Changes in Body composition and Maintenance efficiency during periods of restricted and maintenance feeding in immature and mature sheep.

By Alexander James Ball
Bachelor of Rural Science, 1st Class Honours (UNE)

A thesis submitted for the degree of Doctor of Philosophy of the University of New England
October 1996
Declaration:

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.

Alexander Ball
Acknowledgments

A number of people have contributed to the completion of this thesis. Firstly, I would like to thank all of the staff members (there are too many to name individually) of the Livestock Industries Institute at the University of New England, that have either given practical or intellectual help during the period in which I have been enrolled in this degree.

I am greatly indebted to both John Thompson and Geoff Hinch, who extended their help and time beyond that required as a supervisor. John never ceases to amaze me with his endless enthusiasm and energy, which he continually directs towards experimental design and statistical analysis. He fostered and continues to promote my drive to explore new technologies. He was always ready to spend time listening, helping with analysis or discussing problems with the methodology of the experiments. I am grateful to Geoff for his patience and willingness to listen to more personnel problems, aspects of animal husbandry and his continual reminder of the “biology” of the system.

I am forever reminded that the success and accuracy of any experiment relies on having excellent technical assistance. To this end, Pat Littlefield, Andrew Blakely, and briefly Kath Baker, provided technical help that could not have been matched. Their personal input into the practical management of the experiment, the countless hours weighing and feeding sheep and the professionalism which they displayed at all times is much appreciated. Gudrun Cacho helped immensely, by dissecting some of the thousands of CT-images that I collected.

To my fellow Ph.D students, Neville Jopson and Markus Weber, I owe a great deal of thanks. The support, friendship, discussions they offered helped to make the completion of the thesis enjoyable and rewarding. Neville deserves particular thanks for developing the CT-software that enabled the countless number of images to be analysed in the shortest possible time. Markus helped immensely with the practical components of the experiment and those little “gems” of German wisdom that continually kept me amused.
The staff of the Regional Veterinary Laboratory of NSW Agriculture Armidale, deserve special thanks for their help in identifying and providing solutions for several of the health problems for the sheep that occurred in the experiments.

One of the critical aspects of this thesis was the analysis of the repeated measures of body composition that were obtained using the CT-scanner. I think that I have been extremely lucky that many statisticians were able to give their time to help me. Dave Johnson, Tony Pleasants and Bob Murison spent many hours looking at the structure of my data and helped in proposing and testing new forms of analysis. Just when it appeared nothing would work, Brian Cullis and Arthur Gilmour introduced the concept of random effects models with cubic splines which proved to be an outstanding technique to analyse the data that I had collected. Clair Alston has been nothing short of fabulous. Without her help and explanation of the statistical results, this thesis would not be finished today.

Several people helped with discussions about experimental design and the implications of my results. Hutton Oddy and Peter Fennessy have always challenged me with new ideas and concepts, which has strengthened my ability to be critical of both my own and other published results. Discussions with Peter Parnell were a great help at the start of the Ph.D. I feel fortunate that new technologies have enabled me to communicate with many people throughout the world. A number of international people aided in discussions about the experimental design that I followed and the experimental results that I obtained. I hope in future that I will be able to meet some of these people on a personal basis, rather than communicating across the world of “email”. Special thanks go to many people of AgResearch in New Zealand (John McEwan, Jimmy Suttie, Peter Speck, Dave McCall and Deon Goosen to name a few) that have provided time and access to their ideas and animal resources.

I am deeply indebted to my father, mother and brother who have put up with three years of “being myself” and very frequent requests for help to feed sheep, weigh feed, check results etc. As both my parents are technicians within the department, their
continual reminder of “becoming an academic” served to place reality on a number of situations.

Finally to my wife (Melissa), thanks for putting up with me over the last two years. Your patience and support has been fantastic. Learning to “Hang Loose” was great and finishing before the wedding, if only a day before, had been the focus to submit.
Abstract

Improvements in production and quality can occur, without the need for increased inputs, through the use of *Compensatory growth* or by reducing the maintenance requirements during growth and at maturity. A series of studies were used to examine the changes in body composition that occurred during weight loss and realimentation in immature and mature sheep. The effect of variations in body composition, induced through manipulation of nutrition, on estimates for equilibrium maintenance efficiency of mature sheep was examined. Statistical methods developed, tested for seasonal cycles in body composition in an attempt to determine the impact that any endogenous pattern in tissue deposition has on estimates of efficiencies for growth and maintenance.

**Maintenance efficiency**

Differences in maintenance requirements between genotypes selected for variation in body composition when compared at the same weight were shown to be a function of response of body components to selection. No reduction in the true energetic costs of maintaining the various body tissues was achieved through selection for changes in body fatness. These results indicate that differences in body composition do contribute to variation in maintenance requirements observed both within and between breeds. Improvements in biological efficiency gained by selection for proportionally fatter animals are diminished by a proportional reduction in the final product (muscle mass) from the dam/offspring unit. Sex differences in maintenance requirements at the same weight are not explained by differences in body composition.

The implications of previous nutritional history on estimates for equilibrium maintenance efficiency were examined in mature sheep. Utilisation of CT-scanning allowed estimates for maintenance efficiency to be adjusted for differences in retained energy over the test period. A period of severe weight loss resulted in higher maintenance requirements during a realimentation period relative to that recorded prior to the weight loss period, when expressed per kilogram of body weight. In contrast, less severe
restriction resulted in no deviation in the relationship between equilibrium feed intake and equilibrium weight. After realimentation, the maintenance costs per kilogram of body weight remained higher in those sheep that had previously lost greater weights of body tissues. Higher maintenance requirements may be a cause or an effect of the inability to completely recover empty body weight during the realimentation period. It appears that prior nutritional history can affect estimates of maintenance requirements for mature sheep. The assumption that energy costs for protein and fat deposition and depletion are constant was proposed as a limitation to attempts to estimate true maintenance costs. Equilibrium body weight and body composition at the end of a realimentation period differed for immature sheep that had undergone a previous period of weight loss. Higher body weights were maintained after immature sheep had gained weight and been restricted back to an equilibrium feeding level. This suggests that maintenance requirements do decrease with age or maturity.

**Body composition and Compensatory growth**

More precise methods of describing the magnitude of fixed treatment effects and random animal variation were developed using random effects models with cubic splines. This technique, combined with accurate estimates of body components in vivo via CT-scanning, removed some of the previous confounding effects of differences between animals and biases in allocation of animals to treatment groups. The novel description of the treatment effects using this combination of techniques enhanced the level of understanding of the dynamics of body tissues.

In mature sheep, it was evident that two phases for tissue depletion (that is muscle followed by fat depletion) existed during weight loss. Depletion of carcass fat was used by both sexes to meet the major part of a net energy deficit. Relative to total fat depletion, lean tissues of the body were conserved during the weight loss phase. Changes in endocrine levels were proposed as mechanisms that enabled protein to be conserved during weight loss. Catabolism of lean tissues or muscle from the carcass, that was observed in
the initial phase of weight loss, may be part of a mechanism that protects the animal from ketones formed during lipolysis.

The sheep that were faced with a milder nutritional restriction were able to conserve greater levels of adipose tissue and visceral organs. There was a difference between rams and ewes during weight loss, although unexpectedly it appeared as though females adapted to the energy deficit by reducing metabolic requirements of the tissues rather than mobilising higher levels of lean tissue. There was no effect of fatness genotype (as examined by comparing sheep from lines that differed in backfat thickness) on the patterns of tissue mobilisation during weight loss. Mature sheep fed at a previously defined level for weight maintenance, demonstrated a clear priority for the deposition of carcass fat, whilst carcass muscle remained at depleted levels. A shift to a fat biased metabolism during realimentation appears to be a response of mature sheep that have experienced a period of weight loss.

The patterns of tissue depletion observed for immature sheep clearly differed from those obtained for mature sheep. No hierarchy for tissue depletion in the immature sheep was identified as similar weights of fat and muscle tissue were mobilised from the carcass. Lean conservation was much more pronounced during weight loss in the immature rams when compared to the immature ewes. Elevated levels of growth hormone during feed restriction in the male may contribute to the level of lean conservation that was observed. A distinct sex effect was also observed for the priority for tissue deposition during restricted gain in immature sheep. Females gained greater weights of total fat, whilst males deposited higher weights of carcass muscle as total body weight increased. Differences in priorities for reproductive function as sheep mature may be associated with this result. Clear differences due to sex, were apparent for the proportions of tissues that were deposited during realimentation. Carcass muscle was fully recovered by immature rams, whilst total fat was recovered by both sexes. The influence of elevated growth hormone levels was suggested as a mechanism that promoted lean tissue deposition in the male. Clearly the severity of the nutritional limitation and the stage of maturity at which the restriction was enforced were identified as critical factors that contribute to variation in
the final body composition of sheep from different growth paths. For sheep, it appears as though the sexual dimorphism that exists for body tissue responses to nutritional manipulation, diminishes with maturity.

**Seasonality**

After adjusting for differences in body composition attributable to growth using an allometric function, seasonal oscillations for total body fat and carcass muscle were apparent in growing sheep. The magnitude and phase of the sine oscillations for fat and carcass muscle suggested that seasonal cues affect the priorities for tissue deposition. Seasonal oscillations were present for mature sheep that had been fed at a constant feed level. However, a more precise method of describing the patterns of change in body tissues using random effects models and cubic splines did not reveal the presence of any time-based deviation in total fat, carcass muscle or visceral lean. Nevertheless, the possibility of oscillations in body composition must be considered when estimating the efficiency of growth and maintenance or when evaluating the effects of nutritional manipulation on tissue development in immature and mature sheep.
# Table of Contents

Acknowledgments iii

Abstract vi

Table of Contents x

List of Tables xiii

List of Figures xv

Chapter 1. General Introduction 1

Chapter 2. Literature Review 5

## 2.1 Maintenance efficiency 5

2.1.1 Definition 5

2.1.2 Measurement of maintenance efficiency 7

2.1.2.1 Fasting heat production/Basal metabolic rate 7

2.1.2.2 Equilibrium weight 11

2.1.2.3 Partial regressions 14

2.1.2.4 Residual feed intake 17

2.1.3 Physiological effects on maintenance efficiency 18

2.1.3.1 Growth and maturity 18

2.1.3.2 Sex 20

2.1.3.3 Feeding level 21

2.1.3.4 Body composition 24

2.1.3.5 Compensatory growth 28

2.1.3.6 Seasonality 30

2.1.3.7 Endocrine 31

2.1.4 Selecting for maintenance efficiency 33

2.1.5 Conclusions 36

## 2.2 Tissue mobilisation and accretion patterns during natural and enforced periods of feed restriction: Aspects of Compensatory growth 38

2.2.1 Introduction 38

2.2.2 Ad libitum or Normal growth 38

2.2.3 Responses of animals to a period of feed restriction 40

2.2.3.1 Restricted positive growth 40

2.2.3.2 Weight stasis 42

2.2.3.3 Weight loss 45

2.2.4 Compensatory growth or Realimentation 49

2.2.5 Conclusions 55

Chapter 3. Changes in body composition of mature rams and ewes during periods of feed restriction and realimentation 57

3.1 Introduction 57
Chapter 4. Changes in maintenance efficiency of mature sheep fed at different levels of feed intake. 104

4.1 Introduction 104
4.1.1 Null Hypothesis 106
4.2 Materials and methods 107
4.3 Results 110
4.3.1 Deviations over time for $M_{e,K\%}$ 111
4.3.2 Deviations over time for $M_{e,Ln}$ 112
4.3.3 Deviations over time for $M_{e,En}$ 113
4.4 Discussion 115
4.5 Conclusion 121

Chapter 5. Body compositional changes in immature Merino rams and ewes during periods of feed restriction and realimentation. 122

5.1 Introduction 122
5.1.1 Null Hypotheses 125
5.2 Materials and methods 126
5.2.1 Experimental design 126
5.2.2 Animals 128
5.2.3 Feeding and handling procedures 129
5.2.4 Diet 129
5.2.5 Animal health 129
5.2.6 CT-scanning procedure 130
5.2.7 Statistical methods 131
5.2.7.1 Modeling procedure 132
5.3 Results
   5.3.1 Empty body weight
   5.3.2 Carcass muscle
   5.3.3 Non fat visceral components
   5.3.4 Bone
   5.3.5 Total fat
   5.3.6 Carcass fat
   5.3.7 Internal fat

5.4 Discussion
   5.4.1 Empty body weight and maintenance
   5.4.2 Changes in Body composition
      5.4.2.1 Maintenance feeding
      5.4.2.2 Changes during the treatment period
      5.4.2.3 Changes during the realimentation period

5.5 Conclusion

Chapter 6. Seasonal oscillations in body composition of growing and mature sheep. 165

6.1 Introduction 165
6.2 Seasonal changes in body composition of growing merino sheep 168
6.3 Seasonal oscillations in the mass of body components of mature ewes fed at a constant intake 186
6.4 Conclusion 188

Chapter 7. Summary and Conclusions. 189
7.1 Compensatory growth 190
7.2 Maintenance efficiency 193
7.3 Seasonality 195

References 197

Appendix 235
   A1) Feed requirements for maintenance of mature rams and ewes from lines selected for differences in body composition. 236
   A2) The effect of selection for differences in ultrasonic backfat depth on the feed utilisation for maintenance and biological efficiency in sheep. 243
List of Tables

Table 3.2.1 Timetable of events and scanning dates for the restricted and realimentation phase respectively. 65

Table 3.2.2 Components and dry matter composition of the experimental pellet. 66

Table 3.3.1 Mean fleece free empty body weight (EBW), carcass lean, viscera and total fat weights (±sem) at the start of the experimental period for control and fat rams and ewes. 73

Table 3.3.2 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 empty body weight. 75

Table 3.3.3 Significant variance components (Random effects) of the final models for the seven body components. 75

Table 3.3.4 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 muscle, visceral lean and total fat. 82

Table 3.3.5 Significance and t-values for the overall mean (μ (kg)), deviations for fixed effects (kg) from the overall mean and deviations for the linear time effects for carcass fat and internal fat depots. 84

Table 4.3.1 Significance and t-values for the overall mean (μ), deviations for fixed effects from the overall mean and deviations for the linear time effects for the derived variables of $\text{Mem}_Kg$, $\text{Mem}_Ln$ and $\text{Mem}_En$. 110

Table 4.3.2 Significant variance components (Random effects) of the final models for the derived parameters of $\text{Mem}_Kg$, $\text{Mem}_Ln$ and $\text{Mem}_En$. 111

Table 5.2.1 Timetable of experimental events. 128

Table 5.2.2 Components and dry matter composition of the pelleted feed ration. 129

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. 135
Table 5.3.2 Significance and t-values for the overall mean, deviations for fixed effects and deviations for the linear time effects for empty body weight, carcass muscle, NFVC and total fat.

Table 5.3.3 Significance and t-values for the overall mean, deviations for fixed effects from the overall mean and deviations for the linear time effects for carcass and internal fat depots.
List of Figures

Figure 2.1 Partition of feed energy in animals. 6
Figure 2.2 The Taylor Diagonal. 13
Figure 3.2.1 Feeding levels of the three treatment groups during the experimental period. 64
Figure 3.3 Changes in empty body weight for all individual sheep over the restriction and realimentation phases of the experiment. 74
Figure 3.3.1 Deviations for empty body weight (kg) from initial empty body weight and the 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment. 77
Figure 3.3.2 Deviations for carcass muscle (kg) from initial carcass muscle weight and 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment. 79
Figure 3.3.3 Deviations for visceral lean (kg) from initial visceral lean weight and 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment. 80
Figure 3.3.4 Deviations over time for total fat (kg) with 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment. 83
Figure 3.3.5 Deviations for carcass fat (kg) from initial carcass fat weight with 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment. 84
Figure 3.3.6 Deviations for internal fat (kg) from initial internal fat weight with 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment. 86
Figure 4.3.1 Deviations for $\text{Me}_n$Kg (MJ ME kg$^{-1}$ day$^{-1}$) from initial estimate for the feed required to maintain a kilogram of empty body weight (scaled to zero) for the three treatment groups during the restriction and realimentation phases of the experiment. 112
Figure 4.3.2 Deviations for Me_mLn (MJ ME / kg LN day⁻¹) from initial estimate for the feed required to maintain a kilogram of total body lean (scaled to zero) for the three treatment groups during the restriction and realimentation phases of the experiment.

Figure 4.3.3 Deviations for Me_mEn (MJ ME/MJ day⁻¹) from initial estimate for the feed required to maintain a megajoule of body energy (scaled to zero) and the 95% confidence limits for the three treatment groups during the restriction and realimentation phases of the experiment.

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.

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

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

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

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

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

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 immature sexes during the maintenance, treatment and realimentation periods of the experiment.