

Grazing Management and Sheep Production  
on Improved Pastures

by

J.R. Donnelly B.Agr.Sc.

Submitted in fulfilment  
of the requirements for the degree of  
Master of Agricultural Science

UNIVERSITY OF TASMANIA

HOBART

July 1976.



# STATEMENT

The work presented in this thesis is my own.  
Specific contributions by others are referred to in  
the Acknowledgements and in the text.



J.R. Donnelly

CSIRO Division of Plant Industry,  
P.O. Box 1600,  
Canberra City.,  
A.C.T., 2601.

## Acknowledgements

In any study of grazing management systems the active collaboration of many people is required. Hence I am indebted to a large proportion of the research and technical staff of the Agricultural Systems section of the CSIRO Division of Plant Industry for guidance and assistance in the field and laboratory.

The work described in this thesis is only part of a much larger study in the broad field of grazing management. This study commenced when I was granted leave from the Tasmanian Department of Agriculture to work with Dr. F. Morley at the CSIRO Canberra Laboratories. The financial assistance granted by the Australian Wool Board was much appreciated.

My sincere thanks are due to Dr. Morley, Dr. J. Davidson and Dr. M. Freer for their friendship and their encouragement and assistance while working on this thesis. I owe them much in coming to appreciate the value of the systems approach in agricultural research. I am also indebted to Dr. K. Christian for many hours of fruitful discussion.

I am also grateful to Dr. J. Yates and Prof. G. Wade of the University of Tasmania for the opportunity to

present this work as a thesis in the Department of Agricultural Science.

The text for this thesis was punched on standard IBM 80 column punch cards and I am indebted to Mrs. M. Clark for her co-operation in this task. I developed a series of programs to run on a PDP 11/10 computer to convert the upper case card images to full upper and lower case text. The terminal on which the text was printed uses a dot matrix printing head. Hence the lower case of the letters 'G', 'Q', 'P', and 'S' are printed as 'g', 'q', 'p' and 's' and may seem unusual at first sighting. Initially I had hoped to produce the text on an IBM Selectric Typewriter attached to the computer as a peripheral but the facility became unavailable.

## Contents

	Page
Summary	1
Part 1            General Introduction	4
Part 2            The effect of flock size and grazing management on sheep production	9
2.1    Introduction	9
2.2    Experimental treatments	10
2.3    Experimental procedure	12
2.4    Statistical analysis	14
2.5    The analysis of variance	24
2.6    The effect of flock size on production	26
2.7    The effect of grazing management on production	27
2.8    Comparison of breed effects	29
Part 3            The estimation of feed intake by grazing sheep : a review	32
3.1    Introduction	32
3.2    The estimation of food intake from faecal analysis and diet digestibility	34

3.3	The estimation of nutrient intake from animal production	42
3.4	The prediction of pasture growth under grazing	45
3.5	Conclusions	47
Part 4	The estimation of body composition of live sheep	49
4.1	The statistical analysis of the available data	51
4.3	Prediction of body composition	53
4.4	Conclusions	57
Part 5	The effect of body composition on the intake of food by mature sheep	60
5.1	Introduction	60
5.2	Experimental details	61
5.3	Experimental procedure	63
5.4	Results	66
5.5	Discussion	71
Part 6	General discussion and conclusion	76
Part 7	References	82

## Summary

This thesis emphasizes the need to use a systems approach when examining the effects of management on the efficiency of animal production from grazed pastures. The three experiments that are described were designed to increase the understanding and precision of some of the relationships that are used in the simulation of grazing systems.

Conventional tests of farm management systems are usually of small scale and involve considerable handling of stock. Extrapolation of results to normal farm practice is therefore uncertain. An experiment carried out over 12 months with sheep in flocks of various sizes and managed under various grazing systems was analysed by estimation of the variance components of a non-orthogonal linear model. No effect on liveweight gains or wool production was detected in weaner sheep whether they were in flocks of 3, 9, 27 or 135 or whether they were set-stocked, rotated around three subdivisions of a rotationally grazed pasture, or rotated around three subdivisions of a pasture which was continuously grazed. These results indicate that within these limits neither flock size nor movement of animals has any important effect on animal production and thus can be ignored when establishing relationships between variables of basic biological importance to grazing systems.

Increased precision in the relationships describing the interaction between the grazing animal and the pasture is limited in part by the technical difficulties in measuring food intake and in interpreting liveweight changes in terms of tissue energy retention. A review of the literature suggests that estimates of intake obtained by current techniques may be subject to biases that are at present undefined. Although these techniques may be useful in comparative studies of animal production, they are unlikely to be sufficiently precise for estimating the growth of pastures under grazing.

A substantial improvement to the technique for predicting chemical composition in the live sheep was achieved in the second experiment. New and published data from sheep of widely different ages were used to derive regressions of body components on parameters measured in the live animal. Allometric models including body weight, tritiated water space and maturity as predictors substantially reduced the residual standard deviation for all components and largely eliminated bias from the predicted values, yielding equations of general rather than local application.

These regressions and the best available methods for measuring intake were used in the third experiment to



examine the effect of body condition (energy status) on intake by mature sheep. Energy status within the range 220-389MJ had no effect on the intake of herbage by grazing animals or of a standard feed offered to animals in pens. Sheep which were moved from a sparse pasture (low energy status) to an abundant pasture gained at least as much liveweight, but only 20% as much energy as sheep in better condition (high energy status) because more of their gain was water.

The results indicate that feed intake is likely to be unaffected by body condition under a variety of management regimes, but that changes in efficiency of feed conversion may have important implications in the field.

## Part 1

### General Introduction

Increasing the productivity of grazing systems by linking animal requirements more effectively with seasonal patterns of herbage production is a major objective of grazing management. The conventional approach to research in this field has concentrated on empirical tests of management systems over a range of stocking rates. However, the extrapolation of the results of such experiments to farm practice may be criticized on at least two counts. Firstly, the scale of experiments is smaller and the degree of handling the stock generally greater than on a commercial farm. This may contribute to the discrepancy that Davidson (1965) has observed between experimental and farm yields; the experiment described in Part 2 of this thesis was designed to test the effects of flock size and movement of flocks on animal production. The second important criticism of conventional grazing experiments is that the small number of systems and restricted range of environmental conditions that can be sampled in any one trial impose serious limitations on the value of the information gained. Although these experiments clearly show that improved pastures may carry more animals than was previously thought possible, they have failed to show, with few exceptions (e.g. Bennett et al. 1970), that management leads to consistent or worthwhile increases in animal production. It is possible that there are few gains to be obtained from management, although the negative results are more likely to

arise partly because the majority of trials have relied on wool production of dry sheep as the criterion for comparison, and partly because the few trials with animals more sensitive to management, such as weaners or breeding ewes, have used experimental designs which are inadequate to cope with the increased variability which is a feature of these forms of production.

Although stocking rate experiments yield data that allow broad generalisations useful to farmers in decision making, stocking rate is scarcely a quantitative variable for use in research and needs to be qualified in terms of climate and soil fertility, or perhaps pasture production or grazing intake. In large scale grazing trials resources usually limit the opportunity to make these observations.

An alternative approach using computer simulation to overcome these problems was first suggested by Arcus (1963). Briefly this involves constructing and linking together mathematical equations which describe the biological processes of grazing systems. External factors such as weather can be incorporated in the model from historical data or generated as stochastic or deterministic variables. The model is then used to study the consequences of management decisions.

The level of complexity in the model will depend on

the type of decisions that need to be made. Thus Morley and Graham (1971) examined fodder conservation as a drought strategy without including a detailed biological model. In contrast a model to examine the effect of supplementary feeding on animal production would require a complex series of equations to describe, for example, the consequences of feeding the supplement on the intake of any pasture that might be available. The models referred to in this thesis are of the latter type.

Morley (1968a) has discussed the impact that the simulation approach should have on the design and application of agricultural research, and although simulation procedures as applied to this field have become well established (Morley 1972; Hutchinson and Vickery 1973), it is questionable whether the technique has yet made a worthwhile contribution towards increasing the efficiency of grazing management. The diversity of the functions used to describe similar relationships in the numerous models which have been produced (e.g. Freer et al. 1970; Vickery and Hedges 1972; Smith and Williams 1973) emphasizes that our knowledge of the biological processes involved in grazing systems is imprecise. If models are to guide the synthesis of new and more efficient management systems, research must be concentrated on improving the precision of relationships which describe biological processes.

The major difficulty with the simulation approach lies in the fact that it requires that the system be split into its component processes. In the grazing system the two principal processes are the growth of the pasture and the intake of pasture by the animals, and whereas each may be measured when the other is excluded, the complexity of their interaction renders direct measurement impossible. Because of this, numerous indirect techniques have been developed to estimate the intake of grazing animals. These techniques are evaluated in Part 3. The associated problem of estimating the growth of pasture under grazing is also briefly discussed.

The prediction of intake is, however, only the first step in a model simulating the production of animals grazing on pastures. Recent work by Keenan (1967) with penned sheep suggests that standard nutritional factors cannot be used to convert food energy to body tissue in animals differing in nutritional history. Similar studies in grazing animals have been hampered by a lack of simple and reliable techniques to allow serial estimates of body composition to be made in the same animals. The estimation of body composition by the dilution of hydrogen isotopes, especially tritium, is sufficiently simple for use in field studies with sheep; but the equations published so far (e.g. Keenan 1967; Searle 1970a) do not give consistent predictions of composition. It appears that the two

predicting variables that have been used, liveweight and tritiated water space are insufficient as predictors of all body components. The development of general equations to predict body composition of live sheep which include a function of the age of the animal as an additional predictor is described in Part 4. The application of these techniques to predict the effect of body condition on intake is described in Part 5.

## Part 2

### The effect of flock size and grazing management on sheep production

#### 2.1 Introduction

Most experiments with grazing sheep necessarily involve small flocks, but there is little information to justify extrapolation of the results to flocks of larger sizes. At low stocking rates on native pasture, Southcott, Roe and Turner (1962) found that liveweight gain and wool production were lower in flocks of 2 than in flocks of 4, 8, 16 or 30 sheep. On improved pastures, Suckling (1962) reported that ewes stocked at five per acre in 5, 10, and 50 acre paddocks had similar liveweight changes and wool production. Elliott (1966) also reported that liveweight changes and wool production were similar for wethers stocked at four per acre in a paddock of 107 acres and in paddocks of 5 acres.

Experiments comparing grazing systems may confound two consequences of rotational grazing. Firstly, rotation may affect pasture production (Morley 1968b) and therefore, in some circumstances, animal performance. Secondly, movement of the animals may affect their behaviour and therefore their performance independently of pasture production (e.g. Suckling 1956).

In this experiment the performances of three breeds of young sheep in flocks of 3, 9, 27 and 135, grazing under three systems of management are compared. The effects of various managements on weight gain of young sheep in this experiment and the direct effect of rotation on weight gain of old ewes in a supplementary experiment are also examined.

## 2.2 Experimental treatments

The experimental area had been subdivided using Imperial units of measurement. Hence for convenience I have used these measurements in the discussion of 'experimental units' in this part of this thesis.

Mixed flocks - Equal numbers of Merino (Mo), Comeback (CBK), and Border Leicester x Merino (XB) weaners were stocked at nine per acre on Phalaris tuberosa-Trifolium subterraneum pastures, under three systems of management as follows :

CC - Three flocks of 3 sheep and three flocks of 9 sheep were set stocked; pastures and flocks continuously grazed.

RR - Flocks of 9, 27, and 135 sheep were each rotated around three subdivisions of a pasture; pastures and flocks rotationally grazed.



CR - Three flocks of 3 sheep and three flocks of 9 sheep were each rotated around three subdivisions of a continuously grazed pasture; pastures continuously grazed but flocks rotated.

Pure flocks - Separate flocks of nine weaners of each breed were rotated around three subdivisions of a pasture; pastures and flocks rotationally grazed.

All the weaner flocks were replicated twice, except the 135 RR treatment which included areas of both replications in each subdivision of five acres. In all flocks, two-thirds of the sheep were ewes and the remainder wethers.

A schematic representation of these treatments is shown in Figure 2.1, and the actual field layout of the plots is shown in Figure 2.2.

Ased ewes - Five flocks of ased Merino ewes were set stocked, and five flocks were rotated around five subdivisions of a Phalaris tuberosa-Trifolium subterraneum pasture. The plots were stocked at 12 sheep per acre and each flock contained 4 ewes.

Figure 2.1

Schematic diagram showing experimental treatments.

Single headed arrows indicate rotations.

The subdivisions were not contiguous in the field layout.

Pastures and flocks  
continuously grazed.

Set-stocking

CC

3 sheep
3 sheep
3 sheep

9 sheep
9 sheep
9 sheep

Pastures grazed  
continuously but

flocks rotated.

CR

↑	3 sheep	↓
↑	3 sheep	↓
↑	3 sheep	↓

↑	9 sheep	↓
↑	9 sheep	↓
↑	9 sheep	↓

Pastures and flocks  
rotationally grazed.

RR

9 sheep	↓
	↓
	↓

27 sheep	↓
	↓
	↓

135 sheep	↓
	↓
	↓



### 2.3 Experimental Procedure

Young sheep were allocated to flocks by stratified random sampling, so that initial total liveweight per acre was similar for all flocks. Within each replicate the allocation of paddocks to the continuously grazed flocks and of subdivisions to the rotationally grazed flocks was at random.

The experiment started on March 23, after the sheep were shorn. The Comebacks were then six to eight months old, and Merinos and Border Leicester x Merinos were five to six months old. Between March 23 and August 30 (Period 1) the sheep were weighed each month and those flocks under rotational grazing were moved at the same time. Monthly movements were initially chosen because Morley (1968b), in theoretical arguments, suggested that in winter maximum pasture production is likely to be approached if each subdivision in a three-paddock system is grazed for one month and spelled for two months, provided moisture and nutrients do not limit plant growth.

Since monthly movements had no noticeable effects on liveweight gains in Period 1, the effect of more frequent movement was examined between August 30 and December 20 (Period 2) by rotating the flocks each week and weighing them every two weeks. As this was done during spring it was unlikely that the change in management would increase animal

growth through increased pasture growth, since growth of the latter would generally exceed consumption. However, even this increased speed of rotation had little effect on liveweight, so monthly movements were resumed on December 20, for the start of Period 3.

From February 14 to March 11, during the final three weeks of Period 3, the following changes were made to some flocks to examine possible effects on liveweight of a sudden change in management:

(1) One of the 27 RR flocks was divided into three groups comprising two ewes and one wether from each of the three breeds. One of these groups was interchanged with a 9 CC flock and another with a 9 CR flock.

(2) One of the 9 RR flocks was interchanged with a 9 CC flock.

(3) These changes were made within one replicate and flocks in this replicate under rotational treatments were moved every three days and weighed every nine days.

(4) A 9 RR flock from the second replicate was moved every three days and weighed at nine-day intervals.

The experiment finished on March 11, when the sheep

were shorn. During the experiment no supplementary feed was given. Only seven deaths were recorded, and sheep that died were replaced by animals of corresponding breed, sex, and weight, whose measurements were not included in the results.

Pasture availability was estimated in July by cutting three quadrats per one third acre unit to ground level with a modified shearing handpiece, and obtaining dry weights of green and dead matter.

The investigation with old ewes commenced on October 21 and finished on December 16. Initial total liveweight per acre was similar for all flocks. Ewes under the rotational treatment were moved weekly and all ewes were weighed periodically. Throughout the experiment the amount of pasture was in excess of 1000 kg per ha on all plots.

## 2.4 Statistical analysis

Morley (1951) reported heterogeneity of variance for fleece weight and body weight in Merino sheep where means differed greatly, and used logarithmic transformation to remove the correlation between mean and variance in such data. Since means for sex and breed differed in the present experiment, all analyses and results are expressed as natural logarithms ( $\log_e$ ) of variables, unless otherwise stated.

#### 2.4.1 The model

The general linear model fitted to the data is

$$Y_{ijklm} = \mu + H_i + p_j + G_k + B_l + (HG)_{ik} + (HB)_{il} + (GB)_{kl} \\ + (HGB)_{ikl} + s_{ijklm}$$

where  $Y_{ijklm}$  is the value for the  $m^{\text{th}}$  sheep of the  $l^{\text{th}}$  breed of the  $k^{\text{th}}$  sex on the  $j^{\text{th}}$  paddock in the  $i^{\text{th}}$  flock size and  $\mu$  is the mean of an infinite conceptual population of such sheep.  $H$ ,  $G$ ,  $B$  and their interactions represent effects due to flock size, gender and breed and are considered to be fixed. The  $p_j$  and  $s_{ijklm}$  represent attributes of the particular paddock and sheep which are assumed to be random samples from populations with zero means and variances  $\sigma_p^2$  and  $\sigma_s^2$  respectively. The  $p_j$  includes a flock component and possibly a component due to changes in the pastures in time. Although these three components are completely confounded, it is probable that the paddock component is the major contributor to variance; the flock component is almost certainly very small since the mean liveweight of each flock was similar at the start of the experiment.

Analyses of variance are complicated for the following reasons:

- (1) Variances of different flock means are likely

to be heterogenous because differences caused by paddock effects will be averaged for flocks under rotational grazing, but not for flocks set-stocked on single paddocks.

(2) The numbers of animals in each flock varied, and the flock of 135 sheep, which was unreplicated, grazed over portions of both replicates. In addition comparisons for sex and breed are not orthogonal in flocks with only three sheep. Table 2.1 shows the number of sheep in each cell in the CC and CR systems of management. The non-orthogonal comparison for sex and breed in flocks of three sheep is clearly evident.

Consequently separate analyses are calculated for each management system to obtain estimates of the variance components  $\sigma_p^2$  and  $\sigma_s^2$  defined in the general model. Appropriate error terms can then be constructed from functions of  $\sigma_p^2$  and  $\sigma_s^2$  for testing differences between treatment means.

The analyses of variance are based on a split-plot design with flock size as a main plot effect and breed and sex as sub-plot effects. Table 2.2 shows the skeleton analysis of variance used in the experiment for the CC and CR management systems.

The nature of the fixed effects model (Eisenhart



TABLE 2.1

The number of sheep in each cell in the  
CC and CR systems of management

		Flock Size														
		3							9							
		Flocks							Flocks							
		1	2	3	4	5	6	T*	1	2	3	4	5	6	T	GT**
M	E <sup>#</sup>	1		1	1		1	4	2	2	2	2	2	2	12	16
M	W		1			1		2	1	1	1	1	1	1	6	8
C	E	1	1		1	1		4	2	2	2	2	2	2	12	16
C	W			1			1	2	1	1	1	1	1	1	6	8
X	E		1	1		1	1	4	2	2	2	2	2	2	12	16
X	W	1			1			2	1	1	1	1	1	1	6	8
Total		3	3	3	3	3	3	18	9	9	9	9	9	9	54	72

\* T = Total; \*\* GT = Grand Total.

# M = Merino; C = Comeback; X = Crossbred;

E = Ewe; W = Wether.

TABLE 2.2

The quantities to be estimated in the analysis of variance

Source	df	Quantity to be estimated as crude Sum of Squares
Total	72	$\sum_{ijklm} y_{ijklm}^2$
CF	1	$1/72 (y_{\dots\dots})^2$
H	1	$1/18 (y_{1\dots\dots})^2 + 1/54 (y_{2\dots\dots})^2$
Flocks (in size)	10	$\sum_j (1/3 (y_{1j\dots\dots})^2 + 1/9 (y_{2j\dots\dots})^2)$
G	1	$1/48 (y_{\dots 1\dots\dots})^2 + 1/24 (y_{\dots 2\dots\dots})^2$
B	2	$\sum_l (1/24 (y_{\dots\dots l\dots\dots})^2)$
H x G	1	$1/12 (y_{1.1\dots\dots})^2 + 1/6 (y_{1.2\dots\dots})^2 + 1/36 (y_{2.1\dots\dots})^2 + 1/18 (y_{2.2\dots\dots})^2$
H x B	2	$\sum_l (1/6 (y_{1\dots\dots l\dots\dots})^2 + 1/24 (y_{2\dots\dots l\dots\dots})^2)$
G x B	2	$\sum_l (1/16 (y_{\dots 1\dots\dots l\dots\dots})^2 + 1/8 (y_{\dots 2\dots\dots l\dots\dots})^2)$
H x G x B	2	$\sum_l (1/4 (y_{1.1\dots\dots l\dots\dots})^2 + 1/2 (y_{1.2\dots\dots l\dots\dots})^2 + 1/12 (y_{2.1\dots\dots l\dots\dots})^2 + 1/6 (y_{2.2\dots\dots l\dots\dots})^2)$

1947) implies that the mean square for each fixed effect in the analysis of variance has for its expectation a linear sum of a quadratic term in the fixed effects and the variance components  $\sigma_p^2$  and  $\sigma_s^2$ . The error terms "flocks(within sizes)" and "residual" or "between sheep" consist solely of a sum of  $\sigma_p^2$  and  $\sigma_s^2$ . Therefore unbiased estimates of  $\sigma_p^2$  and  $\sigma_s^2$  can be obtained by equating observed and expected mean squares for these error terms and solving the resulting simultaneous equations for  $\sigma_p^2$  and  $\sigma_s^2$ .

#### 2.4.2 The assumptions involved in the components of variance analysis

The component analysis to estimate the composition of the error mean squares implies the following assumptions. Firstly, paddock effects are considered to be proportional to the time sheep spend grazing on each paddock. Secondly, the experimental area is considered to consist of units of one-third acres with paddock effects independent of those of other units. Where these basic units are contiguous, such as in one acre plots, each unit is assumed to contribute the same amount to the total paddock effect. While this assumption may not be entirely valid it seems reasonable at the high stocking rate of nine sheep per acre.

Although the most obvious heterogeneities were associated with small gullies and rocky outcrops, which generally occupied less than one-third acres, gradients over

larger areas could increase the covariance between contiguous units. The most obvious example of increased covariance was in one of the subdivisions grazed by one flock of 27 sheep, where the three one-third acre units contributing to the subdivision always had an abundance of feed relative to other units in the experiment. Consequently, an alternative unit based on individual plots regardless of size was also considered. The most suitable unit was taken to be that which gave best agreement between predicted and observed mean squares for flocks of each size within each system of management.

#### 2.4.3 The estimation of the components of variance

The procedure for estimating the expected composition of mean squares for sources of variation such as those in Table 2.2 is similar to Method 1 described by Henderson (1953). From the general model for each management system, and taking account of the assumptions made in Section 2.4.2, the composition of mean squares for each source can be derived fairly simply, although the algebra is tedious. For the purposes of the analysis only  $\sigma_p^2$  and  $\sigma_s^2$  need to be estimated. Hence the quadratic terms in the fixed effects have not been calculated. This is a valid procedure since the expectation of a cross product between a fixed effect and a random effect is zero.

Considering the CC system first, and assuming whole

plots as the basic experimental unit, the quantities that must be estimated are shown in Table 2.2. For clarity the relevant quantities for the flocks of three and nine are shown separately since they must be calculated individually due to the unequal numbers involved. The notation used is similar to that of Henderson where a dot in place of a subscript implies summation over that subscript.

The calculations to derive expected composition of the uncorrected sums of the squares for the flock size effect are shown in the following example.

From Table 2.2,

$$E\{H\} = E\{1/18 (y_{1.....}^2) + 1/54 (y_{2.....}^2)\}$$

where E denotes "expected" or "average" value.

Substituting the random effects  $p_j$  and  $s_{ijklm}$  in the general model,

$$E\{H\} = 1/18 E\{\sum_j^6 \sum_m^3 (p_j + s_{1j..m})^2\} + 1/54 E\{\sum_j^6 \sum_m^9 (p_j + s_{2j..m})^2\}$$

Since the  $p_j$  effects are common to all sheep grazing on the same paddock the last expression can be rewritten as

$$E\{H\} = 1/18 \sum_j^6 E\{3p_j + \sum_m^3 s_{1j..m}\}^2 + 1/54 \sum_j^6 E\{9p_j + \sum_m^9 s_{2j..m}\}^2$$

Expanding,

$$E\{H\} = 1/18 \sum_j^6 E\{9p_j^2 + \sum_m^3 s_{1j..m}^2 + \text{cross products}\} \\ + 1/54 \sum_j^6 E\{81p_j^2 + \sum_m^9 s_{2j..m}^2 + \text{cross products}\}$$

From the definition of random effects in the linear model the following apply:

$$E\{p_j^2\} = \sigma_p^2 \quad \text{for } j \neq j';$$

$$E\{s_{ijklm}^2\} = \sigma_s^2 \quad \text{for } j \neq j' \text{ and } m \neq m';$$

and  $E\{\text{of any cross product}\} = 0$ .

$$\begin{aligned} \text{Thus } E\{H\} &= 1/18 \sum_j^6 (9\sigma_p^2 + \sum_m^3 \sigma_s^2) + 1/54 \sum_j^6 (81\sigma_p^2 + \sum_m^9 \sigma_s^2) \\ &= 1/18 (54\sigma_p^2 + 18\sigma_s^2) + 1/54 (486\sigma_p^2 + 54\sigma_s^2) \\ &= 12\sigma_p^2 + 2\sigma_s^2 \end{aligned}$$

The expected composition for other quantities in Table 2.2 can be derived similarly and are shown in Table 2.3.

The composition of the corrected sums of squares is calculated by subtracting the appropriate correction factors and the expected composition of mean squares in terms of  $\sigma_p^2$  and  $\sigma_s^2$  is obtained as usual by dividing through by the appropriate degrees of freedom. The results of these calculations for the CC system of management are shown in Table 2.3.

TABLE 2.3

The expected composition of sources of variation within  
the CC systems of management using experimental units  
equivalent to subdivision size (random parameters only)

Source	df	$E \left( \begin{matrix} \text{Crude} \\ \text{SSQ} \end{matrix} \right)$		$E \text{ (SSQ)}$		$E \text{ (MSQ)}$	
		$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$
Total	71	72	72	71	64.5		
CF	1	1	7.5				
Size (H)	1	2	12	1	4.5	1	4.5
Flocks (in size)	10	12	72	10	60	1	6.0
Sex (G)	1	2	7.5	1	0	1	0
Breed (B)	2	3	7.5	2	0	1	0
H x G	1	4	12	1	0	1	0
H x B	2	6	12	2	0	1	0
G x B	2	6	8.25	2	.75	1	0.375
H x G x B	2	12	15	2	2.25	1	1.125
Residual	50			50	-3	1	-0.06

The estimation of  $\sigma_p^2$  in the CR and RR systems of management, and in the CC system when the experimental units are considered as one-third acres is more complex. For example, in the CR system of management the assumptions in Section 2.4.2 imply that each sheep in the flocks of three spent one-third of its time on each of the three one-third acre units over which it grazed, and each sheep in the flocks of nine spent one-ninth of its time on each of the nine one-third acre units over which it grazed. That is,  $1/3(p_1+p_2+p_3)$  and  $1/9(p_1 + p_2 + \dots + p_9)$  are the paddock effects for each sheep in flocks of three and nine respectively, where  $p_1, p_2, \dots, p_9$  refer to each of the one-third acre units over which the sheep grazed. The example below shows the derivation of the expected composition of the uncorrected sum of squares for the flock size effect (H) in the CR system assuming basic experimental units of one-third acres.

Again from Table 2.2,

$$\begin{aligned} E\{H\} &= E\{1/18 (y_{1.....}^2) + 1/54 (y_{2.....}^2)\} \\ &= 1/18 E\{\sum_j^6 \sum_m^3 y_{1j..m}^2\} + 1/54 E\{\sum_j^6 \sum_m^9 y_{2j..m}^2\} \end{aligned}$$

Substituting the random effects in the general model, heeding the assumptions above and recognising that the design involved two sets of three flocks for each size



(see Figure 2.1),

$$\begin{aligned}
 E\{H\} &= 1/18 E\{2\sum_{j=1}^3 \sum_{m=1}^3 (1/3 (p_1 + p_2 + p_3) + s_{1j..m})^2\} \\
 &\quad + 1/54 E\{2\sum_{j=1}^3 \sum_{m=1}^9 (1/9 (p_1 + p_2 + \dots + p_9) + s_{2j..m})^2\} \\
 &= 1/9 E\{(1/3 (9p_1 + 9p_2 + 9p_3) + \sum_{j=1}^3 \sum_{m=1}^3 s_{1j..m})^2\} \\
 &\quad + 1/27 E\{(1/9 (27p_1 + 27p_2 + \dots + 27p_9) + \sum_{j=1}^3 \sum_{m=1}^9 s_{2j..m})^2\} \\
 &= 1/9 E\{(3p_1 + 3p_2 + 3p_3 + \sum_{j=1}^3 \sum_{m=1}^3 s_{1j..m})^2\} \\
 &\quad + 1/27 E\{(3p_1 + 3p_2 + \dots + 3p_9 + \sum_{j=1}^3 \sum_{m=1}^9 s_{2j..m})^2\}
 \end{aligned}$$

Expanding

$$\begin{aligned}
 E\{H\} &= 1/9 E\{9p_1^2 + 9p_2^2 + 9p_3^2 + 9s_{1j..m}^2 + \text{cross products}\} \\
 &\quad + 1/27 E\{9p_1^2 + 9p_2^2 + \dots + 9p_9^2 + 27s_{2j..m}^2 + \text{cross products}\}
 \end{aligned}$$

Thus

$$\begin{aligned}
 E\{H\} &= 1/9 (27\sigma_p^2 + 9\sigma_s^2) + 1/27 (81\sigma_p^2 + 27\sigma_s^2) \\
 &= 6\sigma_p^2 + 2\sigma_s^2
 \end{aligned}$$

Other expectations are derived similarly and are shown in Table 2.4.

The expected composition of each mean square and the intermediate results using experimental units of one-third acres for the CC system are shown in Table 2.5; those for the CR system using whole plots as the experimental unit are shown in Table 2.6.

The observed mean squares for liveweight change in

TABLE 2.4

Expected composition of sources of variation within the OR  
system of management using experimental units of one-third  
acres (random parameters only)

Source	df	$E \left( \begin{matrix} \text{Crude} \\ \text{SSQ} \end{matrix} \right)$		$E \text{ (SSQ)}$		$E \text{ (MSQ)}$	
		$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$
Total	71	72	12	71	9		
CF	1	1	3				
Size (H)	1	2	6	1	3	1	3
Flocks (in size)	10	12	12	10	6	1	0.6
Sex (G)	1	2	3	1	0	1	0
Breed (B)	2	3	3	2	0	1	0
H x G	1	4	6	1	0	1	0
H x B	2	6	6	2	0	1	0
G x B	2	6	3	2	0	1	0
H x G x B	2	12	6	2	0	1	0
Residual	50			50	0	1	0

TABLE 2.5

Expected composition of sources of variation within the CC  
system of manatement using experimental units of one-third  
acres (random parameters only)

Source	df	$E \left( \begin{matrix} \text{Crude} \\ \text{SSQ} \end{matrix} \right)$		$E \text{ (SSQ)}$		$E \text{ (MSQ)}$	
		$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$
Total	71	72	36	71	33		
CF	1	1	3				
Size (H)	1	2	6	1	3	1	3
Flocks (in size)	10	12	36	10	30	1	3
Sex (G)	1	2	3	1	0	1	0
Breed (B)	2	3	3	2	0	1	0
H x G	1	4	6	1	0	1	0
H x B	2	6	6	2	0	1	0
G x B	2	6	3.75	2	0.75	1	0.375
H x G x B	2	12	9	2	2.25	1	1.125
Residual	50			50	-3.0	1	-0.06

TABLE 2.6

The expected composition of sources of variation within  
the CR system of management using experimental units  
equivalent to subdivision size (random parameters only)

Source	df	$E \left( \begin{matrix} \text{Crude} \\ \text{SSQ} \end{matrix} \right)$		$E \text{ (SSQ)}$		$E \text{ (MSQ)}$	
		$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$	$\sigma_s^2$	$+$ $\sigma_p^2$
Total	71	72	24	71	16.5		
CF	1	1	7.5				
Size (H)	1	2	12	1	4.5	1	4.5
Flocks (in size)	10	12	24	10	12	1	1.2
Sex (G)	1	2	7.5	1	0	1	0
Breed (B)	2	3	7.5	2	0	1	0
H x G	1	4	12	1	0	1	0
H x B	2	6	12	2	0	1	0
G x B	2	6	7.5	2	0	1	0
H x G x B	2	12	12	2	0	1	0
Residual	50			50	0	1	0

Periods 1 and 2 are shown in Tables 2.7, 2.8, 2.9 and 2.10 for the CC and CR systems of management respectively; observed values for fleece weight are shown in Table 2.11 and 2.12 for the CC and CR systems respectively. The random parameters that are estimated by each mean square are based on experimental units of whole plots for wool and liveweight in Period 1, and on experimental units of one-third acres for liveweight in Period 2. Reasons for the choice of experimental unit in each instance are discussed below in Section 2.5. For convenience Table 2.13 shows the mean squares and expected compositions for the terms 'flocks (within sizes)' and 'residual' or 'between sheep (within flocks)'. Unbiased estimates of  $\sigma_p^2$  and  $\sigma_s^2$  were obtained by equating observed and expected mean squares for the terms "flocks (within sizes)" and "residual" or "between sheep" for the CC and CR systems, and solving the resulting simultaneous equations for  $\sigma_p^2$  and  $\sigma_s^2$ .

Expected mean squares for the RR system were not used to estimate  $\sigma_p^2$  and  $\sigma_s^2$  for two reasons. Firstly, each subdivision grazed by the 135 RR flock extended over five acres, and possible gradients over such large portions of the experimental area could introduce important biases. Secondly, the term "flocks (within sizes)" is based on only 2 degrees of freedom, compared with 10 each in the CC and CR systems, and it is unlikely this would allow accurate estimation of  $\sigma_p^2$ .

TABLE 2.7

Analysis of variance on change in  $\log_e$  liveweight for  
CC management system, Period 1

Source	df	SSQ	MSQ	Random parameters estimated
Size (H)	1	0.0507	0.0507	$\sigma_s^2 + 4.5\sigma_p^2$
Flocks (in size)	10	0.7698	0.0770	$\sigma_s^2 + 6.0\sigma_p^2$
Sex (G)	1	0.0028	0.0028	$\sigma_s^2$
Breed (B)	2	0.0329	0.0164	$\sigma_s^2$
H x G	1	0.0029	0.0029	$\sigma_s^2$
H x B	2	0.0064	0.0032	$\sigma_s^2$
G x B	2	0.0450	0.0225	$\sigma_s^2 + 0.375\sigma_p^2$
H x G x B	2	0.0086	0.0043	$\sigma_s^2 + 1.125\sigma_p^2$
Residual	50	0.3756	0.0075	$\sigma_s^2 - 0.06\sigma_p^2$

TABLE 2.8

Analysis of variance for change in  $\log_e$  liveweight for  
CR management system, Period 1

Source	df	SSQ	MSQ	Random parameters estimated
Size (H)	1	0.1712	0.1712	$\sigma_s^2 + 4.5\sigma_p^2$
Flocks (in size)	10	0.1166	0.0117	$\sigma_s^2 + 1.2\sigma_p^2$
Sex (G)	1	0.0018	0.0018	$\sigma_s^2$
Breed (B)	2	0.0388	0.0194	$\sigma_s^2$
H x G	1	0.0075	0.0075	$\sigma_s^2$
H x B	2	0.0005	0.0002	$\sigma_s^2$
G x B	2	0.0136	0.0067	$\sigma_s^2$
H x G x B	2	0.0135	0.0067	$\sigma_s^2$
Residual	50	0.3577	0.0072	$\sigma_s^2$

TABLE 2.9

Analysis of variance on change in  $\log_e$  liveweight for  
CC management system, Period 2

Source	df	SSQ	MSQ	Random parameters estimated
Size (H)	1	0.0333	0.0333	$\sigma_s^2 + 3\sigma_p^2$
Flocks (in size)	10	0.3537	0.0354	$\sigma_s^2 + 3\sigma_p^2$
Sex (G)	1	0.0142	0.0142	$\sigma_s^2$
Breed (B)	2	0.0819	0.0409	$\sigma_s^2$
H x G	1	0.0037	0.0037	$\sigma_s^2$
H x B	2	0.0370	0.0185	$\sigma_s^2$
G x B	2	0.0297	0.0148	$\sigma_s^2 + 0.375\sigma_p^2$
H x G x B	2	0.0164	0.0082	$\sigma_s^2 + 1.125\sigma_p^2$
Residual	49	0.2410	0.0049	$\sigma_s^2 - 0.06\sigma_p^2$



TABLE 2.10

Analysis of variance on change in  $\log_e$  liveweight for  
CR management system, Period 2

Source	df	SSQ	MSQ	Random parameters estimated
Size (H)	1	0.0118	0.0118	$\sigma_s^2 + 3\sigma_p^2$
Flocks (in size)	10	0.0840	0.0084	$\sigma_s^2 + 0.6\sigma_p^2$
Sex (G)	1	0.0301	0.0301	$\sigma_s^2$
Breed (B)	2	0.0260	0.0130	$\sigma_s^2$
H x G	1	0.0000	0.0000	$\sigma_s^2$
H x B	2	0.0019	0.0009	$\sigma_s^2$
G x B	2	0.0005	0.0002	$\sigma_s^2$
H x G x B	2	0.0144	0.0072	$\sigma_s^2$
Residual	50	0.2875	0.0058	$\sigma_s^2$

TABLE 2.11

Analysis of variance on  $\log_e$  fleece weight for CC management system

Source	df	SSQ	MSQ	Random parameters estimated
Size (H)	1	0.0026	0.0026	$\sigma_s^2 + 4.5\sigma_p^2$
Flocks (in size)	10	0.3973	0.0397	$\sigma_s^2 + 6.0\sigma_p^2$
Sex (G)	1	0.0336	0.0336	$\sigma_s^2$
Breed (B)	2	0.2267	0.1133	$\sigma_s^2$
H x G	1	0.0085	0.0085	$\sigma_s^2$
H x B	2	0.0066	0.0033	$\sigma_s^2$
G x B	2	0.0112	0.0056	$\sigma_s^2 + 0.375\sigma_p^2$
H x G x B	2	0.0148	0.0074	$\sigma_s^2 + 1.125\sigma_p^2$
Residual	49	0.5740	0.0117	$\sigma_s^2 - 0.06\sigma_p^2$

TABLE 2.12

Analysis of variance on  $\log_e$  fleece weight for CR management system

Source	df	SSQ	MSQ	Random parameters estimated
Size (H)	1	0.0011	0.0011	$\sigma_s^2 + 4.5\sigma_p^2$
Flocks (in size)	10	0.2492	0.0249	$\sigma_s^2 + 1.2\sigma_p^2$
Sex (G)	1	0.0399	0.0399	$\sigma_s^2$
Breed (B)	2	0.2401	0.1200	$\sigma_s^2$
H x G	1	0.0008	0.0008	$\sigma_s^2$
H x B	2	0.0692	0.0346	$\sigma_s^2$
G x B	2	0.0390	0.0195	$\sigma_s^2$
H x G x B	2	0.0046	0.0023	$\sigma_s^2$
Residual	50	1.1816	0.0236	$\sigma_s^2$

TABLE 2.13

Mean squares and their expected composition for  $\log_e$  (kg) fleece weight and change in  $\log_e$  (kg) liveweight for Periods I and II

Treatment and source	df†	Wool MS $\times 10^4$	Period I MS $\times 10^4$	Expected values	Period II MS $\times 10^4$	Expected values
CC Flocks (within sizes)	10	397	770	$\sigma_s^2 + 6\sigma_p^2$	354	$\sigma_s^2 + 3\sigma_p^2$
Between sheep (within flocks)	50	117	75	$\sigma_s^2 - 0.06\sigma_p^2$	49	$\sigma_s^2 - 0.06\sigma_p^2$
CR Flocks (within sizes)	10	249	117	$\sigma_s^2 + 1.2\sigma_p^2$	84	$\sigma_s^2 + 0.6\sigma_p^2$
Between sheep (within flocks)	50	236	72	$\sigma_s^2$	58	$\sigma_s^2$

† Adjusted for missing values where appropriate

#### 2.4.4 The comparison of treatment means.

The variance of a treatment mean if a total of  $S_n$  sheep graze a total of  $P_n$  units is  $\frac{\sigma_p^2}{P_n} + \frac{\sigma_s^2}{S_n}$ .

The corresponding standard error is  $\sqrt{\frac{\sigma_p^2}{P_n} + \frac{\sigma_s^2}{S_n}}$ .

Differences of mean liveweight change and mean fleece weight between flocks of various sizes and management systems were tested by the t distribution with 20 degrees of freedom, since 20 is the number of degrees of freedom associated with the estimation of  $\sigma_p^2$  which is the source of most of the variance of each mean. Although 20 is only an approximation of the actual degrees of freedom associated with the means, a more exact estimate using a formula of Satterthwaite (1946) gave almost the same value.

#### 2.5 The analysis of variance

The approach to the analysis of variation in this experiment depended on the choice of a suitable experimental unit to obtain reliable estimates of paddock effects. Broad gradients across the experimental site and local departures from these may have contributed to between-plot variation, but their relative importance was by no means clear. If co-variance between adjacent one-third acre units was important, then the estimate of  $\sigma_p^2$  obtained from the 9 CC flocks would be larger than that from 3 CC flocks for

experimental units based on Plots of one-third acres. Reference to Table 2.14 shows this was so for fleece weight and for liveweight change in Period 1. The alternative unit based on whole Plots, however, gave good agreement between the estimates of  $\sigma_p^2$  in Period 1 and reduced the difference between estimates of  $\sigma_p^2$  for fleece weight. This was also true for 3 CR and 9 CR flocks (Table 2.14). In Period 2 the estimates were more consistent if units were of one-third acres. While agreement between observations and predictions does not prove the accuracy of a model, it does indicate reliability within the range of observations under consideration. Hence the most consistent measure of Plot variation was chosen, although there was little difference between the models. This approach must tend slightly to underestimate the standard errors of differences between means, because the estimates used for  $\sigma_p^2$  have been generally lower than the estimates given by the alternative model.

In Period 3 a reliable estimate of  $\sigma_p^2$  could not be calculated due to changes in management of certain flocks in the final three weeks of that period.

Table 2.13 shows portions of the analyses of variance, and the variance and the variance components (based on the appropriate unit), for each management system. The expected residual mean square in the CC treatment

TABLE 2.14

Estimates of variance components from flocks 3 and 9  
sheep in CC and CR systems, assuming independent basic  
units of one-third acres, or of whole units

Basic unit and Flock size	Fleece weight ( $\log_e \text{ kg}^2$ )		Change in $\log_e$ (kg) liveweight			
	$\sigma_s^2 +$	$\sigma_p^2 +$	Period 1		Period 2	
	$\sigma_s^2 +$	$\sigma_p^2 +$	$\sigma_s^2 +$	$\sigma_p^2 +$	$\sigma_s^2 +$	$\sigma_p^2 +$
<u>CC System</u>						
1/3 acres						
3 CC	31	2	108	104	91	87
9 CC	129	210	79	347	42	94
Whole plots						
3 CC	31	2	108	104	91	87
9 CC	129	70	79	116	42	31
<u>CR System</u>						
1/3 acres						
3 CR	363	0	131	0	67	122
9 CR	216	23	92	27	56	0
Whole plots						
3 CR	363	0	131	0	67	131
9 CR	216	8	92	9	56	0

+  $\times 10^4$  in all columns.

includes the term  $-0.06 \sigma_p^2$ , due to the non-orthogonal design and consequent confounding of breed and sex with plots in flocks of three sheep. Plots are not confounded with breed and sex in the CR treatment because all flocks in each replicate grazed over the same three subdivisions.

Using Barlett's test (Snedecor 1956, page 287) the estimates of  $\sigma_s^2$  obtained for fleece weight in each management system were found to be heterogeneous while estimates of  $\sigma_s^2$  were homogeneous for liveweight change in Periods 1 and 2. A more detailed analysis (Table 2.15) showed that the lower between-sheep variance for fleece weight in CC flocks was entirely due to a greatly reduced variance amongst the Comebacks.

## 2.6 The effect of flock size on production

No important effect of flock size on animal production was evident (Table 2.16). Total liveweight gains over the year were remarkably similar; any differences in one period seem to have been compensated by opposite differences in another period. The superior performance of sheep in flocks of 27 in Period 1 was related to the greater amount of green pasture which happened to be on the subdivision grazed by one of these flocks (Figure 2.3).

These results may not be wholly applicable to large commercial flocks, especially on pastures with lower



TABLE 2.15

Residual variance among sheep within breeds for fleece weight  
and change in liveweight over periods 1 and 2 under each system  
of management

Attribute and System	Residual variance for		
	Merino	Comeback	X-bred
Fleece weight ( $\log_e \text{ kg}^2$ )			
CC	0.0128	0.0116	0.0171
CR**	0.0042	0.0476	0.0224
RR**	0.0159	0.0307	0.0148
Change in $\log_e$ (kg) liveweight			
Period 1			
CC	0.0055	0.0132	0.0110
CR	0.0046	0.0100	0.0048
RR	0.0100	0.0096	0.0141
Period 2			
CC	0.0035	0.0074	0.0039
CR	0.0032	0.0090	0.0033
RR*	0.0048	0.0050	0.0088

\*\*  $P < 0.01$ ; \*  $P < 0.05$

TABLE 2.16

Means and S.E. of means for fleece weight and change in liveweight for flocks of various sizes. Figures in parenthesis show mean fleece weight (kg) and percentage change in liveweight

Flock size	Fleece weight		Period I		Period II		Period III		Total	
	$\log_e$ (kg)		Change in $\log_e$ (kg) liveweight							
		(kg)		(%)		(%)		(%)		(%)
3	$1.18 \pm 0.029$	(3.26)	$0.01 \pm 0.033a$	(1)	$0.55 \pm 0.030$	(73)	$0.01$	(1)	$0.57$	(75)
9	$1.19 \pm 0.019$	(3.26)	$0.08 \pm 0.025$	(9)	$0.52 \pm 0.016b$	(68)	$-0.02$	(-2)	$0.58$	(75)
27	$1.19 \pm 0.032$	(3.26)	$0.13 \pm 0.043a$	(14)	$0.49 \pm 0.025c$	(63)	$-0.06$	(-6)	$0.56$	(71)
135	$1.13 \pm 0.024$	(3.08)	$0.04 \pm 0.034$	(4)	$0.60 \pm 0.032bc$	(82)	$-0.10$	(-10)	$0.54$	(76)

Means followed by the same letter differ ( $P < 0.05$ ).

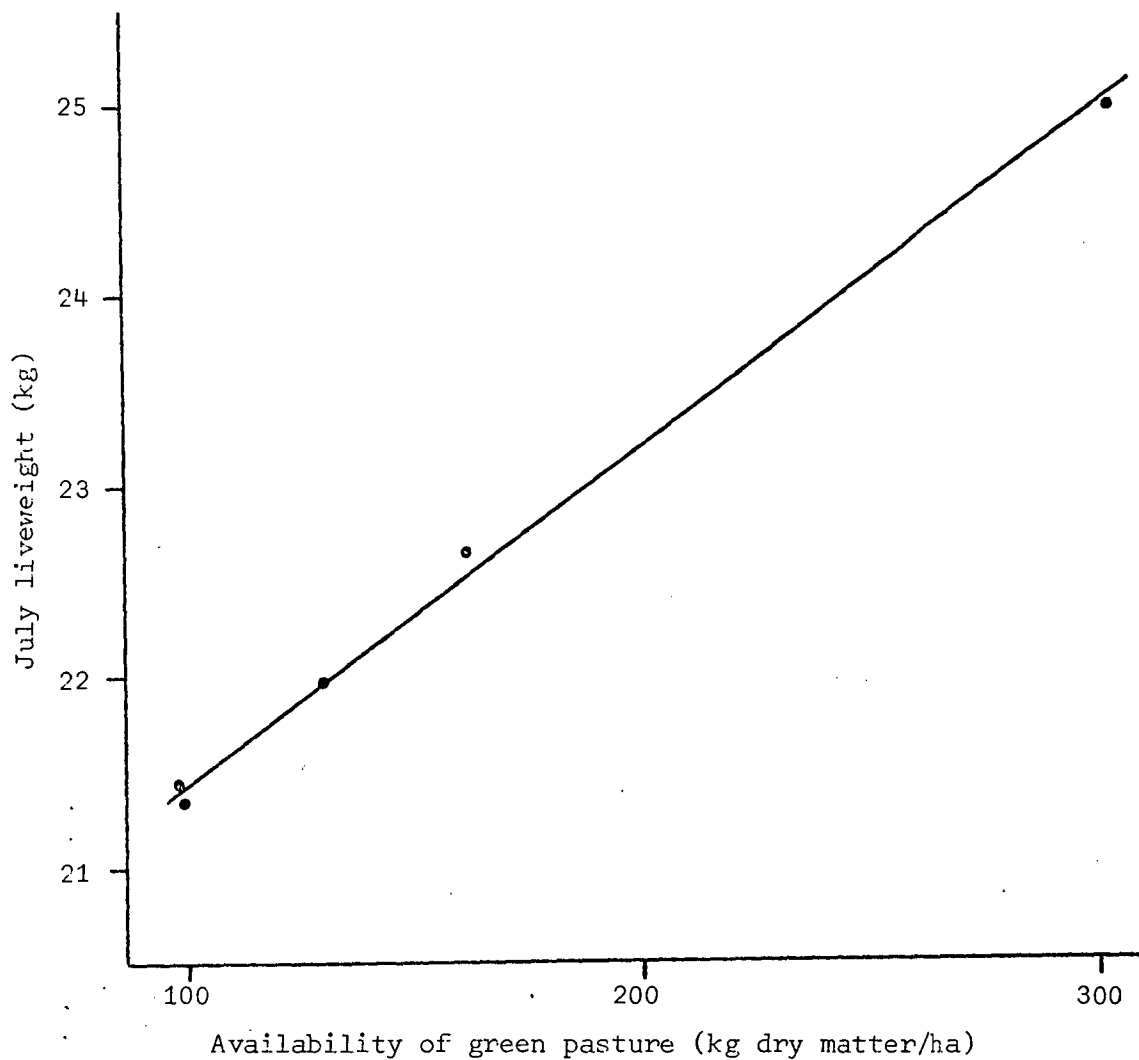


Figure 2.3 - The relationship between availability of green pasture and July liveweight for sheep rotationally grazing three subdivisions of a pasture. The availability of green pasture has been averaged over the three subdivisions on which each flock grazed.

carrying capacities. Distances between water, shelter and feed could then be an important determinant of behaviour, with perhaps consequent changes in plant production. Nevertheless the levels of performance of experimental flocks on small paddocks seem likely to indicate performance of larger flocks, since there were no suggestions of a consistent regression on flock size.

## 2.7 The effect of grazing management on production

Stock movements, either around continuously grazed or rotationally grazed pastures had little or no effect on liveweight changes or wool production in young sheep or old ewes (Table 2.17, Figures 2.4 and 2.5). The rainfall and temperature in April and May were relatively low (Morley, Bennett and McKinney 1969), so that pasture growth was inadequate to support normal animal growth during Period 1; hence rotational grazing was unlikely to have been beneficial. The slightly better performance by RR sheep in Period 2 probably resulted from some compensatory growth, as the weight of these groups fell considerably below that of the others during the winter. In no period did rotation per se appear to affect animal performance. In the comparison between CC and CR flocks the effect of management on pasture growth was virtually eliminated, and any difference in animal production between treatments would be due to movement of the animals. The comparison with RR treatments

TABLE 2.17

Means and S.E. of means for fleece weight and change in liveweight for sheep under three systems of management

Management system	Fleece weight		Period I		Period II		Period III		Total	
	$\log_e$ (kg)				Change in $\log_e$ (kg) liveweight					
		(Kg)		(%)		(%)		(%)		(%)
CC	1.19 $\pm$ 0.024	(3.26)	0.09 $\pm$ 0.031	(10)	0.51 $\pm$ 0.021	(67)	-0.03	(-3)	0.57	(74)
CR	1.20 $\pm$ 0.024	(3.31)	0.05 $\pm$ 0.031	(5)	0.53 $\pm$ 0.021	(70)	0.02	(2)	0.60	(77)
RR	1.15 $\pm$ 0.017	(7.0)	0.06 $\pm$ 0.023	(6)	0.56 $\pm$ 0.017	(75)	-0.09	(-9)	0.53	(72)

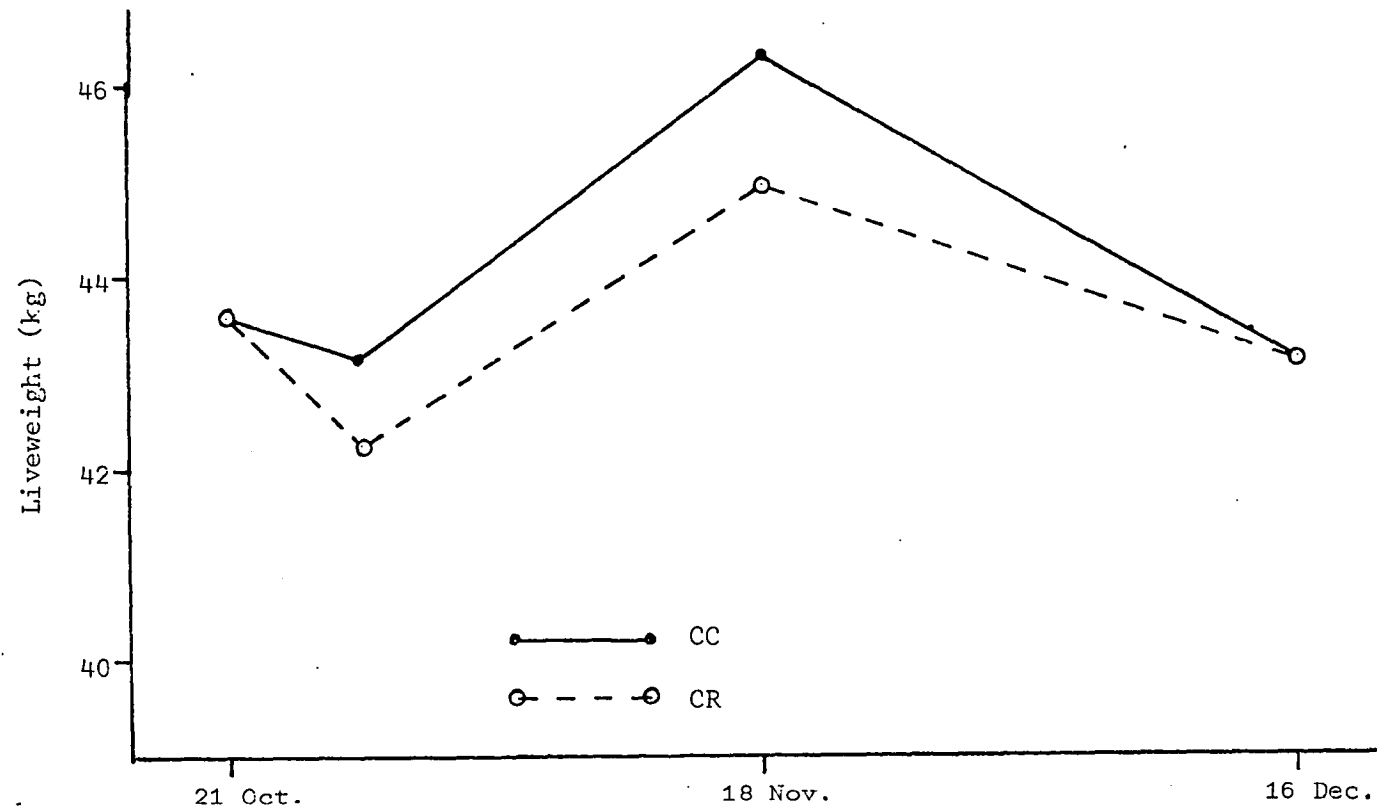


Figure 2.4 - Liveweight change of old ewes under two systems of management - CC and CR.

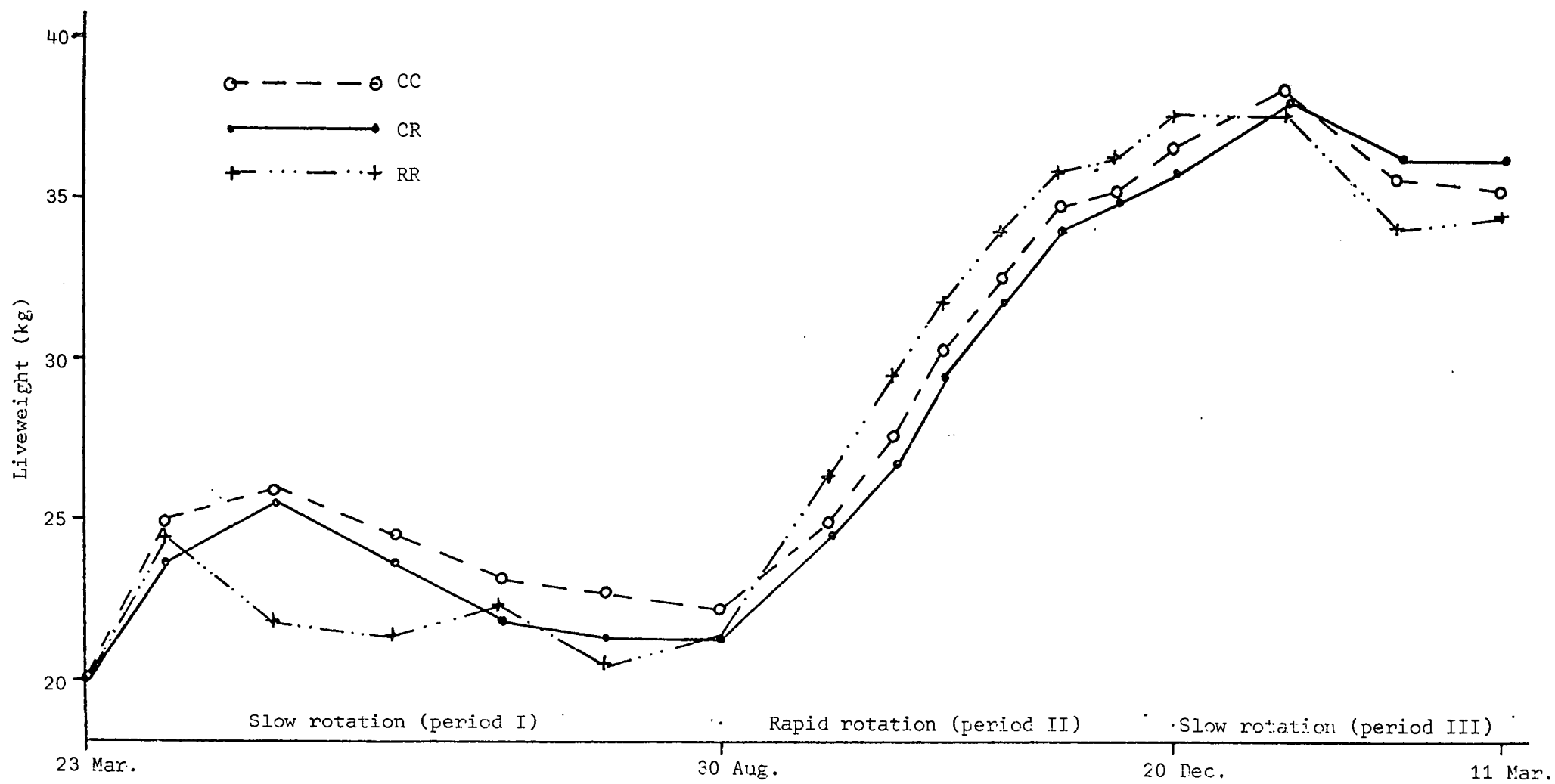


Figure 2.5 - Average liveweight (kg) for each management system

measures, in addition, the effect of pasture growth due to management on animal production. As expected CR flocks were less variable than CC flocks for fleece weight and liveweight change in Period 1 (  $\sigma_p^2$  in Tables 2.13 and 2.14). It was not possible to make a similar observation in the RR flocks since only two degrees of freedom were available for obtaining the estimate of  $\sigma_p^2$ , hardly sufficient to give a reliable estimate of variance.

Rotation per se had no detectable effect on weight changes of old ewes (Figure 2.4). Presumably because feed was always abundant there was no reduction in variance among flocks that were rotated compared with those set-stocked.

Although speed of rotation was confounded with pasture growth and availability in this experiment, more rapid rotation than that used in Period 1 for a three-paddock system would be unlikely to increase pasture growth (Morley 1968b); during Periods 2 and 3 so much feed was present that the system of rotation used was unlikely to affect animal performance or variation amongst flocks.

The changes in management experienced by some flocks at the end of Period 3 had only small effects on liveweight. Over a nine-day period those sheep that moved from CC flocks to RR flocks lost 1% liveweight. Also sheep moved from RR flocks to CC flocks gained about 1% liveweight, while sheep



remaining in CC flocks gained 2%. As before, a reliable estimate of plot variability is not available so tests of significance are not possible. However, the results suggest the RR system did not enhance liveweight gain when pasture growth ceased and feed was not plentiful.

## 2.8 Comparison of breed effects

Merinos in pure flocks gained more weight during Period 1 ( $P < 0.01$ ) and less weight during Period 2 ( $P < 0.05$ ) than Merinos in mixed flocks (Table 2.18), but there was no difference in fleece weight. Comeback and Border Leicester x Merino sheep did not differ in liveweight change or fleece weight whether in pure or mixed flocks. Since the latter breeds were heavier than Merino sheep they probably ate more. Therefore, the comparison of the breeds running as separate flocks may be confounded by different grazing pressures. Thus the greater liveweight gain of the Merinos when run as a pure flock during Period 1 could have been due to lower effective grazing pressure, with reduced competition for forage. During Period 2 when feed was abundant, the Merinos in mixed flocks gained more weight than those in pure flocks. This may have been compensatory gain.

Although all data were transformed to ensure independence of mean and variance, Bartlett's test showed

TABLE 2.18

Mean fleece weight and mean change in liveweight during periods 1, 2 and 3 for each breed in mixed and pure flocks

Breed	Fleece weight		Period 1		Change in $\log_e$ liveweight				Total	
	Pure	Mixed	Pure	Mixed	Period 2 Pure	Period 2 Mixed	Period 3 Pure	Period 3 Mixed	Pure	Mixed
MO	1.96	1.90	0.14**	0.04	0.43*	0.53	-0.03	-0.08	0.54	0.49
CBK	2.03	2.02	0.08	0.11	0.57	0.58	-0.07	-0.11	0.58	0.58
XB	1.94	1.90	0.08	0.03	0.55	0.59	-0.06	-0.08	0.57	0.56

\*\*  $P < 0.01$ ; \*  $P < 0.05$

Comebacks were more variable in fleece weight than either Merino or Border Leicester x Merino sheep in CR and RR flocks ( $P < 0.01$ ) but not in CC flocks (Table 2.15). It is possible that the greater variability in fleece weight amongst Comebacks was due to a sharp segregation in genotype since they were a backcross generation. If this is so, then depending upon the range in wool quality, rapid progress could be achieved through selection for fleece weight. However, there was a slightly greater range in the age of the Comebacks compared with the other two breeds.

Variances amongst the breeds in live weight were homogeneous for each management system in Period 1, but in Period 2 the Border Leicester x Merino sheep were more variable than Merinos or Comebacks ( $P < 0.05$ ) in RR flocks though not in CC or CR flocks ( $P > 0.05$ ). At the start of the experiment the Merinos were significantly less variable in liveweight than Border Leicester x Merinos ( $P < 0.001$ ), which were significantly less variable than the Comebacks ( $P < 0.05$ ).

The higher variability amongst Border Leicester x Merino sheep compared with Merinos and Comebacks in Period 2 seems surprising, since McLaren and Michie (1954) have reported that  $F_1$  hybrid laboratory animals used for bioassay are less variable in response than inbred strains. Apparently homeostatic mechanisms buffer hybrid animals

against environmental variation. Although neither Merinos nor Comebacks used in this experiment can be considered inbred, there is no apparent explanation for the increased variability in the Border Leicester x Merinos.

Interactions between breed, sex and treatment were generally small and not significant. Merino ewes (17.7kg) were significantly lighter at the start of the experiment than the Merino wethers (20.4kg) ( $P < 0.001$ ); Comeback ewes were significantly lighter (19.1kg) than Comeback wethers (20.4kg) ( $P < 0.05$ ); however, both Border Leicester x Merino ewes and wethers weighed approximately 22.7kg. There was no difference in liveweight change over Periods 1 and 2 between ewes and wethers, except that Comeback wethers in RR flocks gained significantly more weight than ewes during Period 2.

Fleece weights of ewes and wethers within breeds and management systems were generally similar, although in CR flocks Merino wethers cut significantly more wool (0.41kg) than did Merino ewes ( $P < 0.01$ ). However, the test is based on only 10 degrees of freedom for error and, since there was no difference in other flocks, this result is probably a sampling variation.

### Part 3

## The estimation of feed intake by grazing sheep : a review

### 3.1 Introduction

Whether the overall aim of a grazing model is to predict the effect of management on the growth of grazed pasture (e.g. by measuring net primary production (Weisert and Evans 1964; Hutchinson 1971)) or on the productivity of grazing animals, the model must contain functions to predict their intake of pasture. The development of relationships between herbage availability and pasture intake has been hampered by the difficulties of measuring intake and by the lack of understanding of other factors that may affect intake.

Although the nutritional requirements of pen-fed animals are reasonably well defined (A.R.C. 1965), those for grazing animals remain uncertain. This is largely due to the lack of direct methods of estimating nutrient intake by grazing animals and the large errors associated with indirect methods. In the main these stem from the difficulty in obtaining an adequate sample of the diet eaten in order to estimate its quality or digestibility. McDonald (1968) has listed 12 major features ranging from physical aspects of the pasture grazed (e.g. herbage availability) to aspects of animal behaviour and internal parasitism which render estimates obtained from pen-fed animals inappropriate for grazing animals. Nevertheless estimates are essential if

computer modelling is to play a useful role in the synthesis and understanding of management systems.

Nutrient intake by grazing animals can be estimated from the product of faecal output and the function  $(1/(1-D))$  where D is the digestibility coefficient of the diet consumed. Alternatively nutrient intake can be deduced by using feeding standards to calculate the food required for the levels of animal production observed. Pasture sampling techniques to estimate herbage removed during grazing are generally very imprecise (Corbett and Greenhalgh 1960). The change in available food must be measured over very short time intervals, otherwise growth of the pasture and reduction of pasture from other causes such as trampling, senescence and decay could introduce large biases. Furthermore pasture sampling techniques are unsuitable to estimate the intake of individual animals or groups of animals undergoing different treatments when grazing in a common flock. Another method described by Alden (1969) estimates the herbage removed by weighing animals before and after a restricted grazing period; this method is laborious and not suitable where the dry matter content or botanical composition of the diet can change. In view of these restrictions this method and the pasture sampling techniques are not considered further.

### 3.2 The estimation of food intake from faecal analysis and diet digestibility

#### (a) The estimation of faecal output

Faecal output by the grazing animal can be measured directly by the use of a harness (Arnold 1960) and collection bag. However, the harness may affect grazing behaviour and hence nutrient intake; Hutchinson (1956) found a marked decline in faecal output by wethers over a 10 day collection period, but Arnold (1960) found no difference in grazing time between harnessed and unharnessed wethers in the 24h following harnessing. With young lambs at Ginninderra, Freer, Dennis and Donnelly (unpublished) found no effect of bagging on body weight gain over 16 day periods. Even so the technique is not particularly suitable for faecal collection with ewes and very young lambs; also individual animals may react to wearing the harness and are thus unsuitable subjects for collection purposes. Possible sources of error result from loss of faeces from the collection bag and from end-period errors (Blaxter et al. 1956), depending on whether an animal defaecates immediately prior to or after the beginning or end of a collection period. The latter errors decrease with  $1/\sqrt{n}$  where  $n$  is the number of individual collections made in a collection period. Nevertheless, loss of faeces must always be a possible and unknown source of bias.

Indigestible markers especially chromium sesquioxide ( $\text{Cr}_2\text{O}_3$ ) have been widely used to estimate faecal output (Kobt and Luckey 1972), and avoid some of the problems associated with total faecal collection. The accuracy of the technique depends on (a) the exact measurement of the amount of marker administered and determination of its concentration in the faeces, (b) the quantitative recovery of the marker in the faeces, and (c) the accuracy with which faeces can be sampled to give an aliquot containing the marker with a concentration representative of the total faecal output (Brisson 1960). The administration of  $\text{Cr}_2\text{O}_3$  in small discrete doses, usually in an oil suspension contained in a soluble capsule, results in diurnal fluctuations of its concentration in the faeces (Lambourne 1957). Furthermore at Ginninderra, Freer, Dennis and Donnelly (unpublished) have observed large seasonal trends in the excretion pattern of  $\text{Cr}_2\text{O}_3$  by young lambs. On three occasions during the year lambs were harnessed for total faecal collection and dosed twice daily with  $\text{Cr}_2\text{O}_3$ . They were moved onto a fresh pasture every two days. Analysis of faeces taken from the collection bags showed complete recovery of chromium, but samples taken from the rectum twice daily at dosing times (0900h and 1600h) always had a lower concentration of chromium than the true mean value. The resulting over-estimate of faecal output increased from 25% in November and February to 63% in May. This suggests a possible interaction between the effect of



daylength on the grazing pattern of the lambs and the diurnal pattern of excretion of the marker. Interactions between daylength and grazing have been reported in cattle (Hughes and Harker 1950; Waite et al. 1951) and are evident in data published by Lancashire and Keogh (1966) for sheep. The use of chromic oxide paper to give a slower release of chromium (Corbett 1960) may overcome these problems, but preparation of the paper doses is laborious and the paper is bulky to administer.

(b) The estimation of diet digestibility

The in vivo digestibility of food eaten by animals in pens can be estimated by feeding a measured amount and collecting the faeces produced. The food and faeces can be analysed for dry matter, organic matter and other chemical constituents. The apparent digestibility (D) of the feed is then estimated as  $\frac{F-f}{F}$  where F is the food consumed and f is the faeces produced. However, D depends partly on the amount of food that is consumed (Blaxter 1964) being significantly higher when F is close to a maintenance ration than when F is close to the limit of voluntary intake. The estimate of D is also subject to end-period errors in the collection of faeces, and errors associated with feed refusals and individual animal variation.

With grazing animals in vivo digestibility cannot be determined directly but can be estimated from in vitro

digestibility of diet samples or by the use of faecal index methods whereby the concentration of a suitable marker substance occurring in the feed or faeces or both is determined. Both techniques relate in vitro digestibility or concentration of the marker substance to in vivo digestibility in a conventional digestibility trial. The difficulty of feeding the same material to the penned animals as that selected by the grazing animals is a major limitation. The relative merits of the two techniques are discussed critically in the following section.

(1) Faecal index techniques

From observations on a large number of digestibility trials with relevant faecal analyses, Lancaster (1947) suggested it was possible to predict the digestibility of the diet eaten by a grazing animal from the nitrogen concentration in its faeces. Prediction equations for the digestibility of herbage eaten ( $D$ ) or the related function ( $1/(1-D)$ ), called the intake factor or feed/faeces ratio, were developed by Lancaster (1949, 1954) and Raymond et al. (1954). Basically these equations depend on the assumption that the output of nitrogen in the faeces of the animal is largely dependent on dry matter intake, an observation initially made in a study on rats by Mitchell (1924).

It follows from this that the nitrogen

concentration in the faeces is a function of the intake factor. However, Lancaster (1949) also found a significant effect of the nitrogen content in the feed, and Raymond (1954) suggested that a restricted regression obtained from a limited range of feeds would improve the precision of predicting digestibility of the diet selected by ruminants grazing on a similar range of feeds. A large number of "local" regressions have since been published. These have been reviewed by Streeter (1969) and Kott and Luckey (1972). Christian (1972) pointed out that these "local" regressions, while embodying substantial statistical refinement (e.g. Arnold and Dudzinski 1963), have hardly improved the accuracy of prediction.

The study of nitrogen wastage in the ruminant is complicated by the large metabolic faecal component in addition to undigested food residues and the difficulty of identifying these fractions by chemical analysis. Metabolic faecal nitrogen contains true endogenous nitrogen from intestinal secretions and gut debris sloughed-off by the passage of food material, but about 70% is thought to consist of undigested bacterial protein from the rumen (Hogan and Weston 1968). In an early study with rats Schneider (1935) partitioned metabolic faecal nitrogen into a constant fraction and a fraction dependent on food intake. Hutchinson (1958) in examining data from a variety of sources where sheep had been fed various levels of

nitrogen-free diets found evidence of a constant fraction as suggested by Schneider, but considered it impossible to confirm its existence since observations on nitrogen intakes approaching zero are impractical with ruminants. He also examined the effect of level of nitrogen intake and dry matter intake on total faecal nitrogen output, and concluded that dry matter intake was the only significant influence on nitrogen output in the faeces provided nitrogen intake was between 8 and 45g/day. This observation would justify the use of faecal nitrogen concentration as a predictor of diet digestibility but for the following. Firstly, as Hutchinson pointed out, the nitrogen intake of grazing sheep may frequently be greater than 45g/day and at these levels nitrogen intake will affect total faecal nitrogen; and secondly, the interaction between dry matter intake and nitrogen intake in their effect on nitrogen output may be different on types of feed other than the restricted range examined by Hutchinson. If such differences exist (e.g. between grasses and legumes) they can be expected to affect the precision of regressions as the botanical composition of the diet changes through seasonal variation or by the selective grazing habits of the animal. It seems unlikely therefore that faecal nitrogen can be used as a reliable index of diet digestibility until there is further elucidation of the factors determining faecal nitrogen output in ruminants.

Other marker substances such as chromogen and lignin have been proposed but difficulties mainly with chemical determination have generally made them even less satisfactory than faecal nitrogen.

(2) In vitro digestibility techniques

In vitro digestibility techniques involve a more or less standard procedure following the 2-stage microbial incubation with rumen flora and acid-pepsin digestion method of Tilley and Terry (1963). This method is essentially an empirical test whereby the different stages may continue for times determined by the closeness of agreement with in vivo values for the same material. The source of rumen inoculum appears important and donor animals should be maintained on feed of high quality (Freer pers. comm.). Barnes (1967) reported large differences between laboratories for a 24h incubation but noted these were reduced for a 48h incubation. Drew (1966) found in vitro figures very close to in vivo figures when the test forage was incubated with rumen fluid for 72h followed by a 24h acid pepsin digestion. At the CSIRO Canberra Laboratories similar times to those used by Drew give close agreement with in vivo values on standard test forages (Christian pers. comm.); the standard error of prediction of an in vivo digestibility value is about  $\pm 2$  digestibility units.

The successful application of the technique depends

upon efficient sampling of the diet consumed by grazing animals. The development of improved techniques in oesophageal fistulation of ruminants (McManus et al. 1962) has allowed sampling of the diet actually consumed by a grazing animal. However the degree to which the diet sample collected from fistulated animals represents the true diet consumed by a grazing animal is unknown (Van Dyne and Torell 1964). These authors concluded that while the technique may not be highly precise, variation between samples collected by different animals is greater than variation between samples for a given animal. Langlands (1966, 1967a, 1967b) also considers the technique is imprecise and "may be subject to biases at present undefined" (Langlands 1969). However in the latter paper he also states that it "seems unlikely that the bias in the fistula technique would exceed 5 units of digestibility". Obviously estimates of herbage intake using this technique to measure digestibility of the diet must be treated with caution since at high levels of digestibility a bias of 5 units leads to a bias of about 25% in the corresponding estimate of intake.

Clipping or plucking herbage from a pasture generally does not give representative samples of the diet where animals can select for the more digestible components on offer. For example, Leish and Mulham (1966) found the diet selected by Merino sheep grazing on a bladder saltbush (Atriplex vesicaria) - cottonbush (Kochia aphylla) community

contained the grass Sporobolus caroli as the major diet component (>56%), although it was present in the pasture as only 1%. In contrast on a pure sward of Phalaris tuberosa, Freer (Pers. comm.) has found that during spring the diet selected by sheep fitted with oesophageal fistulae was similar in digestibility to material cut from the pasture. However on lucerne he observed that sheep selected a diet more digestible than the material that could be cut from the same pasture. Thus selection by grazing animals of the more digestible fractions within a single species may bias the result of digestibility studies on pure swards, especially where leaf:stem ratios are low (Christian et al. 1970).

### 3.3 The estimation of nutrient intake from animal production data

If the maintenance requirements of grazing animals and the energy content of changes in body composition or gains or losses in body weight can be determined, it should be possible to calculate nutrient intake using feeding standards (e.g. A.R.C. 1965). The heat of combustion of grass is relatively constant at 18.1 to 19.1J/g of dry matter (Blaxter 1964). The main determinant of metabolizable energy (ME) is the digestibility (D) of the organic matter in the grass which governs energy loss in the faeces; the energy loss in methane and urine is relatively constant and amounts to 19% of the digestible energy of the

grass. In addition D has a direct influence on the level of intake of herbage if it is freely available and also on the efficiency of use of ME for maintenance and gain (Blaxter 1964). The composition of body weight gains can vary widely in energy content depending on the amounts of water, fat and protein in the gains.

Changes in body composition are usually assumed to be zero in animals which have been maintained at a given liveweight and fed a standard ration for a prolonged period. Under these conditions an estimate of fasting metabolism is possible using calorimetric techniques. The additional requirements for animal activities such as standing and walking can also be estimated. Using this approach Blaxter (1964) estimates the requirement of ME for an adult grazing sheep to be approximately  $360\text{KJ/kgW}^{0.75}/24\text{h}$  and Graham (1964) gives a similar estimate of  $377\text{KJ/kgW}^{0.75}/24\text{h}$ . These estimates represent a 40% increase in the requirements of a grazing animal compared to a penned animal.

Using gaseous exchange techniques on sheep grazing in the field Young and Corbett (1968, 1972a) estimated the requirement of ME for maintenance at  $552\text{KJ/kgW}^{0.75}/24\text{h}$  for sheep that had been maintained in body conditions ranging from emaciated to fat for a prolonged period. They suggest the estimates of Blaxter (1964) and Graham (1964) are imprecise since they do not take account of the complex



interactions between the grazing animal and its environment. However, their own estimates show considerable variation and Whitelaw (1974) has pointed out difficulties and likely errors associated with the techniques. A more serious criticism however lies in the possibility that sheep were making substantial changes in body composition during the two experimental periods when body weight was assumed to be nearly constant. Estimates of in vitro digestibility of the diets selected increased from 62.9 to 70.2 units during this time (Young and Corbett 1972b), and percentage fat in the bodies of the sheep changed considerably (Young and Corbett 1972a). Hence it seems the requirement of energy balance throughout the experiment was not met and the estimates of ME for maintenance, at least for the sheep in fat and moderate body condition, are probably excessive.

Farrell et al. (1972) estimated ME requirements for maintenance from 493 to 849 KJ/kgW<sup>0.75</sup> /24h for grazing sheep ranging in condition from emaciated to fat by measuring rates of production of volatile fatty acids (VFA) in the rumen and predicting changes in body composition by the tritiated water technique. However, they state that their technique for measuring VFA concentrations in the rumen is imprecise. Furthermore they used the prediction equations of Farrell and Reardon (1972) to estimate changes in body composition. Those equations appear to be biased (see Figure 3.1a and b) since the coefficients in the equations

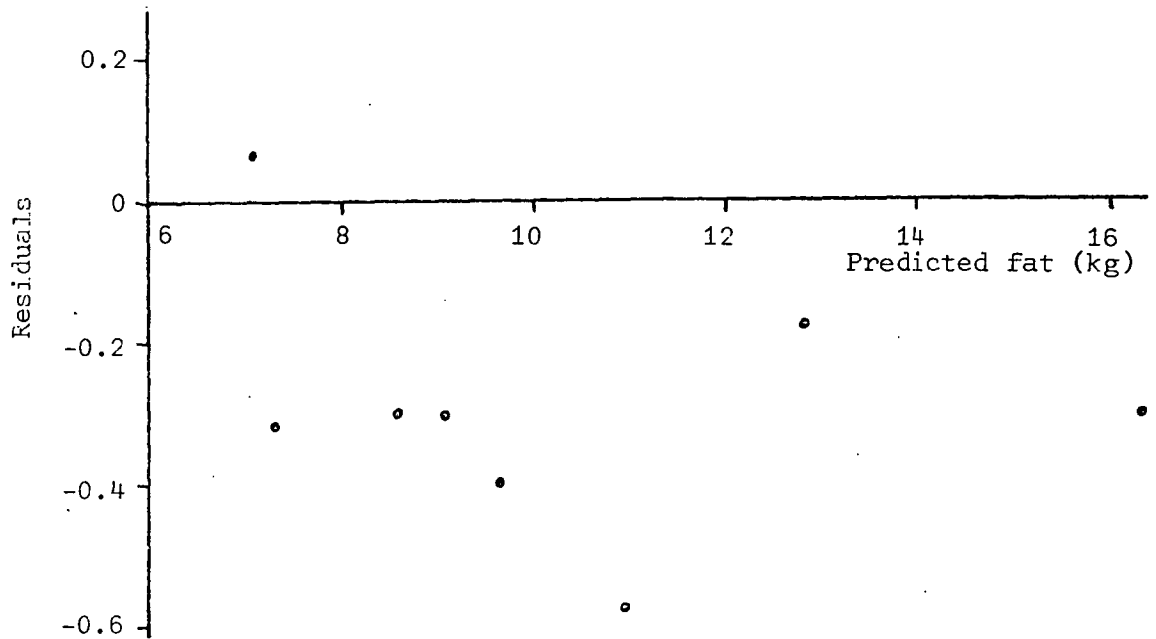


Figure 3.1(a) - Residuals for well-nourished sheep obtained from the equation  $\text{fat} = 0.87W - 0.81T - 3.48 \pm 0.21$  (Farrell and Reardon 1972)

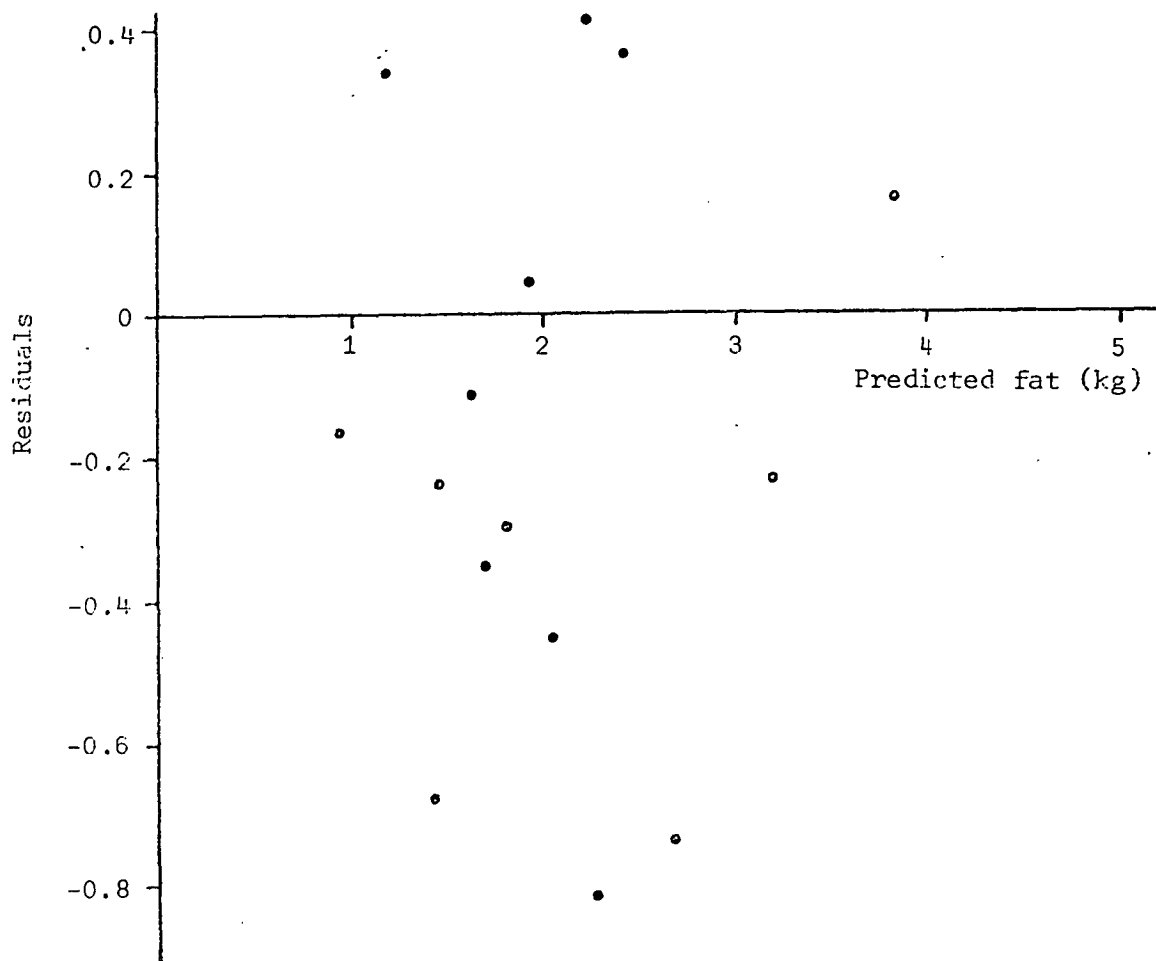


Figure 3.1(b) - Residuals for under-nourished sheep obtained from the equation  $\text{fat} = 0.60W - 0.66T + 0.39 \pm 0.44$  (Farrell and Reardon 1972)

for predicting fat do not appear to be least square estimators derived from the data they published.

Another approach to estimating maintenance requirements is based on regression analyses relating estimates of food intake, body weight and body weight change of animals grazing at pasture (e.g. Arnold et al. 1965; Doney and Russell 1968). However, the estimates of intake are very imprecise and changes in energy composition of gains have not been considered.

In view of these complications the estimates of Blaxter (1964) and Graham (1964) are likely to be the most reliable; at least the additional energy requirements over and above fasting metabolism can be clearly accounted for.

#### 3.4 The prediction of pasture growth under grazing

Whereas the methods discussed above for estimating the intake of grazing animals may be adequate for comparative studies of animal production, it is by no means clear that such estimates would be useful when attempting to measure pasture growth under grazing. There are however theoretical advantages in attempting to measure pasture growth by a combination of pasture intake and change in pasture availability. The advantages arise mainly from the difficulty of reproducing the overall effects of grazing in

any other way than by the grazing animal. Throughout grazing the pasture remains subject to the effects of selective defoliation, trampling and nutrient return. These latter effects are excluded if cage techniques are used, and indeed pasture growth may also be modified by changes to the microenvironment inside the enclosed area (Cowlshaw 1951).

The techniques for estimating intake are most reliable where diet selection is limited (e.g. on pure swards). However, such situations are rare in real systems of production or apply only to rotational systems of grazing with a substantial level of subdivision (e.g. McKinney 1974). In the latter situation the growth of pasture during grazing is relatively unimportant since the grazing period is short. Hence cutting techniques are more appropriate to measure regrowth during recovery from grazing in management systems involving rapid rotation.

Where pastures must be set-stocked for prolonged periods (e.g. on heavily grazed pastures during winter in southern areas), the diet of the animal is not homogenous with respect to digestibility (see Part 5) and may contain substantial amounts of dead plant material of very low digestibility. Also the growth of the pasture during grazing may roughly equal consumption. Hence the errors in measuring intake (up to 25%) are directly applicable to the pasture growth estimates. Other sources of error arise from

the necessity to separate the green component (growth) from the dead, and from those associated with measuring the change in pasture availability. Thus it seems unlikely that these techniques are sufficiently precise to give worthwhile estimates of growth under grazing.

### 3.5 Conclusions

The lack of precision in existing techniques to estimate diet digestibility remains a major obstacle to the accurate measurement of feed intake by grazing ruminants. The potential advantages of the faecal nitrogen technique to account for between-animal variability in digestibility cannot be realised while the factors controlling faecal nitrogen output in ruminants remain unclear. Nevertheless for many purposes satisfactory estimates of diet digestibility may be obtained from extrusa samples collected from animals fistulated at the oesophagus, although such estimates may be subject to unknown biases. Indeed the technique is the only suitable means of getting diet samples where the herbage on offer is in a mixed sward or where selection for more digestible structural components in a pure sward is possible. If pastures are pure swards and show little segregation into leaf and stem, reliable estimates of diet digestibility may be obtained from material cut from the pasture. This procedure would avoid some of the bias that may be associated with the oesophageal fistula technique. It would certainly reduce the effort

required to collect representative samples of the diet of grazing animals. The alternative approach of using feeding standards to predict nutrient intake from animal production data is subject to speculation on the maintenance needs of grazing animals. At present the most reliable estimates of maintenance needs are those derived from calorimeter studies on penned animals and while the estimated requirements in excess of fasting metabolism seem reasonable, the actual energy expenditure of a grazing animal is still unknown.

## Part 4

### . The estimation of the body composition of live sheep

#### 4.1 Introduction

Indirect methods for measuring the chemical composition of living animals are required in nutrition experiments in order to estimate the effect of treatments on the storage of tissue energy. For field studies the technique must be simple as well as reliable. The possibility of predicting the total body water (TBW) by measuring the tritiated water (TOH) space of the live sheep (Till and Downes 1962), coupled with the relative constancy of the composition of the fat-free body mass, has led to the use of multiple regression equations with liveweight and TOH space as predictors for each of the main chemical components (Panaretto 1963; Keenan *et al.* 1969; Searle 1970a). However, it is clear on casual inspection that these equations, which were derived from Merino and Merino crossbred sheep aged from 3 days to adult, predict widely different values when used on the same set of data. In addition, Farrell and Reardon (1972) found that these earlier equations underestimated, to different extents, the weight of fat in thin adult sheep and suggested the use of separate equations for well-nourished and undernourished animals. However, as this approach will result in discontinuities in predicted values for sheep undergoing large changes in nutrition, it would be preferable to



increase the precision of general prediction equations.

The inadequacies of published equations support the suggestion of Seebeck (1968) that liveweight and TOH space are insufficient to specify body composition. However, it is not at present clear what additional predictors, measurable in the live animal, could be usefully added to them. It might be expected that an index of skeletal development would merit inclusion, as this would differentiate between a fat young animal and a thin adult of the same liveweight. Age is one such index, and Searle (1970a) found that its inclusion as an additional parameter increased the correlation coefficients for all components. However, he regarded the improvement as too small, except in the case of ash, to warrant the use of age in prediction equations.

I have examined five groups of published data and some data from two groups of sheep covering a wide range of ages and nutritional status, in an attempt to analyse the reasons for differences between existing equations and to derive more precise general equations. The latter data were collected by Dr. M. Freer at the Ginninderra Experiment Station, A.C.T. Details of the killing procedure and the estimation of TOH space and the analysis of body tissue are described by Donnelly and Freer (1974). In fitting regressions to the available data, liveweight, TOH space and

The sources of the seven groups of data that were available for analysis are shown below. The data collected by Dr. Freer was divided into two groups of Border Leicester x Merino lambs as follows:

Group 2      20 wether lambs about 6 months old.

Group 3	23 adult Merino wethers	Keenan (1967)
Group 4	11 adult Merino wethers and ewes	Panaretto (1968)
Group 5	46 young Merino wethers	Searle (1970a)
Group 6	15 young Corriedale and crossbred wethers and ewes	Searle (1970a)
Group 7	23 adult Merino ewes	Farrell & Reardon (1972)

These data included two crossbred sheep and two Merino

wethers that were heavier than 80ks. For each group the mean age, liveweight, TOH space, weight of total body water (TBW) and weights of fat, protein and ash in the empty body are shown in Table 4.1.

Constants were fitted for linear and non-linear functions predicting body constituents from a number of variates, by using the computer programs for regression analysis prepared by McIntyre and Ward (1970). These variates include the liveweight of the fasted shorn animal (W), TOH space (T) and age as a proportion of 2 years, the assumed age at which mature size is reached in sheep (Brody 1945). This last predictor was designated maturity (M) with a maximum value of 1.0.

In comparing different regressions not only was the residual standard deviation (RSD) used, but also the mean difference between the predicted and actual values (bias) for the separate groups of data, expressed as percentages of the mean actual values. The equations presented in Table 4.2 include, for each body constituent, the allometric equations that incorporate the best single predictor, the best combination of two predictors and the combination of all three predictors. For comparison the appropriate multiple linear regressions are also included.

TABLE 4.1

MEAN AGE AND BODY COMPOSITION OF SHEEP IN EACH OF SEVEN GROUPS\*

	1	2	Group 3	4	5	6	7
Age (months)	2.5	6.7	>24	>24	7.3	3.7	>24
SD( $\pm$ )	0.60	0.41			6.42	1.45	
Fasted live weight (kg)	14.51	30.30	30.53	37.56	20.90	24.62	29.18
SD( $\pm$ )	4.358	2.621	4.402	5.112	11.312	5.753	6.633
TOH space (l)	11.12	19.92	20.40	23.95	14.12	16.09	21.11
SD( $\pm$ )	3.054	1.389	2.562	1.978	6.394	2.773	2.441
TBW (kg)	10.24	17.97	19.36	22.14	13.07	14.50	18.53
SD( $\pm$ )	2.794	1.331	2.416	1.815	5.906	2.696	2.104
Fat (kg)	1.40	6.73	4.45	7.96	3.70	5.75	4.66
SD( $\pm$ )	0.891	1.712	1.711	3.484	3.813	2.485	4.385
Protein (kg)	2.09	4.07	4.77	4.97	3.07	3.24	4.63
SD( $\pm$ )	0.601	0.356	0.608	0.588	1.496	0.583	0.772
Ash (kg)	0.52	1.05	1.53	1.54	0.78	0.72	1.26
SD( $\pm$ )	0.147	0.103	0.133	0.245	0.426	0.147	0.215

\* Origin of data shown in text.

TABLE 4.2

REGRESSIONS OF INDIVIDUAL BODY COMPONENTS  
ON FASTED LIVE WEIGHT (W), TOH SPACE (T) AND MATURITY (M)  
USING ALLOMETRIC AND MULTIPLE LINEAR REGRESSION MODELS

(These regressions include the data from the 149 sheep in  
Groups 1 - 6.)

Component, regression model and equation number	Constants in regression model				RSD (±)
	a	b	c	d	
TBW (kg)					
aT <sup>c</sup> (1)	0.901		1.008		0.442
aT <sup>c</sup> M <sup>d</sup> (2)	1.179		0.926	0.031	0.354
aW <sup>b</sup> T <sup>c</sup> M <sup>d</sup> (3)	1.180	0.002	0.923	0.031	0.355
a + cT (4)	-0.081		0.928		0.443
Protein (kg)					
aW <sup>b</sup> (5)	0.200	0.897			0.324
aW <sup>b</sup> M <sup>d</sup> (6)	0.408	0.708		0.092	0.264
aW <sup>b</sup> T <sup>c</sup> M <sup>d</sup> (7)	0.333	0.474	0.333	0.081	0.253
a + bW + cT (8)	-0.029	0.072	0.107		0.302
Ash (kg)					
aW <sup>b</sup> (9)	0.033	1.048			0.192
aW <sup>b</sup> M <sup>d</sup> (10)	0.305	0.460		0.290	0.100
aW <sup>b</sup> T <sup>c</sup> M <sup>d</sup> (11)	0.260	0.284	0.252	0.281	0.099
a + bW + cT (12)	-0.163	0.017	0.043		0.185
Fat (kg)					
a(W - T) <sup>b</sup> (13)	0.253	1.341			0.816
a(W - T) <sup>b</sup> M <sup>d</sup> (14)	0.117	1.592		-0.225	0.444
aW <sup>b</sup> T <sup>c</sup> M <sup>d</sup> (15)	0.006	4.377	-2.772	-0.224	0.505
a + bW + cT (16)	0.367	0.898	-1.086		0.746

#### 4.3 Prediction of body composition

##### (1) Total Body Water

Since TOH space overestimates TBW, mainly as a result of the slow equilibration of tritium with the non-aqueous hydrogen pool, TBW is usually predicted from equations derived by regression on TOH space. When these equations were calculated for each group of data, the regression coefficient for group 7 differed widely from the others. In no equation did the value of the intercept differ significantly from zero, and, for groups 1-6, TBW represented 92% of the TOH space, whereas in group 7 it was 87%. This group was therefore excluded before pooling the data to fit the regressions shown in Table 4.2.

Inclusion of maturity in the allometric model decreased the RSD (Table 4.2) by reducing the mean difference between actual and predicted values for most of the groups (Figure 4.1). The form of equation (2) indicates that in younger animals TBW represented a smaller proportion of the TOH space. This is in agreement with the suggestion of Lewis and Phillips (1972) that the rate of exchange of tritium with the non-aqueous hydrogen pool depends on the age or growth rate of the animal. The inclusion of liveweight as an additional predictor in any combination did not reduce the RSD.

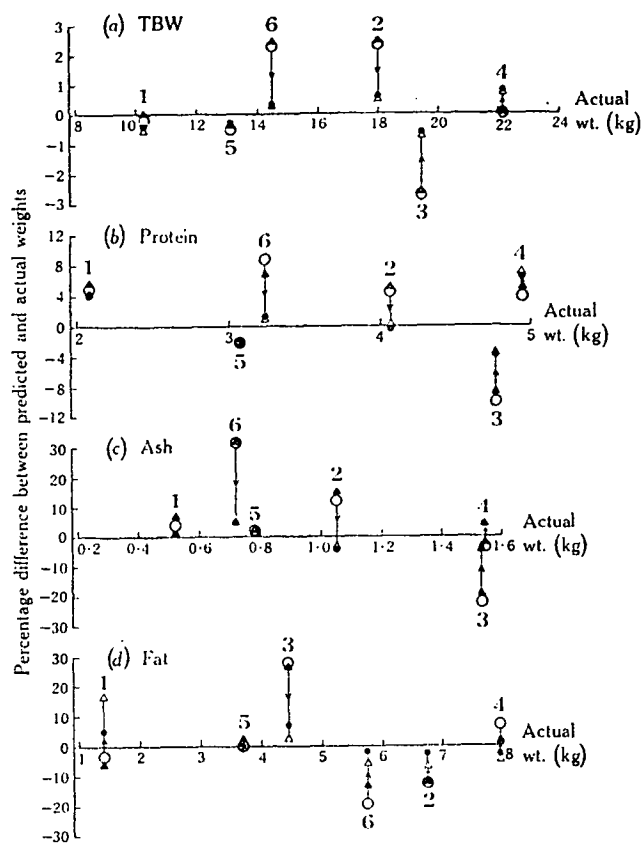


Figure 4.1 - The percentage difference between the mean predicted weight of each body constituent and the mean actual weight for each of the six groups of sheep, on using four different prediction equations. For each body constituent  $\circ$ ,  $\bullet$ ,  $\Delta$  and  $\blacktriangle$  indicate the first, second, third and fourth equations respectively in Table 4.2, and the numeral adjacent to each set indicates the group number. The arrow on the line joining each set of differences for each group points towards the equations that include M as a predictor.

When group 7 was included the RSD of equation (2) was increased by 50% to  $\pm 0.538$ ; as I was unable to explain why these data differ I have excluded them from the general regressions for all body components.

## (2) Protein and Ash

For both these constituents liveweight alone was almost as good a predictor as the combination of W and T in either the allometric or linear form (Table 4.2). However, the combination of maturity and liveweight (equations 6 and 10) substantially reduced the RSD and the mean differences of individual groups from the predicted values (Figure 4.1). The combination of all three variates (equations 7 and 11) gave only a slight further improvement.

## (3) Fat

The relative constancy of the proportion of water in the fat-free empty body of the chemically mature animal (Moulton 1923) provides a biological basis for the multiple regression model commonly used for predicting the weight of fat:

$$\text{fat} = a + bW - cT$$

Equations of this form were calculated for the individual



TABLE 4.3

REGRESSIONS OF FAT (KG) ON FASTED LIVE WEIGHT (W)  
 AND TOH SPACE (T) FOR SHEEP IN INDIVIDUAL GROUPS  
 AND FOR POOLED DATA FROM GROUPS 1-6

Group	Constants in equation of form Fat = a + bW + cT			RSD (±)
	a	b	c	
1	-0.4792	0.6169	-0.6357	0.206
2	-0.1342	0.8525	-0.9520	0.569
3	-0.8560	0.8999	-1.0862	0.386
4	-0.6698	0.8688	-1.0024	0.508
5	-0.0365	0.8976	-1.0629	0.493
6	-0.1383	0.8201	-0.8888	0.304
Mean	0.3667	0.8976	-1.0863	0.746

groups (Table 4.3), but when the common equation for all data was applied to the separate groups the predicted weights of fat were clearly biased (Figure 4.1).

The reasons for this variability can be more clearly visualized (Figure 4.2) by expressing the model in the simple linear form

$$\text{fat} = d + f(W - T).$$

This approximation can be justified by the similarity of the regression coefficients for W and T in each equation in Table 4.3, and in fact it increased the average RSD by only 0.153 kg. Two conclusions are clear from the lines plotted for individual groups in Figure 4.2: that the overall relationship is curvilinear, and that for any value of W - T the weight of fat is greater in younger animals. These conclusions are borne out by the relationships shown in Table 4.2. As a single predictor, W - T (equation 13) was substantially better than W alone (RSD  $\pm$  1.36) and only marginally worse than W and T used together as independent variates in either the allometric form (RSD  $\pm$  0.761) or the multiple linear regression model (equation 16). The inclusion of maturity in addition to W - T (equation 14) gave a further reduction in RSD and in the mean differences

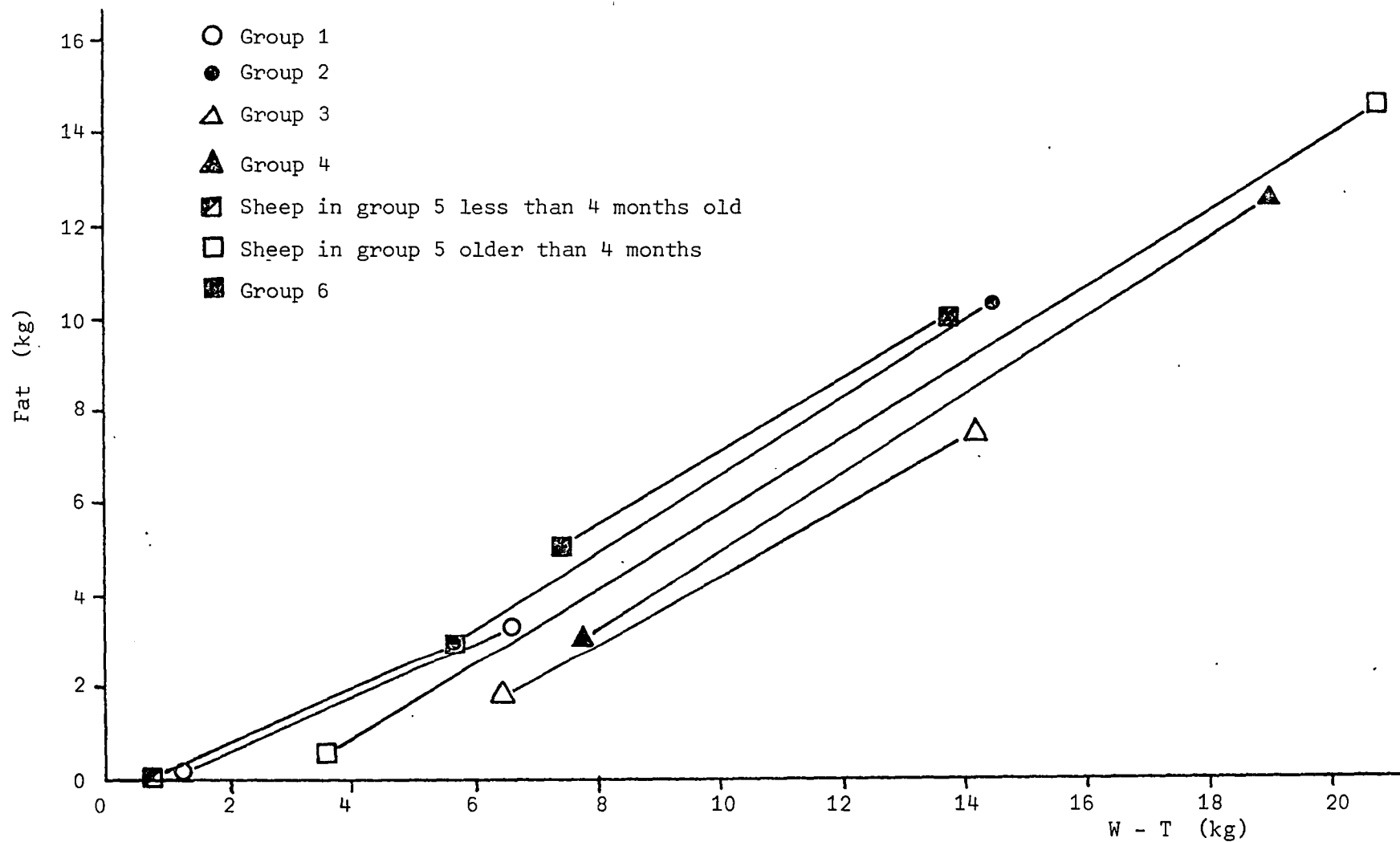


Figure 4.2 - Relationship between W - T and the weight of fat in the empty body for sheep in groups 1 - 6.

of individual groups (Figure 4.1). The superiority of this model over the combination of W, T and M as separate predictors (equation 15) may lie in the greater scope it offers for interaction between the predictors.

The relationship implied by this model is in agreement with the conclusion of Farrell and Reardon (1972) that a single equation of the form,  $\text{fat} = a + bW - cT$  cannot be used to predict the weight of fat in both well-nourished and undernourished mature sheep. However, the constants that are fitted in equation (14) are not suitable for predicting fat values in any of Farrell and Reardon's sheep regardless of their nutritional status. It is possible that this results from the difference in the relationship between TOH space and TBW already discussed.

By using the general equations calculated here, the predicted weight of fat has the highest RSD of any single component. As an alternative, fat could be predicted by subtracting from liveweight the predicted weights of all other components including dry gut contents. From the data for groups 1-6 the weight of dry gut contents was best predicted by the equation

$$\text{dry gut contents} = 0.016W^{-0.569}T^{1.700} \quad (\text{RSD } \pm 0.0936)$$

The RSD of a fat value estimated by difference would therefore be  $\pm 0.45$ , almost the same as the RSD of equation

(14) for the direct prediction of fat. Clearly the estimation of any other component by difference would be less precise than by direct prediction.

#### 4.4 Conclusion

The best equations obtained for the prediction of body composition from the data available are (2), (6), (10) and (14) in Table 4.2. The standard error of a value predicted from an animal or group of animals not in the original sample may be calculated more readily if the appropriate equation is in the linear form that is obtained by converting the model

$$Y = aX_1^{b_1}X_2^{b_2}$$

to

$$\log_e Y = \log_e a + b_1 \log_e X_1 + b_2 \log_e X_2$$

However, to derive coefficients for the linear model by regression analysis after the logarithmic transformation of the original data will lead to bias in the predicted values (Beauchamp and Olson 1973), so the non-linear procedures already described were used. The linear form of each of the four selected equations with the necessary statistics for calculating the errors of predicted values are shown in Table 4.5.

All of the selected equations indicate the importance of including some index of the maturity of

TABLE 4.4

MEAN PERCENTAGE DIFFERENCES BETWEEN PREDICTED AND ACTUAL WEIGHTS (KG)  
 OF EACH BODY COMPONENT IN GROUPS 5 AND 6 USING THE BEST GENERAL  
 REGRESSION EQUATION\* AND THE MULTIPLE LINEAR REGRESSION EQUATION  
 DERIVED FROM THESE GROUPS ALONE†

Component	Regression	Group	
		5	6
TBW	$1.179T^{0.926}M^{0.031}$	-0.22	0.32
	$-0.015 + 0.920T$	-0.69	2.02
Protein	$0.408W^{0.708}M^{0.092}$	-1.90	1.50
	$0.0060 + 0.0494W + 0.139T$	-2.27	6.59
Ash	$0.305W^{0.460}M^{0.290}$	2.70	5.64
	$-0.085 + 0.0123W + 0.0400T$	-6.08	19.69
Fat	$0.117(W-T)^{1.592}M^{-0.225}$	0.35	-1.65
	$0.014 + 0.898W - 1.053T$	5.14	-10.13

\* Equations (2), (6), (10) and (14) from Table 4.2

† Calculated from the data of Searle (1970a).

skeletal development of the animal when predicting body composition over a wide range of age, liveweight and plane of nutrition. Even so it is unlikely that maturity would be a suitable parameter where, for example, young sheep had been fed rations in pens which resulted in very high fat contents in their bodies (fat in excess of 30%). Such conditions, however, are unlikely to occur with lambs fed normal diets or at pasture. Breed differences might also be expected to influence the role of skeletal size in the prediction of body composition. Although data were available from only a narrow range of breeds, there are indications that the general equations including maturity as a predictor can account for breed differences in composition not detected by the standard multiple linear regression model incorporating liveweight and TOH space. For example, the general equations give a more precise prediction of composition (Table 4.4) for groups 5 (Merinos) and 6 (Corriedales and Merino crossbred sheep) than does the multiple linear regression equation derived specifically from these data. This may explain the bias that Searle (1970b) found when he tested his equations with crossbred sheep.

In mature sheep (where  $M=1$ ) the ability of the present equations to predict body composition is limited to an allometric function of the single variate  $W$  or  $T$  or  $(W - T)$  in the case of fat. These results show (Figure 4.1) that

TABLE 4.5

STATISTICS OF REGRESSIONS (2)\*, (6), (10) AND (14)

WHEN TRANSFORMED TO THE MODEL:  $\ln Y = \ln a + b_1 \ln X_1 + b_2 \ln X_2$ 

Y	TBW	PROTEIN	ASH	FAT
$X_1$	T	W	M	(W-T)
$X_2$	M	M	M	M
Mean $\ln X_1$ †	2.694	3.052	3.052	1.805
Mean $\ln X_2$ †	-1.504	-1.504	-1.504	-1.504
$\ln a$	0.1647	-0.8965	-1.1874	-2.1456
$b_1$	0.9260	0.7084	0.4596	1.5919
$b_2$	0.0308	0.0920	0.2898	-0.2253
RSD (±)	0.0238	0.0778	0.1088	0.1057
Elements of inverse matrix †				
$C_{11}$	0.1608	0.1100	0.1100	0.0472
$C_{12}$	-0.05262	-0.04186	-0.04186	-0.02105
$C_{22}$	0.02161	0.02033	0.02033	0.01527

\* See Table 4.2

† Calculated after logarithmic transformation of the individual values.



this is adequate for uniform groups of animals within one breed changing in composition as a result of changes in nutrition. But prediction equations for mature sheep covering a wider range of size or breed may need an index of the mature skeletal size as an additional variate.

## Part 5

### The effect of body condition on the intake of food by mature sheep

#### 5.1 Introduction

A Preliminary attempt by Freer et al. (1970) to construct a model of a grazing system for comparing alternative management strategies, indicated that the predicted liveweight gain of mature sheep was particularly sensitive to the relationships used for calculating their intake of food. The equations used in the model were based on local experimental results relating food intake to the amount and quality of herbage available. However, other determinants of intake may modify these relationships and their effects must be understood if the model is to be sufficiently accurate for predictive purposes.

The previous nutrition of the animal as reflected in its body condition or energy status, may influence food intake. Kennedy (1961) suggested that the level of food intake is regulated by the amount of fat in the body and Graham (1969) observed that mature sheep in pens ate less food when their fat content reached 30% of live weight. At lower fat levels, which are more typical of grazing sheep, little is known of the effect of body condition on intake, yet it is under grazing that fluctuations in condition are most likely to occur.

In young ruminants the effect of dietary restriction on their subsequent voluntary intake of food has been widely studied but no clear conclusion can be reached. Positive or negative effects may be inferred from the results reviewed by Allden (1970) depending on whether intakes are compared in terms of the age, live weight, metabolic size or alimentary capacity of the animal; at present there is no unequivocal basis for comparing intakes by animals at different stages of development.

An experiment was designed to measure the intake of food by mature sheep in poor or good condition when given access to sparse or abundant pasture or to food in pens. The original differences were imposed either by grazing conditions or by restricted feeding in pens to test the possibility that restricted experience of grazing sparse pasture might reduce food intake.

## 5.2 Experimental details

### (a) Design

From 70 three-year-old merino wethers that had grazed together for several months, 16 were prepared with oesophageal fistulae. Nine groups of six were formed from the remaining sheep by random allocation after stratification on the basis of live weight (mean 33kg). During Period A (Table 5.1), from May 14 to July 2, three

TABLE 5.1  
TREATMENTS APPLIED TO NINE GROUPS OF  
SHEEP

Treatment	Groups	
	Period A	Period B
Abundant pasture (H)	1, 2, 3	1 (HH); 4 (LH); 7 (PH)
Sparse pasture (L)	4, 5, 6	2 (HL); 5 (LL); 8 (PL)
Pen feeding* (P)	7, 8, 9	3 (HP); 6 (LP); 9 (PP)

\* Pen feeding treatments described in text.

groups and four fistulated sheep grazed together on abundant pasture (about 2500kg/ha green herbage dry matter) and three groups and eight fistulated sheep on sparse pasture (about 800kg/ha green herbage dry matter). The remaining three groups and four fistulated sheep were fed individually in indoor pens where they received 206g/day digestible organic matter. This was intended to maintain their mean live weight close to that of the sheep on sparse pasture.

On July 2, when Period B started, one group and two fistulated sheep from each of the three initial treatments were divided equally between two plots of abundant pasture. One group and the remaining fistulated sheep from each treatment in Period A were divided between two plots of sparse pasture. The third group from each treatment was offered food ad libitum in pens. Period B ended on August 4 but the measurement of the voluntary intake of food by the penned sheep continued for a further four weeks. The nine groups are referred to below by combinations of H, L and P as shown in Table 5.1.

(b) Pastures

A pasture, predominantly Phalaris tuberosa and Trifolium subterraneum, was divided into four plots, each of 0.4ha. During the autumn these were prepared by mowing and grazing so that two plots had over 2000kg/ha green herbage dry matter and the other two about 800kg/ha.

(c) Pen feeding

A single batch of lucerne hay was hammer-milled to pass through a 3.2mm (1/8") screen and pelleted. Separate measurements using standard collection procedures showed that the digestibility of the organic matter was 62% at a daily intake of 800g dry matter and rose or fell by one percentage unit for each decrease or increase respectively of 120g dry matter. Food was offered once daily at 1000 hours and when offered ad libitum the amount was about 15% in excess of the intake during the previous 24h. Samples of diet and residues were dried and bulked for ash determination. Water was freely available and the intake of minerals and vitamins A and D was adequate.

### 5.3 Experimental procedure

(a) Herbage measurements

On July 6 and July 27 the weight of green herbage dry matter was estimated on the four plots. On each of the two plots with abundant pasture 20 readings of an electronic capacitance meter were taken at sites selected on a stratified random basis. To calibrate the meter four additional sites were cut to ground level with an electric shearing handpiece and the remaining herbage was estimated by taking four cores, each 47.5cm<sup>2</sup>, from each of these sites and removing all plant material from the soil surface of each core. Equations were calculated by regression analysis

to predict the weight of green herbage dry matter per ha. On the sparse pasture virtually no material was accessible to a shearing handpiece, and 40 cores were taken from each plot on a stratified random basis on each sampling date. The herbage from each core was sorted into green and dead fractions, dried and weighed.

The methods used for both pastures give estimates of herbage weight appreciably greater than those obtained by the shearing handpiece alone.

(b) Diet selection

Between July 10 and July 29, samples of ingested herbage were collected from the fistulated sheep on six occasions on the abundant pasture and on ten occasions on the sparse pasture. For each collection the sheep were removed from the pasture for 30-60min before being allowed to graze for about 30min. When the collection bags were removed a sub-sample was stored in alcohol and later separated into green and dead fractions. The remainder was freeze-dried and ground for the estimation of digestibility in vitro.

(c) Live weight and tritiated water (TOH) space

During Period A the sheep were weighed each fortnight after an overnight fast. On July 2 and August 4 the TOH space of each sheep was measured by the method

described by Keenan et al. (1969). Each sheep was weighed after food and water had been withheld for 24h and its fleece marked with a dyeband (Chapman and Wheeler 1963). On September 4 each sheep was shorn and a staple was cut at the dyebands to estimate the weight of fleece and hence the fleece-free live weight on each occasion when TOH space was measured.

The weight of total body water, and the weights of fat and protein in the empty body of each sheep at the start and end of Period B were predicted from the regression equations derived in Part 4. The energy content of each body was estimated from its content of fat and protein (Paladines et al. 1964).

(d) Output of faeces and intake of food by grazing sheep

The sheep wore complete collection harnesses from June 29 and faeces were collected for 3-5 days in each week between July 6 and August 3. Each day the faeces were weighed and a 10% sample dried. The dry samples were bulked weekly for each sheep for ash and nitrogen analysis. The mean daily intake of organic matter by the grazing sheep was calculated from the output of faeces and the mean estimated digestibility of the diet.

(e) Time spent grazing

Throughout each of the last three faecal collection



periods, the time spent grazing by all sheep on one plot of both abundant and sparse pasture was measured with vibracorders (Allden 1962).

(f) Analytical methods

The methods have been described by Christian et al. (1970).

(g) Statistical analysis

The measurements of live weight and faecal output and the calculated values of herbage intake for individual animals were examined by analysis of variance. After testing for heterogeneity of variance the standard error of a mean was calculated for all treatment groups. For body components predicted from regression equations the standard error of the mean value for each treatment was calculated as the error of a value predicted from the mean of  $n$  animals (where  $n = 6$  or  $18$ ) in each group (Raymond et al. 1954).

## 5.4 Results

(a) Herbage present and diet selected

Near the start and end of Period B the dry weight of green herbage barely fell below 2000kg/ha on the plots of abundant pasture and was less than 1000kg/ha on the sparse plots (Table 5.2). The patchy cover on the latter plots is reflected in the high standard errors relative to the means

TABLE 5.2

WEIGHT OF HERBAGE DRY MATTER (KG/HA) PRESENT ON  
EACH OF FOUR PLOTS ON TWO SAMPLING DATES.

Pasture	Plot	Herbage	Sampling date			
			July 6		July 27	
			Mean	C.V.*	Mean	C.V.
Abundant	1	Green	3670	19.4	2320	12.5
		Dead <sup>†</sup>	2918		3307	
	2	Green	2270	27.6	1960	12.8
		Dead <sup>†</sup>	2449		2058	
Sparse	3	Green	958	44.7	820	46.2
		Dead	1499	65.0	1446	55.5
	4	Green	780	57.8	859	54.6
		Dead	1601	62.8	1369	59.8

\* Coefficient of variation between sampling sites

† Estimates from the four sites used to calibrate the capacitance  
meter

(Table 5.2).

Although a large proportion of both pastures consisted of dead material, the mean percentage of green material in the diet of the sheep was  $95 \pm 3$  (S.D. of samples) on abundant pasture and  $80 \pm 7$  on sparse pasture. The corresponding digestibility of organic matter in the selected material was  $73.2 \pm 2.5\%$  and  $53.9 \pm 4.3\%$  respectively. These measurements did not differ between plots, were not affected by treatment in Period A and showed no consistent trend during Period B. Clearly the digestibility of green material eaten from the sparse pasture was considerably lower than that selected from the abundant pasture.

(b) Changes in liveweight and composition

At the end of Period A sheep that had grazed sparse pasture were 23% lower in live weight than those that had grazed abundant pasture (Table 5.3), but 39% and 43% lower in estimated mean dry weight and energy content respectively. It was intended that the pen-fed sheep would lose weight at the same rate as those on sparse pasture and measurements after overnight fasts during Period A indicated that the mean weights of the two groups were the same. However after a 24h fast at the end of Period A the pen-fed sheep proved to be only 17%, 26% and 31% lower in live weight, dry weight, and energy content respectively than those on abundant pasture.

TABLE 5.3

MEAN FLEECE-FREE LIVEWEIGHT, THE ESTIMATED WEIGHTS  
OF BODY COMPONENTS AND THE ESTIMATED ENERGY CONTENT  
AT THE END OF PERIOD A

	Treatment in Period A					
	Abundant pasture (H)		Sparse pasture (L)		Pen feeding (P)	
	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)
Live weight (kg)	36.7	0.45*	28.4		30.4	
Body water (kg)	22.2	0.18†	19.5	0.15	19.7	0.15
Dry matter (kg)	14.5	0.18†	8.9	0.15	10.7	0.15
Fat (kg)	6.9	0.23†	3.1	0.10	4.2	0.13
Energy (MJ)	389	9.7 †	220	4.6	268	5.9

\* SE of a mean, calculated from analysis of variance

† SE of the value predicted from the mean of 18 animals

Of the sheep that grazed sparse pasture during Period B, the LL group maintained their mean live weight without change in composition (Table 5.4) whereas the HL group lost significant ( $P < 0.05$ ) amounts of all components except water. On abundant pasture the liveweight gain by the LH sheep was little more ( $P < 0.1$ ) than that by HH sheep. However as most of the gain made by the LH sheep consisted of water, their increase in dry weight was less ( $P < 0.001$ ) than that of the HH sheep. On both pastures the mean changes in dry weight of sheep moved from pens were intermediate between those of sheep initially on sparse and abundant pastures.

The sheep from sparse pasture that were offered food ad libitum in pens during Period B (LP) gained four times as much dry matter as those in the LH group although their mean gains in live weight were not significantly different ( $P > 0.05$ ). On the other hand the HP and HH groups did not differ significantly in dry matter gain. The HP sheep gained less live weight ( $P < 0.01$ ) and dry matter ( $P < 0.001$ ) than did the LP or PP sheep; these last two groups differed in gain of live weight ( $P < 0.001$ ) and water ( $P < 0.001$ ) but not dry matter.

(c) Output of faeces by grazing sheep

The mean daily output of faecal organic matter

TABLE 5.4

MEAN DAILY GAIN IN THE FLEECE-FREE FASTED LIVE  
WEIGHT, BODY COMPONENTS AND ENERGY CONTENT  
DURING PERIOD B.

Treatment in period B		Treatment in period A					
		Abundant pasture (H)		Sparse pasture (L)		Pen feeding (P)	
		Mean	SE	Mean	SE	Mean	SE
Liveweight (g)	H	102		151		179	
	L	-66		10		-10	
	P	130	17.8 <sup>A</sup>	194		296	
Body water (g)	H	17	11.4 <sup>B</sup>	123	10.1	111	10.3
	L	-9	10.3	-5	9.0	14	9.5
	P	72	11.4	82	10.0	160	10.6
Dry matter (g)	H	85	11.4 <sup>B</sup>	28	10.1	69	10.3
	L	-57	10.3	15	9.0	-24	9.5
	P	58	11.4	112	10.0	135	10.6
Fat (g)	H	69	14.4 <sup>B</sup>	6	6.9	37	9.2
	L	-46	13.7	11	7.3	-18	8.6
	P	43	19.2	66	7.7	86	11.9
Energy (MJ)	H	2.96	0.598 <sup>B</sup>	0.60	0.315	1.88	0.401
	L	-1.97	0.569	0.44	0.324	-0.73	0.375
	P	1.98	0.782	3.08	0.344	4.08	0.500

<sup>A</sup> SE of a mean, calculated from analysis of variance.

<sup>B</sup> SE of the gain calculated from values predicted from the mean of six animals at the start and end of period B.

(Table 5.5) by sheep grazing abundant pasture in Period B was not affected by their treatment in Period A. On sparse pasture sheep which had been in pens during Period A produced less ( $P<0.01$ ) than those which had been grazing.

Throughout Period B the mean concentration of nitrogen in the faecal organic matter from the sheep on abundant pasture was more than one percentage unit higher than that from those on sparse pasture (Table 5.5). Initially, nitrogen in the faeces of sheep moved from pens was lower ( $P<0.05$ ) by about one half of a percentage unit than in the faeces of all other grazing sheep, but the difference was not significant after the first week. The mean concentration of ash in the faecal dry matter was  $19.6\pm0.40\%$  on abundant pasture and  $26.0\pm1.40\%$  on sparse pasture.

#### (d) Intake of food

On neither pasture was the estimated mean daily intake of organic matter affected by the body condition of the sheep (Table 5.6) but on sparse pasture the previously penned animals ate less ( $P<0.01$ ) than those that had been grazing.

During Period B there was an upward trend in the intake of organic matter by all groups (Figure 5.1). The amount eaten in the first week was lower than that in the

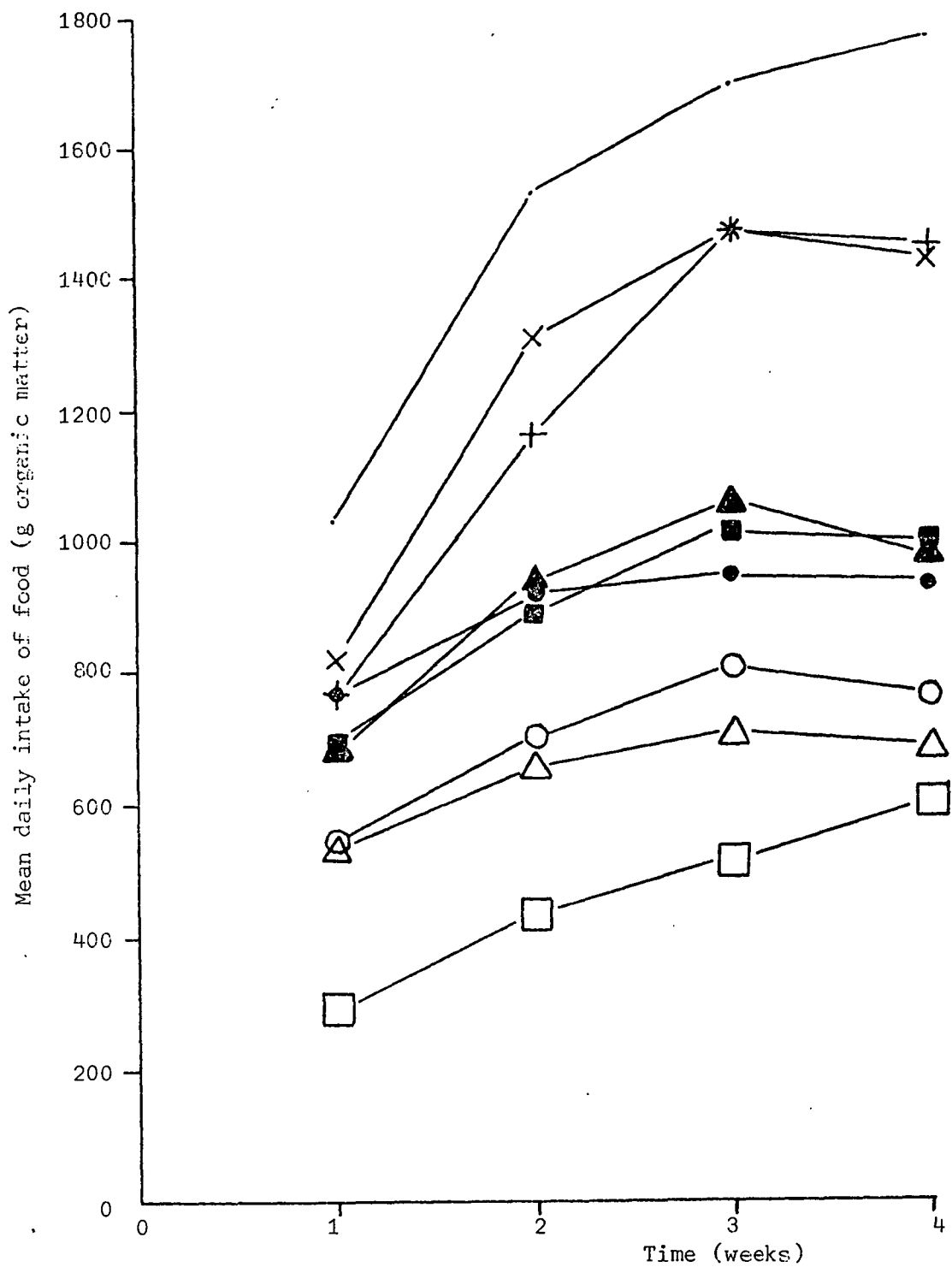


Figure 5.1 - The mean daily intake of organic matter during each week of period B by nine groups of sheep.

X HP      + LP      • PP      ● HH      ▲ LH  
 ■ PH      ○ HL      △ LL      □ PL



TABLE 5.5

MEAN DAILY OUTPUT OF FAECAL ORGANIC MATTER (G) BY GRAZING  
SHEEP DURING PERIOD B AND THE MEAN PERCENTAGE CONCENTRATION  
OF NITROGEN IN THE ORGANIC MATTER OF THE FAECES

	Treatment in Period B	Treatment in Period A			Standard error of a mean ( $\pm$ )
		Abundant pasture (H)	Sparse pasture (L)	Pen feeding (P)	
Faecal organic matter	Abundant pasture (H)	239	245	240	10.3
	Sparse pasture (L)	324	297	212	24.7
Nitrogen	Abundant pasture (H)	4.47	4.45	4.09	0.075
	Sparse pasture (L)	3.27	3.27	3.29	0.122

fourth week by 20% for the HH and LL groups, by 30% for the HL, LH and PH groups and by 50% for the PL group. Even so, in the last week of Period B the intake of food by the PL sheep remained lower than that of the other sheep on sparse pasture.

Sheep that were in pens during both periods ate more food ( $P < 0.01$ ) throughout Period B than did sheep brought in from grazing. The body condition of the latter sheep did not affect their voluntary intake of food. The mean daily intake of food by all groups in pens increased for the first three weeks (Figure 5.1). Over the next five weeks the mean daily intake by the HP and LP groups remained unchanged at about 1500g organic matter while that of the PP group fell to within 6% of this level.

The sheep moved to pens ate about twice as much digestible organic matter during Period B as those on sparse pasture (Table 5.6) but not significantly more than those on abundant pasture.

(e) Time spent grazing

Sheep on sparse pasture grazed for about 2.8h longer per day than sheep on abundant pasture (Table 5.7). Previous treatment had no effect on the total time spent grazing but on sparse pasture animals that had come from pens ate more slowly than the other sheep.

TABLE 5.6

MEAN DAILY INTAKE OF ORGANIC MATTER (G) AND DIGEST-  
IBLE ORGANIC MATTER (G) DURING PERIOD B

Treatment in Period B	Treatment in Period A			Standard error of a mean ( $\pm$ )
	Abundant pasture (H)	Sparse pasture (L)	Pen feeding (P)	
<u>(a) Organic matter</u>				
Abundant pasture (H)	893	915	898	37.9
Sparse pasture (L)	704	645	460	53.6
Pen feeding (P)	1255	1209	1502	70.3
<u>(b) Digestible organic matter</u>				
Abundant pasture (H)	653	669	657	28.1
Sparse pasture (L)	379	348	248	28.9
Pen feeding (P)	708	687	815	30.4

TABLE 5:7

MEAN DAILY TIME SPENT GRAZING AND RATE OF EATING  
DURING PERIOD B

Treatment in Period B	Treatment in Period A		
	Abundant pasture (H)	Sparse pasture (L)	Pen feeding (P)
<u>(a) Total time (h)</u>			
Abundant pasture (H)	7.43	7.61	7.96
Sparse pasture (L)	10.55	10.65	10.24
<u>(b) Rate of eating (g OM/h)</u>			
Abundant pasture (H)	120	120	113
Sparse pasture (L)	67	61	45

## 5.5 Discussion

The main results of this experiment show firstly that the intake of herbage by mature grazing sheep was unaffected by body condition and secondly that rapid changes in plane of nutrition led to marked changes in the water content of liveweight gain and in the efficiency with which energy was retained.

On abundant pasture voluntary intake was not restricted by the availability of green material as this was well in excess of the limiting value suggested by Willoughby's (1959) data. Under these conditions no differences were detected in the intake of food by sheep that differed by 8kg in live weight and ranged in fat content from 11% (L) to 19% (H) at the start of Period B. When these results are considered with those of Graham (1969) they suggest that the amount of fat in the body of a mature wether has little effect on its voluntary intake of food until the fat level exceeds at least 20% of its fasted live weight. It seems unlikely that the depletion of fat below this level causes a further stimulus to intake. The possibility that social facilitation increased the intake by the HH sheep to that by the LH sheep grazing with them appears to be excluded by the lack of difference between the HP and LP sheep.

Of the sheep that grazed sparse pasture in Period B, those with recent experience of similar grazing (LL) ate no more than those from abundant pasture (HL) . However sheep moved from pens (PL) adapted only slowly to field conditions, as shown by their intake of food during successive weeks and by their slow mean rate of eating. The diet they selected was, overall, as high in green material as that of the sheep grazing throughout. The concentration of nitrogen in the faeces of these sheep (PL) was lower during the first week than it was subsequently, but as this was evident also in the sheep moved to abundant pasture (PH) it may indicate a slow adjustment of the gut contents to field conditions rather than a lower digestibility of the diet.

While the sheep in poor condition failed to eat more food than those in better condition they retained a smaller proportion of their energy intake. All three groups on abundant pasture during Period B gained live weight but the greater the change in plane of nutrition compared with Period A, the greater was the contribution of water to this gain - 17, 62, and 81% respectively for the HH, PH, and LH groups. As a result the mean dry matter content of the sheep that moved from sparse to abundant pasture changed little.

This conclusion is not affected by the partition of

the water gain between gut contents and body tissue. But the predicted amounts of fat, and hence energy, in the dry matter gain of the LH and PH sheep would be inaccurate if the amounts of water in their gut contents were markedly greater than those in the animals from which the prediction equations were derived. From measurements made on similar sheep killed after a 24h fast Keenan (1967) found that water in the gut contents increased from 3.40kg to 3.77kg when the daily food intake was increased from 600g to 1600g dry matter. This suggests that the water in the gut contents of the LH and PH sheep would have increased by no more than 0.15kg during Period B compared with the estimated total gain of about 4kg water (Table 5.4).

A comparison of the estimated daily gain in body energy by the grazing groups with the expected daily retention of dietary energy (Table 5.8) shows close agreement for the three groups that remained on a similar plane of nutrition throughout the experiment (HH,LL,PL). The other three groups (LH,PH,HL) were much less efficient and, on the abundant pasture, the difference between the two estimates was directly related to the size of the change in plane of nutrition. Keenan et al. (1969) observed a similar depression in the efficiency of energy retention by mature sheep offered food ad libitum in pens after a period of restricted feeding. The losses in live weight and energy in their animals were similar to those observed in this study.

TABLE 5.8

EXPECTED AND ACTUAL MEAN DAILY RETENTION OF ENERGY  
FROM THE DIET OF THE GRAZING ANIMALS DURING  
PERIOD B (Feeding standards taken from Agricultural  
Research Council (1965))

Treatment during period B:	Abundant pasture			Sparse pasture		
Treatment during period A:	H	L	P	H	L	P
Daily intake of ME <sup>A</sup> (MJ)	10.85	11.11	10.91	6.29	5.78	4.11
Mean liveweight (kg)	38.1	30.7	32.8	35.5	28.9	30.9
Daily liveweight gain (g)	99	146	174	-64	9	-9
ME required for maintenance <sup>B</sup> (MJ)	5.47	4.66	4.88	5.56	4.76	5.01
ME surplus to maintenance (MJ)	5.38	6.45	6.83	0.73	1.02	-0.9
Expected retention of energy <sup>C</sup> (MJ)	2.80	3.35	3.55	0.28	0.40	-0.63
Actual retention of energy (MJ)	2.96	0.60	1.88	-1.97	0.44	-0.73

<sup>A</sup> Metabolizable energy (MJ) = (digestible organic matter (kg))  $\times$  16.6.

<sup>B</sup> ME required for maintenance =  $W^{3/4} \times 0.26/k_m$ ,  
where  $k_m$  = 0.73 for abundant pasture; 0.68 for sparse pasture.

<sup>C</sup> Expected retention of energy = ME surplus to maintenance  $\times k_f$ ,  
where  $k_f$  = 0.52 for abundant pasture; 0.39 for sparse pasture.



Hence the body composition changes they described could be expected in this experiment. Associated with a 16% loss of live weight was a 50% reduction in the weight of the liver. Differential gains in the weights of different organs during the period of recovery may be the cause of the apparently low energy retention by previously undernourished animals since the synthesis of these tissues may have energy requirements different from those ascribed to fat and protein in these calculations.

There is the additional possibility that during the recovery from undernutrition the relationship between TOH space and total body water is different from the one used here because of increased incorporation of tritium into organic compounds. There was no evidence of this in the sheep of Keenan et al. (1969) but the point needs further examination. It is even less likely that the low estimated efficiency of energy retention by sheep moved to abundant pasture resulted from errors in estimating the digestibility of their diet since a difference of 14 units would have been required between the diets selected by the LH and HH sheep to equate the actual and expected values of energy retention (Table 5.8).

The wide fluctuations that occur during the year in the food supply for grazing sheep will result in short-term changes in body condition and these may be accentuated by

some management practices such as a move from yard feeding to pasture. These results suggest that such changes can be ignored when predicting the intake of pasture by mature grazing sheep but must be taken into account when predicting the efficiency with which dietary energy is retained. In experiments done under such conditions large errors could result from the use of feeding standards to predict the energy content of liveweight change in grazing sheep, or worse still, their intake of pasture from measurements of liveweight change, even if these are made after a 24h fast.

## Part 6

### General discussion and conclusions

The experiments described in this thesis have resolved a number of questions concerning the application of experimental findings to practical farm situations. Firstly, flock size within the range of 3 to 135 sheep has little or no effect on animal production, and secondly, in a rotational grazing system, movement of the animals as distinct from the possible effect of rotation on pasture growth, does not influence their production. The results also indicate that frequent disturbance of experimental animals as a result of rotational grazing management has no discernible effect on performance.

These findings represent a clarification of issues which had been poorly defined and existed mainly as a source of unease in the minds of experimental investigators. The absence of consistent effects is indeed fortunate, otherwise interpretation and extrapolation of data from animal experiments would be extremely hazardous. Most of the sheep used in this experiment were weaners of various breeds and sex and can be considered particularly sensitive to management compared to adult dry sheep. Hence the results are probably applicable to many classes of sheep.

The statistical analysis of the data has been

presented in considerable detail, as it could be useful in aiding the design and analysis of other experiments in grazing management. The area of land and number of animals available placed severe restrictions on the experimental design that could be used, and the likelihood of heterogeneity of variance in the different systems of management added a further complication. These restrictions precluded using standard methods of analysis and an alternative approach was used to derive appropriate error terms from an analysis of the components of variance. While the approach used in the analysis is novel, it does not contain any new statistical concept. Although the procedure is difficult to follow and the algebra is tedious, the alternative approach involving a fully replicated experiment, apart from absorbing resources beyond those available, would still involve the problem of heterogeneity of variance in the different systems of management.

The lack of precision in the current methods for measurement of intake of grazing sheep (Part 3) suggests that the problem remains a major source of error in the study of grazing systems. For many purposes, however, collection of oesophageal fistula samples and total faecal output may give estimates adequate for comparative studies in animal nutrition, even though these estimates may be biased. However, the lack of precision suggests that current methods of estimating the intake of grazing animals have little

value when attempting to estimate the growth of hard grazed pastures. Where feed is plentiful or where pastures are rotationally grazed, caging techniques are more appropriate, provided the period of grazing is short. On hard grazed pastures, the use of moveable cages to exclose areas of the pasture for varying intervals and calculating the regression of pasture growth rate against exclosure period offers most promise of getting true estimates of growth under grazing. The main difficulty is that as exclosure time is reduced the problems of measuring the increasingly small growth increments are substantially increased.

For the present, pasture growth must be represented in models by functions that are largely derived from data in cutting experiments. Although in his review on the growth of grazed pastures Davidson (1968) observed that the response of various pasture species in numerous cutting trials to the frequency and intensity of defoliation was not consistent, growth curves such as those obtained by Brougham (1956) appear to be broadly consistent with theory. Indeed Morley (1968b) examined numerous such curves in a computer analysis of the parameters which determine their shape and concluded that the response of pasture growth to grazing management was relatively stable without sharply defined conditions for optimum growth. Such analyses lend confidence to existing models of pasture growth and suggest that gross errors in model response are unlikely to arise

from this source.

The equations derived in Part 4 to predict the body composition of live sheep from their liveweight, tritiated water space and maturity appear to have general application, and indeed are at least as accurate as the "local" regressions derived from the individual sets of data where maturity is excluded as a predictor. Obviously more work is required to check whether the equations will apply to different breeds and species and to animals in different physiological states. More particularly there is a need to check that tritium equilibrates with foetal fluids in pregnant animals before they can be confidently used to examine energy changes in the reproductive animal. Further development is also required to examine the use of parameters other than maturity as an index of skeletal size. Of the numerous measurements that can be made in the live animal some composite measurement obtained perhaps by use of principal components analysis may be appropriate.

The efficiency with which food intake is converted to animal tissue is greatly influenced by the energy status of the animal (Part 5). Yet models of liveweight change in animal production systems have so far neglected this important aspect. Although much more work on this topic is required before energy storage in tissues following re-alimentation is understood, models are likely to be in

error when energy status of the animal is ignored. The

following approach may be a useful approximation. If adult animals are assumed to asymptote towards a standard body composition at a particular live weight, then the greater the degree of undernutrition the greater will be the imbalance in composition of subsequent liveweight gains, with proportionally more water. Thus liveweight will rise rapidly since the composition of the gains is energetically lower than the standard. Liveweight may then decline slightly while the composition equilibrates and fat replaces water.

The work illustrates the way in which simulation has affected the experimental approach to agricultural problems. Conventional analysis of experiments usually requires a more or less formal design, so that standard procedures such as analysis of variance can be readily applied and a precise statement made about treatment differences. However, systems analysis requires quantitative rather than descriptive statements of relationships between variables, and regression techniques may be more appropriate. For example, Axelsen et al (1972) examined the effect of calving time and stocking rate on production of beef cows over four years. They concluded that because seasonal conditions interacted with calving time, much larger resources than those available would be required to accurately estimate the management effects. Morley et al. (1976) re-examined this

data, to see whether the effect on fertility of the management controls applied to the various treatment groups would be related primarily to nutrition as indicated by liveweight parameters. They found that group average liveweight in relation to age and current nutritional status was strongly related to reproductive performance and derived equations to predict the probability of pregnancy for mature Angus cows from liveweight parameters. This result is not only of immediate practical use, but is expressed in a quantitative form that can be used directly in models.

The change in emphasis that is implied in the analysis of experiments similar to that above, suggests that the 150 stocking rate experiments referred to by Allden (1968) contain much data that would greatly increase the precision of models of management systems. While such a re-appraisal of results should have a high research priority, the relationships so obtained will generally be correlative and not causative, and other factors could distort them. In new research into grazing management problems, much more emphasis than in the past must be placed on consideration of the system as a whole rather than on isolated aspects. Attention must be directed to the determination of parameters dealing with basic biological relationships and hence to critical experiments designed for this purpose. Available knowledge must then be synthesized into generalized and consistent patterns.



Part 7

References

- Agricultural Research Council (1965). 'The Nutrient Requirements of Farm Livestock. No. 2, Ruminants.' (Agric. Res. Coun.: London.)
- Allden, W.G. (1962). Proc. Aust. Soc. Anim. Prod. 4, 163.
- Allden, W.G. (1968). Aust. Grassl. Congr. Proc. 2, 213.
- Allden, W.G. (1969). Aust. J. Agric. Res. 20, 499.
- Allden, W.G. (1970). Nutr. Abstr. Rev. 40, 1167.
- Arcus, P.L. (1963). Proc. N.Z. Soc. Anim. Prod. 23, 159.
- Arnold, G.W. (1960). Anim. Prod. 2, 169.
- Arnold, G.W. (1962). J. Br. Grassl. Soc. 17, 41.
- Arnold, G.W., and Dudzinski, M.L. (1963). J. Agric. Sci., Camb. 68, 33.
- Arnold, G.W., McManus, W.R., and Dudzinski, M.L. (1965). Aust. J. Br. Anim. Husb. 5, 396.
- Axelsen, A., Bennett, D., Larkham, P.A., and Coulton, L. (1972). Proc. Aust. Soc. Anim. Prod. 9, 165.
- Barnes, R.F. (1967). J. Anim. Sci. 26, 1120.
- Beauchamp, J.J., and Olson, J.S. (1973). Ecology 54, 1403.
- Bennett, D., Morley, F.H.W., Clark, K.W., and Dudzinski, M.L. (1970). Aust. J. Exp. Agric. Anim. Husb. 10, 694.
- Blaxter, K.L. (1964). Proc. Nutr. Soc. 23, 62.
- Blaxter, K.L., Graham, N. McC., and Wainman, F.W. (1956). Br. J. Nutr. 10, 69.
- Brisson, G.J. (1960). Proc. 8th Int. Grassl. Congr.

Readings, p 435.

Brody, S. (1945). Bioenergetics and Growth. (Hafner:New York).

Brougham, R.W. (1956). N.Z. J. Sci. Tech. Sect. A  
38, 78.

Chapman, R.E., and Wheeler, J.L. (1963). Aust. J. Sci. 26, 53.

Christian, K.R. (1972). J. Aust. Inst. Agric. Sci. 38, 14.

Christian, K.R., Jones, D.B., and Freer, M. (1970). J. Agric.  
Sci., Camb. 75, 213.

Corbett, J.L. (1960). Proc. 8th. Int. Grassl. Congr. 438.

Corbett, J.L., and Greenhalgh, J.F.D. (1960). In "Chemical  
Aspect of the Production and Use of Grass".  
pp 167-180. Ed. H.S. Rooke. London.

Cowlishaw, I.J. (1951). J. Br. Grassl. Soc. 6, 179.

Davidson, B. (1965). J. Aust. Inst. Agric. Sci. 31, 252.

Davidson, J.L. (1968). Proc. Aust. Grassl. Congr. 2, 125.

Doney, J.M., and Russell, A.J.F. (1968). J. Agric. Sci.  
Camb. 71, 343.

Donnelly, J.R., and Freer, M. (1974). Aust. J. Agric.  
Res. 25, 825.

Drew, K.R. (1966). Proc. N.Z. Soc. Anim. Prod. 26, 52.

Eisenhart, C. (1947). Biometrics 3, 1.

Elliott, N.M. (1966). Proc. Aust. Soc. Anim. Prod. 6, 177.

Farrell, D.J., Lang, R.A., and Corbett, J.L. (1972).  
Aust. J. Agric. Res. 23, 483.

Farrell, D.J., and Reardon, T.F. (1972). Aust. J. Agric.  
Res. 23, 511.

- Freer, M., Davidson, J.L., Armstrong, J.S., and Donnelly, J.R.  
(1970). Proc. 11th Int. Grassl. Congr., Surfers Paradise,  
913.
- Graham, N. McC. (1964). Aust. J. Agric. Res. 15, 969.
- Graham, N. McC. (1969). Aust. J. Agric. Res. 20, 375.
- Henderson, C.R. (1953). Biometrics 9, 226.
- Hogan, J.F., and Weston, R.H. (1968). Proc. Aust. Soc.  
Anim. Prod. 7, 364.
- Hughes, G.P., and Harker, K.W. (1950). J. Agric. Sci. 40, 403.
- Hutchinson, K.J. (1956). Proc. Aust. Soc. Anim.  
Prod. 1, 52.
- Hutchinson, K.J. (1958). Aust. J. Agric. Res. 9, 508.
- Hutchinson, K.J. (1971). Herb. Abstr. 41,1.
- Hutchinson, K.J., and Vickery, P.J. (1973). In "The Pastoral  
Industries of Australia." Eds. G. Alexander and O.B.  
Williams. Sydney University Press.
- Keenan, D.M. (1967). Ph.D. Thesis Univ. of N.S.W.
- Keenan D.M., McManus, W.R., and Freer, M. (1969). J.  
Agric. Sci., Camb. 72, 139.
- Kennedy, G.C. (1961). Proc. Nutr. Soc. 20, 58.
- Kobt, A.R., and Luckey, T.D. (1972). Nutr. Abstr.  
Rev. 42, 813.
- Lambourne, L.J. (1957). J. Agric. Sci. 48, 415.
- Lancashire, J.A., and Keogh, R.G. (1966). Proc. N.Z.  
Soc. Anim. Prod. 26, 22.
- Lancaster, R.J. (1947). Proc. N.Z. Soc. Anim. Prod. 7, 75.
- Lancaster, R.J. (1949). N.Z. J. Sci. Technol. Sect. A, 31.

- Lancaster, R.J. (1954). N.Z. J. Sci. Technol. Sect. A, 36.
- Langlands, J.P. (1966). Anim. Prod. 8, 253.
- Langlands, J.P. (1967a). Anim. Prod. 9, 167.
- Langlands, J.P. (1967b). Anim. Prod. 9, 325.
- Langlands, J.P. (1969). Anim. Prod. 11, 379.
- Leish, J.H., and Mulham, W.E. (1966). Aust. J. Exp. Agric. Anim. Husb. 6, 460.
- Lewis, L.D., and Phillips, R.W. (1972). Am. J. Physiol. 223, 74.
- McDonald, I.W. (1968). Nutr. Abstr. Rev. 38, 381.
- McIntyre, G.A., and Ward, M.M. (1970). CSIRO Aust. Div. Math. Stat. Manual No. 3.
- McKinney, G.T. (1974). Aust. J. Exp. Agric. Anim. Husb. 14, 726.
- McLaren, Anne and Michie, D. (1954). Nature. 173, 686.
- McManus, W.R., Arnold, G.W., and Hamilton, F.J. (1962). Aust. Vet. J. 38, 275.
- Mitchell, H.H. (1924). J. Biol. Chem. 58, 873.
- Morley, F.H.W. (1951). N.S.W. Dept. of Agric., Sci. Bull. No. 173.
- Morley, F.H.W. (1968a). Aust. J. Sci. 30, 405.
- Morley, F.H.W. (1968b). Aust. J. Exp. Agric. Anim. Husb. 8, 40.
- Morley, F.H.W. (1972). Proc. Aust. Soc. Anim. Prod. 9, 1.
- Morley, F.H.W., Axelsen, A., and Cunningham, R.B. (1976). Proc. Aust. Soc. Anim. Prod. 11, 201.

- Morley, F.H.W., Bennett, D., and McKinney, G. (1969). Aust. J. Exp. Agric. Anim. Husb. 9, 74.
- Morley, F.H.W., and Graham, G.Y. (1971). In "Systems Analysis in Agricultural Management", pp 212-236.
- Moulton, C.R. (1923). J. Biol. Chem. 57, 79.
- Paladines, O.L., Reid, J.T., Bensadoun, A., and Niekirk, B.D.H. Van (1964). J. Nutr. 82, 145.
- Panaretto, B.W. (1963). Aust. J. Agric. Res. 14, 944.
- Panaretto, B.W. (1968). Aust. J. Agric. Res. 19, 267.
- Raymond, W.F. (1954). J. Br. Grassl. Soc. 9, 61.
- Raymond, W.F., Kemp, C.D., Kemp, A.W., and Harris, C.E. (1954). J. Br. Grassl. Soc. 9, 69.
- Satterthwaite, F.E. (1946). Biometrics 2, 110.
- Schneider, B.H. (1935). J. Biol. Chem. 109, 249.
- Searle, T.W. (1970a). J. Agric. Sci. 74, 357.
- Searle, T.W. (1970b). J. Agric. Sci. 75, 497.
- Seebeck, R.M. (1968). Anim. Breed. Abstr. 36, 167.
- Smith, R.C.G., and Williams, W.A. (1973). J. Range Mgt. 26, 454.
- Snedecor, G.W. (1956). Statistical Methods. (Iowa State University Press : Ames, Iowa, U.S.A.)
- Southcott, W.H., Roe, R., and Turner, Helen Newton (1962). Aust. J. Agric. Res. 13, 880.
- Streeter, C.L. (1969). J. Anim. Sci. 29, 757.
- Suckling, F.E.T. (1956). Proc. N.Z. Soc. Anim. Prod. 16, 39.
- Suckling, F.E.T. (1962). Sheep Farming Annual 1962.
- Till, A.R., and Downes, A.M. (1962). Aust. J. Agric. Res. 13, 335.

- Tilley, J.M.A., and Terry, R.A. (1963). J. Br. Grassl. Soc. 18, 104.
- Tulloch, N.M. (1964). In "Carcass Composition and Appraisal of Meat Animals". Ed. D.E. Tribe (CSIRO Aust : Melbourne).
- Van Dyne, G.M., and Torell, D.T. (1964). J. Range Mgt. 17, 7.
- Vickery, P.J., and Hedges, D.A. (1972). Proc. Aust. Soc. Anim. Prod. 9, 16.
- Waite, R., MacDonald, W.B., and Holmes, W. (1951). J. Agric. Sci. 41, 163.
- Whitelaw, F.G. (1974). Proc. Nutr. Soc. 33, 163.
- Wiesert, R.G., and Evans, F.C. (1964). Ecology 45, 49.
- Willoughby, W.M. (1959). Aust. J. Agric. Res. 10, 248.
- Young, B.A., and Corbett, J.L. (1968). Proc. Aust. Soc. Anim. Prod. 7, 327.
- Young, B.A., and Corbett, J.L. (1972a). Aust. J. Agric. Res. 23, 57.
- Young, B.A. and Corbett, J.L. (1972b). Aust. J. Agric. Res. 23, 77.