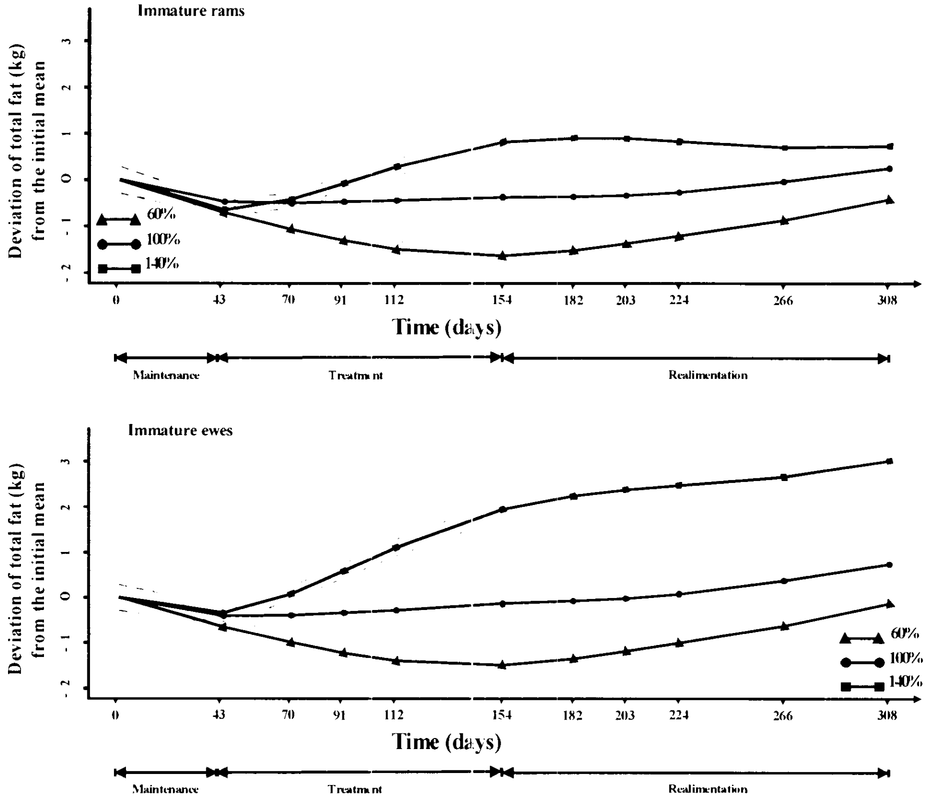


Figure 5.3.5 Deviation for total body fat weight (kg) from initial total body fat weight (scaled to zero) and the 95% confidence limits (dotted lines) for the three treatment groups of both sexes during the maintenance, treatment and realimentation periods of the experiment.

5.3.6 Carcass fat

As shown in tables 5.3.1 and 5.3.3, there were significant effects of treatment* spline time, animal*spline time and treatment*sex*linear time in the final model for carcass fat. In contrast to total fat, figure 5.3.6 shows that there was a relative loss of carcass fat during the initial maintenance period. With respect to the initial weight of 1.81 kg, the average loss for both sexes was 0.5 kg, or 28% of the initial weight. The immature sheep fed at 60% of maintenance during the treatment period continued to lose carcass fat, at the end of the treatment period both sexes had lost a further 0.5 kg, which was a proportional loss of 38% of the weight of carcass fat at the start of the treatment period (Figure 5.3.6). The immature rams fed at 140% of maintenance during the treatment period gained 1.05 kg of carcass fat or 80% of the weight of carcass fat at the start of the treatment period. During the treatment period the immature ewes fed at 140% also gained significant weights of carcass fat; however, as shown in figure 5.3.6, the increase of 1.50

kg represented an even greater gain of 115% of the weight at the start of the treatment period.

The immature sheep fed at maintenance gained carcass fat during the treatment and realimentation periods. The immature rams from this treatment were able to recover the 0.5 kg that was lost during the initial maintenance period (Figure 5.3.6), whilst the ewes gained 0.7 kg so that their weight of carcass fat was not significantly different to that at the start of the experiment. Both the immature rams and ewes fed at 60% of maintenance gained carcass fat during the realimentation period. The rams were able to recover the weight of carcass fat lost during the treatment period, whilst the ewes gained more carcass fat so that they had higher weights of carcass fat than at the start of the treatment period. However, both sexes still had lower carcass fat weights at the end of the realimentation period relative to the start of the experiment.

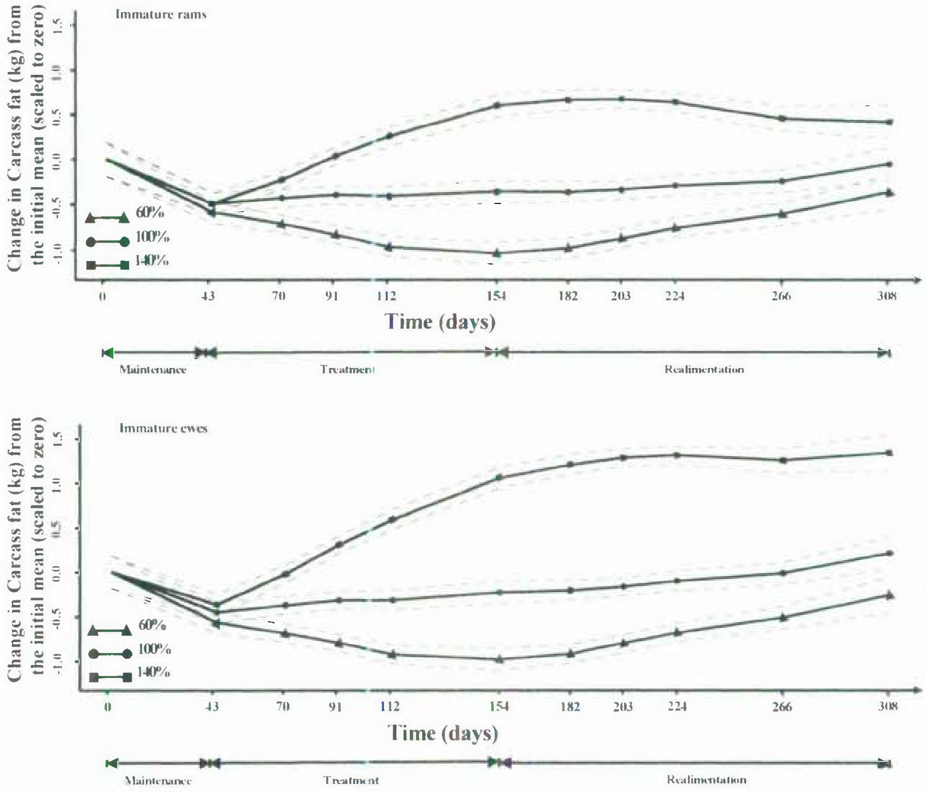


Figure 5.3.6 Deviation for carcass fat weight (kg) from the initial carcass fat weight (scaled to zero) and the 95% confidence limits (dotted lines) for the three treatment groups of both immature sexes during the maintenance, treatment and realimentation periods of the experiment.

Immature rams fed at 140% of maintenance were able to maintain their weight of carcass fat during the realimentation period. In contrast, as shown in figure 5.3.6 the ewes continued to gain 0.37 kg of carcass fat during the realimentation period. At the end of the experiment there were clear differences in the weights of carcass fat between the treatments within each sex group. Ewes fed at 140% of maintenance had significantly higher weights of carcass fat relative to both maintenance and 60% of maintenance fed ewes. The maintenance fed immature ewes had a higher weight of carcass fat then the ewes fed at 60% of maintenance. The immature rams fed at 140% of maintenance had a higher weight of carcass fat than the other two treatment groups. In contrast to the ewes, there was no significant difference in the weight of carcass fat between the maintenance and 60% of maintenance fed rams at the end of the experiment.

5.3.7 Internal fat

The final model for internal fat contained significant effects for treatment*spline time, animal*spline time and treatment*sex*linear time (Tables 5.3.1, 5.3.3). In contrast to carcass fat as shown in figure 5.3.7 there was no significant change in internal fat weight for either immature rams or ewes during the six week maintenance feeding period. Relative to the initial weight of 1.166 kg, both immature rams and ewes fed at 60% of maintenance during the treatment period mobilised internal fat. The 0.4 and 0.5 kilogram loss represented 34 and 43% of the initial internal fat weight for the rams and ewes respectively. It was evident that there was a significant sex effect on the change in internal fat weight for the immature sheep fed at 140% of maintenance during the treatment period. The immature ewes gained 0.85 kg or 73% of the initial internal weight during this period, whilst there was no significant change in internal fat for the rams.

For the sheep fed at maintenance there was a small but significant change of approximately 0.2 kg in internal fat over the entire experimental period. During the realimentation period both the immature rams and ewes fed at 60% of maintenance recovered the internal fat that had been previously lost. The immature rams that had been fed at 140% of maintenance showed no real gain in internal fat during the realimentation period, although at the end of the experiment they had gained approximately 0.2 kg of internal fat. In contrast, as shown in figure 5.3.7, the immature ewes that had been fed at 140% of maintenance continued to gain internal fat during the realimentation period. At the end of the experiment they had gained 1.65 kg of internal fat which represented an overall gain of 142% of the initial internal fat weight at the start of the experiment.

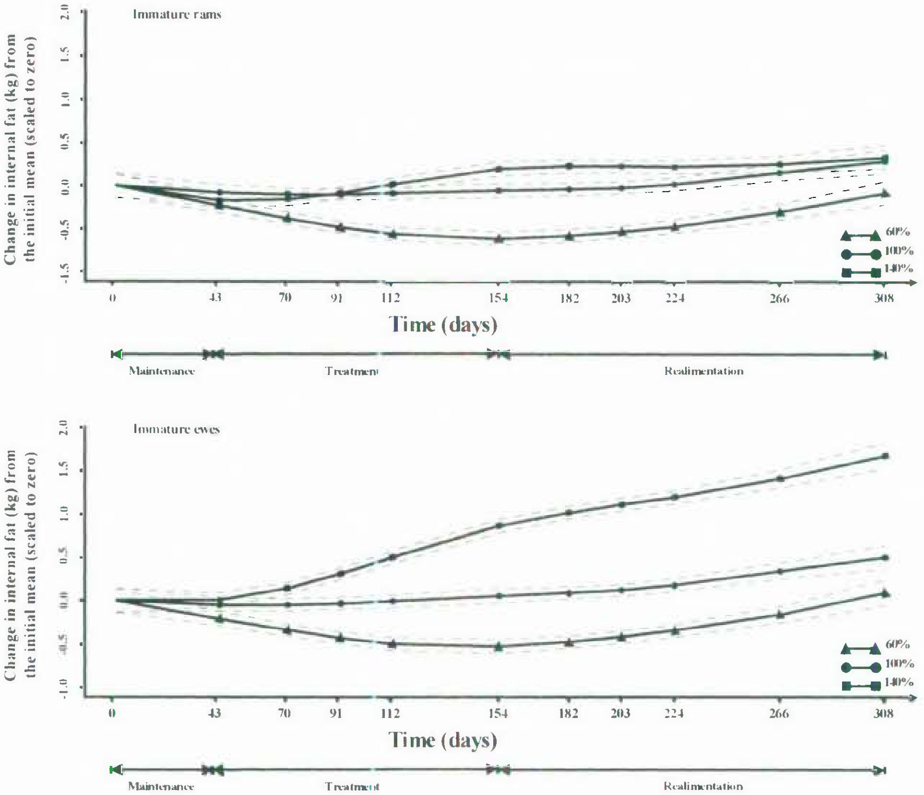


Figure 5.3.7 Deviation for internal fat weight (kg) from the initial internal fat weight (scaled to zero) and the 95% confidence limits (dotted lines) for the three treatment groups of both sexes during the maintenance, treatment and realimentation periods of the experiment.

5.4 Discussion

5.4.1 Empty body weight and maintenance

There is a marked variation between animals within each treatment group as shown in figure 5.3. Graham (1967) observed a 18% greater loss in lean and 5% greater loss of fat between the lightest and heaviest sheep despite identical treatments of successive fasting and realimentation periods. Recently Kamalzadeh (1996) also reported a between animal difference of 25% (5 vs 30%) in body weight loss of restricted lambs. Graham (1967) stated that this variation results in an impediment to practical application of experimental work, as between animal differences that exist in one experimental environment may not be apparent in another. The use of the random effects model with cubic splines (Green and Silverman, 1992; Cullis *et al.*, 1996) provides a more robust analysis by describing the variation that exists between animals.

The primary aim of the experiment was to examine the affect of manipulating feeding levels on the relationship between equilibrium weight and feed intake or the *Equilibrium Maintenance Constant* (T_o; Taylor *et al.*, 1981; Parks, 1982) in immature animals. It was apparent that the immature sheep fed at either 140% (weight gain) or 60% (weight loss) of maintenance, after being returned to previously determined feeding levels for liveweight maintenance, differed substantially in the weight of body tissue that could be maintained. This suggests those sheep that had gained weight were more efficient than sheep that had lost weight when returned to equilibrium feeding levels.

From these results it was apparent that the original hypothesis of Taylor and Young (1968), (that is a constant relationship between equilibrium weight and feed intake as an animal matures whose exponent was not significantly different from unity), does not appear to apply to situations other than where animals have been fed at increasing levels of feed intake. The difference in empty body weight at the end of the experiment that existed between these two groups (4 kg) translated into a mean difference of 21% of the initial equilibrium weight. However it must be noted that although the differences existed after a 21 week period of equilibrium maintenance feeding, it appears as though there was potential for continued gain for those sheep fed at 60% of maintenance (Figure 5.3.1) whereas the potential for gain for the sheep fed at 140% of maintenance appears to be approaching zero. Turner and Taylor (1983) indicated the lag phase required for metabolism to adjust to a change in feed intake is considerable. Given sufficient time the equilibrium requirements of these two groups may converge.

Ferrell *et al.* (1979) and Ferrell *et al.* (1986) showed that lambs that had been fed at higher planes of nutrition during a preliminary period had higher maintenance requirements than lambs fed at lower planes of nutrition when adjusted to the same metabolic weight during a subsequent period of feeding at the same level. This result contrasts with the present experiment where at the end of the experiment the sheep fed at 140% of maintenance had lower maintenance requirements per kilogram of empty body weight than the sheep fed at 60% of maintenance. The present experimental result however does agree with the results obtained for the mature Coopworth sheep in chapter 4. The sheep that had been fed at higher levels (100%) had lower maintenance requirements (after adjusting for differences in retained body energy) than sheep that had been fed at 60% of maintenance. More importantly, the results from this experiment and those described in chapter 4, differ significantly from the results obtained by Koong *et al.* (1982) and Olthoff *et al.* (1989) where animals fed at higher feeding levels (*ad libitum*) had higher maintenance requirements than animals fed at maintenance. Clearly the hypothesis that compensatory growth is partially a function of reduced maintenance requirements of restricted animals when compared to "normally grown" animals (Gingens *et al.*, 1980; Ryan, 1990; Ryan *et al.*, 1993a; Carstens *et al.*, 1991; Carstens, 1995) must be questioned. Further studies where animals are fed repeatedly at varying levels over a full range of maturity and allowed to stabilize at equilibrium weights, are required to unravel the dynamics of maintenance requirements of body tissues.

It is clear that the results obtained for the immature sheep fed at 60% of maintenance differed significantly from the results obtained for the mature sheep in chapter 3. In the present study, the immature sheep were able to fully compensate during the realimentation period, whilst mature sheep that had been fed at 60% of maintenance were unable to fully compensate. Thornton *et al.* (1979), Butler-Hogg and Tulloh, 1982, Carstens *et al.* (1991), all suggested that immature animals have the ability to compensate fully after a period of feed restriction.

Previously Graham *et al.* (1975) had shown that the maintenance requirements of immature sheep, that had been restricted to weight stasis, declined. This would lead to a reduction in the feed required to maintain weight as noted in immature steers (Foot and Tulloh, 1977; Ledger and Sayers (1977) and in immature lambs maintained at approximately 30 kg (Murray and Slezacek, 1988a; Afonso, 1992). Alternatively a reduction in maintenance requirements would lead to an increase in body weight if feed intake had been fixed. In this experiment there was no significant increase in empty body weight for the sheep fed at maintenance. This suggests that maintenance requirements of immature sheep, scaled for empty body weight or its derivative of metabolic weight ($w^{0.75}$), did not change over the 308 days of the present experiment. These results agree with those of Luiting *et al.* (1995) where restriction of pigs to a constant feed intake resulted in no gain in body tissue weight. It is possible that the small non-significant increase in empty body weight that was observed in the present study reflects a slight decrease in maintenance requirements with age, which is included in current feeding standards (SCA, 1990; NRC, 1996)

5.4.2 Changes in body composition

5.4.2.1 Maintenance feeding

Although empty body weight did not change for the immature sheep fed at maintenance, there were significant sex effects which promoted changes in the partitioning of body tissues of the immature sheep during weight stasis. For the immature rams there was a clear redistribution of body protein, with a marked decline in NFVC weight and an increase in carcass muscle weight. A number of studies have shown that during weight stasis in immature sheep, there is a reduction in visceral organ weight and an increase in carcass weight (Notter *et al.*, 1983; Murray and Slezacek, 1988a,b; Ryan and Williams, 1990; Iason and Mantecom, 1993) as was the case for the immature rams. However the present experiment contrasts to those experiments where carcass weight increases were primarily in carcass fat. Drouillard *et al.* (1991a) indicated that carcass muscle accretion can occur in lambs when dietary protein levels are adequate, however this was at the expense of carcass fat rather than visceral organs. It is interesting to note that the same pattern of redistribution of body tissues that occurred for the rams was also apparent in a similar study involving pigs, where body compositional changes were measured within individual animals using CT-scanning (Kolstad *et al.*, 1995; Kolstad and Vangen, 1996). Pekas (1995) also showed that pigs that were terminally restricted to a maintenance feeding level catabolised gastrointestinal organs and used nutrients salvaged for continued carcass muscle accretion organ. Perhaps the accuracy of measurement that obtained by using the CT-scanner (Afonso, 1992), has contributed to the differences between this study and that of Kolstad *et al.* (1995) with those other studies that have used less precise methods.

In contrast to the rams, the magnitude of the changes in body components of the immature ewes that occurred during maintenance feeding were of a smaller scale. There was a reduction in NFVC, although the loss was much less than that for the rams. There was no change in the weight of carcass muscle and only a small change in total fat. Min *et al.*, (1996) stated that body growth in immature sheep that are being fed at a constant level can only occur through changes in efficiency, or through repartitioning of nutrients within the body. A reduction in the mass of the NFVC that was observed for both sexes indicates that immature sheep adapt to maintenance feeding by reducing the mass of those organs with a high metabolic demand (Koong *et al.*, 1985; Ferrell *et al.*, 1986; Iason and Mantecom, 1993). Although the decline in visceral mass may also due a reduction in function associated with the lower feed intake (Pekas, 1995). The evidence from the present experiment is also consistent with an increase in circulating plasma growth hormone levels which would promote the retention or accretion of lean tissue (Min *et al.*, 1996). Although the difference between the sexes suggests that the elevation of GH is only effective in the immature male (Onischuk and Kennedy, 1990). There is no evidence that indicates an enhanced lipolytic effect of IGF-1 in immature sheep fed at near maintenance as proposed by Min *et al.* (1996).

Although total fat did not change for the immature sheep fed at maintenance, there were distinct changes in both carcass fat and internal fat. During the initial six week maintenance period, there was a significant reduction in carcass fat. However, the loss was recovered over the remaining 36 weeks of the experiment. It appears that the early phase of weight stasis is characterised by mobilisation of carcass fat, whilst lean depots and internal fat depots were preserved. Kolstad and Vangen (1995; 1996) and Kolstad *et al.* (1996) also observed a similar trend in pigs fed at maintenance for a period of eight weeks. Kolstad *et al.*(1996) suggested that the different utilisation in the depots may occur through differences in sensitivity to lipolytic and lipogenic stimuli, defining the function of subcutaneous fat as energy yielding and internal fat as insulatory or protective. As the sheep "adapted" to the maintenance feeding level, evidently body metabolism must have been reduced in order for carcass fat to be deposited. This increase in carcass fat has been observed in other studies where immature sheep have been subjected to weight maintenance (Ledin, 1983; Notter *et al.*, 1983; Aziz and Murray, 1987; Murray and Slezacek, 1988a; Ryan and Williams, 1989). Interestingly there was no change in internal fat during the phase of weight maintenance which agrees with the results of Murray and Slezacek (1988b). Yet they differ to those obtained for mature sheep in chapter 3 and those studies of Dulloo and Girardier (1993), Kolstad *et al.* (1996) and Yambayamba *et al.* (1996b) where internal fat weight decreased in animals fed to maintain weight.

5.4.2.2 Changes during the treatment period

The results obtained in this experiment for the immature sheep, differ from those obtained in chapter 3, where there was a reduction in carcass muscle and a maintenance of NFVC tissue for the mature sheep. From this comparison it is evident that the maturity of the animal at the time when maintenance feeding is imposed affects the changes that occur within the body. As mentioned in chapter 3, the difference between mature and immature sheep undergoing weight stasis may be linked to the relative impetus for growth. The immature rams demonstrated the impetus for muscle accretion at the expense of visceral organs, which is consistent with the need for maximising body size and reproductive success.

A number of studies have shown that restriction of feed intake below *ad libitum* results in animals that have higher proportions of lean and lower proportions of total body fat when compared to *ad libitum* fed animals (Turgeon *et al.*, 1986; Bass *et al.*, 1990; Owens *et al.*, 1993; Murphy and Loerch, 1994; Steen *et al.*, 1995). In contrast other studies have shown that feed restricted animals have higher proportions of fat and lower proportions of carcass muscle (Morgan and Owen, 1973; Butler-Hogg and Johnsson, 1986; Greeff *et al.*, 1986b). As there were no *ad libitum* fed immature sheep in the present experimental design it is unknown whether the patterns of tissue development that occurred for sheep fed at 140% of maintenance differ from those of the normally grown animal.

It is evident that there is a marked sex effect on the priorities for tissue deposition during the treatment period for the immature sheep. The immature rams have a priority for the deposition of carcass muscle, whilst for the immature ewes there is a priority for the deposition of body fat. Fourie *et al.* (1970), Thompson *et al.*, (1985b) and Butterfield (1988) all observed strong differences in the relative accretion rates of carcass muscle and total body fat with fat being later maturing and carcass muscle being earlier maturing in the female compared to the male. Morgan and Owen (1973) showed that the difference between rams and ewes became apparent after 25 kg in body weight with a greater emphasis placed on the development of the musculature for the male.

Recently Gatford *et al.* (1996) proposed that the Somatotrophic axis was involved in regulating the sex differences that occur in body tissue development during growth. They showed that IGF-1, IGFBP-3 and the Somatotropin pulse amplitude were all higher in rams compared to ewes and that these differences would promote the accretion of protein at the expense of fat in entire males. Gettys *et al.* (1987) indicated that there was a strong effect of testosterone on carcass muscle development which increases muscle accretion in the entire male.

At the start of the treatment period, although the age of the sheep were similar, relative to mature size the immature rams were less mature than the immature ewes. The sex response observed during the treatment period may be a reflection of a stage of maturity effect on body composition development, as the ewes would be expected to deposit more fat relative to total body weight gains (Thompson *et al.*, 1985b).

The marked sex effect on the relative growth rates of the fat depots for the sheep fed at 140% of maintenance during the treatment period is consistent with the results of Fourie *et al.* (1970); Thompson *et al.* (1985c) and Butterfield (1988). They indicated that carcass fat deposition would be greater in ewes relative to rams as empty body weight increases and that the increase in carcass fat depots would be greater than the increase in internal depots. The results of the present experiment, where there was no increase in internal fat for the rams, support the results of Steen and Kilpatrick (1995) who showed that feed restriction (80% of *ad libitum*) decreased the rate of fat deposition in all depots for bulls, steers and heifers. However, the effect was greater in bulls compared to heifers and the sex effect was more pronounced for the rate of internal fat deposition. In contrast, Morgan and Owen (1973) showed that total fat, and specifically internal fat deposition, was enhanced in both rams and ewe lambs that were restricted to a feeding level of 70% of *ad libitum* for body weights between 25-40 kg. Murray and Slezacek (1976) also indicated that subcutaneous fat has a low priority as a site for fat deposition during restricted growth. Again as there was no *ad libitum* fed sheep against which changes in rates of fat deposition could be compared, it is difficult to speculate whether restricted feeding depressed the rate of carcass fat growth.

The reduction in the NFVC mass for the immature ewes and the small gain for the rams during the treatment period suggests that there is a link between relative tissue deposition in the body and visceral organ metabolism. A reduction in maintenance requirements through a lower mass of metabolically active tissue may enable the ewe to partition more energy into fat deposition, whilst a small gain in the visceral organs may be required to sustain the higher muscle weight of the ram. Overall the sex difference that is expressed during the treatment period is consistent with the hypothesis of Fennessy *et al.*

(1991) that priorities for reproductive success result in changes in the female metabolism which promotes fat accretion, whilst the metabolism of the male results in a higher relative growth of the carcass muscle depot.

There have been a number of studies that have examined the relative changes in body composition that occurs when immature sheep have had feeding levels restricted such that body tissues are catabolised to meet the energy deficit (Drew and Reid, 1975a; Butler Hogg and Tulloh, 1982; Drouillard *et al.*, 1991a; Aziz *et al.*, 1992; Kabbali *et al.*, 1992a,b; Ryan *et al.*, 1993b). However to date, no study has examined the effect that sex has on the priorities for tissue depletion during weight loss and the corresponding effect that is likely to occur during realimentation as a result of differences in body composition at the end of the restriction (Fox *et al.*, 1974; Butler-Hogg, 1984). The was a clear sex effect on the relative loss of carcass muscle during the treatment period for immature sheep fed at 60% of maintenance. The loss was greater for the ewes compared with the rams. Claus and Weiler (1994), indicated that androgens have an anticatabolic function and therefore the conservation of lean in entire males may be greater than in females. Recently Jopson *et al.* (1996) proposed that testosterone or one of its derivatives was responsible for the conservation of carcass muscle in mature Fallow bucks during the "rut". Onischuk and Kennedy (1990) showed that there was a sex effect on the levels of plasma GH in lambs undergoing compensatory growth. Henricks *et al.* (1993) also reported that serum GH rose in young bulls during a feed restriction period and that whilst fat levels declined protein levels remained constant during this period. It is assumed that a higher level was present in the rams and that this may have allowed the conservation of greater levels of carcass muscle (Hart *et al.*, 1992; Henricks, *et al.*, 1993; Adams *et al.*, 1996a,b) than was observed in the present experiment. Wester *et al.* (1995) proposed that Somatotropin was involved in the sex differences that exist in the regulation of fat mobilisation during weight loss, this proposal is supported by recent results of Gatford *et al.* (1996).

There was a sex effect on the relative losses of NFVC from the body during weight loss. The ewes lost more NFVC than the rams which is consistent with the hypothesis that there is a greater conservation of lean tissue in males when compared to females. The results for this experiment support the observations of Drew and Reid (1975a), Thornton *et al.* (1979), Marias *et al.* (1991a), Ryan *et al.* (1993b) and Kamalzadeh (1996) that there is a significant loss of protein from the body during weight loss in immature sheep. The loss of protein from the body during weight loss for immature sheep, is consistent with the hypothesis that some degree of muscle catabolism is required to protect the body from the ketones that are produced during lipolysis (Wolkers et al., 1994b). However the present results contrast with those of Aziz *et al.* (1994) who reported an increase in visceral weight during a weight loss period in young wethers.

In the present experiment, the losses from body lean (carcass muscle and visceral organs) and total fat were of a similar magnitude in weight. However there was no sex effect on the relative losses of total body fat, although it is apparent that the majority of body energy that was lost from the sheep fed at 60% was in the from of fat, with approximately 50% of the initial weight of total body fat mobilised during the treatment period for both sexes. This agrees with the results of Little and Sandland (1975), Kabbali *et al.* (1992b) and Kamalzadeh (1996) who showed that the greatest effect (in energetic terms) was weight loss from the fat depots.

It is evident that the two periods of weight loss that have been described in a number of studies (Meyer and Clawson, 1964; Winter *et al.*, 1976; Thornton *et al.*, 1979; Searle *et al.*, 1979; Aziz *et al.*, 1992; Ryan *et al.*, 1993b) and which were clearly documented for the mature sheep (Chapter 3) are not apparent in the present experiment for the immature sheep. It appears as though carcass muscle, total fat and NFVC are mobilised at equal rates during the treatment period and that the rates of depletion for all tissues were declining towards the end of the treatment period.

A comparison of the results from the present experiment and those from chapter 3 indicate that there is a marked effect of maturity on the relative losses of body tissues during a weight loss period in sheep. Where the mature sheep had demonstrated a clear hierarchy for the tissues that were depleted during the weight loss period, that is carcass muscle, followed by total body fat, it appears as though there is equal rates of depletion for carcass muscle and total fat depletion during weight loss in immature sheep. Although total fat was the largest contributor to total body energy loss during the weight loss period for both immature and mature sheep, the relative loss of fat was greater in the immature sheep. This agrees with the results obtained by Butler-Hogg and Tulloh (1982) who reported a higher proportion of fat loss in immature ewes when compared to mature ewes. The present results also agree with the results of Thornton *et al.* (1979) who showed that weight loss in immature sheep resulted in proportionally more loss of tissue from the carcass. A comparison of the relative losses of carcass muscle for the immature rams in the present experiment with the mature rams (chapter 3) shows that conservation of lean tissue may depend on the maturity of the entire ram at the time when the restriction was applied Henricks *et al.* (1994).

As with the pattern of mobilisation of total fat, there was no sex effect on the relative losses of either carcass or internal fat for the sheep fed at maintenance. It was also evident that the proportion that each of the depots contributed to total fat loss was approximately equal during the treatment period. This contrasts with the results of Kabbali *et al.* (1992b) who indicated that a greater proportion of internal fat was mobilised during the early phase of weight loss, with the contribution by carcass depots increasing as the severity of the weight loss increased. The results of Kabbali *et al.* (1992b) also showed that the rate of weight loss affected the relative proportions of fat mobilised, suggesting that higher rates of weight loss were associated with greater internal fat mobilisation which may contribute to the differences between their results and those of the present study. Little and Sandland (1975) and the results from Chapter 3 indicated that the most labile fat depot during weight loss was the subcutaneous depot. However, in the present study no difference existed in the absolute loss of fat from either the carcass or internal depot. Sainz *et al.* (1995) indicated that the tissue that is most labile during the time when a feed restriction is applied will be the one that is most effected, thus it appears as though the priority for mobilisation of carcass fat only becomes evident as the animal matures.

5.4.2.3 Changes during the realimentation period

During the realimentation period the sheep that had been fed at 140% of maintenance maintained body weight. As previously indicated the maintenance requirements per kilogram of empty body weight for these sheep must have declined in order for the observed result to occur. However there is a definite sex effect on the mechanisms that were adopted to decrease maintenance requirements and to maintain empty body weight. There was no change in the weights of carcass muscle, NFVC and total fat during the realimentation period for the immature rams with respect to the weights of these tissues that were recorded at the end of the treatment period. Waghorn and Wolf (1984) indicated that protein fractional turnover rates decline with age and that lipid turnover remains constant. Lobley (1990) showed that there was a decrease in Na^+/K^- ATPase with increasing maturity and that muscle oxygen consumption and muscle protein synthesis also parallels lower maintenance requirements as animals age. Freetly (1995) also indicated that reductions in maintenance requirements that occur with age arise from both reductions in the proportions and the per unit costs of the metabolically active tissues. It appears as though maintenance requirements may have decreased in the immature rams as a result of lower relative turnover rates within body lean depots as the sheep "matured".

In contrast, maintenance of body weight in the immature ewes (from the 140% maintenance feeding treatment), during the realimentation period was achieved by a reduction in the mass of both body lean depots or carcass muscle and visceral lean, whilst total body fat continued to increase. Ledger and Sayers (1977), Koong *et al.* (1985), Notter *et al.* (1983), Murray and Slezachek (1988b), Aziz and Murray (1987), Ryan and Williams (1990) and Iason and Mantecom (1993), have all shown that immature animals mobilise visceral organ mass and increase total fat mass. This enables animals to reduce maintenance requirements by reducing the proportion of metabolically active tissues (Burrin *et al.*, 1988). Clearly this response observed in the ewes does not differ from previously published results, yet it differs markedly from the results obtained for the immature sheep that had been fed at maintenance for the entire experimental period.

Two possible explanations exist for this observation. Firstly, as the 140% ewes were more mature at the stage where weight stasis occurred compared with the sheep fed at 100% of maintenance, it may be that the response observed is a function of maturity and that a switch occurs at or near puberty, with a shift of the metabolism of the animal towards a fat biased metabolism which is more pronounced in the female (Greeff *et al.*, 1986a; Dulloo and Girardier, 1993; Schadereit *et al.*, 1995). Secondly it is also possible that the increase in total fat for the ewes which occurred during late summer and autumn was a component of a seasonal oscillation in body fat. Laurenz *et al.* (1992); Parker *et al.* (1993), Worden *et al.* (1995), Weber and Thompson (1995), Hewison *et al.* (1996) and Ball *et al.* (1996) have shown that seasonal oscillations in body components exist for both growing and mature animals. Ball *et al.* (1996; Chapter 6) indicated that total body fat increased during the autumn period and that the increase may be related to either a shift in metabolism or a mechanism that enables fat to be deposited prior to the reproductive season. Both scenarios indicate that fat deposition is a key priority of the female as it matures in order for reproductive success to be maximised (Weber, 1996).

The sex effect that was evident for the partitioning of body tissues during the realimentation period for the sheep fed at 140% of maintenance was also present for the partitioning of the fat between the fat depots. The gain in total fat observed for the ewes was primarily associated with increases in internal fat. For sheep that are maintaining weight, increases in total fat have been observed, yet the majority of the gain has been in carcass fat (Murray and Slezacek, 1988a,b; Ryan and Williams, 1989; Afonso, 1993). It is interesting to note that the gain in internal fat by the ewes during this period was associated with a significant decrease in NFVC. Adams *et al.* (1996b) immunised ewes against GHRH during a realimentation phase and noted that these ewes gained greater levels of internal fat and had lighter visceral organ weights when compared to controls. Perhaps the pattern of feeding has altered the response to GHRH by these ewes. Eisemann *et al.* (1996) also indicated that internal fat relative to visceral weight increases with age and perhaps the present result is a function of maturity of the ewes.

During the realimentation period, the sex of the immature sheep clearly dominated the priorities for tissue repletion during body weight compensation for those sheep that had previously been fed at 60% of maintenance during the treatment period. The immature rams were able to fully compensate for the carcass muscle that had been lost during the weight loss period, whilst the ewes only showed a partial compensation. Similarly the level of compensation for NFVC of the immature rams was complete but only partially complete for the ewes. In contrast, there appears to be no sex effect on the level of compensation of total fat that was achieved during the realimentation period. Both rams and ewes were able to fully recover the weight of total fat that had been lost during the treatment period. These results are the first to demonstrate that sex influences the level of compensation. However Marias *et al.* (1991a) did show a sex effect on deposition rates of body tissues during both feed restriction and realimentation. They indicated that rams were more efficient during a realimentation phase at an immature age compared to ewes, which appears to be consistent with the results of the present experiment

A number of studies have indicated that priority is placed on deposition of adipose tissue within the carcass depots and that internal fat appears to be insensitive to nutritional manipulation during compensatory growth (Hodge and Star, 1984; Carstens *et al.*, 1989b; Kabbali *et al.*, 1992a,b; Hayden *et al.*, 1993; Yambayamba *et al.*, 1996b). This pattern of fat partitioning was observed in the mature sheep in chapter 3, however in the present study there appears to be no difference in the relative repletion of fat tissue in the carcass and internal fat depots. These results indicate that maturity does effect the relative priorities for fat deposition during compensatory growth. However it must be noted that results quoted from the literature were from immature animals.

Several authors have stated that compensatory growth occurs in two phases, which are opposite to the phases that have been defined previously for weight loss. The existence of phases during compensatory growth is supported by a number of studies have shown that the initial phase of compensatory growth is associated with the deposition of body protein (Searle and Graham, 1975; Butler-Hogg, 1984; Greeff *et al.*, 1986b; Ryan *et al.*, 1993b; Drouillard *et al.*, 1991; Iason and Mantecom, 1993), with the majority of the gain in protein associated with increases in visceral lean weight (Fox *et al.*, 1972; Drew and Reid, 1975a; Ryan, 1990; Wright and Russel. 1991). The second phase of compensatory growth is usually dominated by an acceleration in fat deposition (Turgeon *et al.*, 1986; Hayden *et al.*, 1993; Ryan *et al.*, 1993b). The results from the present experiment do not indicate clear differences in the rates of either fat or lean deposition during the realimentation period. It appears as though the proportions of fat and total body lean gain are equal.

At the end of the realimentation period, immature rams that had gone through weight loss and realimentation attained similar proportions of body tissues to that recorded at the start of the experiment. However the ewes at the end of the experiment were proportionally fatter than at the start of the experiment. Onischuk and Kennedy (1990) indicated that although GH was elevated during compensatory growth in both ram and ewe lambs, the levels were six times higher in rams which would promote an increased deposition of protein. They also showed that insulin levels and the ratio of Insulin:GH were significantly lower in rams compared to ewes, that favoured lean deposition in the ram and promotes fat accretion in the ewe. As mentioned previously, it appears as though the female places emphasis on fat deposition at the expense of muscle tissue and that this may be associated with maximising reproductive success (Fennessy *et al.*, 1991; Weber, 1996). The ability of the immature ram to regain carcass muscle and NFVC tissue contrasts with the results obtained in chapter 3, where mature sheep from either sex were unable to regain carcass muscle. A possible explanation for this difference is that an elevation of GH is responsible for the ability of the immature ram to increase protein synthesis during the realimentation period and that the inability of the immature ewes and the mature sheep of chapter 3 to recover carcass muscle may be related to depressed GH levels during realimentation which restricts protein synthesis and accretion.

The contrast in the fat depots between the sheep that had been fed at 140% and 60% during the treatment period, after the realimentation period, particularly for the immature ewes, indicates that the growth path does influence the proportions of body tissues within the body when compared at the same age (Butler-Hogg and Johnsson, 1986).

From these results it is evident that the sheep that followed a 140:100 growth path had greater weights of both carcass and internal fat, but the magnitude of the difference was influenced by sex. Murray and Slezacek (1976), Thatcher *et al.* (1992) and recently Kirton *et al.* (1995) have shown that fat deposition was greater in lambs that had a higher rate of growth during an initial feeding phase. Although Butler-Hogg and Johnsson (1986) indicated that slower growing lambs (LH vs HL) had greater weights of fat in both the carcass and internal fat depots. Kirton *et al.* (1995) suggested that changes in fat partitioning in response to nutritional manipulation are unpredictable and that the mechanisms responsible may be complex. Clearly the ability to describe changes within individual animals, as shown by the present results, has provided some insight into the mechanisms that may be responsible for the variation, particularly the influence that sex has on the patterns observed. As mechanistic or dynamic models are developed to predict changes in body composition in response to nutritional manipulation (Oltjen *et al.*, 1986a; Sainz and Wolf, 1990; Williams *et al.*, 1995; Baldwin, 1995), studies which can describe changes in body components within individual animals will be required before the complexity of the relationships can be defined

The results from the present study show that bone growth is altered by nutritional manipulation and that as expected, the response was greater in rams than in ewes. In agreement with the results of Kirton *et al.* (1995), sheep from the HM feeding level, had greater weights of bone than sheep from the LM feeding level. This contrasts with previous studies by Murray *et al.* (1974), Price (1975) and Yambayamba and Price (1991) who showed that bone growth was unaffected by nutritional restriction and compensation. This study also indicates that bone remained constant during nutritional restriction for immature sheep, where Seebeck and Tulloh (1968) had shown that bone was lost in cattle that had undergone weight loss.

5.5. Conclusion

Sex had a marked effect on the priorities for tissue deposition that occurred during restricted growth which may be related to differences in target points for reproductive success. Greater emphasis was placed on carcass muscle development in the ram, whilst for the ewe an increase total body fat and in particular deposition of internal fat appears to be the highest priority. When restricted to a feeding level that had been previously calculated to maintain liveweight, both the immature rams and ewes were able to maintain a higher weight. For the immature ewes a distinct reduction in NFVC, combined with the repartitioning of energy from carcass muscle into adipose tissue, would lower maintenance requirements. The ability of the rams to maintain higher weights suggests that metabolic costs per unit of body tissue decline, which may be a function of age or maturity.

Different phases of weight loss were not apparent for the immature sheep as similar weights of fat and muscle tissue mobilised from the carcass. The depletion of total fat from the body during this phase was severe for both sexes, indicating that body fat reserves are primarily used to meet energy deficits in immature sheep. However, carcass muscle and NFVC conservation is more pronounced for the ram when compared to the ewe. Higher levels of growth hormone or the presence of androgens may be part of a mechanism that maintains body protein (lean) mass in the immature ram.

The mechanisms that were responsible for lean conservation during the weight loss phase may have contributed to the immature rams ability to recover carcass muscle during the realimentation phase. Clearly the ability to regain lost body tissues is much greater for the immature sheep when compared to the mature sheep. The results of this experiment has shown that nutritional manipulation of growth rates can result in distinct differences in body composition within and between sex for immature sheep at the same age and at similar liveweights. The interrelationships between growth paths and sex that have been identified can be used to enhance the construction and to test the accuracy of dynamic models that are being developed to predict the effect of feeding regimes on body tissue development (Oltjen *et al.*, 1986a; Sainz and Wolf, 1990; Keele *et al.*, 1992; Baldwin, 1995).

Chapter 6
Seasonal oscillations in body composition of growing and mature sheep.

6.1 Introduction

Changes in body composition with season have been reported in various breeds of cattle (Laurenz, *et al.*, 1992) and in mature female deer (Parker *et al.*, 1993; Weber and Thompson, 1995). All studies showed that there was an increase in the rate of fat deposition during the summer months, whilst during the winter months there appeared to be a increase in the rate of carcass muscle deposition and a mobilisation of fat reserves. In addition to these seasonal oscillations in body components, seasonal shifts in voluntary daily feed intake were also identified. As these two oscillations have been correlated it is unclear whether the changes in body composition are an effect related to seasonal influences on feed intake or whether they are an inherent response to other seasonal shifts in metabolism, nutrient utilisation or feed digestibility.

The effect of photoperiod *per se* on feed intake in both immature and mature sheep has been clearly established, with a higher feed intake recorded in summer and a lower feed intake recorded in winter (Kay, 1979; Forbes, 1982; Iason and Manetcom, 1991; Loudon, 1994; Iason *et al.*, 1994). These circannual rhythms in voluntary feed intake (Simpson *et al.*, 1984) are considered to be remnants of adaptive responses to environments where there were periods of limited feed supply such that the animal maximised physiological events such as growth, pregnancy and lactation in periods of abundance and minimised its costs during periods where resources were limited (Loudon, 1994). For sheep, the amplitude of the oscillations are dampened when compared to those of deer, as evolution in an environment where feed intake is less restrictive has resulted in a lower degree of seasonality displayed (Kay, 1985; Suttie and Webster, 1995). The question that remains is whether a cyclic change in feed intake drives or is driven by seasonal oscillations in the priorities for tissue deposition and depletion (Tucker *et al.* 1984).

Photoperiod *per se* has been shown to affect the rate and composition of gain during growth (see reviews Tucker *et al.* 1984; Petitclerc and Zinn, 1991). At a constant feed intake per unit of metabolic weight, Forbes *et al.* (1979) showed that lambs exposed to a 16L:8D increased weight by 4-10% above that of lambs exposed to 8L:16D lighting regime. Long-day lengths of 16L:8D also stimulated live weight gain in growing heifers and bulls by 8-16% when compared to animals exposed to light periods of less than 12 hours (Petitclerc *et al.*, 1983; Tucker *et al.*, 1984). Petitclerc *et al.* (1984) showed that the rate of gain in carcass weight (9.8%) and the protein percentage of the 8-11 rib section (11%) was increased for well fed heifers exposed to 16L:8D. In sheep, the results from Forbes *et al.* (1979) and Forbes *et al.* (1981) indicate that long-day length stimulated the growth of non-fat tissue in growing lambs. however Schanbacher and Crouse (1980) showed no difference in backfat thickness, kidney and pelvic fat, or yield. Tucker *et al.* (1984) postulated that for cattle, short day-length stimulates fat deposition and long-day length stimulates protein deposition. For sheep there can be no definite conclusions due to the lack of chemical analyses of carcasses. It is important to note that these experiments present results of an animals reaction to a short term change to a fixed light length pattern and thus establishment of any endogenous effect of photoperiod on the rate and composition of gain in growing animals remains unquantified.

Metabolic indicators such as fasting heat production or basal metabolic rate have indicated that body metabolism is under a seasonal influence. Blaxter and Boyne (1982), showed that sheep fed to maintain body weight, had oscillations in heat production (corrected to either a zero energy retention or to a zero feed intake) that were sinusoidal with time when an annual time period was assumed. The oscillations indicated that minimal metabolism occurred in winter and maximal metabolism in summer with amplitude of 14%. Walker *et al.* (1991) also observed distinct cyclic patterns in metabolic heat production in mature ewes, with the maximum of the amplitude occurring when animals where exposed to increasing daylength and a minimum occurring during exposure to a decreasing daylength. The magnitude of this difference was 26% when regressed to a metabolic weight ($W^{0.75}$). In contrast, several recent studies in deer have found no evidence of a seasonal pattern in metabolism after adjusting for both activity and critical homeothermic temperature (Mautz, *et al.*, 1992; Pekins *et al.*, 1992). Birkelo, *et al.* (1991b) also showed that although there was no effect of season on maintenance requirements as measured by fasting heat production, there was an effect of season on the energy required for weight maintenance. This indicates the influence that the technique used to estimate maintenance requirements has on the interpretation of associated mechanisms such as seasonality.

Overall, photoperiod does have a clear role in the seasonal affects on carcass tissue deposition, possibly through its influence on hormones such as prolactin and IGF-1. Eiseman *et al.* (1984) showed that prolactin was elevated during long daylengths and that this had a positive effect on lipid metabolism and on lean growth, although elevating prolactin without increased light resulted in no change in lean growth. This suggests that the effect of daylength on lean growth must be accompanied by other changes in combination with prolaction. Suttie and Webster (1995) tentatively proposed a causal link between the seasonal release of IGF-1 and growth rate in deer. For sheep this relationship has not been identified although IGF-1 does produce an increase in growth rate (Morel *et al.*, 1991; Flint, 1994).

The presence of seasonal effects on voluntary feed intake, metabolism, tissue growth rates and ultimately in body composition has been clearly established. In most scenarios, the links between the "*drivers*" and the driven parameters have not been established. Two experiments presented here were designed to test the hypothesis that oscillations in body components do exist in both immature and mature sheep. Specifically experiment one, assessed the magnitude and phase responses of total fat, carcass muscle and viscera in immature sheep after adjusting for the growth of tissues that are associated with increased maturity. The second experiment was aimed at identifying seasonal oscillations in body components of mature ewes that were fed at a constant feeding level. The two papers that have been published from these experiments are presented in the form in which they have been submitted for publication.

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6.2 Seasonal Changes in Body Composition of Growing Merino Sheep.

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Abstract

Circannual patterns in feed intake, metabolism and growth for sheep appear to be endogenous rhythms that are entrained to a seasonal photoperiodic pattern. It was considered that body composition, a resulting outcome of the input and utilisation of feed (metabolism), would also demonstrate a seasonal pattern. This study was aimed at establishing the presence of seasonal oscillations in body components of growing sheep, using total body fat, muscle and empty body weight data from a long term serial slaughter experiment in growing Merino sheep from weaning through to maturity. Changes in total fat and muscle weight relative to empty body weight were analysed using the additive allometric model in the non-linear form, to which a sine function was added to account for any seasonal oscillations in the residuals. For total body fat weight, the addition of a sine oscillation to the allometric model was significant for both rams ($P<0.05$) and ewes ($P<0.10$) with mean amplitudes of 1.01 and 0.58 kg, respectively. For muscle weight, the addition of the sine function was significant only for the rams ($P<0.01$), with a mean amplitude of 0.664 kg. In rams, the peak in the oscillation for total fat occurred in mid summer, whilst in ewes the peak occurred 111 days later in autumn. In rams, the oscillation for total muscle was approximately six months out of phase with that for total body fat. Therefore in rams, after adjustment for empty body weight, fat weight increased during summer, whilst muscle weight increased during winter. These oscillations indicate that there is a seasonal effect on the priorities for muscle and fat accretion in growing sheep. Oscillations in body components will have implications for assessing the energy requirements of growth and effect the ability to finish animals to fatness/weight specifications. Oscillations in body components will effect the maintenance energy costs of the mature breeding unit.

Keywords

Sheep, body composition, seasonality, growth

Introduction.

Changes in photoperiod, temperature, rainfall and feed availability are environmental cues that occur in distinguishable cycles, or seasons (Gwinner, 1986; Loudon, 1994). These cues often appear to synchronise physiological events such as reproduction, tissue growth and metabolism to the environmental conditions in which the animal lives (Tucker *et al.*, 1984; Gwinner, 1986). Cyclic patterns in metabolism (Silver *et al.*, 1969; Blaxter and Boyne, 1982; Walker *et al.*, 1991), growth (Simpson *et al.*, 1984; Iason and Mantecom, 1991; Suttie and Webster, 1995) and feed intake (Kay, 1979; Barry *et al.*, 1991; Iason *et al.*, 1994; Loudon, 1994) have been well documented in sheep, cattle and deer. Oscillations in the inputs (feed intake), or their utilisation (metabolism, growth) are likely to produce seasonal patterns in outputs, such as body components. As there is a differential relationship between body weight and component weight, it is important to understand whether changes in components are simply due to changes in body weight, or if there is a direct seasonal effect on the partitioning of nutrients between fat and lean tissues. A seasonal effect on the partitioning of nutrients into fat and lean would contribute significantly to the energy costs of weight gain during growth (Geay, 1984; Koong *et al.*, 1985) and to maintenance costs of mature females in production systems (Thompson and Barlow 1986; Ortigues *et al.*, 1993).

A number of studies have identified seasonal changes in body composition in wild ungulates, particularly in temperate deer species (Drew, 1985; Adamczewski *et al.*, 1987, Parker *et al.*, 1993; Weber and Thompson, 1995), with a higher deposition of tissue during the spring and summer months and a loss of tissue during the autumn and winter months. In temperate deer the greatest oscillations occur in body fat, which perhaps reflected an adaptation for storage and then mobilisation of energy dense tissues. In cattle, changes in body composition and maintenance requirements with season have also been reported (Laurenz *et al.*, 1992), for different breeds with diverse production potentials and mature body composition. They showed that mature Simmental and Angus cows had a cyclic nature in both empty body protein and fat. Body fat was gained and body protein mobilised during summer, whilst empty body protein was regained in winter and spring for both breeds. Although seasonal oscillations in body composition has been shown to exist in mature animals. To date, there is no evidence to indicate whether the same oscillations occur during growth.

Normally, the relative growth of body components is described using the allometric model in which component weight is regressed against empty body weight (Huxley, 1932).

However for *ad libitum* fed animals, body weight increments on a time axis become progressively smaller as growth rate decline as the animal approaches maturity. Therefore using the allometric model, any time based oscillations in body components with respect to empty body weight would become progressively compressed with increments of growth as shown in Figure 1. Given this confounding, it is not surprising that previous studies have not reported any seasonal oscillations in the body components of growing animals.

The present study aimed to establish and quantify seasonal oscillations in total dissectible body fat and muscle with respect to time, above the changes due to normal growth. Data were used from a serial slaughter experiment , in which rams and ewes from three strains of Merino sheep, selected for high and low weaning weight, that were slaughtered from weaning through to maturity (Thompson *et al.*, 1985a). Because the three strains differed in mature weight by a factor of 1.3, this data set had the added advantage that body weight was not confounded with season.

Materials and Methods

Data were from a long term serial slaughter experiment. Details of the selection history, experimental design, and husbandry have been previously reported by Thompson *et al.* (1985a). Briefly, rams and ewes from flocks selected for high (weight plus) and low (weight minus), along with a randomly selected flock, were fed *ad libitum* and slaughtered from birth through to maturity. The analysis used data from the 99 animals slaughtered post-weaning. For the first five slaughters, groups of 12 animals were slaughtered at increments of 10kg in body weight of the random rams (i.e. at 18, 26, 42, 53 and 68 weeks). Thereafter body weight in the remaining animals plateaued, and animals were processed as quickly as facilities allowed at three slaughter times (at 84, 95 and 102 weeks of age).

Details of the slaughter and physical breakdown of the carcass were given by Thompson *et al.* (1985b). The present analysis used data for empty body weight (sum of the fresh weight of both the carcass and non-carcass components), total dissectible fat (sum of the weights of the omentum, mesentery, kidney and channel fat and scrotal/udder fat depots and twice the weight of the dissected half carcass subcutaneous and intermuscular depots) and total dissectible muscle (twice the weight of dissected muscle from the half carcase).

The usual method to analyse compositional data involves fitting the log transformed data to a linear allometric model, [$\log_{10}Y = \log(A) + b \log_{10}(X)$, where Y is the weight of the component (kg), A the scaling factor, b the allometric growth coefficient and X empty body weight (kg)], using conventional least squares analysis. This analysis takes no account of time and as illustrated in Figure 1 any oscillations in fat and muscle weight were confounded with compositional changes due to growth.

In this study, log transformed fat and muscle weights were fitted to models which contained terms for strain, sex, log empty body weight and all first order interactions. After non-significant ($P>0.05$) interactions were removed, the final models for both fat and muscle contained terms for strain, sex, log empty body weight and sex x log empty body weight. A plot of the residuals for total fat and muscle over time indicated oscillations that were independent of changes in empty body weight.

The next phase of the analysis was to describe the patterns of residuals about the allometric model. Although it is possible to linearise the sine function using the first derivative of the fourier transform (Blaxter and Boyne, 1982) and include it in the above log transformed model, it was considered inappropriate as it was not possible to back-transform the log function with a sine term, to the additive form of the allometric equation ($Y=AX^b$). In addition the error associated with the allometric equation may be additive or multiplicative. If the error structure is assumed to be multiplicative then taking the logs of both sides of the allometric model, transforms it into a linear regression equation. However, if the error is additive then there is no transformation to linearity, and the allometric model $Y=AX^b$ must be analysed as a non-linear model.

Therefore rather than using the conventional log transformed least squares approach, the data was fitted to the non-linear additive form of the allometric model ($Y=AX^b$) to which a sine function was then added to account for any regular oscillation in the residuals. The sine function was, $d \sin(\omega t + \phi)$, where d = the amplitude of the sine oscillation in the residuals of the component from the allometric equation (kg), ω = frequency of the sine oscillation (radians/day), t = time at slaughter expressed in Julian days (days) and ϕ = phase angle for the sine oscillation (radians). The allometric model and the sine function was fitted within sex subclass using NLIN in SAS (1988). Within sex, the strain was constrained to a fixed effect by fitting strain as two single degree contrasts.

As the oscillations were considered to be seasonal in nature they were described as a function of time with an annual frequency (ω) that was defined as $2\pi/365$ or 0.0172 radians. The significance of the increase in variance accounted for by the inclusion of the sine function was assessed using F ratios.

Results

Allometric equations

The general agreement between the multiplicative and the additive models suggests that the error structure does not effect the estimation of the parameters. The additive error structure was adopted, since interpretation of the sine regression was more natural in this error structure. Allometric coefficients (b) estimated by either least squares or a non-linear approach are shown in Table 1. There was general agreement between the allometric coefficients estimated by the different techniques, with the exception of the rams for total body fat, where there was a significant decline ($P<0.05$) in the non-linear estimates, compared with the least squares approach.

Oscillations in the residuals.

The addition of a sine oscillation to the allometric function for total fat was significant for the rams ($P<0.05$) and less well defined for the ewes ($P<0.1$). The amplitude of the oscillation for total fat oscillation was 1.01 kg for rams and 0.58 kg for ewes (Table 2). For total muscle weight, the addition of the sine oscillation to the allometric function was significant for the rams ($P<0.01$) and was not significant for the ewes ($P>0.1$). The magnitude of the amplitude of the oscillation for total muscle weight for the rams was 0.66 kg (Table 2).

The phase shift of the oscillations (ϕ') in total fat for rams showed an increase to a maximum in summer relative to empty body weight, whilst there was a decrease to a minimum in winter relative to empty body weight (Figure 2). For ewes, the peak in total fat weight occurred in autumn, 3.5 months (111 days) later than that for rams. Sine oscillations for fat and muscle of the rams are presented in Figure 3. It is apparent that the phase of the oscillation for fat and muscle are approximately six months different (188 days).

Discussion

These results show that there are seasonal effects on the observed weights of components of the empty body during growth. When adjusted for empty body weight, there was a relative increase in fat deposition during the summer months in rams and the autumn months in ewes, whilst in rams there was a relative increase in muscle deposition during the winter months. As illustrated in Figure 2, the amplitude of the oscillations in total fat appeared to be twice the magnitude in rams than for ewes.. Montano-Bermudez and Neilsen (1990) suggested that the amplitude of the seasonality in growth in beef cows was related to function, with those animals having the higher absolute fat weight showing the greatest amplitude of the oscillations in fat. This appears to be a similar result for the sexes of the sheep, although as a proportion of total fat weight at maturity, the sexes had similar amplitudes.

Analysis of feed intake and body weight patterns for these animals by Thompson *et al.* (1985a) showed substantial sinusoidal oscillations in feed intake. They concluded that the amplitude and phase of these oscillations were primarily a result of temperature, with perhaps a minor influence of daylength. They also showed small, regular oscillations in the liveweight / feed intake relationship which they concluded were due to variations in gut fill. Interestingly, the phase of these oscillations was such that the minimum point for feed intake occurred during the summer period, whereas the results from this study showed a maximum in total fat weight for the rams, and where fat was increasing for the ewes. This contrasts with studies in temperate deer, that have shown that phase of fat deposition occurs during the period where annual cycles in feed intake are at the maximum (Adamczewski *et al.*, 1987; Worden *et al.*, 1995; Weber and Thompson, 1995).

These results are in close agreement with previously reported seasonal influences on body components in both cattle and deer. Laurenz *et al.* (1992) showed that mature cows fed at near maintenance stored body fat during the summer and mobilised body protein, when adjusted to a zero weight change. In contrast with the present results for sheep, the study of Laurenz *et al.* (1992) showed that there was little change in fat weight during winter for the mature cows. In black-tailed deer fed *ad libitum*, Parker *et al.* (1993) showed that body mass increased during the summer period and that the major component of this increase was fat, whilst during winter 10-15% of protein reserves and 70-82% of fat reserves were mobilised.

Worden *et al.* (1995) observed that fat deposition in white-tailed deer occurred in late autumn at the same time that maximum feed intake occurred. They indicated that fat deposited during summer, when mobilised supplied between 20-30% of total energy requirements during the winter period. In agreement with the results of Laurenz *et al.* (1992) no seasonal effect on protein mass was observed. It may be that the seasonal patterns in body composition are an evolutionary adaptation to balance the energy requirements of the animal in environments with an annual fluctuating feed supply.

Weber and Thompson (1995) examined oscillations in body components of *ad libitum* fed mature fallow does, in which body composition was estimated *in-vivo* at regular intervals using a CAT-Scanner over an 17 month period. Within individual animals, they found pronounced seasonal oscillation in both muscle and total body fat weights, which appeared to be in phase. The amplitudes of the oscillation in body fat were twice the magnitude of those for muscle, with increases in both tissues occurring during the summer/autumn and decreases during the winter/spring periods. However, when adjusted for empty body weight the differences in the amplitude of the oscillations in fat and muscle weight, had the effect of moving the phase of the oscillation of the smaller component (muscle), six months out of phase with the oscillation in the dominant component (fat). In the present study, where the oscillations in body components were evident after adjustment for empty body weight, it was possible to conclude that differences in the priority of tissue development occurred on an annual basis.

Given that the data reported in this paper were from growing animals in a serial slaughter experiment, it was necessary to adjust for empty body weight. However as demonstrated by the results of Weber and Thompson (1995), adjustment for empty body weight may alter the phase of the oscillations in causing a mirror image effect. Therefore, although the present study clearly showed the presence of oscillations, it was difficult to comment on the physiological mechanisms which control these changes in composition. Clearly, an experiment designed to measure individual component weights in animals that are maintaining weight is needed to identify the phases and magnitudes of oscillations in body components which are not confounded by changes in empty body weight.

Laurenz *et al.* (1991) showed that the requirements for weight maintenance in mature cows was lower during the winter period and higher during summer, and that the seasonal difference in requirements was at least, in part, due to the changes in body components. Importantly, they recognised that the requirements for weight maintenance differed to those for energy maintenance, as a result of the seasonal change in body composition. In contrast to the weight requirements for maintenance being higher in summer, the greatest requirements for energy maintenance occurred during winter due to the higher costs of depositing fat tissue as opposed to lean tissue (Webster, 1977; Solis *et al.*, 1988). Thompson *et al.* (1983) also showed a decline, during winter, of body fat, which correspondingly increased the maintenance requirements of mature cows. These results support the suggestion of Webster *et al.* (1982) that the metabolic rates in cattle change, such that fat accretion is accelerated during late summer prior to the winter period.

For sheep fed to maintain body weight, Blaxter and Boyne (1982) showed that heat production corrected to a zero energy retention and to a zero feed intake, was sinusoidal with time, with an amplitude of ±14% The frequency of this oscillation indicated that minimal metabolism occurred in winter and maximal metabolism in summer. The authors suggested that, although basal metabolic rate had a similar variation to that of feed intake, it was not a result of feed intake as both the level of feeding and the metabolisable energy of the diet were constant throughout. Walker *et al.* (1991) also observed distinct cyclic patterns in metabolic heat production in mature ewes, with a maximum occurring when the ewes where exposed to increasing daylength and a minimum occurring during exposure to a decreasing daylength. The magnitude of this difference was 26% when regressed to a metabolic weight ($w^{0.75}$).

In contrast, Pekins *et al.* (1992) and Sibbald *et al.* (1993) found no evidence of a seasonal pattern in metabolism of white tailed and red deer respectively, and suggested that activity and response to a critical homoeothermic temperature where important controlling factors of basal metabolic rate. Birkelo *et al.* (1991) also showed that there was no seasonal effect on fasting heat production or maintenance requirements in mature cows. However they did show that the energy requirements for weight maintenance changed over the yearly cycle and indicated that seasonal effects on body tissue depletion and accretion patterns would be the most probable effect. Despite the conflict, the cyclic patterns in metabolism observed by Blaxter and Boyne (1982) and Walker *et al.* (1991), suggests that metabolic requirements do vary with season in sheep, but it still remains to be determined whether the changes are either the cause, or a result of seasonal changes in body composition that have been identified in the present experiment.

Conclusions

The body weight at maturity of random rams in this study was 70 kg , with the proportions of fat and muscle being 0.30 and 0.26, respectively (Thompson *et al.*, 1985b). If it can be assumed that the seasonal changes in body components continues at maturity then the amplitude of 1 kg in fat would represent a proportional seasonal oscillation of ±1.05 of the total fat weight in the body. For rams, an amplitude of 0.7 kg represents a proportional seasonal oscillation of ±1.04 in total muscle weight. In energetic terms, the mobilisation and accretion of 2 kg of fat over an annual cycle will impact on the energetic requirements of the animal, with the mobilisation or accretion of fat yielding or requiring up to 1.5 MJ ME/week, respectively. This variation in energy yielded and absorbed by seasonal oscillations in body composition will affect breeding programmes that attempt to measure and compare the maintenance requirements of breeding animals at fixed feeding levels at different times of the year.

The presence of seasonal oscillations in body composition of growing sheep indicates that the energy costs of tissue deposition will alter with season. Although the efficiency of fat deposition is higher than that for lean deposition (Ferrell *et al.*, 1979), the higher energy content in fat tissue when compared to lean tissue would suggest that per kilogram of empty body weight the requirements for body growth would be higher in the summer/autumn months for growing animals. Seasonal oscillations in body components will have an effect on the energy requirements for growth and the absolute nature of the oscillations in total fat will effect the ability of the producer to supply carcasses that meet specific fatness/weight specifications of various markets.

Acknowledgments

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Table 1.

Allometric coefficients (b) from the least squares analysis (± average se.) and the non-linear models of the allometric function with and without the sine function (± asymptotic se.) for total fat and muscle as a function of empty body weight for rams and ewes

		Allometric coefficients (b)*		
	Sex	log transformed allometric function	Non linear allometric function	Non linear allometric function + sine oscillation
Total fat	Rams	1.804^{a} (0.030)	1.430^{b} (0.073)	1.484^{b} (0.070)
	Ewes	1.588^{a} (0.030)	1.541^{a} (0.059)	1.523^{a} (0.064)
Total muscle	Rams	0.974^{a} (0.02)	0.942^{ab} (0.035)	0.895^{b} (0.035)
	Ewes	0.818^{a} (0.02)	0.758^{a} (0.040)	0.764^{a} (0.048)

* Allometric coefficients with different superscripts are significantly different (5% LSD)

Table 2

Amplitudes (d, kg) and phase shift (ϕ, radians) (± asymptotic se.) and the phase shift expressed in days from the photoperiod (ϕ′, days) for the oscillations in dissectible fat and muscle components.

Sex subclass	Dissectible fat			Dissectible muscle		
	d	ϕ	ϕ′	d	ϕ	ϕ′
Rams	1.010	1.052	42	-0.664	0.919	230
	(0.374)	(0.393)		(0.210)	(0.304)	
Ewes	0.582	-0.895	153	0.045	1.565	12
	(0.267)	(0.575)		(0.167)	(4.172)	

Ball, A.J., Thompson, J.M. and Pleasants, A.B. (1996) Seasonal changes in body composition of growing Merino sheep. *Livestock Production Science*. 46:173-180

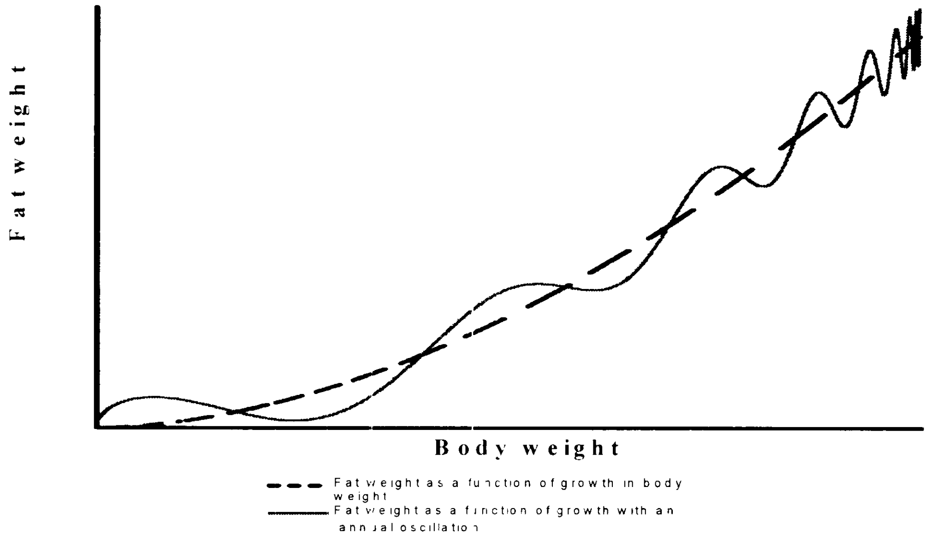

Figure 1. Fat weight as a function of growth in body weight with and without an annual oscillation.

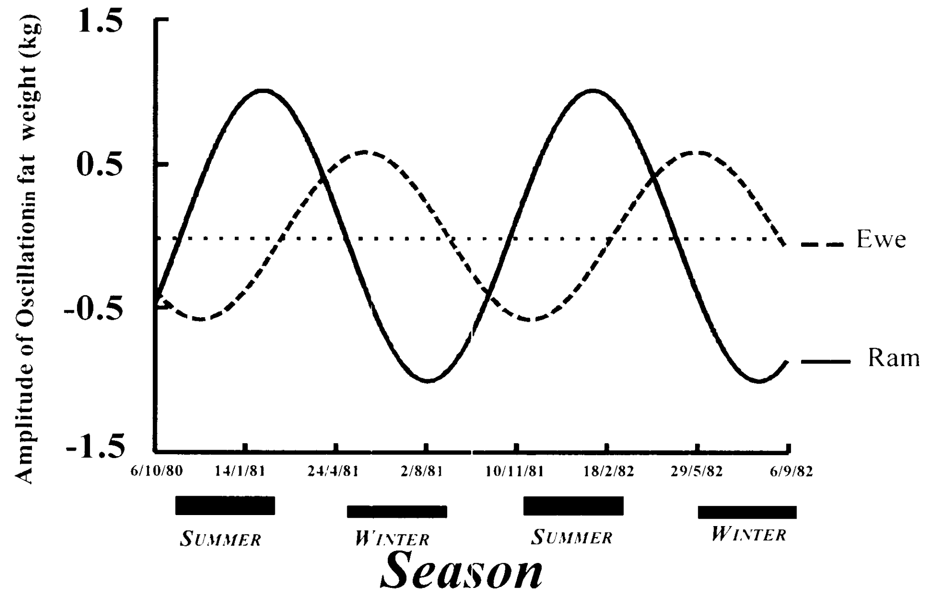

Figure 2. Oscillations in fat weight for rams and ewes from the predicted mean weight deposited during growth.

Ball, A.J., Thompson, J.M. and Pleasants, A.B. (1996) Seasonal changes in body composition of growing Merino sheep. *Livestock Production Science*. 46:173-180

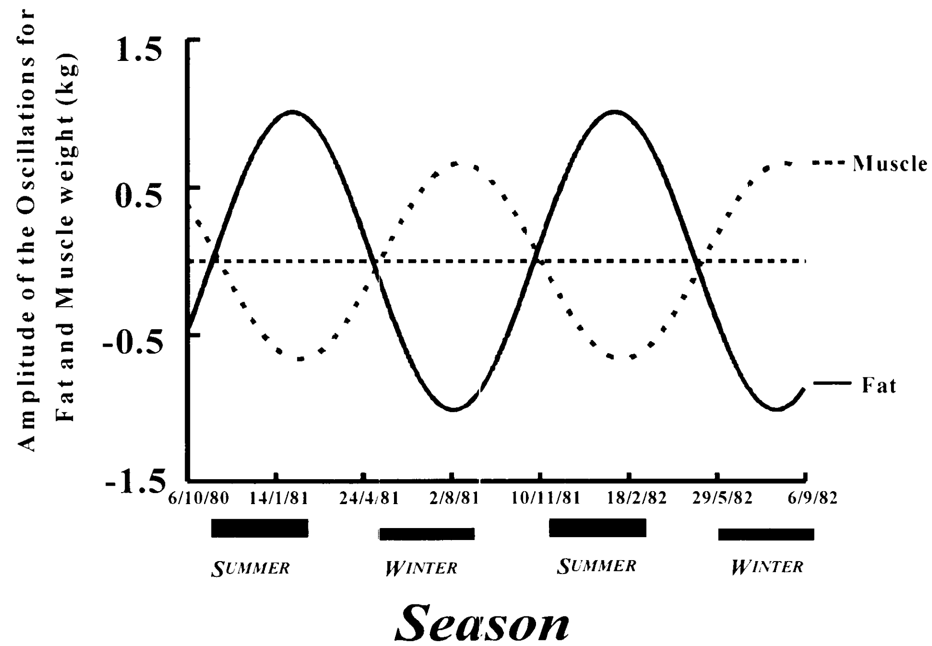

Figure 3. Oscillations in fat and muscle weight for rams from the predicted mean weight deposited during growth.

Ball, A.J., Thompson, J.M. and Ginch, G.N. (1996) Seasonal oscillations in the mass of body components of mature ewes fed at a constant intake. ***Proceedings of the Australian Society of Animal Production.*** **21: 479**

6.3 Seasonal oscillations in the mass of body components of mature ewes fed at a constant intake.

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Seasonal oscillations in total fat and carcass muscle above that due to changes in empty body weight have been identified in growing sheep (Ball *et al.*, 1995) and in mature fallow deer does (Weber and Thompson, 1995). In both experiments there were seasonal oscillations in feed intake, so it was unclear whether the observed changes in body components were a result of differences in nutrient utilisation arising from the variation in feed intake, or whether there was an inherent seasonal shift in metabolism, which was independent of variation in food intake. The present experiment examined whether there were seasonal patterns in body components of mature ewes fed a constant intake of the same pelleted ration (10.3 MJ/kg, 16% CP) for 260 days.

Four mature non-pregnant Coopworth ewes, housed individually in 3x3 metre pens within an open shed with natural light, were fed once daily, from April, 1993 until January ,1994. On nine occasions, repeated *in vivo* estimates for carcass muscle, visceral lean, total fat and empty body weight (EBW) were obtained using a CAT-scanner (Thompson and Kinghorn, 1992). Changes in body components (Y) of EBW, total fat, carcass muscle and visceral lean relative to time (t) were analysed using a non-linear model that contained a linear term and a sine function, $Y = a + b*t + d*\sin(0.0172*(t + \phi))$, where t = days from the first estimate (day 42) and ϕ = the phase shift of the sine oscillation from the starting point (days). As the use of the CAT-scanner provided repeated measurements of body components, changes in the tissues over time were analysed within animals.

The analysis for EBW showed no linear change over time, but did show a significant sine oscillation ($P<0.01$), with an amplitude of 1.10 kg. For total body fat and muscle, the addition of the linear term together with the sine function was significant when compared to the model with a constant (a) (Table 1; $P<0.01$). For total fat and muscle the amplitudes of the oscillation were 2.02 kg and 0.81 kg respectively. For visceral lean the linear term was not significant (P>0.10), so the final model contained only the sine function (P<0.01), which had an amplitude of 0.34 kg.

Table 1. Parameters for linear and seasonal oscillations in EBW, total fat, muscle and viscera with time.

	Model		Linear term		Sine Oscillation	
Component	df	F-ratio[A]	Constant	Linear coefficient (b)	Amplitude (d, kg)	Phase shift (ϕ days)
EBW	2,30	22.02*	43.16	-	1.10	94.
Total Fat	3, 29	13.39*	14.91	0.021	2.02	70
Carcass muscle	3,29	22.24*	18.73	-0.014	0.81	242
Visceral lean	2,30	17.45*	5.22	-	0.34	109

[A] F-ratio for the variance associated with the addition of the linear change and sine oscillation in body components relative to the model that contained only a constant (a).
* (P<0.01)

The peak in the oscillations for EBW and total fat occurred in early summer, whilst the peak for carcass muscle occurred in late autumn. The presence of oscillations in EBW, total fat, carcass muscle and visceral lean in ewes fed at a constant intake, indicates that there are seasonal effects on the priorities for tissue deposition and retrieval that are independent of variations in feed intake. The changes in tissue weights and EBW with time indicate that the utilisation of a given weight of feed by mature ewes does vary with season.

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6.4 Conclusion

Preliminary analyses of the data from the mature Coopworth sheep fed at maintenance (Chapter 3), using the methods of Ball *et al.* (1996) as shown in Ball *et al.* (1996), did show significant oscillations in body components. It is well argued that in order to test for an oscillation, measurements must be made over the time frame at least equal to the frequency of the oscillation examined (Stroup *et al.*, 1987). In both experiments, the original designs included extension of the feeding period for 15 months. Circumstances beyond the control of the experimenter resulted in both experiments (Chapter 3 and 5) being terminated. In both studies a more detailed analysis of the body components for both immature and mature sheep fed at maintenance using the random effects models with spline functions (Cullis *et al.*, 1996) did not show a presence of seasonal oscillations. To date, it is not possible to confirm or dismiss the occurrence of seasonal oscillations in body components of sheep fed at maintenance feeding levels. Further long term studies using CT-scanning will be required to determine whether seasonal oscillations are an endogenous rhythm in sheep.

It is evident from a comparison of the magnitude of seasonal oscillations in feed intake of the various species of deer with those of immature sheep, that the pressure for maintaining an endogenous link to the seasonal conditions has been dependent on the environment in which they have evolved. The less seasonal breeds of sheep show less seasonality in the observed traits of growth and voluntary feed intake (Kay, 1979). Temperate deer species show a much more pronounced circannual pattern in feed intake and growth then tropical deer species (Suttie and Webster, 1995). It is important that these relationships with the environment be understood when attempting to introduce a new species or breed into a environmental situation that differs to the one in which they have evolved.