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**Genetic control of lean tissue growth rate in sheep:
Genetic parameters and responses to selection**

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Doctor of Philosophy

at

Lincoln University

by

Shalaulani James Nşoso

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for Napong

Dedication

**In memory of Nsoso Dumuwa
father, mentor and a dear friend
1919 - 1996**

Abstract of a thesis submitted in partial fulfilment of the
requirements for the degree of Doctor of Philosophy

GENETIC CONTROL OF LEAN TISSUE GROWTH RATE IN SHEEP:

Genetic parameters and responses to selection

by

S.J. Nsoso

Performance data sets were available from lean tissue growth rate (LTGR) selection experiments for Border Leicester (n=1070), Coopworth (n=3720) and Dorset Down (n=1439) flocks as well as a Corriedale progeny test flock (n=1495). LTGR flocks had been selected for an aggregate breeding value (ABV) incorporating lean and fat weights with positive and negative economic weightings, respectively. The economic selection indices used comprised liveweight (LW), fat depth (FD) and muscle depth (MD) were:

- | | |
|--------------------------------|--------------|
| (a) $0.44LW - 0.58FD$ | 1986 - 1988 |
| (b) $0.25LW - 0.58FD + 0.48MD$ | 1989 - 1992. |

Parameter and response estimates for index component traits were derived from multivariate AIREML analyses, fitting an individual animal model. Responses in index component traits and greasy fleece weight were obtained by regression of BLUP breeding values on time. Responses of ABV component traits and a correlated response in bone were measured as differences between LTGR and control lines of the Dorset Down flock in 1995 only.

Performance in index component traits was significantly affected by birth rank, age of dam, year and age at measurement. The magnitude of these fixed effects varied between breed, sex and season, indicating that standardised corrections are not valid.

Index component traits and greasy fleece weight had medium (0.10-0.30) to high (0.31-0.70) heritability estimates but low (0.20-0.40) to moderate (0.40-0.60) genetic and phenotypic correlations. Differences observed in genetic parameters between breed, sex and season could not be attributed solely to season or genotype, due to confounding with management and time of the year.

LW increased in response to selection for all data sets (+0.095 to +0.489kg/year). Generally MD increased (+0.04 to +0.09 mm/year) although in one instance it decreased (-0.05 mm/year). Generally fat depth decreased (-0.001 to -0.10mm/year) although it appeared to increase slightly in one data set (+0.01mm/year). Greasy fleece weight increased (+7.58 to +17.01 g/year). Relative responses were

greatest in FD ($-1.23 \pm 1.26\%$ per year) and least in MD ($+0.20 \pm 0.19\%$ per year) with LW being intermediate ($+0.54 \pm 0.22\%$ per year). Correlated responses in greasy fleece weight were similar to those of LW in magnitude ($0.46 \pm 0.14\%$ per year). Response rates varied between traits, seasons, sexes and breeds, although most of the variation was small and insignificant. Generally, differences between data sets for responses in index component traits reflected differences in genetic parameter estimates.

Desirable responses were observed in ABV component traits (+72 and -40g/year for lean and fat weight, respectively) measured *in vivo* by X-ray computer assisted tomography in one year. There was a correlated response in bone weight (+30g/year). Responses exhibited by the sexes, differed significantly ($P < 0.05$), rams having a greater response in lean weight (+136 vs +9 g/year) and a lesser response in fat weight (-3 vs -78 g/year) than ewes. A correlated response in bone weight was significantly ($P < 0.05$) greater in rams than in ewes.

Key words: Lean tissue growth rate, liveweight, fat, muscle, lean, computer tomography, heritability, genetic correlation, selection index , response, sheep

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LIST OF ABBREVIATIONS

a) traits

ALW	autumn liveweight
AFD	autumn fat depth
AMD	autumn muscle depth
WLW	winter liveweight
WFD	winter fat depth
WMD	winter muscle depth
SLW	spring liveweight
SFD	spring fat depth
SMD	spring muscle depth
GFWT	greasy fleece weight, measured in winter for rams and spring for ewes
GFW	rams' greasy fleece weight measured in winter
GFS	ewes' greasy fleece weight measured in spring
LW	liveweight
FD	fat depth
MD	muscle depth
GR	total tissue depth between the surface and the rib bone at a point 11cm from midline of the last rib (Frazer, 1976; Kirton, Sinclair and Dobbie, 1978)
A	maximum width of <i>Longissimus</i> muscle at cut surface between thoracic and first lumbar vertebrae (Palsson, 1939)
B	maximum depth of <i>Longissimus</i> muscle at right angle to location A (Palsson, 1939)
C	fat depth at the point adjacent to measurement B (Palsson, 1939)
J	depth of thickest fat layer over the rib (Palsson, 1939)
S2	fat thickness on the shoulder after it has been removed by a cut between the fifth and sixth rib (Kirton, Clarke and Carter, 1967)

b) fixed effects

AGE	age at measurement in autumn, winter or spring
AOD	age of dam
BR	birth rank
RR	rearing rank

c) nomenclature for data sets

- (i) *season-trait analysis* refers to within sex, within breed across season analyses
- (ii) *sex-trait analysis* refers to within breed, within season across sexes analyses
- (iii) *breed-trait analysis* refers to within season, same sex, across breed comparisons
- (iv) *seasonXsex-trait analysis* refers to combined sexes within breed, within season analyses
- (v) *seasonXbreed-trait analysis* refers to combined sexes across breeds, within season comparisons
- (vi) *seasonXsexXbreed-trait analysis* refers combined sexes and breeds within season analysis

d) identity of data sets and subsets

BLE	Border Leicester ewe autumn data subset
BLR	Border Leicester ram winter data subset
DDE	Dorset Down ewe autumn data subset
DDR	Dorset Down ram winter data subset
CORE	Corriedale ewe winter data subset
CORR	Corriedale ram winter data subset
CPWE	Coopworth ewe spring data subset

e) parameters

V_A	additive genetic variance
V_E	environmental variance
r_G	genetic correlation
r_P	phenotypic correlation
h^2	heritability
r_{IAB}	correlation between index and aggregate breeding value
r_{IA}	correlation between index with either lean weight or fat weight
IAM	individual animal model

f) statistical methods

BLUP	best linear unbiased prediction
DFREML	Derivative free restricted maximum likelihood
AIREML	Average information restricted maximum likelihood
ML	Maximum likelihood
REML	Restricted maximum likelihood

g) units

kg	kilogram
mm	millimetre
g	gram
s	seconds
kV	kilovolts
mA	milliamperes

h) others

vs	versus
SD	selection differential
CPU	central processing unit
GLM	general linear model
LTGR	lean tissue growth rate
SYB	Simm, Young and Beatson (1987)
sem	standard error of the mean
sed	standard error of difference

CHAPTER 1

SELECTION FOR LEAN TISSUE GROWTH RATE IN SHEEP

1.0 Introduction

The broad aim of the present work was to critically look at breeding strategies for lean tissue growth rate in meat and dual purpose breeds of sheep under New Zealand intensive pastoral farming conditions.

1.1 Decline in lamb consumption

Decline in lamb consumption has been the major impetus leading to selection for changed body composition in sheep (Simm, 1986; Glimp and Snowden, 1989) to result in an ideal meat animal. An ideal meat animal is one which has a high ratio of muscle to bone and a high proportion of the most valuable joints, while possessing the ability to be within acceptable limits of fatness (Berg and Walters, 1983; Berg and Butterfield, 1985; Thorgeirsson and Thorsteinsson, 1989) at the most economic time of slaughter (Thorgeirsson and Thorsteinsson, 1989).

Circumstantial evidence (*i.e.* from surveys) has accumulated that consumers in developed countries prefer to purchase and consume meat with lower levels of fat than previously, mainly because of the possible association between high levels of dietary saturated animal fats and cardiovascular disease (Kempster, Cook and Grantley-Smith, 1986; Simm, 1987; Allen, 1990; Dransfield, Nute, Hogg and Walters 1990; Fisher, 1990; Wood, 1990). For example, in the United Kingdom, Kempster (1983) estimated that since 1945, consumption of lamb and mutton have fallen from near 12kg/person/year to about 7kg/person/year, and that it constitutes only 10% of total meat consumed, compared to 24% in the 1940s. Furthermore, Meat and Livestock Commission (1987) estimated a lower figure of lamb meat consumption per person per year for 1986 (4kg) than the early 1980s figure (7kg) of Kempster (1983). Australian figures show similar trends, though consumption is still relatively high; 24.4kg/person/year in 1971-72 falling to 16.6kg/person/year in 1980-81 (Thatcher and Couchman, 1983).

Other reasons for producing lean carcasses as opposed to those with excess fat are that in biological and economic terms lean carcasses are more efficient to produce (Glimp and Snowden, 1989; Cameron and Bracken, 1992) due to fat being a more energy intensive tissue.

1.2 Lamb production pattern in New Zealand

New Zealand lamb is produced from flocks fed pasture based diets with supplementation from hay, silage or crops. Animals are run outside all year round. Lambing is usually in spring (August - October)

with weaning in summer (November - December). Lambs are drafted for slaughter from weaning until prior to the emergence of their 2 permanent teeth (typically 12-14 months of age) when they are graded as hoggets and receive lower returns than lambs.

1.3 Description of lamb carcasses graded and proportion of lambs in each grade

The majority of lamb carcasses in New Zealand are for export markets. These carcasses are graded by weight and total tissue depth (GR), a measure of fat development (Kirton, 1989). The carcass that produces the greatest income has a heavy weight and a low GR measurement (Waldron, Clarke and Rae, 1991).

Over the years 1991-1993, between 22 and 27 million lambs were slaughtered annually. About 8-10% required trimming of excess fat before export, while 0.1-0.8% were below export minimum weight (9 kg). These received lower payment per kg than the 89-91% that fell into acceptable ranges for weight and fatness and which were able to be exported whole (New Zealand Meat Producers Board, 1992b & 1993b). In the 1992 and 1993 financial years the value of export lamb was 1 625 and 1 547 million New Zealand dollars respectively (New Zealand Meat Producers Board, 1992a & 1994). Increasing the proportion of lamb exported as carcasses would increase financial returns to different sectors of the meat industry. For example, the proportion of PM class (13.3 to 17.1 kg with over 7 mm and up to and including 12 mm GR) were 22 and 23% respectively in 1992 and 1993. Average premium price paid for a 14.5 kg PM compared to "all grades average" was NZ\$2.00 per head in 1992 (Anon, 1993). Using this premium payment, increasing the proportion of PM carcasses from 22 to 50% would increase earning for the industry by 13.7 million dollars. This figure relative to the gross of all carcasses is very small but indicates the magnitude of extra financial gains that are possible with carcasses required by consumers. In reality the premium may be more than NZ\$2.00 per head, given that different carcass classes receive different premiums (Anon, 1993).

1.4 National targets for carcass weight and fat

Targets for lamb carcasses envisaged by the New Zealand Meat Producers Board as possible for the medium term (time frame not specified) were 15 kg with less than 23% fat and with GR of 8mm (Frazer, 1983). The average lamb carcass weight at that time was 13.5 kg with 24% fat and 9mm GR (Frazer, 1983). Average lamb carcass weight in 1993 was 14.97 kg, an increase of 6.2% over the previous year with 51% of the carcasses classified as Y or lean (6-9mm GR) (New Zealand Meat Producers Board, 1994). For 1991 and 1992 the percentages of Y or lean carcasses were both 54% (New Zealand Meat Producers Board, 1992a). The recent average carcass weight target is 15.5kg by the year 2000 (New Zealand Meat Producers Board, 1993a). Targets of average carcass weight have

almost been achieved, however, more work is needed in improving the percentage of animals classified as lean. A further increase in carcass weight is desirable to reduce costs of killing and processing as it is cheaper per kg to kill and process heavier carcasses than lighter ones (Frazer, 1983; Glimp and Snowden, 1989). However, increasing carcass weight inevitably increases carcasses graded as overfat since carcass weight and fat weight are positively correlated (Kirton and Johnson, 1979; Waldron, Clarke, Rae, Kirton and Bennett, 1992a). Therefore, selection strategies aiming at increasing lean tissue growth rate have to work against this genetic antagonism between desirable changes in lean weight and undesirable changes in fat weight.

1.5 Increasing the proportion of lean carcasses

Management practices (*e.g.* nutritional manipulation, ceasing castration of ram lambs, slaughtering animals at lighter weights) and genetic means (*e.g.* breed substitution, within breed selection) can be used to increase the percentage of lean carcasses (Simm and Dingwall, 1989; Simm, 1992). Management practices are preferred over the short to medium term but they need to be repeated every year. Comparatively genetic improvement through within breed selection is permanent and cumulative. Thus it is to be preferred over the longer term (Simm, 1989; Simm and Dingwall, 1989).

Several alternative breeding objectives may be used to increase the percentage of carcasses classified as lean. One is to simultaneously hold lean weight at current levels while decreasing fat weight; alternatively, the aim may be to increase lean weight while holding fat weight; and thirdly increase lean weight while decreasing fat weight. The latest breeding objective is preferred because it increases efficiency of production (Glimp and Snowden, 1989; Cameron and Bracken, 1992). The most efficient way of realising the latest objective is through use of economic selection indices (Simm, 1986; Simm, Young and Beatson, 1987; Simm and Dingwall, 1989). Of concern to such an approach is that genetic and phenotypic parameters required for index construction are scarce in the literature. Furthermore, important factors such as sex and breed which have been shown to significantly influence genetic and phenotypic parameter estimates in other ruminants species *e.g.* beef cattle (Davis, 1993; Koots, Gibson, Smith and Wilton, 1994a; Koots, Gibson and Wilton, 1994b), have received either brief or scant attention in sheep. A few studies in sheep have shown that sex (*e.g.* Parratt, Nicoll and Alderton, 1989; Maria, Boldman and van Vleck, 1993) and breed (*e.g.* Brash, Fogarty, Gilmour and Luff, 1992) differences exist in genetic parameters for traits important in lean tissue growth rate such as liveweight and ultrasonic fat depth. However, more extensive work similar to that in beef cattle is required if improvement in lean tissue growth rate is to be more effective.

CHAPTER 2

A REVIEW OF LITERATURE

GENETIC CONTROL AND MANIPULATION OF LEAN TISSUE GROWTH AND BODY COMPOSITION

2.0 Introduction

Many studies have estimated responses to selection from single trait selection experiments in sheep and beef cattle (*e.g.* growth rate). Most of these experiments were summarised in the reviews of Barlow (1978 & 1984), Scholtz and Roux (1984), Clarke and Johnson (1993) and Nicoll and Morris (1993) who have reported desirable responses in beef cattle and sheep. However, selection using such an approach is often not adequate since other traits of economic importance are ignored leading to possible undesirable correlated responses *e.g.* increase in mature size of breeding animals. As emphasised in later sections of this Chapter, selection should take into account all important economic traits in order to maximise overall economic returns from a breeding enterprise.

The reviews of Davis (1993) and Koots *et al.* (1994a & b) have identified factors such as sex and breed in beef cattle as being important in causing differences between genetic and phenotypic parameters of traits of economic importance *e.g.* those of body composition, and as such likely to affect responses to selection. Relatively, there is less such information for sheep.

In order to understand and extend the current state of knowledge in the genetic control and manipulation of growth and body composition, this Chapter will describe and examine fundamental concepts in animal growth, genetic theory and experimental animal breeding in order to identify opportunities for research.

2.1 Growth and development

A major objective of modern meat production is to simultaneously enhance the deposition of lean tissue and decrease that of fat, to increase efficiency of production and to produce a product suitable for the demands of Western markets (Simm, 1987; Glimp and Snowden, 1989; Grant and Helferich, 1991; Cameron and Bracken, 1992). In order to accomplish this objective, an understanding of the biology of growth and development is necessary (Grant and Helferich, 1991).

In this thesis growth is defined as an increase in animal size (Hammond, Mason and Robinson, 1971; Johnson, 1977; Widdowson, 1980; Butterfield, 1988). This is to distinguish it from development, which is the change in shape and body proportions associated with growth (Butterfield, 1988). The distinction between growth and development is necessary because although the two processes are related and one is

the consequence of the other, they are measured in different units. Growth can be measured in units of weight *e.g.* as liveweight, fat weight or muscle weight or in linear dimensions *e.g.* length of carcass or width of bone whereas development is measured in indices of shape *e.g.* conformation, muscularity or proportions of weight. A contentious issue is that both in live animals and carcass studies, measures of growth and development are not precisely defined and are frequently used to mean different things by different authors (De Boer, Dumount, Pomeroy and Weniger, 1974; Young, 1989; Purchas, Davies and Abdullah, 1991; Waldron, *et al.*, 1992a; Waldron, Clarke, Rae and Woods, 1992b). All these publications provide working definitions for measures of growth and/or development but as stressed by De Boer *et al.* (1974) and Waldron *et al.* (1992b) specific universal definitions are desirable. Standard definitions for measures of growth in sheep carcass assessment are reported by Fisher and De Boer (1994) for The European Association for Animal Production. These authors point out that universal adoption of these definitions would enable ready comparison of carcass data and research results.

In this thesis carcass fat weight is defined as the sum of subcutaneous fat and intermuscular fat weights (Carroll and Coniffe, 1967; Butterfield, 1988) and muscle weight as the sum of muscle fibres and intramuscular fat weight (Carroll and Coniffe, 1967; De Boer *et al.*, 1974). This definition of muscle weight will also be used for lean weight. The definitions of fatness and muscularity are those of De Boer *et al.* (1974), which are; (i) fatness (fat covering) is the development of fat cover relative to dimensions of the skeleton (fat cover is interpreted to mean subcutaneous fat thickness) and (ii) muscularity is the thickness of muscle relative to linear dimensions of the skeleton.

Generally, as animals grow towards maturity, in absolute terms, body, carcass, bone, fat and muscle weights all increase. Comparatively, the development process is different. Relative to carcass weight, the proportion of fat weight (fatness) increases. In contrast proportions of muscle weight (leanness) and bone decrease. However, the proportion of muscle weight decreases less than that of bone (McClelland, Bonaiti and Taylor, 1976; Wood *et al.*, 1980; Butterfield, 1988). Success in enhancing lean tissue deposition while decreasing fat entails breeding from animals which are genetically superior for lean tissue deposition and inferior for fat deposition.

The objectives of efficient meat production are to increase lean meat deposition in the body and minimise deposition of fat at a defined point in the animal's life *e.g.* at weaning or in autumn or at all times. In addition to altering body composition, increases in carcass weight are also desirable because heavier carcasses reduce unit costs in slaughter, processing and marketing phases compared to smaller carcasses (Frazer, 1983; Glimp and Snowden, 1989; Bennett, 1990; Wood and Fisher, 1990; Harper and Buttery, 1992).

The definition of lean tissue growth rate which will be used in this thesis is that of Fowler, Bichard and Pease (1976) and of Kempster, Cuthbertson and Harrington (1982), which is the ratio of lean weight produced to days on performance test. This is a working definition which suffices in most practical situations. However, Fowler *et al.* (1976) drew attention to the drawback of this definition, which is lack of a sufficiently accurate *in vivo* method to predict lean at the start of test. Hence a fixed percentage of liveweight at the start of the test has to be assumed. This leads to residual effects of differences in starting composition included in the assessment of carcass composition at the conclusion of the test, but these would only be important if they were much less heritable than lean deposition during test (Fowler *et al.*, 1976). Non-genetic or environmental effects *e.g.* year, birth rank and age of dam are corrected for in such assessments.

Success in enhancing lean tissue deposition and reducing fat through breeding depends on the genetic parameters (heritability and the genetic correlations) of the traits under selection (Wolf, Smith, King and Nicholson, 1981; Hill and Meyer, 1988; Meyer, 1989a). Accurate estimates of the genetic parameters would lead to most rapid improvement (Land, 1985; Meyer, 1990; Webb and Bampton, 1990). Both overestimation and underestimation of these parameters would lead to breeding objectives which do not maximise economic returns (Sheridan, 1988).

2.2. Statistical methods of estimating genetic and phenotypic parameters

Over the last decade, statistical methods employed to estimate (co)variance components for continuous traits in most fields such as animal breeding and population biology have generally evolved from analysis of variance (ANOVA) and related types (*e.g.* General linear model (GLM)) to maximum likelihood (ML) and related methods (Shaw, 1987; Meyer and Hill, 1992). Increases in the power of computers and development of specialised algorithms have aided this evolution (Meyer, 1989a & b; Klassen and Smith, 1990).

In fields such as animal breeding, this evolution has come about because ANOVA and related methods are based on assumptions commonly violated in typical animal breeding data sets. Firstly, that data are balanced, that is with equal numbers of individuals in each subclass. Secondly, that data are a random sample from an unselected population. Thirdly, that the data structure conforms to certain standard or stereotype designs *e.g.* paternal half-sibs or parent(s)-offspring and therefore only one type of relatedness is exploited in the analysis (Shaw, 1987; Meyer, 1989a; Searle, 1989). However, typically animal breeding data are unbalanced, from selection experiments or livestock improvement schemes where animals are continuously culled for poor performance and animals are related in a variety of ways. Hence estimates from ANOVA and related types are biased and those of ML and related procedures are preferred (Shaw, 1987; Meyer, 1989a).

Interest in ML and related methods has risen because they are based on sufficient statistics, consistent, asymptotically normal and efficient (Harville, 1977; Kennedy, 1981). Furthermore, constraints on parameters are imposed in ML to exclude estimates out of bounds (Harville, 1977; Shaw, 1987; Searle, 1989; Meyer, 1990). However, out of bounds estimates serve to raise doubts about the validity of the model fitted (Shaw, 1987; Searle, 1989; Klassen and Smith, 1990).

Drawbacks of ML are that firstly, it is downwardly biased because the loss of degrees of freedom due to estimating fixed effects is not taken into account. This loss can be severe if the number of fixed effects are large in the model (Harville, 1977; Kennedy, 1981; Meyer, 1990). Secondly, ML may be further biased because data are required to be normally distributed (Shaw, 1987; Harville, 1977). However, Harville (1977) inferred without proof that ML and related methods may be appropriate even when the distribution of data is not specified. Proof that indeed in certain instances ML and related procedures are not biased by asymmetric distribution was furnished from the simulation works of Banks, Mao and Walter (1985) and Westfall (1987).

Bias in ML caused by failure to take account of the loss of degrees of freedom due to fitting fixed effects has been corrected for by the modified method called restricted maximum likelihood (REML) developed by Patterson and Thompson (1971). REML is equivalent to performing ML on data that has been standardised to have a mean of zero (Meyer, 1989a; James, 1991). This modification leads to estimates being identical to those of ANOVA if data are balanced and if out of bounds estimates are not excluded. REML shares all the desirable properties of ML (Shaw, 1987).

Use of ML and REML in animal breeding has brought about change in the random effects fitted in the infinitesimal additive genetic model (Henderson, 1988; Foulley, 1990). In traditional ANOVA and related methods, (co)variances are described in terms of random effects due to a single parent (*e.g.* sire model) or both parents (sire-dam model) uniquely partitioning total sum of squared deviations of the observation from the grand mean into sums of squares contributed by each factor in the design (Harville, 1977; Shaw, 1987). However, ML and REML allow the random effects of models to be expressed in terms of the genetic merit or breeding value of animals. These models are called Individual Animal Models (IAM) and incorporate information on relationships between all animals (Meyer, 1989a & b & 1991a). It is intuitively obvious that IAM is more correct in animal breeding data since it exploits all known relationships and can therefore account for changes in genetic variances due to both inbreeding and the established linkage disequilibrium (Kennedy and Sorensen, 1988; Henderson, 1990a). Furthermore, use of IAM allows fitting more random effects like maternal or dominance effects which are known to bias some genetic estimates (Barlow, 1978; Falconer, 1989; Meyer, 1989a; Webb and Bampton, 1990).

Both ML and REML are based on maximising the likelihood of error contrasts (Patterson and Thompson, 1971; Smith and Graser, 1986; James, 1991). Of note is that, similar to other methods, accuracy and precision of REML estimates increase with size of sample regardless of design and criterion for choosing estimates (Shaw, 1987). However, even with best method of analysis, variance components are only as good as the data on which they are based (Meyer, 1989a & 1990).

2.2.1 REML

REML is more difficult computationally than ML as it requires inversion of the portion corresponding to the random effects of the complete coefficient matrix including the fixed effects (Kennedy, 1981; Meyer, 1989a & 1993). Except for simple and balanced designs, REML estimates require the numerical solution of a constrained non-linear optimisation problem. Analytical solutions are impossible and iterative procedures must be used (Harville, 1977; Kennedy, 1981; Klassen and Smith, 1990; Meyer, 1993).

Iterative methods which use both first and second derivatives have been found to converge quickest (Meyer, 1989a & 1990; Klassen and Smith, 1990). However, these are difficult to calculate in highly unbalanced data typically found in animal breeding (Klassen and Smith, 1990). Therefore, it is more common to use numerical techniques *e.g.* simplex method or statistical approximations of either first or second derivatives *i.e.* quasi Newton-Raphson methods (Graser, Smith and Tier, 1987; Klassen and Smith, 1990).

2.2.1.1 Derivative free (DF) REML

The minimum or maximum of a function can be found without knowing its derivatives using numerical techniques called DF algorithms (Meyer, 1989a & 1990). The DF approach using the simplex procedure of Nelder and Mead (1965) has proven to be easy and robust (against starting values far from the estimate) to use in animal breeding data (Meyer, 1989b & 1991a). This procedure allows the simplex to rescale itself automatically in each iteration, changing shape and size according to the landscape of the surface searched. This adaptability is achieved by a combination of reflection, expansion and contraction (Meyer, 1990). Furthermore, it is highly flexible, accommodating a wide range of models of analysis, differing in random effects fitted and assumptions about covariances between them, of interest for analysis of animal breeding data (Meyer, 1989a & 1993).

2.2.1.2 Average information (AI) REML

Use of numerical approximations based on Expectation-Maximisation algorithms, which calculate expected second derivatives have proved to be highly computational demanding if not prohibitive and slow to converge, especially for traits of low heritability (Meyer, 1989a; 1990). However, recently

Johnson and Thompson (1995) developed univariate IAM using the average of observed and expected information. Sparse matrix techniques are employed to derive the coefficient matrix required to calculate the first derivatives of the likelihood. Second derivatives of the likelihood are calculated by averaging their observed and expected values. This leads to an algorithm called AI-REML which is a compromise between the Newton-Raphson and the Fisher scoring algorithms (Madsen, Jensen and Thompson, 1994; Johnson and Thompson, 1995). The development of AI-REML algorithms followed the observation that the average of observed and expected information matrices as second derivatives is considerably easier to compute than either of the components due to cancellation of some terms (Madsen *et al.*, 1994; Johnson and Thompson, 1995). AI-REML was extended to multivariate analyses by Madsen *et al.* (1994) and Johnson (pers. comm.). These extensions to multivariate algorithms were from similar mathematical backgrounds (Johnson, pers. comm.).

2.2.1.3 DF-REML vs AI-REML

Criticisms of the use of DF algorithms have been based on their slow convergence in multivariate analyses and poor numerical properties which has led to interest in other methods (Madsen *et al.*, 1994). Particular criticisms of the simplex procedure are that its performance becomes less successful as the dimension of search increases with an increase in the number of traits and random effects in the model (Meyer, 1989b & 1991a). For example, comparison of bivariate AI-REML and those based on DF-REML algorithms resulted in almost identical parameter estimates. However, AI-REML methods converged faster (341.2s CPU time) than DF-REML (1837.6s CPU time) on a CRAY C92A computer. For 3, 4 or 5 jointly analysed traits AI-REML converged in 13 rounds of likelihood evaluations or less but DF-REML analyses were not run due to constraints on CPU time (Madsen *et al.*, 1994; Johnson, pers. comm.). Furthermore, algorithms utilising the second derivative of the likelihood provide estimates of sampling variances of parameters as a by-product. In contrast, for DF based algorithms, additional computational effort is required to estimate sampling errors which can be quite considerable if the number of parameters estimated are many (Meyer and Hill, 1992). In conclusion, AI-REML algorithms are currently more efficient in utilising computer time and resources than those based on DF multivariate analyses of 2 or more traits with one random effect. However, for univariate analyses DF-REML performs similarly to AI-REML. Despite savings in computing time and resources multivariate IAM AI-REML are at an early stage of development compared to DF-REML methods of Meyer (1989a) as described by Misztal (1994). Further work is needed in developing AI-REML to the current standard of DF-REML if AI-REML is to be a worthwhile competitor.

2.2.2 Comparing parameter estimates from ANOVA and related types to those from REML

Few comparisons have been reported of parameter estimates based on REML fitting an IAM and traditional sire models based on ANOVA and its related types. Generally, the results have shown that there are no differences in the parameter estimates from the two methods of estimation (*e.g.* Young,

1989; the review of Koots *et al.* 1994a; Conington, Bishop, Waterhouse and Simm, 1995). The studies of Young (1989) and Conington *et al.* (1995) are based on selection experiments spanning approximately two generations with most selection being on sires and little on ewes, which may explain their failure to demonstrate superiority of individual animal models over sire models. The review of Koots *et al.* (1994a) may have been based on either experiments of animals which did not have extensive pedigree data or from selection experiments spanning only a few years, or both, hence their failure to find differences between ANOVA and ML based methods. A further likely explanation of this discrepancy, is that if there is no effective selection in an experiment, there will be no reduction in genetic variance, hence genetic parameter estimates will not be affected by method of analysis (Koots *et al.*, 1994a). In conclusion, despite lack of demonstration of the superiority of IAM REML from early stages of selection experiments, their superior mathematical properties appeal in analysing long term selection experiments with extensive pedigree data.

2.3 Breeding value estimation

In order to make rapid genetic progress in performance through selection for traits of economic importance in farm animals, selected animals must be chosen for their superior breeding values (the genetic worth of individuals as parents) (Dalton, 1985; Bichard, 1988; Dempfle, 1988; Falconer, 1989; Nicholas, 1993). There are many sources of information which can provide clues to an individual's breeding value. These include individual performance, family performance and, combined performances of individual and family weighted appropriately (Dalton, 1985; Falconer, 1989; Nicholas, 1993) after correction for known environmental effects. Conditions under which the use of these different sources of information are appropriate are well documented in the literature (*e.g.* Falconer, 1989; Nicholas, 1993). A point worth highlighting is that when heritability is low combining individual and family performances appropriately weighted provides maximum response to selection (Falconer, 1989). This is because the estimated breeding value of an individual from different relationships is more accurate than a single estimate from the individual alone (Falconer, 1989; Nicholas, 1993).

Traditionally, when there is no selection and mating is at random, breeding values are estimated as individual or progeny deviation from contemporary performance within an environment (Dalton, 1985; Falconer, 1989; Wills, 1991; Nicholas, 1993) after adjusting for most identifiable environmental sources such as birth rank, rearing rank, age of dam and age. In contrast, when selection has occurred and/or animals are compared across environments or assortatively mated, estimates of breeding values from this traditional method would be biased due to the ignoring of relationships between animals which accumulates with selection. In this situation Best Linear Unbiased Prediction (BLUP) (Kennedy, 1981; Falconer, 1989; Nicholas, 1993) developed by Henderson (1949 & 1973) is the better method (Henderson, 1973; 1980; Kennedy, 1981; Falconer, 1989; Nicholas, 1993) particularly when the more recent IAM is employed for analyses. Under BLUP the model of analysis takes into account the fixed

effects (*e.g.* years, herds, age) and relatedness between animals, therefore providing less biased estimates of breeding values (Falconer, 1989; Henderson, 1973; 1990b; Nicholas, 1993). Thus in animal breeding where animals are selected or culled on performance, employing BLUP to estimate breeding values results in less biased estimates than using other methods. Although BLUP was developed in 1949 its wide application has only become possible in the last 10 to 15 years due to increases in computing speed (Hill and Meyer, 1988; Henderson, 1990a) and the discovery of a rapid method of inverting the coefficient matrix (Henderson, 1990a).

2.4 Selection theory

The economic value of farm animals generally depends on more than one trait. Hence to maximise economic value of animals, selection has to be applied to more than one trait at a time (Hazel and Lush, 1942; Hazel, 1943; Bichard, 1988; Falconer, 1989). Following the decision to select for many characters simultaneously, the important question to answer is, “how should selection be applied to the characters to achieve maximum economic value?” Falconer (1989). The method(s) of choice should be efficient, that is, result in maximum genetic improvement per unit time and per unit effort expended (Hazel and Lush, 1942).

2.4.1 Selection methods

Although many traits can influence the economic value of farm animals, they do so to varying degrees (Hazel, 1943). In addition, all traits do not have the same heritability, while phenotypic and genetic relationships between traits vary (Warwick and Legates, 1979). The most appropriate method(s) of selection such as selection index and multivariate BLUP take these into account. The selection index is the most efficient method for simultaneous selection of several traits (Hazel and Lush, 1942; Hazel, 1942; Warwick and Legates, 1979; Falconer, 1989) in a single environment where there is no selection or assortative mating (Henderson, 1973; 1980; 1984 & 1990b). However, when selection has occurred and/or animals are compared across environments or assortatively mated, selection index is no longer the method of choice because it would provide biased breeding values. In this situation BLUP is the preferred method (see section 2.3).

2.4.2 Measuring responses to selection

A paramount feature of sheep selection experiments is that sheep are exposed to environmental influences which vary widely, with corresponding effects on performance (Hill, 1972d; McGuirk, Atkins and Thompson, 1986; Falconer, 1989). Therefore, any attempt to measure responses to selection must account for yearly fluctuations, as well as long-term environmental changes (McGuirk *et al.*, 1986; Falconer, 1989). The most common way of eliminating environmental effects is to keep an

unselected control population (Hill, 1972a; b; c & d; McGuirk *et al.*, 1986; Falconer, 1989). The implicit assumption is that major environmental influences affect the selected and control populations alike and the phenotypic difference between the two populations is an estimate of the genetic improvement made by selection (Falconer, 1989). Further advantages of this method are that a single control population can be used for more than one selected line and that control flocks provide information on genetic variances and covariances without the complicating effects of selection (McGuirk *et al.*, 1986). The use of a control line has an added advantage in terms of selling the research to non-scientists (*e.g.* extension officers and farmers).

The use of a control population does not always improve the precision with which the response is estimated because of random genetic drift and sampling errors (Falconer, 1989). In addition, the use of a control population utilises extra resources (McGuirk *et al.*, 1986) which normally reduces the population size of the selected line due to limited facilities (Falconer, 1989). If the selected line and the control line both have half the population number of a single selected line, then the use of control quadruples the sampling variance of the response measured as a deviation from the control, and so doubles the standard error (Falconer, 1989). This loss in accuracy may counterbalance the gain from eliminating environmental influences (Falconer, 1989).

Loss in accuracy of selection response due to genetic drift can be minimised by dividing control flocks into families and using rams with index scores closest to their family mean (Simm, Dingwall, Murphy and Brown, 1990a). Another strategy to increase the relative accuracy of the response measured by the use of a control is selection in the opposite direction, in a two-way or divergent selection (Hill, 1972a & c; Falconer, 1989). However, divergent selection may not be desirable in selection to improve economic merits of farm animals since the interest is to increase production and hence value of produce. Due to the inherent problems in the use of control populations, the use of frozen semen and embryos to provide an occasional measure of response in future seems attractive (Hill, 1972c & d; McGuirk *et al.*, 1986). However, this method may be risky due to accidents rendering stored genetic material useless.

2.5 Selection for lean tissue growth rate

In the short term, consumer-acceptable ways farmers could respond to increases in financial incentives for lean meat or penalties for fat are by slaughtering animals at lighter weights, ceasing castration of males and manipulating the quality or quantity of feeding (Simm and Dingwall, 1989; Simm, 1992). Several of these short-term non-genetic measures have disadvantages; for example, reducing the slaughter weight of animals may lead to lower output per unit of land or capital, and altering feed quality and quantity may be impractical in extensive production systems (Simm, 1992). Furthermore, the time when feed is manipulated is critical since intermuscular fat, the fat depot which affects carcass

value the most, is early maturing (Wood, MacFie, Pomeroy and Twinn, 1980; Berg and Walters, 1983; Kadim, Purchas, Rae and Barton, 1988; Harrington and Kempster, 1989). Comparatively, genetic improvement is relatively slow but it provides permanent and cost-effective improvement in carcass composition (Simm and Dingwall, 1989). Thus genetic improvement, either alone or in combination with some of the measures outlined above, is an attractive option for affecting long-term, permanent improvement in carcass composition (Simm *et al.*, 1987; Simm and Dingwall, 1989; Simm, 1992). The quickest route to genetic improvement can be through breed substitution where better genotypes exist.

2.5.1 Selection between breeds

Genetic variation in body composition between breeds can be due to differences in degree of maturity, appetite and partitioning of metabolites between tissues. After adjusting for differences in degree of maturity, remaining genetic variation is probably small, perhaps less than 10% (Wood, 1982). Therefore, when selecting an appropriate breed, these intrinsic genetic differences have to be taken into account.

Choosing an appropriate genotype to be used in a breeding enterprise involves comparing genotypes when they are equal age, weight, level of fatness (Wolf and Smith, 1983; Rae, 1984) or maturity (Wolf and Smith, 1983; Taylor, 1985), or over defined ranges of these variables (Wolf and Smith, 1983).

The concept of comparison at equal degree of maturity is theoretically elegant but practically limited because mature size is not known for individual farm animals. Mature size of farm animals is hard to measure, since animals destined for slaughter are killed before they reach maturity and breeding animals rarely reach mature weight because of nutritional and other environmental factors (McClelland *et al.*, 1976; Butterfield, Griffiths, Thompson, Zamora and James, 1983). A working definition of mature weight coined by Taylor (1985) is the body weight of a normally grown, skeletally mature, normally active adult animal maintained in a state of body weight equilibrium on a standardised diet, in a thermo-neutral, disease free environment with, or adjusted to, a chemical body fat of 20% or less for feral mammalian species. The conditions specified in this definition are unlikely to be controlled in many practical situations, therefore mature weight would be imprecisely defined. To circumvent this problem, workers may define a simple definition of maturity in line with the practicalities of each particular situation (Taylor, 1985; Butterfield, 1988) such as a standardised growth state *e.g.* equal estimated carcass subcutaneous fat proportion of Kempster, Croston, Guy and Jones (1987). This has been the case in most studies (McClelland *et al.*, 1976; Butterfield *et al.*, 1983; Croston, Kempster, Guy and Jones, 1987; Kempster *et al.*, 1987; Thonney, Taylor and McClelland, 1987). The important thing is that criteria adopted as measures of maturity should be reported (McClelland *et al.*, 1976; Taylor, 1985; Butterfield, 1988).

The concept of comparison at equal maturity was formalised by Taylor (1985) into two genetic size scaling rules. These rules provide the conceptual framework for comparison at the species level but whether they can be validly applied to within breed or strain studies requires confirmation. Results to date are ambivalent (Taylor, 1987). In the absence of conclusive results on mature liveweight of farm animals, comparisons of animals have to be on the basis of “guessed” mature weights (*e.g.* McClelland *et al.*, 1976; Butterfield *et al.*, 1983; Thonney *et al.*, 1987) or a standardised growth state. For example, Kempster *et al.* (1987) and Croston *et al.* (1987) compared 10 sheep sire breeds at the same estimated carcass subcutaneous fat proportion. The rationale behind comparison at a constant external fat cover is that animals with the same estimated carcass subcutaneous fat proportion are at the same degree of maturity (Kempster *et al.*, 1987; Croston *et al.*, 1987) which is true when animals differ in frame size.

Comparisons of most modern breeds at a given age or weight have shown that there are differences in fat weight but not lean weight. However, differences in fat weight disappeared when comparison was at a common degree of maturity (McClelland *et al.*, 1976). Comparison at a constant estimated carcass subcutaneous fat proportion also showed that there was no variation in lean proportion in most traditional breeds (Kempster *et al.*, 1987). Breed variants that do exist in all these comparisons are either of no economic importance at present (Young, 1989) *e.g.* the exceptionally lean Soay is very small (McClelland *et al.*, 1976) or their benefits may be offset by disadvantages *e.g.* the lean Texel has a slow growth rate hence takes longer to reach acceptable slaughter fat levels (Kempster *et al.*, 1987; Glimp and Snowden, 1989). In conclusion therefore, selection between breeds probably offers very little scope to improve lean tissue growth rate under the present farming systems.

2.5.2 Selection within breed

Butterfield *et al.* (1983) compared carcass composition of small and large size Merinos at the same age, weight and equal maturity. Comparison at the same age and weight resulted in the small size Merinos having a higher proportion of fat than the large Merinos with no difference in lean proportion. However, comparison at equal maturity (mature size defined as mean weight when weekly liveweight gain were minimal and where muscle plus bone weight had ceased to increase) reversed the previous ranking in carcass fat proportion, the large Merinos had higher proportion of fat than the small strain, but the lean proportion were still not different. Furthermore, the maturing patterns of tissues were similar. This probably is further evidence that genetic size scaling rules need to be fully tested within species, breed and strains before they can be universally adopted as pointed out by Taylor (1985 & 1987). In conclusion, there appears to be variation within breed although the results are only based on one experiment. This warrants further investigation using more meat breeds and may provide the genetic diversity required to improve lean tissue growth rate.

2.5.3 Selection objectives

As defined previously, the selection objective is to simultaneously increase lean weight and decrease fat weight. This objective is particularly suitable for terminal sires where the main goal is to improve carcass composition with little emphasis on reproduction and other traits of economic importance (Cameron and Bracken, 1992). However, even in terminal sires, improvement in production of lean meat concerns several aspects of production including survival, liveweight growth, carcass shape and palatability. Thus selection for lean tissue can not be considered in isolation from other traits (Kempster *et al.*, 1982; Wolf and Smith, 1983; McEwan, Dodds, Davis, Fennessy and Hisson, 1991).

2.5.4 Selection criteria

In sheep farming where production is usually linked to seasonal pasture growth, the main objective is to maximise production in a given time interval. For this, and operational reasons, selection of breeding animals will often be made at a fixed time. There are many possible selection criteria, (i) single trait (*e.g.* growth rate), (ii) single ratio trait (*e.g.* estimated carcass lean proportion) (Simm, 1986; Simm *et al.*, 1987), (iii) biological index (*e.g.* estimated lean tissue growth rate) and (iv) economic selection indices (*e.g.* for lean tissue growth rate) (Fowler *et al.*, 1976; Simm, 1986).

With the exception of major genes, selection using single trait criteria does not maximise economic returns because undesirable correlated responses are possible in other traits of economic importance. Barlow (1978 & 1984) and Scholtz & Roux (1984) concluded that selection using growth rate as the selection criterion results in increased fatness at, or after, the age of selection due to increased feed intake. Scholtz and Roux (1984) also concluded that selection for growth rate decreased viability and reproductive fitness. A more appropriate strategy is to use index selection to minimise undesirable correlated responses. Index selection can either be through the use of a biological index (Fowler *et al.*, 1976) or an economic index (Simm, 1986; Simm *et al.*, 1987).

The biological index approach of Fowler *et al.* (1976) is based on the concept of biological efficiency of production (*e.g.* of lean tissue growth rate and lean tissue conversion). A biological index attempts to define in terms of physiological concepts the nature of the changes (*e.g.* genetic or technical characters) which are desirable to improve overall value of a meat producing animal (Fowler *et al.*, 1976).

Biological indices were formulated because of inherent deficiencies in the derivation of traditional economic indices. The derivation of economic selection indices requires estimates of phenotypic and genetic parameters for traits in the selection criteria and the aggregate breeding value, and estimates of relative economic values of traits in the aggregate breeding value (Simm, 1986; Simm *et al.*, 1987;

Simm and Dingwall, 1989). Genetic and phenotypic parameters may vary with breed or strain and with conditions of testing (Simm, 1986; Simm *et al.*, 1987) and are expensive or difficult to obtain (Simm and Dingwall, 1989). Relative economic values of traits in the aggregate breeding value may not remain stable (Hazel, 1943), are expensive or difficult to obtain (Simm and Dingwall, 1989) and can be derived from different viewpoints with corresponding different outcomes *e.g.* individual breeder, investor or government (Moav, 1973; Simm *et al.*, 1987).

Biological indices do not require estimation of phenotypic and genetic parameters or of relative economic values (Fowler *et al.*, 1976; Simm, 1986). However, biological indices have implied economic values which are uncontrolled and may be far from the true value. Most importantly, the most variable component trait (*e.g.* growth rate in ruminants) dominates the index. Hence they may not maximise economic returns from a breeding enterprise (Simm, 1986, Simm, 1992). Theoretically, economic selection indices for lean meat production use all genetic and phenotypic parameters and relative economic values to optimally weight different measurements in the selection criteria (such as liveweight and *in vivo* measurements) to maximise response in overall economic merit (Simm, 1986; Simm *et al.*, 1987; Simm and Dingwall, 1989).

Traditionally, there have been problems assigning economic values to lean and fat weight in sheep and beef cattle because carcass payments do not always reflect carcass composition (Kempster *et al.*, 1982; Kirton, 1989). Most carcass payment schemes in sheep are based on weight and eye appraisal *e.g.* for conformation and/or fatness (Kempster *et al.*, 1982; Kirton, 1989; Kempster, 1990). Furthermore, other factors such as commercial procurement strategies and international marketing affect meat prices and premiums for fatness which further “blur” the economic signals used to predict such relative economic values. The popularity of economic selection indices in lean tissue growth rate studies in sheep breeding have been revived by solutions to the inherent problems involved in derivation of relative economic values for lean and fat weights which have been formulated by among others Simm *et al.* (1987) and more recently by Waldron *et al.* (1991). These authors have explicitly defined the selection objectives as simultaneously increasing lean weight and decreasing fat weight. Following this, they then set the economic value of fat weight to negative (-1) and estimated that of lean weight from market signal data. This has only been possible in meat markets like New Zealand where carcass payments reflect composition. However even in markets where carcass payments do not reflect composition, setting the economic value of the trait to be reduced to negative one and giving a positive economic value to the trait to be increased has been shown theoretically to result in desirable economic responses (Simm and Dingwall, 1989; Clarke and Rae, 1991; Clarke, Waldron and Rae, 1991) although not optimal. Furthermore, early experimental results show that such indices result in reduction in fat depth and increase in muscle depth (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). In conclusion economic selection indices which aim to maximise overall economic returns are the most appropriate to improve lean tissue growth rate.

2.5.5 Measuring body composition *in vivo* to aid in selection

Accurate estimation of carcass composition in live sheep is important if selection for lean tissue growth rate is to be effective. Traditional carcass evaluation techniques involving slaughter and dissection can not be employed to measure carcass composition of potential breeding animals and it is not economic to slaughter and dissect their relatives (Sehested, 1986; Sehested and Vangen, 1989). Hence there is much interest in methods for estimating carcass composition *in vivo* (Sehested, 1986; Sehested and Vangen, 1989; Simm, 1992).

2.5.5.1 Subjective techniques

Only non-invasive *in vivo* techniques will be considered here because they are publicly acceptable and do not compromise the welfare of animals. Subjective or visual assessments *e.g.* conformation and condition scoring are generally of poor accuracy as indicated by their low coefficient of determination (relationship between predictors and predicted variable) *e.g.* in cattle (0.14-0.33) (Glodek, 1984). Visual assessments are also highly dependent on operator skill. Hence, in the long term, selection for lean tissue growth rate based on these is unlikely to be effective (Alliston, 1983; Glimp and Snowden, 1989). However, visual assessments appear attractive since they are cheap and easy to apply (Alliston, 1983).

2.5.5.2 Objective techniques

Compared to subjective techniques, objective techniques are more accurate as indicated by higher coefficient of determinations *e.g.* ultrasound devices (0.31-0.53 in cattle and 0.22-0.90 in pigs) (Glodek, 1984). There are many objective *in vivo* techniques employed for measuring body composition in human medicine. However, only ultrasound devices are commonly used in animal studies. In applied animal breeding, some of the factors that lead to slow uptake of these *in vivo* techniques are practicability (constraints associated with use of particular technique *e.g.* speed, ability to resist harsh environment), portability, cost, public acceptability, precision and accuracy (Alliston, 1983; Kempster, 1984 & 1989) and physical requirements such as space, services needed and level of skill required for successful operation (Allen, 1990).

In the balance of this review the term *in vivo* techniques will be used to refer to objective techniques.

2.5.5.2.1 Ultrasound *in vivo* measurements

Ultrasound devices are widely used because they are easy to operate, free from hazard at exposure level, portable and relatively inexpensive (Busk, 1984; Wells, 1984). Most, if not all ultrasound devices

measure linear dimensions or areas of predictors of carcass composition (Berg and Butterfield, 1976). Lean weight predictors measured are area, width and depth of muscles and those of fat weight are depths of subcutaneous fat. In addition, to measurements *in vivo*, overall size especially liveweight is measured simply and cheaply. Failure to account for variation in carcass composition due to liveweight differences can lead to overestimation of the value of *in vivo* techniques particularly if tested on a population of animals varying widely in liveweight and carcass composition (Simm, 1987). When using liveweight measurements, gutfill can have an appreciable effect in ruminants particularly if weighing is prolonged and animals have been grazing highly digestible pasture. Therefore, "starved" weights (*e.g.* 24 hours removal off feed) are to be preferred (Woolaston, 1984; Simm, 1987).

The use of ultrasound devices in their present form to measure *in vivo* body composition may not be appropriate for at least five reasons.

Firstly, ultrasound measurements are either linear or 2-dimensional but the entities to be predicted are 3-dimensional (Groeneveld, Kallweit, Henning and Pfau, 1984). Therefore, entities may either be over or underestimated, possibly because distribution/conformation effects mean a predictor changes relatively more or relatively less than the predicted entity. Hence *in vivo* measuring devices which measure 3-dimensional entities may be preferred.

Secondly, ultrasound measurements of subcutaneous fat depth in sheep have given less precise predictions of carcass composition than that achieved in pigs and in cattle (Berg and Walters, 1983; Simm, 1989). This is probably partly due to dependence of pulse-echo ultrasonic techniques on the amount of subcutaneous fat in the body. A lower proportion of total carcass fat in sheep and cattle is in the subcutaneous depot compared with pigs (Berg and Walters, 1983; Kempster *et al.*, 1986; Simm, 1989). Estimates of these fat proportions quoted by Kempster *et al.* (1986) are 0.12 in sheep and 0.08 in cattle compared to 0.16 in pigs. In addition to the lower proportion of subcutaneous fat, sheep are smaller in absolute terms, so total depth of subcutaneous fat is shallower (Simm, 1989). Measurement error will be proportionately greater in sheep than cattle or pigs.

Thirdly, measurement of subcutaneous fat in live animals may not provide a sufficiently accurate indication of total amount of fat available in the body if there is substantial between animal variation in the ratio of subcutaneous fat to other depots (Kempster, 1984). To avoid such bias, *in vivo* techniques should measure carcass lean weight directly (Kempster, 1984 & 1986). Therefore, more accurate *in vivo* techniques have to be sought (Skjervold, Gronseth, Vangen and Evensen, 1981).

Fourthly, although there are positive and moderately high (>0.40) genetic correlations between

subcutaneous fat depot and other fat depots (Wolf *et al.*, 1981; Waldron *et al.*, 1992a), there is experimental evidence that correlated responses in other depots may be undesirable. For example, Kadim *et al.* (1988) studied two lines of sheep selected for high and low subcutaneous fat depth. They found that the benefits of reduction in subcutaneous weight depot in the low line (2.40 kg) compared to the high line (2.52 kg) was offset by a change in fat partitioning which led to an increase in weight of intermuscular fat in the low line (1.91 kg) compared to the high line (1.78 kg). Both lines had the same average carcass weight.

Lastly, subcutaneous fat depot in ruminants is of less importance because of its lower proportion in the carcass compared to intermuscular fat (Kempster *et al.*, 1986; Simm *et al.*, 1987). Estimates of intermuscular fat proportions are 0.11 in sheep and 0.13 in cattle compared to 0.05 in pigs (Kempster *et al.*, 1986). Compared to subcutaneous and internal fat, not only is intermuscular fat difficult to measured particularly with ultrasound devices, but it is also expensive to remove from the carcasses without mutilation (Kadim *et al.*, 1988; Harrington and Kempster, 1989; Simm, 1989). Therefore, selection using *in vivo* techniques which measure all fat depots is expected to lead to greater progress in response to selection for lean tissue growth rate (Parratt and Simm, 1987; Simm, 1989).

2.5.5.2.2 More advanced *in vivo* imaging technologies

Techniques such as computer tomography (CT) and nuclear magnetic resonance imaging (NMR) have had limited use in animal research to date (*e.g.* in assessing body composition) with little commercial application (Glodek, 1984; Kempster, 1989). The relative precision of these techniques have not been compared under standardised conditions, hence their relative accuracy is hard to quantify, because different studies have used animals varying greatly in weight, breed, age and carcass composition. Furthermore, operators of different skills are involved and carcass traits or indicators vary between trials (Kempster, 1984). Despite this, the technologically more advanced of these methods *e.g.* CT and NMR should permit extra response to selection to be achieved (Simm, *et al.*, 1987) since they have extremely high resolution and good tissue discrimination (Wells, 1984).

Comparatively, the more accurate and precise *in vivo* techniques (*e.g.* CT and NMR) are more expensive and less mobile than ultrasound devices (Simm, 1987 & 1989). These may be cost-effective if the higher running costs were widely spread such as in centralised breeding schemes or where superior genotypes are widely used *e.g.* through artificial insemination (Allen, 1990). Their potential also lies in applications in research or second stage selection following mass screening with cheaper techniques like ultrasound (Simm, 1987 & 1989). These techniques allow multi-dimensional appraisals of the body (Busk, 1984).

NMR has greater potential than CT since it differentiates between soft tissues better (Wells, 1984 ; Groeneveld *et al.*, 1984). It should allow assessment of meat quality when it is manifested as changes in proportion of chemical composition in muscle (*e.g.* in pigs Groeneveld *et al.*, 1984). More accurate and precise assessments of carcass composition would make it possible and efficient to terminate costly progeny test stations and use the money and facilities to increase the capacity of performance stations (Standal, 1984), which would lead to greater genetic progress in selecting for lean tissue growth rate.

2.5.6 Estimates of genetic and phenotypic parameters for carcass composition traits

The few studies which have estimated genetic and phenotypic parameters for lean and fat weight traits have concluded that, when characterised as weight or percentages they have moderate to high heritability estimates (0.2-0.40) (Wolf *et al.*, 1981; Waldron *et al.*, 1992a) with very low (-0.20 to 0.20) to low (0.20-0.40) correlations (genetic and phenotypic) (Waldron *et al.*, 1992a). Due to the few parameter estimates reported, conclusions as to whether differences in parameter estimates are true or due to factors such as, sampling errors, size of data set, methods of estimation and nutrition which vary between experiments are hard to reach. Nevertheless, medium to high heritability and low genetic correlations indicate that improvement of these traits through selection is possible.

2.5.6.1 Estimates of genetic and phenotypic parameters for liveweight, fat and muscle depths

Tables 2.1 and 2.2 show moderate to high heritability estimates and Tables 2.1 and 2.3 show very low to moderately high genetic correlations and predominantly moderate phenotypic correlation estimates from lean tissue growth rate and body composition experiments using *in vivo* ultrasound measurements. Similar but more extensive tables were compiled by Young (1989) and Fogarty (1995) for growth and body composition traits. Young (1989) concluded that parameter estimates were clearly variable, in part reflecting different statistical methods of analyses (*e.g.* offspring-parent regression or sib-correlation), high sampling errors (experiments vary in size) and environmental influences (*e.g.* nutrition and maternal effects). These conclusions of Young (1989) are applicable to results summarised in Tables 2.1, 2.2 and 2.3 except environmental influences like maternal and nutritional effects would be negligible for indoor *ad libitum* fed sheep where experiments were designed to minimise these (see Table 2.1, Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). Another important influence on genetic parameter estimates is the effect of selection over time.

Selection is known to alter genetic variances and covariances between individuals (Robertson, 1977; Henderson, 1980; Kennedy, 1981; Henderson, 1986 & 1988; Kennedy and Sorensen, 1988), therefore biasing estimates of genetic parameters. Hence the effects of selection should be taken into account when estimating genetic parameters.

As shown in Tables 2.1-2.3 the magnitude of genetic and phenotypic parameter estimates varied in the different studies. However, due to the large sampling errors of these parameters relative to parameter estimates, no conclusions could be drawn. The study of Brash *et al.* (1992) which studied parameter estimates of body composition traits for five sheep breeds (Border Leicester, Suffolk, Corriedale, Coopworth and Gormark) also found that genetic parameter estimates were variable and no firm conclusions could be reached due to large standard error relative to parameter estimates. The difference in parameter estimates could indicate real differences. The studies of Young (1989), Cameron and Bracken (1992) and Bishop (1993) were conducted with one breed and one sex (rams) only. Factors such as breed and sex have been identified as significantly affecting parameter estimates in beef cattle by the reviews of Davis (1993) and Koots *et al.* (1994 a & b). The effect of such factors on genetic and phenotypic parameter estimates could be important in designing effective breeding programmes in sheep.

2.5.7 Responses to selection

Due to the many selection criteria used in lean tissue growth rate studies in sheep, predicted responses based on indirect selection including ultrasonic measurements have generally varied depending on the strategy adopted (Simm *et al.*, 1987; Simm and Dingwall, 1989; Clarke and Rae, 1991). This variation in predicted responses should be mirrored in realised responses.

Realised responses from divergent selection studies based on ultrasonic measured backfat adjusted for liveweight to reduce (low line) or enhance (high line) fatness in different sheep breeds have generally resulted in significant differences in subcutaneous fat measures between the low and high lines *e.g.* Coopworth (Fennessy, Greer and Bass, 1982; Fennessy, Bain, Greer and Johnstone, 1992), Southdown and Suffolk (Bennett, Meyer and Kirton, 1988) and Southdown (Kadim, Purchas, Rae and Barton, 1989). The reported classical subcutaneous fat C measurement of Palsson (1939) and other subcutaneous fat measures *e.g.* GR and S2 and kidney fat weight have been reduced in low fat lines compared to high fat lines with no changes in liveweight.

Most of these studies did not report changes in muscle measurements which are important as indicators of leanness. Kadim *et al.* (1989) reported that compared to the low fat line, high fat line sheep had significantly lighter weights of muscle and bone and also more dissectible fat. These studies have shown that indicators of body composition can be favourably manipulated by selection for ultrasonic measured backfat depth on the live animal. However, the objective best suited to biologically and economically efficient meat production is simultaneous increasing lean weight and decreasing fat weight.

Only a few selection experiments with the objective of increasing lean tissue growth rate in sheep have

been reported in the literature. In general, selection on an economic index comprising liveweight, ultrasonic muscle and fat depths in Suffolk breed (Young, 1989) or estimated lean based on liveweight and fat depth in Texel-Oxford breed (Cameron and Bracken, 1992) or estimated lean based on liveweight and fat depth in Scottish Blackface breed (Bishop, 1993) led to increases in muscle depth (an indicator of lean weight) and reduction in fat depth (an indicator of fat weight) per year. These early realised responses support theoretical predictions, although the realised responses were smaller in magnitude than predicted. However, none of these experiments measured direct responses to selection in lean and fat weight.

Lower realised than predicted responses may reflect the way the economic indices were constructed. Most of the genetic and phenotypic parameters were taken from the literature or unpublished estimates or were assumed (Simm *et al.*, 1987; Simm and Dingwall, 1989; Cameron and Bracken, 1992). The studies of Young (1989), Cameron & Bracken (1992) and Bishop (1993) estimated genetic and phenotypic parameters differing in magnitude to those used in their index construction. For example, in constructing their selection index, Cameron and Bracken (1992) assumed a genetic correlation of 0.15 between liveweight and the selection index based on the work of Wolf *et al.* (1981). However, analysis of their data resulted in an estimate of 0.67. This probably highlights the problems that can occur using genetic parameters from different breeds or strains or different testing conditions as described by Simm *et al.* (1987).

Lower realised than predicted responses to selection could also be an effect of lower selection intensity and longer generation interval. The above experiments selected sires within family instead of mass selection to reduce overall rates of inbreeding (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). This lowers selection differential and ultimately response to selection (Falconer, 1989). A further possible reason to explain the lower realised responses may be that genetic parameters for lean and fat weight and their indicator traits may differ between breeds and, if this is the case, then using assumed genetic parameters which are different from those of the population they are applied to would reduce responses to selection. Such a hypothesis could be addressed by estimating genetic and phenotypic parameters and responses to selection in lean and fat weight directly for each population.

2.5.8 Correlated responses

In most selection experiments to improve lean tissue growth rate, correlated responses in important traits such as mature liveweight, fertility, prolificacy, meat quality and wool production have not been reported. While these are less important for terminal sires, they are critical for dual purpose sheep where emphasis is placed on other traits in addition to lean tissue growth rate (Wolf and Smith, 1983).

An increase in mature liveweight of breeding ewes would further lower the already low efficiency of lamb production compared to pig and beef production (Large, 1970; Webster, 1989). The ideal situation would be to decrease fat weight in the carcass without altering adult ewe size (Webster, 1989) or shifting fat deposition from carcass to non-carcass depots (Kempster *et al.*, 1982; Glimp and Snowden, 1989), where it affects carcass value less. Shifting fat deposition from carcass to internal depots would be ideal for ewes which mobilise this energy store during periods when energy from pasture intake fails to meet requirements.

Although results from selection for reduced fatness in pigs are conflicting, there is evidence that ultra-lean meat (about 10mm backfat thickness at P2 position, 65mm from the dorsal mid-line at the last rib) has undesirable properties (such as toughness) due to low levels of intramuscular (marbling) fat which affect eating quality (Wood and Fisher, 1990; Wood and Warris, 1992). Toughness has not yet been found in sheep meat from experimental flocks but continuously monitoring for this is required, as it would seriously affect selection objectives.

McEwan *et al.* (1991) reported low or zero genetic correlations between ultrasonic fat depths and ewe hogget fleece weight in three wool breeds (Coopworth, Romney and Perendale) selected for increased ovulation rate. Based on these findings they concluded that reducing fat content in dual purpose breeds may have little effect on wool production. Since wool is economically important in New Zealand and Australian farming, more research is needed to validate these results in these and other sheep breeds.

2.6 Opportunities for research

There has been considerable research on the genetic control of growth in sheep, but relatively less on body composition and lean tissue growth rate. Furthermore, there is no information on responses to selection in aggregate breeding value traits or to what extent variation in genetic and phenotypic parameters and responses to selection estimates are due to differences between sexes and breeds. There is also relatively little information on correlated responses to selection for lean tissue growth rate.

Table 2.1: Heritability, genetic and phenotypic parameter estimates (standard errors in brackets) of traits of economic importance in lean tissue growth rate experiments - LW140 and LW150, liveweights at 140 and 150 days respectively, FD140 and FD150, ultrasonic fat depths at 140 and 150 days respectively and, MD140 and MD150, ultrasonic muscle depths at 140 and 150 days respectively for rams fed high energy and high protein diets (indoors). Heritability estimates are along diagonal (bold), phenotypic correlations above diagonal and genetic correlations below diagonal.

	LW150*	FD150*	MD150*	LW140 ⁺	FD140 ⁺	MD140 ⁺	LW140 [#]	FD140 [#]	MD140 [#]
LW150*	0.26 (0.10)	0.40 (0.05)	0.43 (0.04)	-	-	-	-	-	-
FD150*	0.02 (0.23)	0.55 (0.11)	0.26 (0.05)	-	-	-	-	-	-
MD150*	0.61 (0.20)	0.19 (0.21)	0.29 (0.11)	-	-	-	-	-	-
LW140 ⁺	-	-	-	0.20 (0.13)	0.35 (0.06)	0.50 (0.05)	-	-	-
FD140 ⁺	-	-	-	-0.58 (0.49)	0.35 (0.14)	0.25 (0.06)	-	-	-
MD140 ⁺	-	-	-	0.07 (0.36)	-0.12 (0.30)	0.43 (0.14)	-	-	-
LW140 [#]	-	-	-	-	-	-	0.23 (0.12)	0.45	0.52
FD140 [#]	-	-	-	-	-	-	0.13 (0.32)	0.39 (0.13)	0.38
MD140 [#]	-	-	-	-	-	-	0.41 (0.27)	0.41 (0.24)	0.36 (0.14)

* - estimates from Young (1989)

+ - estimates from Cameron and Bracken (1992)

- estimates from Bishop (1993)

Table 2.2 Weighted[‡] literature heritability means (\pm standard errors in brackets)(adapted from Fogarty, 1995). The number (n) of estimates in brackets.

Breed [#]	Trait ^a					
	PWWT	YWT	HWT	GFWT	UFD	UMD
Dual	0.26 \pm 0.09 (n=42)	0.33 \pm 0.12 (n=26)	0.31 \pm 0.17 (n=17)	0.36 \pm 0.14 (n=29)	-	-
Meat	0.28 \pm 0.09 (n=15)	0.22 \pm 0.14 (n=6)	0.25 \pm 0.10 (n=5)	0.19 \pm 0.12 (n=3)	-	-
All	-	-	-	-	0.28 \pm 0.13 (n=30)	0.24 \pm 0.19 (n=16)

dual (dual purpose), all (dual and meat)

[‡] - by inverse of the variance derived from standard error of estimate

a PWWT (post weaning weight), YWT (yearling weight), HWT (hogget weight), GFWT (greasy fleece weight), UFD (ultrasonic fat depth) and UMD (ultrasonic muscle depth).

Table 2.3 Weighted^a literature mean phenotypic (above diagonal) and genetic (below diagonal) correlations (\pm standard error) (adapted from Fogarty, 1995). The number (n) of estimates in brackets.

	PWWT	YWT	HWT	GFWT	UFD	UMD
PWWT	-	0.78 \pm 0.04 (n=4)	0.69 \pm 0.09 (n=5)	0.43 \pm 0.09 (n=7)	0.50 \pm 0.06 (n=13)	0.53 \pm 0.07 (n=9)
YWT	0.89 \pm 0.10 (n=4)	-	0.74 \pm 0.12 (n=4)	0.38 \pm 0.08 (0.08)	0.51 \pm 0.10 (n=10)	0.60 \pm 0.13 (n=3)
HWT	0.89 \pm 0.03 (n=5)	0.97 \pm 0.03 (n=4)	-	0.37 \pm 0.10 (n=21)	0.47 \pm 0.04 (n=8)	0.49 \pm 0.06 (n=2)
GFWT	0.50 \pm 0.25 (n=7)	0.28 \pm 0.12 (n=7)	0.21 \pm 0.17 (n=22)	-	0.15 \pm 0.02 (n=3)	0.19 \pm 0.06 (n=1)
UFD	0.46 \pm 0.23 (n=13)	0.42 \pm 0.17 (n=9)	0.44 \pm 0.17 (n=8)	-0.08 \pm 0.27 (n=3)	-	0.37 \pm 0.12 (n=18)
UMD	0.51 \pm 0.12 (n=9)	0.46 \pm 0.09 (n=3)	0.44 \pm 0.04 (n=2)	-0.06 \pm 0.39 (n=1)	0.33 \pm 0.25 (n=18)	-

‡ - by inverse of the variance derived from standard error of estimate

a PWWT (post weaning weight), YWT (yearling weight), HWT (hogget weight), GFWT (greasy fleece weight), UFD (ultrasonic fat depth) and UMD (ultrasonic muscle depth).

CHAPTER 3

DATA AND ANALYTICAL APPROACHES

3.0 Objectives

The objectives of this study were:

1. to examine whether the effects of environmental factors on lean tissue growth rate traits were consistent between seasons, sexes and breeds,
2. to estimate genetic and phenotypic parameters associated with lean tissue growth rate traits and their variability, to verify whether they are universally applicable across seasons, sexes and breeds,
3. to evaluate lean tissue growth rate indices for different genotypes to determine whether they are generally applicable across seasons, sexes and breeds,
4. to assess responses to selection for lean tissue growth rate to validate the selection approach;
 - (a) *in vivo* for aggregate breeding value traits (lean and fat weights),
 - (b) *in vivo* for index component traits (liveweight, fat depth and muscle depth)
 - (c) for correlated responses in greasy fleece weight and bone weight.

Responses to selection and genetic and phenotypic parameters for lean and fat weight were intended to be measured *in vivo* using an X-ray computer assisted tomography (CT) scanner. The CT scanner became operational only towards the end of the present work. Therefore, the genetic control and the responses to selection in bone, muscle and fat weights *in vivo* could not be measured in all animals. Only the 1994 born Dorset Down animals were CT scanned (Chapter 8).

3.1 Data source

Four data sets from Lincoln University's sheep breeding programmes were used. The first three data sets were for three genotypes (Border Leicester, Coopworth and Dorset Down) comprising five lines. The lines were established during the 1986 autumn mating and flocks subsequently closed except the Coopworth flock which was closed in 1988. The lines were:

- (i) Dorset Down - one control line and one line selected for lean tissue growth rate
- (ii) Border Leicester - one line selected for lean tissue growth rate
- (iii) Coopworth - one control line and one line selected for lean tissue growth rate

Data from these 5 lines were collected from 1984 to 1992 inclusive. These data sets were used to evaluate parts 1 to 3 and 4(b) and 4(c) of the objectives (see 3.0). Animals were run at pasture under similar management in a similar environment.

The fourth data set was from the Lincoln University Corriedale progeny test for the years 1989 to 1992 inclusive and was used to evaluate parts 1 to 3 of the objectives.

3.2 Establishment of the lines in different genotypes

For all genotypes of this study ewe flocks were existing at Lincoln university prior to data collection for lean tissue growth rate traits.

3.2.1 Border Leicester

For several years prior to 1986 rams were either leased or borrowed from ram breeders, the aims being for the flock to be representative of the New Zealand Border Leicester breed, to have genetic diversity to allow for rapid selection and so that results obtained from any future studies would be applicable and of benefit to the farming industry as a whole.

At the 1986 autumn mating, selection for lean tissue growth rate began with 150 ewes and 6 2-Tooth sires born at Lincoln University and the flock was closed. Subsequently, similar ewe numbers were kept each year until 1989. At the 1990 autumn mating the ewe flock was reduced from 150 to 120 ewes for management reasons.

3.2.2 Coopworth

For the 1984 and 1985 matings, 10 sires were either leased or bought from 5 stud breeders and 10 were from the Lincoln University flock *i.e.* 20 industry and 20 Lincoln sires were used during this period. The dual aims were to make the flock representative of the New Zealand Coopworth breed and to compare progeny performance of industry and Lincoln University sires.

Formation of the lines began at the 1986 autumn mating using sires born in 1984. That year (1986) 20 sires were mated to 980 ewes and each sire was represented in all lines subsequently set up. The ewes were randomly allocated according to age, sire, production index and mating weight to four lines, with 42, 23, 23 and 12% of the ewes allocated to production index, lean tissue growth rate, clean fleece weight and control lines respectively. The age structure of ewes in each line was similar. Subsequently, all progeny were born into their allocated line.

At the 1987 autumn mating 20 sires (born in 1985) were mated to approximately 1000 ewes which were reallocated to lines (same proportions as in 1986) and again all progeny were born into their allocated line. In the 1988 autumn mating (sires born in 1986), sires were selected from rams born into each line. The numbers of sires used in each line were as follows: 6 for clean fleece weight, 6 for lean tissue growth rate, 8 for production index and 6 for control. Thirty percent (30%) of 2-tooth (2-T) ewes were selected as replacements from within the line they were born into. Mixed age ewes born prior to establishment of the lines were reallocated among lines as in 1986 and 1987.

At the 1989 autumn mating 20 sires (born in 1987) were selected within each line, with the same number of sires per line as in 1988 being used. Two-T and 4-T ewes were also selected within line but 6-T and older ewes were reallocated to lines as in previous years. For the 1990 to 1992 autumn matings, 5 sires per line were used except for the production index line, where eight sires were used. The sires were born within line. All ewes were also born within line except those born in 1985 or earlier. These older ewes were reallocated to lines each year until they were culled or cast for age. The reallocation of ewes each year was done to make lines similar and also to create strong genetic links between the lines.

3.2.3 Dorset Down

Prior to 1986, industry and Lincoln sires were used to broaden the genetic base and make the flock representative of the New Zealand Dorset Down breed for similar reasons as in Border Leicesters. Two identical flocks were established and closed in 1986. One flock of 100 ewes was nominated as the control line and the other of 150 ewes was nominated for selection for lean tissue growth rate. Ewes and rams were randomly allocated to the two lines and then the rams were selected within line.

The Dorset Down control line also serves as the control line for the Border Leicester selected line. The Dorset Down and Border Leicester selected lines were established at the same time, and have the same: (i) breeding objectives, (ii) selection criteria, (iii) mating design and (iv) are run together. For these reasons, it was considered valid to have the selected Dorset Down and Border Leicester lines controlled by one line.

3.2.4 Corriedale

The Corriedale progeny test was run from 1989 to 1992 inclusive, with twelve industry and two Lincoln rams being progeny tested over Lincoln University Corriedale ewes each year. Rams were selected from individual farms for superiority in greasy fleece weight and/or liveweight. Each ram was mated to 25 ewes to produce at least 30 progeny. The Corriedale flock was not selected for lean tissue growth rate.

3.3 Description of data sets

Annual distributions of progeny per sire, birth rank, rearing rank, the number of ram and ewe lambs performance tested and age of dam for all data sets are presented in Appendix A.

In this Chapter means are presented with their standard deviations (*e.g* 17.8±8.3).

Between 53 and 128 sires were used in the breeds. The average number of progeny per sire ranged between 17.8±8.3 and 29.2±18.2. Average age of dam ranged between 3.5±1.3 and 3.9±1.4, giving weighted generation intervals of between 2.74 and 2.93 years (Table 3.1).

Ewes were predominantly performance tested for index component traits in autumn for all breeds except Coopworth and Corriedale ewes which were performance tested in spring and winter respectively. Generally, rams were tested in winter with few autumn observations (Table 3.2).

Most animals were born and reared as singles or twins, with very few born and reared as triplets in Border Leicester, Dorset Down and Corriedale. Comparatively, in Coopworth most animals were born as singles, twins or triplets with a few quadruplets. Rearing rank was not recorded for animals born between 1984 and 1987 inclusive in Coopworth. The Coopworth breed had highest proportion of multiple births (90%) and Dorset Down the least (65%), with Border Leicester (77%) and Corriedale (74%) being intermediate (Table 3.3).

Most of the dams were aged between 2 and 7 years in all breeds. Only in Coopworth and Dorset Down breeds were there dams aged 8 years or older (Table 3.4).

Table 3.1: Total number of sires (NOS), average progeny number (AVP) (±standard deviation), average age of dam (AOD) (±standard deviation) and weighted generation interval (GI) for animals performance tested from 1984 to 1992 for Border Leicester (BL), Coopworth (CPW), Dorset Down (DD) and 1989 to 1992 for Corriedale (COR) flocks[#].

Variable	Breed			
	BL	CPW	DD	COR
NOS	59	128	98	53
AVP	22.6±10.0	29.2±18.2	17.8±8.3	28.2±5.9
AOD (year)	3.5±1.3	3.6±1.5	3.8±1.5	3.9±1.4
GI (year)	2.74	2.81	2.88	2.93

[#] - combined sexes data

Table 3.2: Number of rams and ewes in autumn (TOTA) and winter (TOTW), average age in autumn (AGEA) and winter (AGEW) (standard deviation in brackets) for animals performance tested from 1984 to 1992 for Border Leicester (BL), Coopworth(CPW), Dorset Down (DD) and 1989 to 1992 for Corriedale (COR) flocks.

Variable	Breed							
	BL		CPW		DD		COR	
	Rams	Ewes	Rams	Ewes [#]	Rams	Ewes	Rams	Ewes
TOTA [†]	394	647	1183	1407	514	923	-	-
AGEA (d)	214.2 (20.2)	224.6 (21.1)	227.3 (7.0)	228.9 (7.5)	254.2 (16.1)	258.2 (14.0)	-	-
TOTW [†]	608	462	1711	2024	820	607	722	773
AGEW (d)	321.9 (17.0)	316.4 (16.2)	318.0 (11.0)	392.6 (16.5)	347.2 (16.1)	337.1 (13.5)	331.1 (11.0)	358.0 (22.1)

- ewes performance tested in spring not winter

†- number of observations for largest data set (see Appendix B).

Table 3.3: Total frequency of birth and rearing rank for sexes combined for animals performance tested from 1984 to 1992 for Border Leicester (BL), Coopworth(CPW), Dorset Down (DD) and 1989 to 1992 for Corriedale (COR) flocks[†].

Breed	Birth rank				Rearing rank			
	Single	Twin	Triplet	Quad [#]	Single	Twin	Triplet	Quad [#]
BL	309	889	136	-	413	840	81	-
CPW	381	2527	840	31	-	-	-	-
DD	608	1107	27	-	762	966	15	-
COR	389	1045	61	-	474	982	39	-

- quadruplets

†- number of observations for largest data set (see Appendix B).

Table 3.4: Total frequency of age of dam (AOD) for sexes combined for animals performance tested from 1984 to 1992 for Border Leicester (BL), Coopworth(CPW), Dorset Down (DD) and 1989 to 1992 Corriedale (COR) flocks[†].

Breed	TOTAL FREQUENCY OF AOD								
	2	3	4	5	6	7	8	9	10
BL	366	382	301	181	91	13	-	-	-
CPW	1066	936	758	529	280	124	35	13	-
DD	407	434	390	277	165	62	6	1	1
COR	325	332	338	287	155	58	-	-	-

†- number of observations for largest data set (see Appendix B).

3.4 Mating design and general management

Ewes in all lines were single-sire mated for 2-cycles (42 days) in individual paddocks. Ewes were randomly allocated to sires on the basis of age, sire and mating weight. In order to reduce inbreeding sires were not mated to their dams or full-sisters or half-sisters. From the end of mating ewes within breed were run together. Dorset Down, Border Leicester and Corriedale flocks were all run at the Lincoln Sheep Breeding Unit with Dorset Down and Border Leicester ewe flocks run together except at

mating. The Coopworth flock has been run at three different farms; Lyndhurst (mid Canterbury), Lincoln and Orton Bradley Park on Banks Peninsula.

Lambing was in spring (August to October). Lambs were born outside and run at pasture with their dams until weaning in summer (November) at approximately 10 weeks of age. Newborn lambs were tagged either in the morning or evening within 12 hours of birth. After weaning ewe and ram lambs were run separately at pasture. Standard husbandry procedures were performed on all lambs *e.g.* tailing, drenching for internal parasites, vaccination against diseases such as pulpy kidney, tetanus and blackleg.

3.5 Details of selection

3.5.1 Indirect selection for lean tissue growth rate

The breeding objectives (to increase lean weight and simultaneously decrease fat weight), aggregate breeding value and selection criterion for the lean tissue growth rate lines were those of Simm *et al.* (1987). Due to current technology not being able to assess lean and fat weight directly, a decision was made to practice indirect selection. Two indices were used for selection, and are described below.

For 1986, 1987 and 1988 matings, animals were selected on the reduced index of Simm *et al.* (1987), comprising liveweight (LW) and ultrasonic fat depth (FD) (index 1 below). Selection in 1988 for the 1989 and subsequent matings was based on the full index of Simm *et al.* (1987), comprising liveweight (LW), muscle (MD) and fat (FD) depths; index 2 below. Therefore, animals born in 1989 and later were the progeny of rams selected on index 2. Index component traits were standardised deviations corrected for age at measurement and birth rank only within year.

1986 - 1988: 0.44LW - 0.58FD (index 1)

1989 onwards: $0.25LW - 0.58FD + 0.48MD$ (index 2)

Index 1 was used initially because muscle depth could not be measured accurately with the AIDD model 3 ultrasound machine (developed by the Auckland Industrial Development Division of DSIR) in use at the time. Inclusion of MD became possible with procurement of a real time B-mode ultrasound scanner fitted with a UST-58101-5 probe operating at 5-MHz (Aloka SSD-210 DXII, Aloka Co. Ltd., Japan).

Fat and muscle depths were measured over the 12th rib. Muscle depth measurement was the classical B measurement and fat depth was measured over the eye-muscle but in a more lateral position than the C measurement of Palsson (1939) as described by Young and Deaker (1994) (Figure 3.1 on page 43). These positions were chosen because they were readily identified and easily measured (*e.g* Bishop,

1993). Other lean tissue studies in sheep have measured the same or adjacent sites *e.g.* Young (1989), Cameron & Bracken (1992) and Bishop (1993).

For both indices, rams selected for breeding in the lean tissue growth rate lines were those with the highest index ranking within sire line (sire family). Different selection strategies were employed in the control lines. Rams in the Dorset Down control line were chosen such that the average lean tissue growth index was zero and the standard deviation the same as the unselected population. While Coopworth control line rams were selected such that their average production index was zero with a similar standard deviation to the Coopworth production index line. Control line rams were also selected within sire family.

The Coopworth production index line was selected on a weighted aggregate breeding value incorporating number of lambs born, weaning weight, greasy fleece weight and hogget liveweight. All index components were weighted by the relative economic values of the Coopworth Sheep Society of New Zealand. These are 500c/lamb, 25c/kg, 100c/kg and zero for number of lambs born, weaning weight, greasy fleece weight and hogget liveweight respectively. The relative economic value of greasy fleece weight has been changed over the breeding span of this programme. From 1986 to 1990, the relative economic value was 95c/kg which was changed to 200c/kg in 1990 and the current figure is 100c/kg. Hogget liveweight is weighted by zero because the index aims to improve overall production without increasing ewe size which would lower the already low efficiency of lamb production (Large, 1970).

Only one Coopworth control line could be kept due to limited resources. Since the production index line encompassed the aims of the other two lines, a control line was deemed to be more useful if based on this line. The strategy employed in selecting the Coopworth control line ensures that there is no directional change in the production index hence it should be a suitable control line for the other two lines as well. Whatever the genetic correlations between the different selection objectives are, if there is no change in the production index then there should be no change in the other traits as well.

Six two-tooth rams were used from 1986 to 1989 but this number was reduced to 5 in 1990 due to external factors necessitating a reduction in size of the ewe flock. It was considered more desirable to reduce the number of sire families than the size of each sire family in order to minimise rate of inbreeding.

All breeding rams were selected on winter measurements because earlier work at Lincoln University has shown that heritability and predicted responses in fat depth are higher in winter than autumn or spring (Beatson, 1987). In all lines only rams without physical defects were used.

All ewes were performance tested annually. Approximately 50% of ewe hoggets tested in the lean tissue growth rate lines were selected on the basis of high index values and kept as replacements. Ewes in control lines were selected using the same criteria as control line rams (see above). Similar proportions (25-30% per year) of ewes are replaced in selected and control lines. Mixed age ewes are culled for age or poor reproductive performance.

Culling of surplus ewe hoggets soon after the autumn measurement is necessary to provide flexibility in management and allow higher levels of feeding for retained ewe and ram hoggets under test in Border Leicester and Dorset Down flocks. Thus seldom were winter measurements made on ewe hoggets.

3.5.2 Ewe selection in Corriedale flock

The ewes were selected on a production index based on an aggregate breeding value incorporating, number of lambs born, weaning weight, greasy fleece weight and winter liveweight. All index components were weighted by the relative economic values of the Corriedale Sheep Society of New Zealand. These are 500c/lamb, 25c/kg, 150c/kg and 0 for number of lambs born, weaning weight, greasy fleece weight and hogget liveweight respectively. Hogget liveweight was given zero weighting for similar reasons as in the Coopworth production index line. Each year 45% of ewe hoggets were kept as replacements and they constituted 30% of the ewe flock.

3.6 Statistical analyses

Data sets (Appendix B) were tested for normality based on kurtosis and skewness statistics as described by Snedecor and Cockran (1980). No major departures from normality were observed.

3.6.1 Model components

Prior to final analyses, development of analytical approach (Appendix C) was undertaken for two reasons. Firstly, examination of the results from exploratory analyses revealed deficiencies in analytical methods available at that time *i.e* statistical methods had to be sourced that would: (i) allow fitting of appropriate models (ii) allow multivariate analyses (iii) produce suitable sampling errors in estimation. Secondly, the data sets were not specifically collected to address the objectives of this study. Young (1989) encountered problems estimating genetic and phenotypic parameters from data collected for a different purpose. Least squares of Harvey (1985) did not produce useful results and REMLPK of Meyer (pers. comm) either did not converge or crashed trying to estimate negative square root (Young, 1989). The developmental process aimed to identify if such problems would be encountered in this study.

Prior to estimating genetic and phenotypic parameters, and responses to selection, significant ($P < 0.10$) fixed effects and covariables to be included in individual animal model restricted maximum likelihood analyses were determined using SAS GLM procedures (SAS, 1991). This was to find the most parsimonious model. This was done for both DFREML (Meyer, 1993) and AI-REML (Johnson and Thompson, 1995; Johnson, pers. comm.) analyses.

$$Y_{ijklmno} = \mu + BR_i + RR_j + AOD_k + \beta(AGE_{ijklmno} - AGE) + Year_l(\text{or } Year_l * Line_m) + Sire_n(Year_l) (\text{or } Sire_n(Year_l * Line_m)) + \epsilon_{ijklmno} \quad (\text{equation 3.1})$$

where:

$Y_{ijklmno}$	=	observation trait of individual specified by subscripts
μ	=	population mean for that trait
BR_i	=	birth rank effect ($i = 1, 2 \text{ or } 3$)
RR_j	=	rearing rank effect ($j = 1, 2 \text{ or } 3$)
AOD_k	=	age of dam effect ($k = 2, 3 \text{ and } 4$)
β	=	linear regression coefficient of $AGE_{ijklmno}$ on age at measurement
AGE	=	mean age of animals at measurement
$AGE_{ijklmno}$	=	is the age of individual specified by subscripts at measurement
$Year_l$	=	year of measurement effect ($l = 1 \dots 9$)
$Year_l * Line_m$	=	year*line of measurement
$Sire_n(Year_l)$	=	sire nested within year
$Sire_n(Year_l * Line_m)$	=	sire nested with year and line
$\epsilon_{ijklmno}$	=	random error associated with observation, assumed to be normally and independently distributed with mean zero.

Attempts to fit sire-dam models in SAS were abandoned due to the memory requirements being prohibitive. Therefore a sire model was fitted. Main fixed effects fitted were birth rank, rearing rank, age of dam and year or year by line interaction for flocks with two lines (see equation 3.1). All two-way interactions were also fitted. Age at measurement was fitted as a covariable and sire nested within year (or year by line) was fitted as a random effect. All two-way interactions not significant at 10% significance level were dropped from the model and the analysis was continued. Finally all effects significant at 10% confidence level were identified to be included only in AIREML analyses (equation 3.1).

Consideration of SAS outputs, led to classes of birth and rearing ranks being reduced to two (2) for Dorset Down flock and three (3) for the other three flocks since there were few triplets in the Dorset Down flock and few quadruplets in the other flocks. As well, there were only small differences in least squares means for twins vs triplets in Dorset Downs and triplets vs quadruplets in other flocks. Classes

of age of dam were reduced to three (3) due to lack of performance differences between progeny from four (4) year or older ewes.

Birth and rearing rank were largely confounded such that fitting one before the other explained most of the variation in the other. Since rearing rank was not available during the early years in the Coopworth flock a decision was made to fit birth rank in AIREML analyses, since it was recorded for all flocks i.e rearing rank was not fitted.

The significance of fixed effects and covariates from SAS output were not consistent across traits in the different data sets. Therefore, models differing in fixed effects and covariables were fitted to the different traits in multivariate analyses.

3.6.2 Finding the most appropriate statistical method(s) of analyses

This section summaries the results from evaluation of traditional methods such as GLM and modern methods such as DFREML and AI-REML (Appendix C). The method(s) chosen had to be efficient in terms of time and computer resources.

Most of the details of the data sets were covered in section 3.3. For preliminary analyses, data for animals born in 1992 were not used since they were not available until the end of this study.

3.6.2.1 Overall findings for univariate analytical methods

Details of the methods evaluated are reported in Appendix C. Overall heritability estimates for most traits were medium (>0.10) to high (>0.60). These varied between sexes, seasons and breeds. Variation in heritability estimates between sexes, seasons and breeds could be real or biased by selection or unbalanced data. Heritability estimates derived by modern analytical methods were generally greater than those determined by traditional least squares. These results were consistent with theoretical expectations where analysis is performed on data from populations of selected animals with extensive pedigree records (Chapter 2). Progression to multivariate analyses was made to estimate genetic and phenotypic correlations.

3.6.2.2 Overall findings for multivariate analytical methods

Trends in heritability estimates seen in univariate analyses were evident in multivariate analyses. Generally, ram estimates were higher than those from ewe data. Estimates of phenotypic parameters were similar between the sexes. However, some estimates of genetic correlations from ewe data were non-estimable or nonsensical (>1.00) from multivariate SAS GLM. Furthermore, most genetic correlations varied between the sexes, with no trends apparent (Appendix C).

3.6.3 Models of analyses

Preliminary work identified that some analyses of data sets containing both sexes within or across seasons (autumn, winter and spring within year) were not appropriate due to one sex having more measurements in one season than the other (Table 3.5). Hence analyses were performed: (i) within sex, within season and within breed, (ii) combined sexes within breed and within season and (iii) data combined across sexes and breeds within season for Border Leicester and Dorset Down. In most cases, even the smallest data sets *i.e* those within sex, within breed and within season, were of adequate size using the criteria of Koots *et al.* (1994a). All contained at least 500 observations or at least 20 sires (see Appendices A and B).

Dependent variables were based predominantly on three traits or measurements (liveweight, fat depth and muscle depth). These were measured in three seasons (autumn, winter and spring) for two sexes (ewes and rams) of four breeds (Border Leicester, Coopworth, Dorset Down and Corriedale). Potentially analyses involved many data combinations. However, data were not available for all season-sex-breed combinations (see Table 3.5). To avoid confusion and for brevity when referring to a particular data analysis the following nomenclature will be used in the thesis. Aims of the analyses were to evaluate the effects of season, sex and breed on; (i) correction factors for fixed effects, (ii) genetic and phenotypic parameter estimates (parameter estimates) of liveweight, fat depth and muscle depth and responses to selection.

Combinations of traits for the different analyses performed are presented in Table 3.6.

1. Traits measured in autumn and, winter or spring, within sex and within breed were analysed together as separate but related traits. This is referred to as a *season-trait* analysis. These analyses provided first estimates of seasonal influence on correction factors and parameter estimates of the three index component traits.

- 2(a). Ewe and ram traits within season and within breed were analysed together as separate but related traits. This is referred to as a *sex-trait* analysis. These provided estimates of sex influence on correction factors and parameter estimates for the three index component traits.

- 2(b). Responses to selection in index component traits were derived from *sex-trait* analysis but with autumn (or spring) ewe traits and winter ram traits analysed together as separate but related traits. This was employed because ewes were predominantly performance tested in autumn or spring whereas rams were predominantly performance tested in winter.

3. Using outputs from 1 and 2(a) above, the influence of breed was investigated by comparing within sex and within season correction factors and parameter estimates for the three index component traits. This is referred to as *breed-trait* comparison.

4. Data were combined across sex within trait, within season, within breed. Sex was fitted as a fixed effect. Autumn and/or winter traits were analysed together as separate but related traits. This is referred to as *seasonXsex-trait* analysis. Estimates from these larger data sets (compared to 1 above) were thought to provide better estimates of the influence of the season on correction factors and parameter estimates.

5. Using outputs from 4 above, the effect of breed was investigated by comparing correction factors and parameter estimates for the three traits within season, within sex across the different data sets. These comparisons are referred to as *breedXsex-trait* comparisons.

6. In order to provide estimates of the influence of season, sex and breed from large data sets on correction factors and parameter estimates, another strategy of data combination was employed using data from the Border Leicester and Dorset Down flocks which were run together within sex. This analysis combined data across sex and breed within season, within trait. Sex and breed were included in the model as fixed effects. Autumn and winter traits were analysed together as separate but related traits. This analysis is referred to as *seasonXsexXbreed-trait* analysis.

AIREML analyses were performed on *season-trait*, *sex-trait*, *seasonXsex-trait* and *seasonXsexXbreed-trait* data sets. Estimates from *sex-trait* and *seasonXsex-trait* analyses were used for *breed-trait* and *breedXsex-trait* comparisons respectively.

The significance of fixed effects and covariates varied between traits and was determined using SAS GLM procedure (section 3.6.1). Where an effect was significant for one trait but not others, the effect was coded as a constant in the trait where it was non-significant (Johnson, pers.comm). Fixed and covariable effects fitted in AIREML analyses are shown in Table 3.7.

For each analysis style, traits were analysed together as separate but related traits in a single multivariate AIREML analysis using all information from relatives. Full pedigree files were fitted including all animals with recorded identities. Data files included only animals with measurements for each trait.

Joint analyses of traits involved traits being stacked in one column and identified by a right hand side code as described by Meyer (1993). The largest number of traits simultaneously included in a single run was eight and the smallest four. Analyses of fewer joint traits were only carried out where data sets

were too big and caused computer memory shortage. This restriction was required for *seasonXsexXbreed* trait analyses and those of the Coopworth data.

Table 3.5: Number of observations for liveweight (LW), fat depth (FD) and muscle depth (MD) within sex and within season for Border Leicester (BL), Coopworth (CPW), Dorset Down (DD) and Corriedale (COR) data.

Breed	Sex	Season								
		Autumn			Winter			Spring		
		LW	FD	MD	LW	FD	MD	LW	FD	MD
BL	Ewes	647	621	349	462	415	155	-	-	-
	Rams	394	397	123	608	613	377	-	-	-
CPW	Ewes	1407	728	180	-	-	-	2021	1516	598
	Rams	1183	686	174	1711	1525	645	-	-	-
DD	Ewes	923	925	586	607	525	201	-	-	-
	Rams	513	514	223	820	819	557	-	-	-
COR	Ewes	-	-	-	773	773	773	-	-	-
	Rams	-	-	-	721	722	722	-	-	-

Table 3.6: Data combinations for the different types of analyses in Border Leicester (BL), Coopworth (CPW), Dorset Down (DD) and Corriedale (COR) data sets. Traits within each type were analysed together in a single AIREML analysis as separate but related traits.

Analyses type	Data combinations	Number of traits in analysis	Traits
<i>season-trait</i>	BL rams	7	ALW, AFD, AMD, WLW, WFD, WMD, GFWT
	BL ewes	7	ALW, AFD, AMD, WLW, WFD, WMD, GFWT
	CPW rams	7	ALW, AFD, AMD, WLW, WFD, WMD, GFWT
	CPW ewes	7	ALW, AFD, AMD, SLW, SFD, SMD, GFWT
	DD rams	6	ALW, AFD, AMD, WLW, WFD, WMD
	DD ewes	6	ALW, AFD, AMD, WLW, WFD, WMD
<i>sex-trait[†]</i>	BL	(a) 4ram & 4ewe	ram ALW, AFD, AMD, GFWT & ewe ALW, AFD, AMD, GFWT
		(b) 4ram & 4ewe	ram WLW, WFD, WMD, GFWT & ewe WLW, WFD, WMD, GFWT
		(c) 4ram & 4ewe	ram WLW, WFD, WMD, GFWT & ewe ALW, AFD, AMD, GFWT
	CPW	(a) 4ram & 4ewe	ram ALW, AFD, AMD, GFWT & ewe ALW, AFD, AMD, GFWT
		(b) 4ram & 4ewe	ram WLW, WFD, WMD, GFWT & ewe SLW, SFD, SMD, GFWT
		(c) 4ram & 4ewe	ram ALW, AFD, AMD & ewe ALW, AFD, AMD
	DD	(a) 3ram & 3ewe	ram WLW, WFD, WMD & ewe WLW, WFD, WMD
		(b) 3ram & 3ewe	ram WLW, WFD, WMD & ewe ALW, AFD, AMD
		(c) 3ram & 3ewe	ram WLW, WFD, WMD, GFWT & ewe WLW, WFD, WMD, GFWT
<i>seasonXsex-trait</i>	COR	(a) 4ram & 4ewe	ram WLW, WFD, WMD, GFWT & ewe WLW, WFD, WMD, GFWT
	BL rams& ewes	7	ALW, AFD, AMD, WLW, WFD, WMD, GFWT
	CPW rams& ewes	4	ALW, AFD, AMD, GFWT
	DD rams& ewes	6	ALW, AFD, AMD, WLW, WFD, WMD
<i>seasonXsexXbreed-trait</i>	COR rams& ewes	4	WLW, WFD, WMD, GFWT
	BL & DD rams and ewes	6	ALW, AFD, AMD, WLW, WFD, WMD

[†] (c) used to estimate responses to selection

Table 3.7: Fixed and covariable effects fitted in AIREML analyses.

Analysis	Effects fitted	
	Fixed	Covariable
(i) <i>season-trait and sex-trait</i>	BR, YEAR, AOD	AGE
(ii) <i>seasonXsex-trait</i>	BR, YEAR, AOD, SEX	AGE
(iii) <i>seasonXsexXbreed-trait</i>	BR, YEAR, AOD, SEX, BREED	AGE

3.6.4. Parameter estimates

Genetic and phenotypic parameters were estimated from multi-variate AIREML (AIMUL) analyses based on Restricted Maximum Likelihood using the average information matrix as second derivatives in

a quasi-Newton procedure (Johnson, pers.comm). The model of analysis was an Individual Animal Model (equation 3.2) with animal being the only random effect and birth rank, age of dam and year of birth as fixed effects and age at measurement as a covariable.

$y = Xb + Z\mu + e$ --- equation 3.2 (adapted from Henderson, 1973 & 1984)

where, in the terminology of Meyer (1993):

equation 3.2 denotes the multivariate linear model of analysis for q traits with:

- y the vector of N observations for all traits
- X the N x NF incidence or design matrix for fixed effect with column rank NF
- b the vector NF fixed effects (including any linear or higher order covariables)
- Z the N x NR incidence matrix for random effects
- μ the vector of all NR non-observable random effects fitted
- e the vector of N non-observable random residual errors

Under a model with no selection, μ and e have null means and :

variance $= \begin{bmatrix} a \\ e \end{bmatrix} \begin{bmatrix} a & e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & R_e\sigma_e^2 \end{bmatrix}$

A is the numerator relationship matrix and R_e is the identity matrix (Henderson, 1986). However, in these analyses selection has occurred, therefore, μ and e did not have null means.

To estimate responses to selection, complete data sets were available for ewes autumn measurements in Border Leicester and Dorset Down flocks and spring in Coopworth flock, and winter measurements for rams in all flocks. Rams were performance tested in winter for reasons discussed previously. Animals born in 1984 and 1985 prior to establishment of the lines in 1986 were coded as controls as previously described.

3.6.5. Breeding value estimates

BLUP breeding values of index component traits were derived as by-products of AIMUL REML analyses. Mean breeding values of the lean tissue growth rate lines were regressed against year of birth to obtain response rates to selection. For muscle depth, only those years in which it was measured were used for regression.

3.7 Presentation of results and discussions

Results and their respective discussions are presented in three Chapters. Chapter 4 covers environmental effects and their correction factors, Chapter 5 genetic and phenotypic parameters and Chapter 6 responses to selection.

Estimates of fixed effects, genetic and phenotypic parameters from *season-trait* and *sex-trait* analyses were generally similar so either estimates could have been reported. Results presented in Chapters 5 and 6 were from AIMUL *sex-trait* analysis (part 2(b) in section 3.6.4) to provide links between genetic and phenotypic parameters and BLUP breeding values for ewe autumn or spring traits and ram winter traits in Border Leicesters, Coopworths and Dorset Downs.

Where there are many tables and figures for comparison, the descriptive text is presented first and all tables and figures follow in a block. Otherwise tables and figures are presented immediately after the descriptive text.

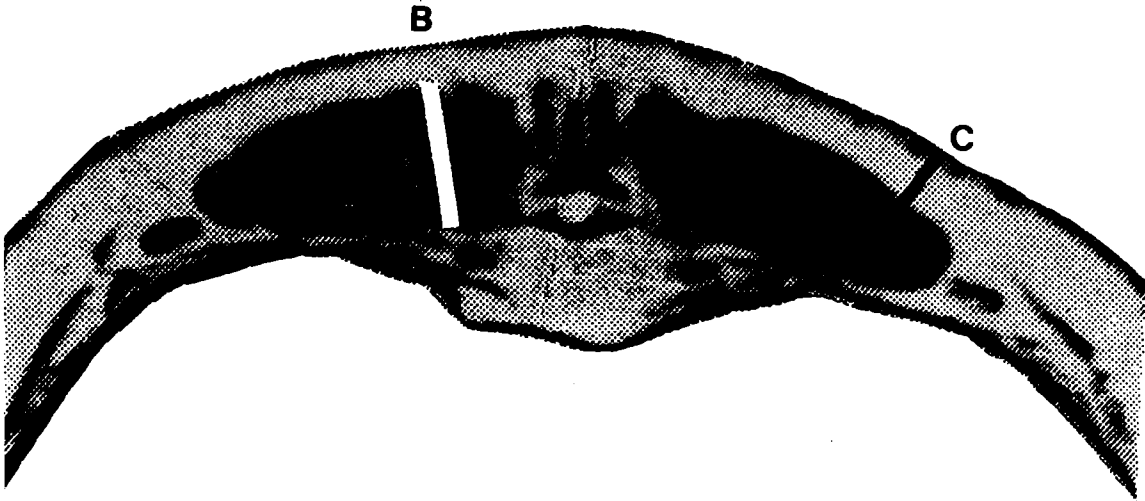


Figure 3.1: Cross-section of a carcass cut transversely at the 12th rib showing the sites at which depth of *M. longissimus dorsi* (B) and subcutaneous fat (C') were measured by ultrasound.

CHAPTER 4

ENVIRONMENTAL FACTORS

4.0 Introduction

Environmental correction factors presented in Tables 4.1 to 4.13 (page 52 onwards) are from univariate SAS GLM procedures. Estimates from multivariate (AIMUL) AIREML were generally similar in magnitude. Where the estimates differed significantly, SAS estimates were consistently greater in magnitude. AIMUL correction factors were not presented because they were estimated without sampling errors. Magnitudes of correction factors are presented as deviations from the first level of each fixed effect.

4.1 Results

4.1.1 Estimates of environmental effects and their correction factors

Generally, year, birth rank, age of dam and age at measurement affected performance in all traits. Twins and triplets had lighter liveweight, lighter greasy fleece weight and shallower muscle depth and fat depth than singles. Where fitted, triplet performance was lower than that of twins for most traits. Progeny from 2 year old dams performed at a lower level than those from older ewes for all traits, while progeny from 4 year and older ewes generally had the greatest performance for most traits. Younger animals had lighter liveweights and lighter greasy fleece weights and shallower fat and muscle depths than older animals. Year effects were variable and essentially random (Tables 4.1 to 4.13).

4.2. Comparison of methods of estimation

In sections 4.2.1 to 4.2.7 differences were judged to be significant ($P < 0.10$) on the basis of *t*-test (Little and Hills, 1978).

Generally, trends and magnitudes of correction factors for liveweight and greasy fleece weight in the present study fall within the range of literature estimates (e.g. Eikje, 1971; Baker, Clarke and Carter, 1974; Warmington and Beatson, 1986; Young, 1989; Cameron and Bracken, 1992). Correction factors for environmental effects affecting muscle and fat depths are scarce in the literature, the few reported being based on ram data only (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993; Olesen and Husabo, 1994). Trends and magnitudes of correction factors for these two traits in the present study fall within the range of these reported estimates.

4.2.1 General magnitudes and trends

Across data sets within breed correction factors for fixed effects in similar traits (*e.g.* liveweight in autumn and winter) were similar in magnitude and did not vary greatly indicating that correction factors were estimated accurately. Correction factors of the larger data sets (*seasonXsex-trait* and *seasonXsexXbreed trait*) were estimated with smaller sampling errors than those of the smaller data sets (*season-trait* and *sex-trait*) (Tables 4.1-4.13).

Although there were no significant differences between similar traits in autumn, winter or spring *e.g.* liveweight, generally animals were heavier and had deeper fat and muscle depths in winter and spring than in autumn. Rams had heavier liveweight and deeper muscle depth in all seasons than ewes, but ewes either had deeper fat depth, or were fatter relative to their liveweight in all seasons. Ewes which were shorn in spring had heavier fleece weights than rams which were shorn in winter in breeds where this trait was recorded (Tables 4.1 to 4.13).

Variation is often correlated with the mean (Snedecor and Cochran, 1980). Thus care must be taken comparing either statistic across populations. However, the coefficient of variation is relatively stable (Snedecor and Cochran, 1980) and generally provides valid comparisons (Lasley, 1978). The coefficient of variation also allows comparison of traits measured in different units (Warwick and Legates, 1979).

Coefficients of variation were greater for winter traits and spring traits than autumn traits except for Border Leicester ewes, where the opposite was true. Fat depth ($30\pm12\%$) showed greater coefficients of variation than both liveweight ($10\pm4\%$) and muscle depth ($7\pm4\%$) which were similar (Tables 4.1, 4.2, 4.4, 4.5, 4.7, 4.8, 4.11 and 4.12).

Sex-trait analyses revealed that coefficients of variation were greater in ewe traits than ram traits, the exception being in Dorset Downs where they were similar for the two sexes. The coefficients of variation for greasy fleece were greater in ewes than rams in breeds where this trait was recorded. Greater coefficients of variation in ewe traits than ram traits were predominantly due to greater standard deviations in ewes than rams, although, occasionally, it was a combination of both a smaller mean and greater standard deviation in ewes than rams (Tables 4.1 to 4.13).

In *breed-trait* analyses, coefficients of variation were greater in Border Leicester ewes than for Coopworth and Dorset Down ewes for all autumn traits. While in winter coefficients of variation were greater in Border Leicester ewes than Dorset Down and Corriedale ewes for tissue depths except for liveweight which was similar in all breeds. For rams there were no apparent trends in coefficients of variation in either autumn or winter (Tables 4.1 to 4.13).

For *seasonXsex-trait* analyses, coefficients of variation were greatest in Border Leicesters, least in Coopworths, and intermediate in Dorset Downs except in winter when coefficients of variation were similar across breeds (Table 4.3 to 4.6 and 4.9). Finally, for *seasonXsexXbreed-trait* analysis the coefficients of variation were similar for autumn traits and winter traits (Table 4.10).

4.2.2 *Season-trait* analyses

For birth rank, there was a tendency for greater correction factor estimates in all traits for autumn than winter for both rams and ewes in most breeds except for Border Leicesters where the opposite was true. With age of dam, there was strong evidence that correction factors for all traits were greater in winter than autumn. For all traits, the between years correction factors were generally greater in winter and spring than autumn (Tables 4.1 to 4.13).

4.2.3 *Sex-trait* analyses

Correction factors were generally similar for autumn traits and winter or spring traits for the two sexes in all breeds.

4.2.4 *Breed-trait* analyses

For both rams and ewes, correction factors for all traits significantly differed for the *breed-trait* analyses. Correction factors were generally greater for Border Leicester ewe traits and ram traits in both autumn and winter than separate sex traits in other breeds (Tables 4.1, 4.2, 4.4, 4.5, 4.7, 4.8, 4.11 and 4.12). For ewe data sets, there was a tendency for between year correction factors for all traits to be significantly greater in Border Leicester than Dorset Down even though the two breeds were run together at pasture in autumn and winter (Tables 4.1 and 4.7).

4.2.5 *SeasonXsex-trait* analyses

For Border Leicester and Dorset Down sex correction factors were significantly greater in winter than autumn except for fat depth where the opposite was true. Rams had greater correction factors for liveweight and muscle depth and less for fat depth than ewes in both autumn and winter (Tables 4.3 and 4.9). Birth rank was significantly greater for winter muscle depth than autumn muscle depth with no obvious trends in liveweight and fat depth for Border Leicesters. In Dorset Downs, birth rank correction factors were significantly less in winter for liveweight and muscle depth than similar traits in autumn. Age of dam was significantly greater for fat depth and muscle depth in autumn than respective traits in winter for Border Leicester, with no obvious trends in liveweight. In contrast, for the Dorset Downs age

of dam was significantly greater in all winter traits than similar traits in autumn. Fat depth and muscle depth had similar age regressions in autumn and in winter. However, liveweight in autumn had significantly greater growth rate than in winter for Border Leicesters and Dorset Downs. Year correction factors for all traits were generally random between seasons (Table 4.3 and 4.9).

4.2.6 *BreedXsex-trait* analyses

For all traits, there was a tendency for correction factor estimates for birth rank to be greater in breeds with a higher proportion of multiple births, especially in winter. Correction factors for these environmental effects were greatest in Border Leicesters and least in Dorset Downs. Comparatively, correction factors for age of dam were greatest in Dorset Downs than other breeds in both autumn and winter. Correction factors for sex were significantly greater for winter than autumn. For autumn traits sex correction factors were greater in Dorset Downs than both Border Leicesters and Coopworths which were similar (Tables 4.3, 4.6 and 4.9). For winter traits sex correction factors were greatest in Corriedales, followed by Dorset Downs and least in Border Leicesters. In all breeds, rams generally had heavier liveweight, lighter greasy fleece weight, deeper muscle depth and shallower fat depth than ewes, except for Corriedale rams which had deeper fat depth and heavier fleece weight than their ewe counterparts (Tables 4.3, 4.6, 4.9 and 4.13).

4.2.7 *SeasonXsexXbreed-trait* analysis Border Leicesters and Dorset Downs

There was a tendency for the Dorset Down to have heavier liveweight, deeper muscle and shallower fat depths both in winter and autumn than the Border Leicester. Breed differences were significantly greater in winter than in autumn.(Table 4.10).

4.3 Discussion

4.3.1 Magnitude of correction factors

Results from the present work indicate that the magnitude of correction factors of fixed effects (birth rank, age of dam, age at measurement and year) affecting performance of the index component traits varies between season, sex and breed. While structure of data sets caused a degree of confounding since ewes and rams were usually tested in different seasons and run as different mobs from weaning onwards, trends were strong and follow patterns that can be readily explained. In Border Leicester and Coopworth flocks birth rank had the greatest effect (multiples were 2-25% less than singles) followed by age of dam (progeny from 2 year old dams were 2-11% less than progeny from older dams). In Dorset Down and Corriedale flocks, birth rank and age of dam effects were of similar magnitude (2-12% and 1-13% respectively). Other studies have reported variation in the effects of these environmental variables (1-15% of the mean) (Ch'ang and Rae, 1970; Baker *et al.*, 1974; Warmington and Beatson, 1986; Young, 1989; Cameron and Bracken, 1992; Bishop, 1993).

Greater differences between birth ranks in Border Leicesters and Coopworth sheep could be due to an interaction between milk production and prolificacy. However, the birth rank-age of dam interaction was not significant ($P > 0.10$) in any data set. Geenty and Jagusch (1974) showed that higher milk production in Dorset (139%) and Corriedale (119%) than in Romney (100%) ewes was correlated with growth rate of progeny (Dorset, 113%; Corriedale, 107%; Romney, 100%). While there are no quantitative reports of milk production in Border Leicester and Coopworth ewes in the literature, it is expected that these two breeds would produce more milk than either Dorset Down or Corriedale. The Border Leicester breed is considered to have high milking ability (Anon., 1977; Geenty and Sykes, 1983) and is one of the two breeds used to derive the Coopworth. If the Border Leicester and Coopworth produce more milk than either Dorset Down or Corriedale then one would expect smaller differences between singles and multiples in the former breeds because milk supply would be less likely to limit lamb growth but the opposite was observed. Examination of the data showed that the proportion of lambs from 2-year old dams was greater in Border Leicester (29%) and Coopworth (34%) than in Dorset Down (19%) and Corriedale (18%). Border Leicester and Coopworth 2-year old dams gave birth to more twins (66-72%) than singles (18-27%) compared to Dorset Down (51% twins vs 48% singles) and Corriedale (61% twins vs 37% singles). Since, 2-year old dams produce less milk than older ewes (Barnicoat, Logan and Grant, 1949), a higher proportion of twins from 2 year old ewes would increase differences between single and multiple born lambs in the Border Leicester and Coopworth flocks which could explain the greater difference between birth ranks in these flocks.

Correction factors varied for year effects in the present study. The studies of Ch'ang & Rae (1970), Baker, Clarke, Carter and Diprose (1979) and Warmington & Beatson (1986) reported similar effects. Year effects in the present study demonstrate that variation in feed supply and other factors affect growth each year. However, in the present selection programmes these are not important since selection is within year not across years.

Unbiased parameter estimates are needed to maximise genetic progress in breeding enterprises (Land, 1985; Meyer, 1990; Webb and Bampton, 1990). Correcting for significant fixed effects is important prior to estimation of genetic and phenotypic parameters in order to yield estimates which are not biased (Harville, 1977; Kennedy, 1981). It is also important to correct for significant fixed effects to improve the accuracy with which breeding values are estimated and hence the efficiency of selection (Eikje, 1971; Fogarty and Luff, 1985; Warmington and Beatson, 1986). Results of this study indicate that corrections should be carried out within season, within sex, within year and within breed.

4.3.2 Trends in correction factors

Effects of birth rank and age at measurement decreased in magnitude as animals grew older. This phenomenon has been attributed to compensatory growth in previously disadvantaged groups (Ch'ang and Rae, 1970; Eikje, 1971; Hight and Jury, 1971; Baker *et al.*, 1974 & 1979). On the contrary, the influence of age of dam remained undiminished for most traits, a phenomenon noted by Ch'ang and Rae (1970) in Romney ewes. The effect of sex increased with age in line with the findings of Baker *et al.* (1979) in Romney sheep.

The effects of age of dam and birth rank essentially reflect the magnitude of pre-weaning nutritional handicap resulting from lower milk production of the younger dams or in case of twins, having to share pre-natal uterine environment and post-natal milk supply (Ch'ang and Rae, 1970). This conclusion can be extended to the present study.

Lack of compensation for age of dam suggests that this environmental effect is more severe than birth rank (Ch'ang and Rae, 1970). Age of dam effects may occur earlier in pregnancy whereas birth rank effects occur later in pregnancy and during lactation. The earlier the effect occurs, the more permanent its influence (Allden, 1970). Black (1983) concluded that severe pre-natal growth retardation in late pregnancy due to restricted maternal nutrition can result in a reduction of up to 10% in liveweight of progeny at 2-2.5 years of age. Liveweight changes were not recorded for dams of the present study but slight loss of liveweight due to low quality and quantity of feed available during the winter period commonly occurs. During this period of nutritional restriction (mid to late pregnancy) intra-uterine growth retardation could be greater in younger than older dams due to competition for metabolites between the dam and foetuses since younger dams are still growing.

Generally, rams were heavier (10-22%), had deeper muscle depth (5-14%) and shallower fat depth (0-28%) than ewes within season in the present study. These differences could reflect true genetic differences since rams have a higher growth rate (Thompson, Butterfield and Perry, 1985; Warmington and Beatson, 1986; Butterfield, 1988), developmental differences (Taylor, 1985) or nutritional differences. Ram flocks have sometimes been given preferential feeding to prepare them for sale (Warmington and Beatson, 1986) and field days particularly in years when feed supply was restricted. While preferential feeding of rams was not a usual management policy (Logan, pers. comm.) the two sexes were run separately at pasture from weaning in summer onwards. However, the consistently large sex differences quantified above suggest that these are due to developmental differences between the sexes rather than preferential feeding.

Greater coefficients of variation were observed in winter or in spring than in autumn in the present study. Eikje (1971) concluded that although the standard deviation increases as lambs grow older and heavier, the coefficient of variation remained constant. Such a conclusion did not apply in the present study. Greater coefficients of variation in winter or in spring than in autumn were predominantly due to greater standard deviation in winter or spring than in autumn.

Variation in correction factors and coefficients of variation between sexes are not readily explained because sex and management were confounded. For most breeds (Border Leicester, Dorset Down and Coopworth) one sex had a greater number of observations in one season than the other. Greater coefficients of variation in ewes than rams could be due to differences in maturity or sex. However, neither of these effects could be resolved because of the confounded data sets. In the Corriedale breed where both sexes were measured in winter and data sets were similar in size, differences in correction factors and coefficients of variation between sexes were also observed suggesting that these are real in other breeds.

4.3.3 Univariate vs multivariate model

It was reassuring to find that most of the correction factors in the present study did not differ significantly ($P > 0.10$) between SAS GLM and AIMUL, indicating that the extra precision of multivariate IAM REML (Meyer, 1991a; Villanueva, Wray and Thompson, 1993) arising from their superior mathematical properties (Harville, 1977; Kennedy, 1981) had relatively little effect on estimation of fixed effects.

There were some significant differences between estimates from AIMUL REML and univariate SAS GLM. Correction factors from univariate and multivariate SAS were similar, indicating that differences between AIMUL and univariate SAS GLM are likely to be due to fitting different models *i.e.* sire model versus individual animal model, rather than differences between univariate and multivariate analysis. A

comparison of univariate (AIUNI) AIREML and univariate SAS GLM procedures produced similar correction factors indicating that differences between univariate SAS and AIMUL estimates were due to fitting, univariate versus multivariate model. In theory multivariate IAM should produce more accurate correction factor estimates than univariate IAM (Meyer, 1991a; Villanueva *et al.*, 1993)). However, the beta version of AIMUL REML used did not estimate sampling errors of estimates of fixed effects.

4.4 Conclusion

Correction factors of fixed effects must be estimated within sex and within flock where this can be done accurately.

Table 4.1: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Border Leicester ewes. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects						
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	0	0	0	0	-	-
	2	-3.65 (0.04)	-0.58 (0.01)	-1.04 (0.04)	-3.24 (0.04)	-1.04 (0.02)	-	-
	3	-4.99 (0.06)	-0.90 (0.02)	-1.36 (0.06)	-4.77 (0.09)	-0.92 (0.05)	-	-
AOD (years)	2	0	0	-	0	-	-	-
	3	+1.07 (0.04)	+0.23 (0.01)	-	+0.80 (0.05)	-	-	-
	4	+1.99 (0.03)	+0.44 (0.01)	-	+1.42 (0.04)	-	-	-
AGE(/day)		0.239 (0.024)	0.07 (0.01)	0.10 (0.02)	0.112 (0.024)	0.04 (0.01)	0.03 (0.02)	-
YEAR OF BIRTH	1984	0	0	-	0	0	-	0
	1985	+8.06 (0.12)	+2.52 (0.04)	-	+2.95 (0.10)	+1.41 (0.05)	-	-0.59 (0.01)
	1986	+10.32 (0.10)	+1.90 (0.04)	-	+7.19 (0.09)	+1.91 (0.04)	-	+0.61 (0.01)
	1987	+7.27 (0.08)	+0.71 (0.04)	0	+0.45 (0.11)	-1.86 (0.06)	0	-0.76 (0.01)
	1988	-	-	-	-	-	-	-
	1989	-10.95 (0.10)	-3.50 (0.04)	-6.74 (0.06)	-8.59 (0.12)	-	-	-1.37 (0.01)
	1990	-0.69 (0.08)	-1.31 (0.03)	-2.22 (0.06)	-	-	-	-
	1991	-0.50 (0.09)	-1.16 (0.04)	-2.58 (0.06)	-	-	-	-
	1992	-	-	-	+3.31 (0.09)	-2.15 (0.05)	+2.40 (0.06)	-1.30 (0.01)
Phenotypic mean		37.03 (7.29)	3.83 (2.07)	22.30 (2.81)	42.27 (5.39)	5.16 (1.84)	24.39 (1.70)	3.52 (0.77)
CV(%) [#]		19.69	53.96	12.61	12.75	35.66	6.95	21.88

- CV based on least squares means and their standard deviations

Table 4.2: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Border Leicester rams. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects						
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	-	-	0	-	0	0
	2	-3.04 (0.06)	-	-	-3.38 (0.04)	-	-1.06 (0.03)	-0.10 (0.003)
	3	-4.91 (0.16)	-	-	-5.94 (0.10)	-	-2.13 (0.06)	-0.23 (0.01)
AOD (years)	2	-	-	-	0	-	-	-
	3	-	-	-	+1.86 (0.05)	-	-	-
	4	-	-	-	+2.06 (0.04)	-	-	-
AGE(/day)		0.209 (0.036)	0.05 (0.01)	0.07 (0.04)	0.197 (0.033)	0.05 (0.01)	0.08 (0.02)	0.01 (0.002)
YEAR OF BIRTH	1984	0	0	-	0	0	-	0
	1985	+3.17 (0.13)	+3.04 (0.04)	-	+4.57 (0.16)	+3.13 (0.04)	-	-0.15 (0.01)
	1986	+7.34 (0.12)	+1.89 (0.04)	-	+12.70 (0.15)	+3.40 (0.04)	-	+0.41 (0.01)
	1987	+6.86 (0.14)	+0.20 (0.05)	0	+10.20 (0.22)	+0.98 (0.06)	0	+0.10 (0.01)
	1988	+0.84 (0.23)	-0.16 (0.08)	-	-2.02 (0.21)	-0.70 (0.06)	-4.50 (0.10)	-0.32 (0.01)
	1989	-	-	-1.66 (0.12)	-1.01 (0.15)	+0.88 (0.04)	-1.44 (0.08)	-0.24 (0.01)
	1990	-	-	-	+4.27 (0.14)	+0.52 (0.04)	-0.51 (0.08)	-0.41 (0.01)
	1991	-	-	-	-2.64 (0.15)	+0.14 (0.04)	-0.21 (0.08)	-0.30 (0.01)
	1992	-	-	-	-2.17 (0.15)	+0.36 (0.04)	+1.11 (0.08)	+0.12 (0.01)
Phenotypic mean		42.06 (3.37)	4.21 (1.41)	24.82 (1.17)	49.46 (5.68)	3.79 (1.40)	26.18 (1.94)	2.59 (0.27)
CV(%)		8.01	33.49	4.72	11.48	36.94	7.40	10.24

- CV based on least squares means and their standard deviations

Table 4.3: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for sexes combined Border Leicester. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects						
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	0	0	0	0	0	0
	2	-3.37 (0.02)	-0.44 (0.01)	-0.92 (0.03)	-3.32 (0.02)	-0.55 (0.01)	-1.17 (0.03)	-0.08 (0.002)
	3	-4.94 (0.05)	-0.84 (0.02)	-1.30 (0.05)	-5.12 (0.06)	-0.56 (0.02)	-1.86 (0.04)	-0.17 (0.01)
AOD (years)	2	0	0	-	0	-	-	-
	3	+0.70 (0.03)	+0.12 (0.01)	-	+1.33 (0.03)	-	-	-
	4	+1.56 (0.02)	+0.19 (0.01)	-	+1.57 (0.03)	-	-	-
SEX [‡]	1	0	-	0	0	0	0	0
	2	-3.90 (0.02)	-	-1.10 (0.03)	-7.39 (0.02)	+1.10 (0.01)	-3.36 (0.02)	+0.97 (0.002)
AGE(/day)		0.220 (0.020)	0.06 (0.01)	0.10 (0.02)	0.133 (0.021)	0.04 (0.01)	0.05 (0.01)	0.01 (0.002)
YEAR OF BIRTH	1984	0	0	-	0	0	-	0
	1985	+5.90 (0.07)	+2.85 (0.02)	-	+2.94 (0.08)	+1.90 (0.03)	-	-0.38 (0.01)
	1986	+8.92 (0.06)	+1.98 (0.02)	-	+9.01 (0.08)	+2.41 (0.02)	-	+0.47 (0.01)
	1987	+6.35 (0.06)	+0.45 (0.02)	0	+3.75 (0.10)	-0.98 (0.03)	0	-0.51 (0.01)
	1988	+1.74 (0.15)	-0.41 (0.06)	-1.75 (0.09)	-3.40 (0.17)	-1.57 (0.06)	-4.19 (0.08)	-0.57 (0.02)
	1989	-11.09 (0.09)	-3.29 (0.04)	-6.18 (0.05)	-4.48 (0.08)	0 (0.03)	-1.27 (0.05)	-0.78 (0.01)
	1990	-1.26 (0.07)	-1.19 (0.03)	-1.82 (0.05)	+2.21 (0.10)	-0.44 (0.03)	-0.53 (0.05)	-0.68 (0.01)
	1991	-0.81 (0.09)	-0.95 (0.03)	-2.07 (0.05)	-3.76 (0.10)	-0.70 (0.03)	+0.24 (0.05)	-0.55 (0.01)
	1992	-	-	-	-2.86 (0.07)	-1.08 (0.07)	+1.74 (0.04)	-0.48 (0.01)
Phenotypic mean		38.00 (6.22)	3.52 (1.91)	22.82 (2.29)	45.66 (4.49)	4.23 (1.35)	24.57 (1.99)	3.05 (0.39)
CV(%)		16.37	54.26	10.03	9.83	31.91	8.10	12.79

- CV based on least squares means and their standard deviations

‡- 1= rams and 2 = ewes

Table 4.4: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Coopworth ewes. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects						
		ALW(kg)	AFD(mm)	AMD(mm)	SLW(kg)	SFD(mm)	SMD(mm)	GFWT(kg)
BR	1	0	0	-	0	0	0	0
	2	-2.43 (0.03)	-0.34 (0.02)		-2.70 (0.03)	-0.18 (0.01)	-0.90 (0.04)	-0.06 (0.002)
	3	-4.20 (0.03)	-0.74 (0.02)		-4.39 (0.03)	-0.62 (0.01)	-1.04 (0.04)	-0.16 (0.002)
AOD (years)	2	0	-	-	0	-	-	0
	3	+1.41 (0.02)			+1.40 (0.02)			+0.10 (0.001)
	4	+0.95 (0.01)			+1.05 (0.01)			+0.04 (0.001)
AGE(/day)		0.194 (0.018)	0.04 (0.01)	0.09 (0.03)	0.130 (0.020)	0.03 (0.01)	-	0.01 (0.002)
YEAR OF BIRTH	1984	0	0	-	0	0	-	0
	1985	-2.48 (0.02)	-		-1.07 (0.02)	-2.57 (0.01)	-	-0.51 (0.002)
	1986	-6.10 (0.02)	-1.33 (0.01)		+5.82 (0.03)	-1.73 (0.01)	-	-0.36 (0.003)
	1987	+0.09 (0.03)	-0.48 (0.01)		-4.05 (0.04)	-5.95 (0.02)	0	-0.97 (0.004)
	1988	-	-		-3.85 (0.04)	-2.82 (0.03)	+7.50 (0.04)	-1.06 (0.003)
	1989	-	-		-4.24 (0.06)	-3.62 (0.03)	+6.88 (0.04)	-0.62 (0.005)
	1990	-	-		+12.72 (0.07)	+0.89 (0.04)	+10.56 (0.08)	+0.20 (0.001)
	1991	-	-		-3.14 (0.04)	-4.57 (0.02)	+6.85 (0.03)	-0.87 (0.003)
	1992	-	-		-1.46 (0.09)	-3.74 (0.04)	+8.13 (0.05)	-1.13 (0.01)
Phenotypic mean		34.01 (2.91)	3.62 (0.67)	21.65 (2.65)	44.26 (5.68)	4.12 (2.15)	24.82 (3.54)	2.91 (0.47)
CV(%)		8.55	18.51	12.24	12.83	52.18	14.26	16.19

- CV based on least squares means and their standard deviations

Table 4.5: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Coopworth rams. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects						
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	0	0	0	0	0	-
	2	-2.75 (0.03)	-0.50 (0.01)	-0.89 (0.09)	-2.44 (0.03)	-0.20 (0.01)	-0.54 (0.03)	
	3	-4.37 (0.04)	-0.71 (0.02)	-1.66 (0.13)	-4.70 (0.03)	-0.41 (0.01)	-1.53 (0.04)	
AOD (years)	2	0	0	-	0	0	-	-
	3	+1.48 (0.02)	+0.02 (0.01)		+1.71 (0.02)	+0.20 (0.005)		
	4	+1.37 (0.02)	+0.25 (0.01)		+1.40 (0.02)	+0.27 (0.004)		
AGE(/day)		0.176 (0.022)	0.04 (0.01)	0.10 (0.03)	0.136 (0.021)	0.01 (0.01)	0.04 (0.01)	0.01 (0.005)
YEAR OF BIRTH	1984	0	0	-	0	0	-	0
	1985	-2.64 (0.02)	-		-5.88 (0.02)	+0.90 (0.01)	-	-0.07 (0.002)
	1986	-2.86 (0.03)	+0.24 (0.01)		+3.86 (0.04)	+1.73 (0.01)	-	-0.13 (0.003)
	1987	-1.28 (0.03)	-1.01 (0.01)		+0.50 (0.03)	+0.85 (0.01)	0	-0.43 (0.002)
	1988	-	-		+0.43 (0.07)	+0.74 (0.02)	+2.27 (0.04)	-0.19 (0.01)
	1989	-	-		-0.76 (0.07)	-0.02 (0.02)	+0.80 (0.03)	-0.34 (0.01)
	1990	-	-		+6.11 (0.05)	+1.51 (0.01)	+3.53 (0.03)	-0.29 (0.003)
	1991	-	-		-10.12 (0.07)	-0.45 (0.02)	-0.36 (0.04)	-0.12 (0.005)
	1992	-	-		-2.38 (0.05)	+1.41 (0.01)	+2.67 (0.03)	+0.45 (0.004)
Phenotypic mean		37.79 (1.33)	2.87 (0.67)	20.06 (2.36)	45.46 (4.87)	3.08 (0.76)	25.60 (1.57)	2.28 (0.26)
CV(%)		3.52	23.28	11.77	10.71	24.68	6.12	11.40

- CV based on least squares means and their standard deviations

Table 4.6: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for sexes combined Coopworth. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects			
		ALW(kg)	AFD(mm)	AMD(mm)	GFWT(kg)
BR	1	0	0	0	0
	2	-2.58 (0.02)	-0.40 (0.01)	-0.92 (0.05)	-0.02 (0.001)
	3	-4.33 (0.02)	-0.74 (0.02)	-1.51 (0.06)	-0.12 (0.001)
AOD (years)	2	0	0	-	0
	3	+1.40 (0.01)	+0.06 (0.01)		+0.10 (0.001)
	4	+1.10 (0.01)	+0.12 (0.004)		+0.07 (0.001)
SEX [‡]	1	0	0	0	0
	2	-3.77 (0.01)	+0.83 (0.003)	+1.73 (0.02)	+1.00 (0.001)
AGE(/day)		0.188 (0.013)	0.04 (0.01)	0.09 (0.02)	-
YEAR OF BIRTH	1984	0	0	-	0
	1985	-2.56 (0.01)	-		-0.30 (0.001)
	1986	-4.69 (0.01)	-0.63 (0.01)		-0.25 (0.002)
	1987	-0.64 (0.01)	-0.78 (0.01)		-0.57 (0.001)
	1988	-	-		-0.65 (0.001)
	1989	-	-		-0.25 (0.003)
	1990	-	-		-0.26 (0.002)
	1991	-	-		-0.32 (0.002)
	1992	-	-		+0.05 (0.002)
Phenotypic mean		35.86 (2.12)	3.21 (0.41)	20.87 (2.63)	2.63 (0.23)
CV(%)		5.90	12.77	12.61	8.75

- CV based on least squares means and their standard deviations

‡ - 1= rams and 2 = ewes

Table 4.7: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Dorset Down ewes. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects					
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)
BR	1	0	-	-	0	-	-
	2	-2.92 (0.02)			-2.12 (0.03)		
AOD (years)	2	0	-	-	0	-	-
	3	+1.74 (0.03)			+2.12 (0.04)		
	4	+1.75 (0.02)			+2.21 (0.04)		
AGE(/day)		0.109 (0.019)	0.02 (0.01)	0.04 (0.01)	0.172 (0.026)	0.04 (0.01)	0.04 (0.02)
YEAR OF BIRTH	1984	0	0	-	0	0	-
	1985	-4.60 (0.07)	+0.40 (0.02)	-	-0.67 (0.08)	+0.90 (0.03)	-
	1986	-0.44 (0.07)	+0.19 (0.02)	-	+3.86 (0.08)	+1.87 (0.03)	-
	1987	-1.67 (0.07)	-0.36 (0.02)	0	-2.54 (0.07)	-0.39 (0.03)	0
	1988	+0.32 (0.07)	-1.36 (0.02)	+0.24 (0.03)	-	-	-
	1989	-7.15 (0.07)	-1.45 (0.02)	-1.75 (0.03)	-10.85 (0.09)	-	-
	1990	-0.77 (0.07)	-0.88 (0.02)	-0.77 (0.03)	-	-	-
	1991	-3.92 (0.07)	-1.20 (0.02)	-1.35 (0.03)	-	-	-
	1992	-	-	-	-4.07 (0.08)	-1.99 (0.03)	-0.60 (0.03)
Phenotypic mean		43.81 (2.67)	4.05 (0.73)	24.75 (0.85)	48.35 (4.94)	5.32 (1.45)	27.93 (0.42)
CV(%)		6.09	18.02	3.44	10.22	27.26	1.51

- CV based on least squares means and their standard deviations

Table 4.8: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Dorset Down rams. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects					
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)
BR	1	0	-	-	0	-	-
	2	-3.53 (0.04)			-2.59 (0.02)		
AOD (years)	2	0	-	-	0	0	0
	3	+0.65 (0.07)			+2.09 (0.05)	+0.08 (0.01)	+0.35 (0.03)
	4	+1.78 (0.05)			+1.92 (0.04)	+0.27 (0.01)	+0.77 (0.02)
AGE(/day)		0.186 (0.033)	0.02 (0.01)	0.08 (0.03)	0.109 (0.029)	-	-
YEAR OF BIRTH	1984	0	-	-	0	0	-
	1985	-9.07 (0.12)			-2.96 (0.13)	+0.05 (0.03)	-
	1986	-4.00 (0.11)			+7.40 (0.12)	+1.39 (0.02)	-
	1987	-0.09 (0.11)			+9.28 (0.12)	+2.34 (0.02)	0
	1988	-1.13 (0.10)			-6.70 (0.12)	-1.49 (0.02)	-5.49 (0.05)
	1989	-			-4.78 (0.12)	+0.28 (0.02)	-2.71 (0.05)
	1990	-			+7.22 (0.11)	+0.51 (0.02)	-0.02 (0.05)
	1991	-			-4.92 (0.13)	-0.08 (0.03)	-1.58 (0.05)
	1992	-			-1.12 (0.13)	+0.63 (0.03)	+1.21 (0.05)
Phenotypic mean		51.87 (3.83)	3.81 (1.37)	28.20 (0.13)	57.98 (6.06)	3.73 (1.05)	28.33 (2.41)
CV(%)		7.38	35.96	0.47	10.45	28.15	8.53

- CV based on least squares means and their standard deviations

Table 4.9: Correction factor estimates for significant (P<0.10) fixed effects and covariables from SAS GLM procedures for sexes combined Dorset Down. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects					
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)
BR	1	0	-	-	0	-	-
	2	-2.98 (0.01)			-2.30 (0.01)		
AOD (years)	2	0	-	-	0	0	0
	3	+1.48 (0.02)			+1.98 (0.02)	+0.09 (0.01)	+0.24 (0.02)
	4	+1.64 (0.02)			+1.87 (0.02)	+0.08 (0.01)	+0.39 (0.02)
SEX [§]	1	0	0	0	0	0	0
	2	-7.80 (0.01)	+0.44 (0.004)	-2.61 (0.01)	-9.11 (0.01)	+1.18 (0.004)	-2.20 (0.02)
AGE(day)		0.145 (0.017)	0.02 (0.005)	0.04 (0.01)	0.125 (0.020)	0.02 (0.01)	0.04 (0.01)
YEAR OF BIRTH	1984	0	0	-	0	0	-
	1985	-6.42 (0.04)	+0.09 (0.01)	-	-1.68 (0.06)	+0.50 (0.02)	-
	1986	-1.93 (0.04)	-0.07 (0.01)	-	+5.56 (0.05)	+1.66 (0.01)	-
	1987	-0.74 (0.04)	-0.04 (0.01)	0	+2.93 (0.05)	+0.82 (0.01)	0
	1988	-0.38 (0.04)	-0.67 (0.01)	+0.10 (0.02)	-8.67 (0.08)	-2.36 (0.02)	-6.08 (0.03)
	1989	-8.29 (0.06)	-1.32 (0.02)	-1.93 (0.03)	-7.60 (0.05)	-0.73 (0.02)	-3.33 (0.03)
	1990	-1.33 (0.06)	-0.77 (0.02)	-0.77 (0.03)	+5.43 (0.07)	-0.10 (0.02)	-0.42 (0.03)
	1991	-4.71 (0.06)	-1.08 (0.02)	-1.43 (0.03)	-7.00 (0.09)	-1.09 (0.02)	-2.21 (0.04)
	1992	-	-	-	-2.28 (0.05)	-0.91 (0.01)	+0.12 (0.02)
Phenotypic mean		47.43 (3.11)	3.79 (0.55)	26.06 (0.89)	52.80 (5.47)	4.24 (1.19)	27.18 (2.43)
CV(%)		6.56	14.51	3.42	10.36	28.07	8.93

- CV based on least squares means and their standard deviations

§ - 1 = rams and 2 = ewes

Table 4.10: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for sexes and breeds combined Border Leicester and Dorset Down. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects					
		ALW(kg)	AFD(mm)	AMD(mm)	WLW(kg)	WFD(mm)	WMD(mm)
BR	1	0	0	0	0	0	0
	2	-3.13 (0.01)	-0.27 (0.003)	-0.96 (0.01)	-2.66 (0.01)	-0.26 (0.003)	-0.75 (0.01)
	3	-4.63 (0.05)	-0.69 (0.02)	-1.26 (0.04)	-4.60 (0.06)	-0.33 (0.02)	-1.53 (0.04)
AOD (years)	2	0	0	-	0	0	0
	3	+1.10 (0.01)	+0.12 (0.004)		+1.68 (0.02)	+0.11 (0.01)	+0.24 (0.01)
	4	+1.64 (0.01)	+0.08 (0.004)		+1.76 (0.01)	+0.15 (0.004)	+0.39 (0.01)
SEX [‡]	1	0	0	0	0	0	0
	2	-6.18 (0.01)	+0.28 (0.003)	-2.18 (0.01)	-8.37 (0.01)	+1.14 (0.003)	-2.67 (0.01)
BREED [†]	1	0	0	0	0	0	0
	2	-1.03 (0.01)	+1.29 (0.004)	-0.73 (0.01)	-3.50 (0.01)	+0.79 (0.004)	-1.04 (0.01)
AGE(/day)		0.177 (0.013)	0.03 (0.004)	0.06 (0.01)	0.131 (0.01)	0.03 (0.004)	0.04 (0.01)
YEAR OF BIRTH	1984	0	0	-	0	0	-
	1985	-1.56 (0.03)	+0.80 (0.01)	-	+0.57 (0.04)	+1.08 (0.01)	-
	1986	+2.28 (0.02)	+0.35 (0.01)	-	+7.20 (0.03)	+1.93 (0.01)	-
	1987	+2.20 (0.02)	-0.07 (0.01)	0	+3.36 (0.04)	-0.06 (0.01)	0
	1988	-0.24 (0.04)	-0.46 (0.01)	-0.84 (0.02)	-6.30 (0.06)	-2.04 (0.02)	-5.10 (0.03)
	1989	-9.77 (0.04)	-2.26 (0.01)	-3.58 (0.02)	-6.22 (0.03)	-0.45 (0.01)	-2.26 (0.02)
	1990	-1.61 (0.03)	-1.14 (0.01)	-1.03 (0.02)	+3.66 (0.04)	-0.32 (0.01)	-0.38 (0.02)
	1991	-2.91 (0.04)	-1.05 (0.01)	-1.36 (0.02)	-5.59 (0.05)	-0.95 (0.01)	-0.93 (0.02)
	1992	-	-	-	-2.72 (0.03)	-1.07 (0.01)	+0.95 (0.02)
Phenotypic mean		42.84 (3.82)	3.74 (0.98)	24.64 (1.34)	48.80 (4.87)	4.24 (1.17)	25.18 (2.15)
CV(%)		8.92	26.20	5.43	9.98	27.59	8.54

- CV based on least squares means and their standard deviations

‡ - 1= rams and 2 = ewes

† - 1= Dorset Down and 2 = Border Leicester

Table 4.11: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Corriedale ewes. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) indicates an effect was not significant or level was missing. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects			
		WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	-	0	0
	2	-2.86 (0.03)		-0.59 (0.02)	-0.13 (0.002)
	3	-3.79 (0.19)		-1.45 (0.08)	-0.31 (0.02)
AOD (years)	2	0	0	0	0
	3	+1.81 (0.05)	+0.52 (0.01)	+0.59 (0.02)	+0.11 (0.005)
	4	+1.56 (0.04)	+0.17 (0.01)	+0.37 (0.02)	+0.12 (0.004)
AGE(/day)		0.140 (0.026)	0.03 (0.01)	0.05 (0.01)	0.01 (0.002)
YEAR OF BIRTH					
	1989	0	0	0	0
	1990	+6.31 (0.07)	+1.64 (0.02)	+0.81 (0.03)	-0.58 (0.01)
	1991	+7.77 (0.08)	+1.12 (0.02)	+1.81 (0.03)	+0.12 (0.01)
	1992	+13.69 (0.07)	+1.46 (0.02)	+3.30 (0.03)	+0.10 (0.01)
Phenotypic mean		46.29 (5.62)	4.10 (0.74)	24.42 (1.42)	3.32 (0.33)
CV(%)		12.15	18.05	5.82	9.94

- CV based on least squares means and their standard deviations

Table 4.12: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for Corriedale rams. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects			
		WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	0	0	0
	2	-3.72 (0.04)	-0.25 (0.01)	-0.56 (0.01)	-0.17 (0.003)
	3	-4.43 (0.19)	-0.45 (0.04)	-1.23 (0.07)	-0.28 (0.01)
AOD (years)	2	0	0	-	0
	3	+1.91 (0.07)	+0.28 (0.01)		+0.16 (0.004)
	4	+1.33 (0.05)	+0.01 (0.01)		+0.13 (0.004)
AGE(/day)		0.215 (0.033)	0.03 (0.01)	0.05 (0.01)	-
YEAR OF BIRTH	1989	0	0	0	0
	1990	+7.35 (0.07)	-0.45 (0.01)	-1.25 (0.02)	-0.49 (0.005)
	1991	-2.57 (0.06)	-0.97 (0.02)	-1.55 (0.02)	-0.20 (0.004)
	1992	-4.44 (0.07)	-1.11 (0.02)	-1.84 (0.03)	-0.30 (0.01)
Phenotypic mean		52.06 (5.17)	3.87 (0.51)	25.88 (0.81)	3.23 (0.20)
CV(%)		9.94	13.18	3.14	6.19

- CV based on least squares means and their standard deviations

Table 4.13: Correction factor estimates for significant ($P < 0.10$) fixed effects and covariables from SAS GLM procedures for sexes combined Corriedale. Standard deviation for covariable and standard error of differences for fixed effect in brackets. Least squares mean weights and tissue depths with their standard deviations and coefficients of variation (CV) are at the bottom of the table. A dash (-) on its own indicates that an effect was not significant whereas within an effect it indicates missing level. The full names of abbreviations are presented in the list of abbreviations.

Effect		Estimates of environmental effects			
		WLW(kg)	WFD(mm)	WMD(mm)	GFWT(kg)
BR	1	0	0	0	0
	2	-3.34 (0.02)	-0.26 (0.004)	-0.61 (0.01)	-0.16 (0.001)
	3	-3.54 (0.12)	-0.48 (0.02)	-1.12 (0.04)	-0.26 (0.01)
AOD (years)	2	0	0	0	0
	3	+1.50 (0.04)	+0.26 (0.01)	+0.40 (0.01)	+0.13 (0.002)
	4	+1.28 (0.03)	+0.04 (0.01)	+0.12 (0.04)	+0.12 (0.002)
SEX [‡]	1	0	0	0	0
	2	-11.04 (0.02)	-1.23 (0.004)	-3.56 (0.01)	-0.19 (0.001)
AGE(/day)		0.166 (0.011)	0.05 (0.002)	0.08 (0.004)	0.01 (0.001)
YEAR OF BIRTH	1989	0	0	0	0
	1990	+6.07 (0.03)	+0.34 (0.01)	-0.31 (0.01)	-0.58 (0.002)
	1991	+1.76 (0.03)	-0.50 (0.01)	-0.34 (0.01)	-0.08 (0.002)
	1992	+5.71 (0.04)	+0.22 (0.01)	+1.00 (0.01)	-0.08 (0.003)
Phenotypic mean		49.61 (2.98)	4.02 (0.37)	25.30 (0.63)	3.30 (0.27)
CV(%)		6.01	9.20	2.49	8.18

- CV based on least squares means and their standard deviations

‡ - 1= rams and 2 = ewes

CHAPTER 5

GENETIC AND PHENOTYPIC PARAMETER ESTIMATES

5.0 Introduction

Parameter estimates presented here were estimated largely by the method described in section 3.6. Parameter estimates involving the index appear in italics because these were derived algebraically as detailed in Appendix D. Index 2 coefficients were used in these derivations because the majority of animals were selected using this index (see Chapter 3). No genetic or phenotypic parameter estimates were derived between the index and greasy fleece weight because there were no coefficients between these traits.

5.1 General trends

Tables 5.1 to 5.22 detail genetic and phenotypic parameters estimated in this study. Average liveweights, tissue depths and greasy fleece weights for these animals were shown in Tables 4.1 to 4.13. Generally, the magnitude of genetic and phenotypic parameters for index component traits and greasy fleece weight estimated in this study were similar across data sets and subsets within breed, suggesting that there were no major artefacts in data structures. Genetic and phenotypic parameter estimates from larger data sets *e.g. seasonXsex-trait* analyses and *seasonXsexXbreed-trait* analyses were estimated with less (33% or more) sampling error than those from smaller data sets. Sampling errors of genetic correlations were relatively large compared to those of corresponding phenotypic correlations (Tables 5.1 to 5.22).

Predominantly moderate (0.10 to 0.30) to high (>0.30) heritabilities were estimated for most index component traits and greasy fleece weight. Of note is the low (<0.10) heritability estimate for muscle depth in autumn and in winter for the Border Leicester ewes and *seasonXsex-trait* analysis of Border Leicesters in autumn. Generally, both genetic and phenotypic correlations between index component traits and between liveweight and greasy fleece weight were positive and of low (0.20 to 0.40) to moderate (0.40 to 0.60) magnitude. However, genetic and phenotypic correlations between muscle depth and greasy fleece weight and between fat depth and greasy fleece weight were generally very low (-0.20 to 0.20) to low with about half of the estimates being negative.

Generally moderate to high heritabilities (0.11-0.50) were derived for the index. High, positive (>0.60) genetic and phenotypic correlations between the index and muscle depth or the index and liveweight were found. However, genetic correlations between the index and fat depth were lower (-0.65 to 0.28) with phenotypic correlations being very low (Tables 5.1 to 5.19).

Comparisons of genetic and phenotypic parameter estimates between data sets showed that while they varied in magnitude, most were not significantly different ($P>0.05$) from each other because of large sampling errors relative to estimates, particularly for genetic correlations.

Generally, genetic correlations between autumn traits and winter traits or spring traits for *season-trait* analyses were high (>0.80) for liveweight ($n=300-1334$) and fat depth ($n=300-696$) and low (>0.25) to moderate for muscle depth ($n=80-170$). Genetic correlations between muscle depth and other traits had higher sampling errors than those of liveweight and fat depth. Similar observations were evident for genetic correlations between winter and autumn or spring for *sex-trait* analyses in Border Leicesters, Coopworths and Dorset Downs, except genetic correlations for muscle depth measurements between seasons were high (Table 5.23). Similarly, for *seasonXsex-trait* analyses Border Leicesters and Dorset Downs and *seasonXsexXbreed-trait* analysis genetic correlations between autumn and winter were high for liveweight ($n=687-1618$) and fat depth ($n=628-1479$), with those of muscle depth ($n=164-440$) being moderate with high sampling errors (Table 5.24).

5.2 Specific trends

In the following sections, significantly different ($P<0.05$) results were based on *t-test*.

5.2.1 Season-trait analysis

Neither genetic nor phenotypic parameter estimates differed significantly between autumn and winter for Border Leicester ewes (Tables 5.1 and 5.2).

In Border Leicester ram data subsets, none of the heritability estimates significantly differed between autumn and winter. However, the genetic correlation between fat depth and greasy fleece weight was significantly greater in winter than autumn. Furthermore, this estimate was positive in winter whereas in autumn it was negative. None of the phenotypic correlations significantly differed between autumn and winter (Tables 5.3 and 5.4).

For Coopworth and Dorset Down ram and ewe data subsets there were no significantly different parameter estimates between seasons (Tables 5.7-5.10, 5.12-5.15).

5.2.2 Sex-trait analysis

Generally, for Border Leicester and Dorset Down, ewe and ram data subsets there were no discernible trends in either heritability or genetic correlations between the sexes either in autumn or in winter. However, the phenotypic correlation between fat depth and muscle depth was significantly greater in Border Leicester ewe than ram data subset in autumn (Tables 5.1-5.4, 5.12-5.15).

A significantly greater heritability estimate for muscle depth was found for Coopworth ewes than rams in autumn. However, there were no discernible trends for either genetic or phenotypic correlations between the sexes in autumn (Tables 5.7-5.10).

For Corriedales, none of the heritability estimates differed significantly between sexes in winter. However, the genetic correlation between muscle depth and greasy fleece weight was significantly greater in ewes than rams. Furthermore, the estimate for ewes was positive whilst that for rams was negative. There were no apparent trends in phenotypic correlations between the sexes (Tables 5.20 and 5.21).

5.2.3 *Breed-trait analyses*

Neither genetic nor phenotypic parameter estimates differed significantly for similar traits within ewe and ram data subsets in autumn and winter (Tables 5.1- 5.4, 5.7, 5.8-5.10, 5.12-5.15).

5.2.4 *SeasonXsex-trait analysis*

Heritability estimates for liveweight, fat and muscle depths were significantly greater for Border Leicesters in winter than in autumn. For this breed generally, all genetic correlations were significantly greater for winter than autumn traits. However, there were no significant trends in phenotypic correlation estimates between seasons for Dorset Downs (Tables 5.5-5.6, 5.16-5.17).

5.2.5 *BreedXsex-trait analyses*

For autumn traits, significantly lower heritability estimates for liveweight and muscle depth were observed in Border Leicesters than either Coopworths or Dorset Downs, which had similar estimates. A significantly greater heritability estimate for fat depth was observed in Border Leicesters than Coopworths. A significantly lower genetic correlation between liveweight and muscle depth was observed in Border Leicesters than either Coopworths or Dorset Downs, which had similar estimates. The genetic correlation between muscle depth and greasy fleece was significantly greater in Coopworths than Border Leicesters. This estimate was positive in Coopworths, but negative in Border Leicesters. For autumn traits, all phenotypic correlation estimates were significantly greater in Border Leicesters than Dorset Downs. Comparatively, between Border Leicesters and Coopworths none of the phenotypic correlations significantly differed in autumn (Tables 5.5, 5.11 and 5.16).

Significantly greater heritability estimates were found for liveweight and fat depth in Border Leicesters than in both Corriedales and Dorset Downs, which had similar estimates in winter. The heritability for muscle depth was significantly greater in Corriedales than Border Leicesters. The only genetic correlation which significantly differed between *breedXsex-trait* analyses was for fat depth and greasy

fleece weight between Border Leicesters and Corriedales only, with Border Leicesters having a greater estimate than Corriedales. Furthermore, the genetic correlation between fat depth and greasy fleece weight was positive in Border Leicesters whereas it was negative in Corriedales. All phenotypic correlations were significantly greater in Corriedales than Border Leicesters except the phenotypic correlation between fat depth and greasy fleece which was not significantly different between the two data sets (Tables 5.6, 5.17 and 5.22).

5.2.6 *SeasonXsexXbreed-trait* analysis

There were no significantly different genetic parameter estimates between autumn and winter. However, phenotypic correlations between liveweight and muscle depth and, fat depth and muscle depth were significantly greater in autumn than in winter (Tables 5.18 and 5.19).

5.2.7 Genetic correlations across seasons and sexes

None of the genetic correlations between autumn traits and winter traits or spring traits differed significantly across sexes within breed and within sex across breeds. However, there was a tendency for genetic correlations between liveweights and fat depths to have greater estimates and lower sampling errors than those for muscle depths (Table 5.23). Similar results were observed in *seasonXsex-trait* and *seasonXsexXbreed-trait* analyses (Table 5.24).

5.3 Discussion

In the present study parameter estimates for the index component traits varied between season, sex and breed. Such variation may have been influenced by size of data sets and management.

5.3.1 Data size

The number of observations of traits of the present study varied within and between data sets. However, most data sets were of adequate size based on criteria of Koots *et al.* (1994a) and larger than those of similar studies which used 265-432 animals (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). Shaw (1987) conducted a simulation study looking at the effect of data set size ($n=60$ vs $n=180$) on estimation of heritability and verified that, larger data sets are preferred over smaller data sets to improve the accuracy of heritability estimates. However, data sets in the present study were an order of magnitude larger in size so the effects of data set size should be smaller. Furthermore, use of multivariate REML individual animal model rather than the sire model used by Shaw (1987) should further improve the precision of parameter estimation.. However, size of the data sets could have affected genetic correlations which are notoriously difficult to estimate accurately (Land, 1985).

5.3.2 Season of measurement

In the present study, heritability estimates were generally greater in winter than autumn in data sets of both ewes and rams. Ch'ang and Rae (1970) and Baker *et al.* (1979) reported similar trends in heritability of liveweight. As animals grow older genetic parameter estimates increase because individuals have had greater opportunity to express their genetic potential independent of maternal effects (Ch'ang and Rae, 1970). Environmental stress such as cold temperatures and low feed availability over winter might accentuate genetic differences, or reduce environmental variance, thereby increasing heritability (Baker *et al.*, 1979). Results from the present study favour one or both of these explanations.

In the present study, a degree of confounding occurred between sex and season of measurement. Ewes had larger data sets in autumn (Dorset Down and Border Leicester) or in spring (Coopworth) while rams had larger data sets in winter. Most often genetic (co)variances were greater and environmental (co)variances less in winter or spring than in autumn. The difference in "split" between genetic and environmental (co)variation for ewes compared to rams may be an artefact of data structure but consideration of sire family size and other statistics did not reveal obvious differences between the ewe and ram data sets. It could be postulated that autumn, spring and winter measurements are different traits insofar as they are controlled by different sets of genes, albeit largely overlapping. Such an argument is plausible if liveweight, fat and muscle depths were influenced by physical changes associated with the onset of breeding in the autumn for ewes, but not for rams in the winter. However,

no data was available to elucidate the effect of reproductive status. Corriedale ram and ewe data which were collected in winter showed that genetic parameters differed for sexes within season. Further evidence in the present study that differences in parameter estimates between seasons are real is from genetic correlations of autumn traits with winter or spring traits within sex. Such correlations were found to be less than unity (0.30 to 0.99, average 0.76), with two of the eighteen estimates being close to unity (0.98 & 0.99), although sampling errors were large relative to parameter estimates.

5.3.3 Sex

Findings from the present study support the conclusions of Baker *et al.* (1979), Parratt *et al.* (1989), Maria *et al.* (1993) and Koots *et al.* (1994a & b) that genetic parameters differ between the sexes. In the present study few significantly different parameter estimates were observed between rams and ewes in the different breeds. Heritability estimates in Coopworth and Corriedale were greater in ewes than rams and consistent with the studies of (Baker *et al.*, 1979; Warmington and Beatson, 1986). While in Dorset Down breed, the heritability estimates were greater in rams than ewes hence being consistent with the study of Parratt *et al.* (1989) who reported greater heritabilities in Romney rams than ewes from weaning to spring. There were no apparent trends in heritability trends in rams and ewes of the Border Leicester breed. Confounding occurred with the two sexes performance tested at different times of the year. In the Corriedale flock both sexes were performance tested in winter and had data sets of similar sizes, sex differences were observed in genetic parameters indicating that such differences are real.

In the present study differences in parameter estimates between sexes were due to variation in both genetic and environmental (co)variances but no consistent patterns were evident. Parratt *et al.* (1989) and Maria *et al.* (1993) who studied liveweight at different ages for rams and ewes observed this also. Differences in genetic and phenotypic parameters between sexes, if real, are important in instances where indices derived using parameter estimates obtained from one sex are applied to the other sex where there is high selection pressure in ewes. Genetic correlations between ewe traits in autumn or in spring and ram traits in winter were less than unity (0.27-0.95 average 0.74), with only one of nine estimates being close to unity (0.95). In the Corriedales where ewes and rams were measured in winter, genetic correlations between ewe and ram traits were 0.90 ± 0.38 , 0.53 ± 0.24 , 0.77 ± 0.20 and 0.80 ± 0.21 for liveweight, fat depth, muscle depth and greasy fleece weight respectively. It can be concluded that ewe and rams traits are genetically different albeit sharing a large proportion of genes.

5.3.4 Breed

Parameter estimates of the present study generally varied in magnitude between breeds. Davis (1993) and Koots *et al.* (1994a & b) have shown that significant differences in genetic parameters between breeds exist but this is not always the case (Eikje, 1974; Brash *et al.*, 1992). Nevertheless, breed

parameter estimates reported by the latter authors were of different magnitude, failing to reach significance due to large sampling errors relative to parameter estimates. Similar to the study of Brash *et al.* (1992) sampling errors in the present study were also large relative to parameter estimates, particularly those for genetic correlations. Parameter estimates of the present study did not show trends between dual purpose and meat breeds, supporting the conclusion of Fogarty (1995). Variation in parameter estimates between breeds bring into question application of a general index to improve meat production based on the premise that the genetic control of body composition is the same in all breeds.

5.3.5 Appropriateness of selection indices

Results of the present study and the other studies (Baker *et al.*, 1979; Parratt *et al.*, 1989; Maria *et al.*, 1993; Koots *et al.*, 1994a & b) demonstrate that parameter estimates differ between male and female animals and between breeds (Eikje, 1974; Brash *et al.*, 1992; Davis, 1993). Genetic and phenotypic parameter estimates derived in the present study were generally greater than those used to derive the selection index (Simm *et al.*, 1987). Young and Simm (1990) and Cameron and Bracken (1992) also reported greater realised parameter estimates than those used to construct their selection indices. The impact of variation in such parameters due to sex and breed on predicted rates of responses to selection is critically examined in Chapter 7.

Table 5.1: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Border Leicester ewes in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	4.203 (1.680)	11.34 (1.247)	0.27 (0.08)	-
LW	FD	0.712 (0.361)	2.303 (0.382)	0.47 (0.25)	0.51 (0.07)
LW	MD	0.088 (0.906)	5.493 (0.689)	0.07 (0.68)	0.59 (0.06)
LW	GFWT	0.240 (0.192)	0.468 (0.113)	0.37 (0.24)	0.43 (0.10)
<i>LW</i>	<i>INDEX</i>	<i>0.680</i>	<i>4.136</i>	<i>0.72</i>	<i>0.79</i>
FD	FD	0.537 (0.153)	1.671 (0.178)	0.24 (0.06)	-
FD	MD	0.233 (0.228)	1.805 (0.263)	0.53 (0.95)	0.57 (0.10)
FD	GFWT	0.053 (0.069)	0.077 (0.041)	0.23 (0.34)	0.21 (0.13)
<i>FD</i>	<i>INDEX</i>	<i>-0.022</i>	<i>0.473</i>	<i>-0.07</i>	<i>0.20</i>
MD	MD	0.363 (0.813)	5.470 (0.567)	0.06 (0.13)	-
MD	GFWT	-0.050 (0.153)	0.310 (0.081)	-0.26 (0.93)	0.26 (0.16)
<i>MD</i>	<i>INDEX</i>	<i>0.061</i>	<i>2.952</i>	<i>0.22</i>	<i>0.81</i>
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	<i>0.212</i>	<i>2.177</i>	<i>0.09</i>	-

Table 5.2: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Border Leicester ewes in winter. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	7.883 (2.719)	7.620 (1.471)	0.51 (0.13)	-
LW	FD	2.658 (1.137)	0.680 (0.602)	0.52 (0.28)	0.42 (0.18)
LW	MD	0.418 (1.422)	3.296 (1.015)	0.23 (0.61)	0.41 (0.13)
LW	GFWT	0.513 (0.267)	0.282 (0.119)	0.57 (0.27)	0.49 (0.16)
<i>LW</i>	<i>INDEX</i>	0.630	3.093	0.25	0.57
FD	FD	3.272 (1.058)	0.730 (0.421)	0.82 (0.24)	-
FD	MD	0.377 (0.872)	0.815 (0.550)	0.32 (1.22)	0.26 (0.23)
FD	GFWT	0.084 (0.214)	0.011 (0.061)	0.14 (0.41)	0.12 (0.28)
<i>FD</i>	<i>INDEX</i>	-1.052	0.138	-0.65	-0.27
MD	MD	0.423 (1.502)	4.864 (0.913)	0.08 (0.27)	-
MD	GFWT	-0.023 (0.239)	0.154 (0.105)	-0.11 (1.19)	0.14 (0.25)
<i>MD</i>	<i>INDEX</i>	0.089	2.686	0.15	0.72
GFWT	GFWT	0.103 (0.088)	0.065 (0.016)	0.61 (0.38)	-
GFWT	INDEX				
<i>INDEX</i>	<i>INDEX</i>	0.811	1.982	0.29	-

Table 5.3: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Border Leicester rams in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	5.503 (2.021)	16.71 (1.792)	0.25 (0.08)	-
LW	FD	0.874 (0.464)	2.139 (0.440)	0.46 (0.27)	0.42 (0.06)
LW	MD	0.839 (1.087)	4.939 (0.950)	0.28 (0.37)	0.48 (0.07)
LW	GFWT	0.030 (0.064)	0.725 (0.082)	0.06 (0.13)	0.45 (0.06)
<i>LW</i>	<i>INDEX</i>	<i>1.272</i>	<i>5.308</i>	<i>0.54</i>	<i>0.71</i>
FD	FD	0.647 (0.187)	1.627 (0.181)	0.29 (0.07)	-
FD	MD	-0.242 (0.324)	0.858 (0.324)	-0.24 (0.33)	0.16 (0.08)
FD	GFWT	-0.040 (0.024)	0.140 (0.030)	-0.23 (0.16)	0.19 (0.06)
<i>FD</i>	<i>INDEX</i>	<i>-0.273</i>	<i>0.003</i>	<i>-0.34</i>	<i>-0.09</i>
MD	MD	1.637 (0.694)	4.894 (0.670)	0.25 (0.10)	-
MD	GFWT	-0.040 (0.045)	0.177 (0.076)	-0.14 (0.17)	0.15 (0.08)
<i>MD</i>	<i>INDEX</i>	<i>1.136</i>	<i>3.086</i>	<i>0.88</i>	<i>0.84</i>
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	<i>1.021</i>	<i>2.806</i>	<i>0.27</i>	-

Table 5.4: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Border Leicester rams in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	10.85 (3.425)	15.98 (2.507)	0.41 (0.11)	-
LW	FD	2.210 (0.574)	0.549 (0.510)	0.69 (0.23)	0.36 (0.06)
LW	MD	2.621 (0.953)	3.453 (0.921)	0.75 (0.28)	0.52 (0.06)
LW	GFWT	0.362 (0.148)	0.540 (0.130)	0.45 (0.18)	0.49 (0.06)
<i>LW</i>	<i>INDEX</i>	2.689	5.334	0.82	0.83
FD	FD	0.941 (0.201)	1.144 (0.181)	0.45 (0.08)	-
FD	MD	0.457 (0.208)	0.906 (0.247)	0.44 (0.18)	0.42 (0.06)
FD	GFWT	0.085 (0.033)	0.053 (0.033)	0.36 (0.14)	0.27 (0.06)
<i>FD</i>	<i>INDEX</i>	0.226	-0.091	0.23	0.05
MD	MD	1.137 (0.402)	3.914 (0.527)	0.22 (0.07)	-
MD	GFWT	0.031 (0.051)	0.168 (0.057)	0.12 (0.18)	0.25 (0.06)
<i>MD</i>	<i>INDEX</i>	0.936	2.216	0.88	0.76
GFWT	GFWT	0.059 (0.014)	0.069 (0.011)	0.46 (0.10)	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.990	2.451	0.29	-

Table 5.5: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes combined Border Leicester flock in autumn. Standard error of estimate in brackets(< stands for less than). A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	4.852 (<0.01)	14.03 (<0.01)	0.26 (<0.01)	-
LW	FD	0.903 (<0.01)	2.070 (<0.01)	0.52 (<0.01)	0.45 (<0.01)
LW	MD	0.496 (<0.01)	5.747 (<0.01)	0.31 (<0.01)	0.58 (<0.01)
LW	GFWT	0.201 (<0.01)	0.462 (<0.01)	0.30 (<0.01)	0.34 (<0.01)
<i>LW</i>	<i>INDEX</i>	0.927	5.065	0.72	0.79
FD	FD	0.610 (<0.01)	1.656 (<0.01)	0.27 (<0.01)	-
FD	MD	0.261 (<0.01)	1.507 (<0.01)	0.46 (<0.01)	0.47 (<0.01)
FD	GFWT	-0.009 (<0.01)	0.135 (<0.01)	-0.04 (<0.01)	0.19 (<0.01)
<i>FD</i>	<i>INDEX</i>	-0.003	0.280	-0.01	0.11
MD	MD	0.524 (<0.01)	5.638 (0.01)	0.09 (<0.01)	-
MD	GFWT	-0.022 (<0.01)	0.233 (<0.01)	-0.10 (<0.01)	0.19 (<0.01)
<i>MD</i>	<i>INDEX</i>	0.224	3.269	0.53	0.81
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.342	2.673	0.11	-

Table 5.6: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes combined Border Leicester flock in winter. Standard error of estimate in brackets (< stands for less than). A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	9.138 (<0.01)	17.47 (<0.01)	0.34 (<0.01)	-
LW	FD	1.716 (<0.01)	1.801 (<0.01)	0.52 (<0.01)	0.40 (<0.01)
LW	MD	1.991 (<0.01)	4.504 (<0.01)	0.66 (<0.01)	0.54 (<0.01)
LW	GFWT	0.514 (<0.01)	0.433 (<0.01)	0.55 (<0.01)	0.41 (<0.01)
<i>LW</i>	<i>INDEX</i>	2.245	5.485	0.78	0.80
FD	FD	1.180 (<0.01)	1.673 (<0.01)	0.41 (<0.01)	-
FD	MD	0.498 (<0.01)	1.176 (<0.01)	0.46 (<0.01)	0.42 (<0.01)
FD	GFWT	0.081 (<0.01)	0.125 (<0.01)	0.24 (<0.01)	0.28 (<0.01)
<i>FD</i>	<i>INDEX</i>	-0.016	0.044	-0.02	0.01
MD	MD	1.004 (<0.01)	4.473 (0.027)	0.18 (<0.01)	-
MD	GFWT	0.027 (<0.01)	0.177 (<0.01)	0.09 (<0.01)	0.20 (<0.01)
<i>MD</i>	<i>INDEX</i>	0.691	2.591	0.73	0.75
GFWT	GFWT	0.094 (<0.01)	0.103 (<0.01)	0.48 (0.01)	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.902	2.590	0.26	-

Table 5.7: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Coopworth ewes in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	5.938 (0.751)	6.961 (0.578)	0.46 (0.04)	-
LW	FD	1.152 (0.226)	0.849 (0.199)	0.59 (0.14)	0.41 (0.04)
LW	MD	2.543 (0.550)	1.510 (0.465)	0.96 (0.24)	0.45 (0.06)
LW	GFWT	0.057 (0.049)	0.457 (0.047)	0.19 (0.18)	0.37 (0.03)
<i>LW</i>	<i>INDEX</i>	2.037	1.973	0.87	0.74
FD	FD	0.633 (0.109)	1.223 (0.109)	0.34 (0.06)	-
FD	MD	0.369 (0.188)	1.324 (0.201)	0.43 (0.23)	0.50 (0.04)
FD	GFWT	0.019 (0.017)	0.066 (0.021)	0.19 (0.20)	0.16 (0.03)
<i>FD</i>	<i>INDEX</i>	0.098	0.138	0.13	0.11
MD	MD	1.178 (0.206)	5.011 (0.437)	0.19 (0.03)	-
MD	GFWT	0.015 (0.014)	0.202 (0.055)	0.11 (0.11)	0.22 (0.06)
<i>MD</i>	<i>INDEX</i>	0.987	2.015	0.95	0.79
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.926	1.380	0.40	-

Table 5.8: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Coopworth ewes in spring. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	9.467 (1.512)	16.98 (1.181)	0.36 (0.04)	-
LW	FD	1.297 (0.337)	2.133 (0.328)	0.45 (0.13)	0.39 (0.04)
LW	MD	1.719 (0.748)	3.354 (0.600)	0.44 (0.23)	0.41 (0.07)
LW	GFWT	0.051 (0.064)	0.720 (0.066)	0.12 (0.14)	0.38 (0.03)
<i>LW</i>	<i>INDEX</i>	2.440	4.618	0.84	0.80
FD	FD	0.881 (0.146)	2.120 (0.151)	0.29 (0.04)	-
FD	MD	0.714 (0.218)	1.488 (0.229)	0.61 (0.37)	0.54 (0.10)
FD	GFWT	-0.024 (0.021)	0.106 (0.023)	-0.19 (0.13)	0.12 (0.04)
<i>FD</i>	<i>INDEX</i>	0.156	0.018	0.18	0.06
MD	MD	1.550 (0.837)	4.116 (0.462)	0.27 (0.11)	-
MD	GFWT	0.002 (0.069)	0.121 (0.044)	0.01 (0.35)	0.13 (0.07)
<i>MD</i>	<i>INDEX</i>	0.760	1.951	0.65	0.66
GFWT	GFWT	0.019 (0.008)	0.135 (0.007)	0.12 (0.06)	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.885	2.081	0.30	-

Table 5.9: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Coopworth rams in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	2.988 (0.954)	13.21 (0.956)	0.19 (0.06)	-
LW	FD	0.389 (0.230)	1.243 (0.250)	0.40 (0.25)	0.36 (0.04)
LW	MD	2.803 (0.756)	2.691 (0.863)	0.90 (0.35)	0.55 (0.08)
LW	GFWT	0.050 (0.064)	0.348 (0.061)	0.16 (0.23)	0.28 (0.06)
<i>LW</i>	<i>INDEX</i>	<i>1.867</i>	<i>3.873</i>	<i>0.88</i>	<i>0.82</i>
FD	FD	0.309 (0.100)	0.935 (0.103)	0.25 (0.07)	-
FD	MD	0.140 (0.250)	1.069 (0.297)	0.14 (0.24)	0.44 (0.08)
FD	GFWT	0.032 (0.021)	0.040 (0.021)	0.31 (0.31)	0.19 (0.06)
<i>FD</i>	<i>INDEX</i>	<i>-0.015</i>	<i>0.282</i>	<i>-0.02</i>	<i>0.14</i>
MD	MD	3.228 (0.993)	2.972 (1.070)	0.52 (0.14)	-
MD	GFWT	0.100 (0.106)	0.058 (0.082)	0.30 (0.54)	0.18 (0.17)
<i>MD</i>	<i>INDEX</i>	<i>2.169</i>	<i>1.479</i>	<i>0.98</i>	<i>0.84</i>
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	<i>1.517</i>	<i>1.514</i>	<i>0.50</i>	-

Table 5.10: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Coopworth rams in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	4.751 (1.200)	19.03 (1.158)	0.20 (0.04)	-
LW	FD	0.291 (0.222)	1.879 (0.225)	0.22 (0.17)	0.37 (0.03)
LW	MD	0.839 (0.534)	4.252 (0.540)	0.37 (0.24)	0.47 (0.03)
LW	GFWT	0.043 (0.066)	0.652 (0.065)	0.11 (0.16)	0.41 (0.03)
<i>LW</i>	<i>INDEX</i>	<i>1.422</i>	<i>5.709</i>	<i>0.77</i>	<i>0.83</i>
FD	FD	0.358 (0.078)	1.074 (0.078)	0.25 (0.06)	-
FD	MD	0.120 (0.133)	0.976 (0.144)	0.19 (0.20)	0.42 (0.04)
FD	GFWT	-0.031 (0.016)	0.089 (0.016)	-0.28 (0.16)	0.14 (0.03)
<i>FD</i>	<i>INDEX</i>	<i>-0.077</i>	<i>0.315</i>	<i>-0.15</i>	<i>0.11</i>
MD	MD	1.078 (0.365)	3.769 (0.386)	0.22 (0.07)	-
MD	GFWT	-0.080 (0.042)	0.240 (0.041)	-0.38 (0.25)	0.20 (0.04)
<i>MD</i>	<i>INDEX</i>	<i>0.658</i>	<i>2.305</i>	<i>0.75</i>	<i>0.77</i>
GFWT	GFWT	0.033 (0.007)	0.090 (0.006)	0.27 (0.06)	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	<i>0.716</i>	<i>2.351</i>	<i>0.23</i>	-

Table 5.11: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes combined Coopworth flock in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	5.062 (0.445)	9.705 (0.368)	0.34 (0.03)	-
LW	FD	0.622 (0.127)	1.400 (0.112)	0.47 (0.10)	0.40 (0.03)
LW	MD	2.636 (0.260)	2.577 (0.242)	0.99 (0.11)	0.52 (0.03)
LW	GFWT	0.079 (0.037)	0.427 (0.035)	0.25 (0.14)	0.31 (0.03)
<i>LW</i>	<i>INDEX</i>	2.170	2.851	0.97	0.79
FD	FD	0.345 (0.045)	1.353 (0.045)	0.20 (0.03)	-
FD	MD	0.385 (0.083)	1.376 (0.086)	0.56 (0.13)	0.52 (0.03)
FD	GFWT	0.012 (0.013)	0.080 (0.014)	0.14 (0.16)	0.17 (0.03)
<i>FD</i>	<i>INDEX</i>	0.140	0.226	0.24	0.17
MD	MD	1.397 (0.064)	5.277 (0.171)	0.21 (0.01)	-
MD	GFWT	0.031 (0.051)	0.214 (0.034)	0.19 (0.03)	0.22 (0.03)
<i>MD</i>	<i>INDEX</i>	1.106	2.379	0.94	0.82
GFWT	GFWT	0.019 (0.010)	0.158 (0.004)	0.11 (0.06)	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.993	1.724	0.37	-

Table 5.12: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Dorset Down ewes in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	5.168 (1.345)	14.19 (1.195)	0.27 (0.06)	-
LW	FD	0.276 (0.320)	1.885 (0.271)	0.21 (0.35)	0.38 (0.10)
LW	MD	1.465 (0.506)	3.951 (0.557)	0.74 (0.58)	0.54 (0.08)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	1.835	4.351	0.94	0.82
FD	FD	0.321 (0.266)	1.319 (0.106)	0.20 (0.14)	-
FD	MD	0.249 (0.365)	1.029 (0.164)	0.50 (0.44)	0.44 (0.08)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.002	0.200	0.04	0.09
MD	MD	0.762 (0.584)	4.478 (0.407)	0.14 (0.10)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	0.588	2.540	0.78	0.80
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.740	2.191	0.25	-

Table 5.13: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Dorset Down ewes in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	5.912 (1.886)	14.82 (1.710)	0.29 (0.08)	-
LW	FD	0.394 (0.561)	2.293 (0.534)	0.17 (0.27)	0.34 (0.08)
LW	MD	1.330 (0.667)	4.130 (0.789)	0.86 (0.85)	0.61 (0.10)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	<i>1.888</i>	<i>4.357</i>	<i>0.81</i>	<i>0.80</i>
FD	FD	0.911 (0.387)	2.101 (0.294)	0.30 (0.11)	-
FD	MD	0.109 (0.358)	1.328 (0.327)	0.18 (0.54)	0.42 (0.10)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	<i>-0.378</i>	<i>-0.008</i>	<i>-0.41</i>	<i>-0.13</i>
MD	MD	0.403 (0.469)	3.406 (0.529)	0.11 (0.11)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	<i>0.463</i>	<i>1.897</i>	<i>0.76</i>	<i>0.71</i>
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	<i>0.913</i>	<i>2.005</i>	<i>0.31</i>	-

Table 5.14: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Dorset Down rams in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	7.941 (2.351)	21.60 (2.172)	0.27 (0.07)	-
LW	FD	0.095 (0.397)	2.12 (0.383)	0.06 (0.23)	0.32 (0.04)
LW	MD	1.599 (1.059)	3.802 (1.049)	0.34 (0.24)	0.39 (0.07)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	2.698	5.995	0.84	0.80
FD	FD	0.378 (0.124)	1.305 (0.120)	0.22 (0.07)	-
FD	MD	0.568 (0.226)	0.469 (0.239)	0.56 (0.27)	0.31 (0.07)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.077	-0.002	0.11	0.03
MD	MD	2.713 (0.744)	3.829 (0.752)	0.42 (0.10)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	1.373	2.516	0.73	0.76
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	1.289	2.708	0.32	-

Table 5.15: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Dorset Down rams in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	14.24 (3.242)	19.82 (2.429)	0.42 (0.08)	-
LW	FD	1.044 (0.424)	1.206 (0.366)	0.42 (0.17)	0.33 (0.04)
LW	MD	2.923 (0.892)	3.326 (0.826)	0.61 (0.20)	0.47 (0.04)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	4.358	5.852	0.93	0.86
FD	FD	0.424 (0.103)	0.944 (0.099)	0.31 (0.07)	-
FD	MD	0.449 (0.146)	0.364 (0.164)	0.54 (0.20)	0.31 (0.04)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.231	-0.071	0.28	0.07
MD	MD	1.616 (0.380)	3.541 (0.455)	0.31 (0.07)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	1.246	2.320	0.79	0.77
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	1.554	2.618	0.37	-

Table 5.16: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes combined Dorset Down flock in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic	Residual	h^2 or	r_P
X	Y	(co)variance	(co)variance	r_G	
LW	LW	7.951 (1.322)	16.33 (1.029)	0.33 (0.04)	-
LW	FD	0.420 (0.233)	1.909 (0.212)	0.25 (0.14)	0.36 (0.03)
LW	MD	1.850 (0.469)	4.202 (0.484)	0.67 (0.18)	0.51 (0.03)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	2.632	4.992	0.93	0.83
FD	FD	0.347 (0.072)	1.388 (0.075)	0.20 (0.04)	-
FD	MD	0.279 (0.096)	0.994 (0.127)	0.48 (0.17)	0.40 (0.03)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.038	0.149	0.06	0.08
MD	MD	0.958 (0.226)	4.854 (0.344)	0.17 (0.04)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	0.761	2.804	0.78	0.79
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	1.001	2.508	0.28	-

Table 5.17: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes combined Dorset Down flock in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	8.612 (0.445)	23.13 (1.384)	0.27 (0.01)	-
LW	FD	0.955 (0.120)	2.383 (0.297)	0.42 (0.07)	0.39 (0.03)
LW	MD	1.470 (0.346)	4.200 (0.533)	0.48 (0.28)	0.45 (0.07)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	2.305	6.416	0.87	0.82
FD	FD	0.594 (0.078)	1.732 (0.110)	0.26 (0.03)	-
FD	MD	0.431 (0.204)	0.827 (0.154)	0.54 (0.25)	0.37 (0.07)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.101	-0.012	0.14	0.03
MD	MD	1.080 (0.761)	3.868 (0.321)	0.22 (0.13)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	0.636	2.427	0.68	0.73
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.822	2.776	0.23	-

Table 5.18: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes and breeds combined Border Leicester and Dorset Down flocks in autumn. Standard error of estimate in brackets. A dash (-) indicates parameter was tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable					
X	Y	Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
LW	LW	8.355 (1.111)	16.93 (0.875)	0.33 (0.04)	-
LW	FD	0.964 (0.212)	2.113 (0.199)	0.44 (0.10)	0.42 (0.03)
LW	MD	1.729 (0.380)	5.476 (0.424)	0.69 (0.16)	0.57 (0.03)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	2.360	5.635	0.94	0.84
FD	FD	0.566 (0.069)	1.543 (0.075)	0.27 (0.03)	-
FD	MD	0.493 (0.120)	1.267 (0.130)	0.60 (0.14)	0.48 (0.03)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.149	0.241	0.23	0.14
MD	MD	0.767 (0.187)	5.489 (0.301)	0.12 (0.03)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	0.514	3.269	0.68	0.80
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.751	2.838	0.21	-

Table 5.19: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes and breeds combined Border Leicester and Dorset Down flocks in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable					
X	Y	Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
LW	LW	9.387 (0.502)	21.41 (1.087)	0.30 (0.01)	-
LW	FD	1.461 (0.122)	2.274 (0.253)	0.52 (0.06)	0.41 (0.03)
LW	MD	1.994 (0.338)	3.862 (0.441)	0.40 (0.14)	0.34 (0.03)
LW	GFWT	-	-	-	-
<i>LW</i>	<i>INDEX</i>	2.456	5.887	0.86	0.82
FD	FD	0.824 (0.054)	1.834 (0.099)	0.31 (0.01)	-
FD	MD	0.618 (0.115)	1.177 (0.148)	0.42 (0.16)	0.30 (0.04)
FD	GFWT	-	-	-	-
<i>FD</i>	<i>INDEX</i>	0.184	0.070	0.22	0.09
MD	MD	1.291 (0.479)	3.926 (0.279)	0.25 (0.07)	-
MD	GFWT	-	-	-	-
<i>MD</i>	<i>INDEX</i>	0.760	2.167	0.72	0.70
GFWT	GFWT	-	-	-	-
GFWT	INDEX	-	-	-	-
<i>INDEX</i>	<i>INDEX</i>	0.872	2.471	0.26	-

Table 5.20: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Corriedale ewes in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	19.43 (5.672)	9.472 (2.241)	0.67 (0.16)	-
LW	FD	2.079 (0.655)	1.359 (0.451)	0.53 (0.20)	0.47 (0.10)
LW	MD	4.298 (0.823)	2.445 (0.735)	0.72 (0.20)	0.59 (0.10)
LW	GFWT	0.817 (0.236)	0.392 (0.150)	0.49 (0.20)	0.50 (0.14)
LW	INDEX	-	-	-	-
FD	FD	0.794 (0.156)	1.076 (0.148)	0.42 (0.07)	-
FD	MD	0.824 (0.174)	0.532 (0.178)	0.68 (0.13)	0.47 (0.06)
FD	GFWT	0.061 (0.054)	0.043 (0.035)	0.18 (0.17)	0.17 (0.10)
FD	INDEX	-	-	-	-
MD	MD	1.832 (0.322)	2.706 (0.354)	0.40 (0.06)	-
MD	GFWT	0.187 (0.078)	0.100 (0.055)	0.37 (0.13)	0.30 (0.08)
MD	INDEX	-	-	-	-
GFWT	GFWT	0.142 (0.030)	0.063 (0.016)	0.69 (0.11)	-
GFWT	INDEX	-	-	-	-
INDEX	INDEX	-	-	-	-

Table 5.21: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for Corriedale rams in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	7.996 (3.005)	26.75 (2.859)	0.23 (0.08)	-
LW	FD	1.492 (0.424)	2.400 (0.491)	0.63 (0.21)	0.52 (0.06)
LW	MD	1.267 (0.813)	6.102 (0.872)	0.33 (0.18)	0.56 (0.03)
LW	GFWT	0.197 (0.158)	1.009 (0.164)	0.26 (0.20)	0.47 (0.04)
LW	INDEX	-	-	-	-
FD	FD	0.704 (0.124)	0.909 (0.133)	0.44 (0.07)	-
FD	MD	0.504 (0.147)	0.799 (0.181)	0.44 (0.16)	0.46 (0.06)
FD	GFWT	-0.040 (0.030)	0.162 (0.033)	-0.18 (0.14)	0.22 (0.06)
FD	INDEX	-	-	-	-
MD	MD	1.844 (0.365)	3.105 (0.410)	0.37 (0.07)	-
MD	GFWT	-0.094 (0.054)	0.317 (0.058)	-0.26 (0.16)	0.23 (0.06)
MD	INDEX	-	-	-	-
GFWT	GFWT	0.070 (0.016)	0.121 (0.016)	0.37 (0.07)	-
GFWT	INDEX	-	-	-	-
INDEX	INDEX	-	-	-	-

Table 5.22: Estimates of genetic and residual (co)variances, heritability (h^2), genetic correlation (r_G), and phenotypic correlation (r_P) from multivariate AIREML analyses for sexes combined Corriedale flock in winter. Standard error of estimate in brackets. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	9.429 (2.578)	34.76 (2.373)	0.21 (0.06)	-
LW	FD	1.229 (0.354)	3.372 (0.385)	0.53 (0.16)	0.51 (0.03)
LW	MD	1.637 (0.615)	8.185 (0.690)	0.44 (0.14)	0.64 (0.03)
LW	GFWT	0.428 (0.130)	1.133 (0.130)	0.44 (0.14)	0.51 (0.03)
LW	INDEX	-	-	-	-
FD	FD	0.575 (0.086)	1.306 (0.099)	0.31 (0.04)	-
FD	MD	0.535 (0.095)	1.066 (0.133)	0.58 (0.13)	0.50 (0.03)
FD	GFWT	-0.014 (0.023)	0.149 (0.024)	-0.06 (0.10)	0.22 (0.03)
FD	INDEX	-	-	-	-
MD	MD	1.490 (0.211)	3.930 (0.287)	0.28 (0.04)	-
MD	GFWT	0.001 (0.037)	0.326 (0.042)	0.003 (0.10)	0.31 (0.04)
MD	INDEX	-	-	-	-
GFWT	GFWT	0.100 (0.013)	0.109 (0.011)	0.48 (0.06)	-
GFWT	INDEX	-	-	-	-
INDEX	INDEX	-	-	-	-

Table 5.23: Genetic correlation estimates (\pm standard error) between autumn and winter or spring from joint multivariate AIREML analyses for separate ewe and ram traits for Border Leicester (BL), Coopworth (CPW) and Dorset Down (DD) flocks and for similar traits across sexes Border Leicester (BLc) and Dorset Down (DDc) and Coopworth (CPWc). Across sexes genetic correlations between traits for ewes in autumn or spring and for rams in winter. Number of observations in brackets. Standard error of estimates for DDrams not presented because they were all less than 0.01. A dash (-) indicates parameter not tabulated. The full names of abbreviations are presented in the list of abbreviations.

Traits		Genetic correlation								
		BLewes	BLrams	BLc	CPWewes	CPWrams	CPWc	DDewes	DDrams	DDc
ALW	WLW	0.92\pm0.14 (n=386)	0.88\pm0.21 (n=301)	0.85\pm0.35 (n=647 & 608)	-	0.80\pm0.18 (n=1109)	-	0.92 (n=509)	0.98\pm0.17 (n=422)	0.95\pm0.25 (n=923 & 820)
AFD	WFD	0.80\pm0.18 (n=322)	0.79\pm0.23 (n=306)	0.91\pm0.28 (n=621 & 613)	-	0.57\pm0.24 (n=668)	-	0.99 (n=430)	0.87\pm0.23 (n=421)	0.59\pm0.34 (n=925 & 819)
AMD	WMD	0.30\pm0.40 (n=84)	0.72\pm0.48 (n=80)	0.27\pm0.78 (n=349 & 377)	-	0.36\pm0.35 (n=170)	-	0.86 (n=106)	0.64\pm0.44 (n=170)	0.85\pm0.44 (n=586 & 557)
ALW	SLW	-	-	-	0.86\pm0.16 (n=1334)	-	-	-	-	-
AFD	SFD	-	-	-	0.84\pm0.16 (n=696)	-	-	-	-	-
AMD	SMD	-	-	-	0.59\pm0.11 (n=159)	-	-	-	-	-
WLW	SLW	-	-	-	-	-	0.72\pm0.20 (n=1711 & 2021)	-	-	-
WFD	SFD	-	-	-	-	-	0.75\pm0.23 (n=1525 & 1516)	-	-	-
WMD	SMD	-	-	-	-	-	0.79\pm0.34 (n=645 & 598)	-	-	-

Table 5.24: Genetic correlation estimates (\pm standard error) between autumn and winter traits from joint multivariate AIREML analyses of autumn and winter data sets for combined sexes Border Leicester (BL) and Dorset Down (DD). Genetic correlations between autumn and winter traits are also presented for sexes and breeds combined Border Leicester and Dorset Down (BD). Number of observations in brackets. Standard error of estimates for BL not presented because they were all less than 0.005. The full names of abbreviations are presented in the list of abbreviations.

Traits		Genetic correlation		
		BL	DD	BD
ALW	WLW	0.88 (n=687)	0.98 \pm 0.08 (n=931)	0.89 \pm 0.07 (n=1618)
AFD	WFD	0.91 (n=628)	0.96 \pm 0.16 (n=851)	0.93 \pm 0.11 (n=1479)
AMD	WMD	0.73 (n=164)	0.81 \pm 0.37 (n=276)	0.60 \pm 0.21 (n=440)

CHAPTER 6

RESPONSES TO SELECTION

6.0 Results

This Chapter examines responses to selection in index component traits for Border Leicester, Coopworth and Dorset Down genotypes and correlated response in greasy fleece weight in Border Leicester and Coopworth flocks. Critical examination of responses requires consideration of selection pressure applied. Responses were derived by the method described in Chapter 3.

6.1 Selection differentials

Two tooth ewes entering the flocks each year were selected on autumn measurements in Border Leicester and Dorset Down flocks and spring measurements in the Coopworth flock (see Chapter 3). All rams were selected on winter measurements. Figures 6.1 to 6.4 show the selection differentials applied to index component traits each year. Figure 6.5 shows correlated selection differentials applied to greasy fleece weight in the Coopworth lines. Selection differentials were calculated as the difference between the mean of the selected animals and the mean of the population to which they belong (Falconer, 1989). These were calculated separately for sexes within line and within breed since sexes were run separately from weaning onwards and different selection pressures were applied to rams and ewes.

In all flocks higher selection differentials were applied to rams than ewes. This is simply the result of rams having a higher reproductive rate than ewes hence less are needed for breeding. Higher selection differentials were applied in lean tissue growth rate lines than in controls, although none were significantly different from each other ($P>0.05$) based on *t-test* except selection differential for liveweight in the Coopworth rams which was significantly greater in the lean tissue growth rate line than the control line.

Standardised selection differentials were used to compare selection pressures applied to rams and ewes within line and between breeds within sex and within line to avoid the confounding effects of season of measurement and grazing mobs since the Coopworth flock was grazed separately from other flocks. Standardised selection differentials were calculated as selection differentials divided by their annual pre-selection phenotypic standard deviations (Falconer, 1989). Table 6.1 shows standardised selection differentials averaged across years for the index and its component traits. These calculations clearly show that higher selection pressure was applied to rams compared to ewes.

Generally, higher average standardised selection differentials were applied to the index, liveweight and muscle depth than fat depth within lines. Average standardised selection differentials for greasy fleece

weight, although not significantly different from each other ($P>0.05$), were greater in rams than ewes and in the lean tissue growth rate lines than the control lines (Table 6.1).

Since the components of aggregate breeding value (lean weight and fat weight) were not measured it was not possible to derive standardised selection differentials on the basis of selection differential and phenotypic standard deviation. Average standardised selection differentials for aggregate breeding value traits were theoretically derived based on mass selection (Falconer, 1989) using Table 2 of Becker (1992). These were calculated on the basis of selecting the 6 highest index ranking rams in the first two years of the selection programme and subsequently the 5 highest index ranking rams for all lean tissue growth rate lines. This led to selecting on average the 5 highest index rams from annual populations of 64, 61 and 93 for Border Leicester, Dorset Down and Coopworth rams respectively (see Appendix A). Resulting average annual selection intensities were 1.829, 1.792 and 1.996 respectively. For ewes on average, annual selected numbers were 43, 47 and 52 from populations of 94, 72 and 91 giving selection intensities of 0.868, 0.532 and 0.671 for Border Leicester, Dorset Down and Coopworth respectively. Therefore, overall annual selection intensities were estimated to be 1.34, 1.16 and 1.33 for Border Leicester, Dorset Down and Coopworth lean tissue growth rate flocks respectively. However, selection intensities for rams in the present study are likely to be less because within sire family selection was practised. The degree to which within family selection compromised responses could not be assessed directly because aggregate breeding value traits were not measured. However, an indirect evaluation of this effect was assessed by examining its impact on selection efficiency of the index and its component traits.

Standard definitions of mass selection and within sire family selection were used (Falconer, 1989). Mass selection differential was defined as selection differential of the 6 highest index rams in the first two years of this selection programme and subsequently the 5 highest index rams based on the index. Within sire family selection differential was defined in the same way as mass selection differential except that selection was practised within sire family, with the highest index ram in each sire family being chosen for breeding. The same number of rams as in mass selection were selected for breeding. No attempt was made to distinguish between within sire family and actual selection because the two are deemed to be the same since by definition the best animal in each sire family was kept for breeding. Selection efficiency was then defined as the selection differential of within sire family relative to selection differential from mass selection.

Table 6.2 shows high (>0.74) average selection efficiencies for the index and its component traits except for muscle depth in the Coopworth which was lower (0.48). Nearly all selection efficiencies were less than 100% except the selection efficiency for winter liveweight in Dorset Down (2.33 ± 3.27) and

Coopworth (1.19 ± 0.16) rams. A greater than 100% selection efficiency is theoretically impossible and is simply an artefact of the calculation method used. The 1.19 selection efficiency for liveweight in Coopworth rams was due to greater selection differentials for liveweight every year from within sire family selection than mass selection. While in Dorset Down rams it was due to one odd year (rams born in 1987) when the family selection differential was 2.148kg, while the mass selection differential was 0.264kg giving a selection efficiency of 8.14. Excluding this extreme value from the calculation gave an estimate of 0.87 ± 0.40 which was consistent with estimates for other traits in the index.

Degree of inbreeding did not differ significantly ($P > 0.05$) between the selected and the control lines (Table 1 Appendix E). Generally inbreeding was low in all lines, ranging between 0 and 2% per year with an average of less than 1% per year in all lines.

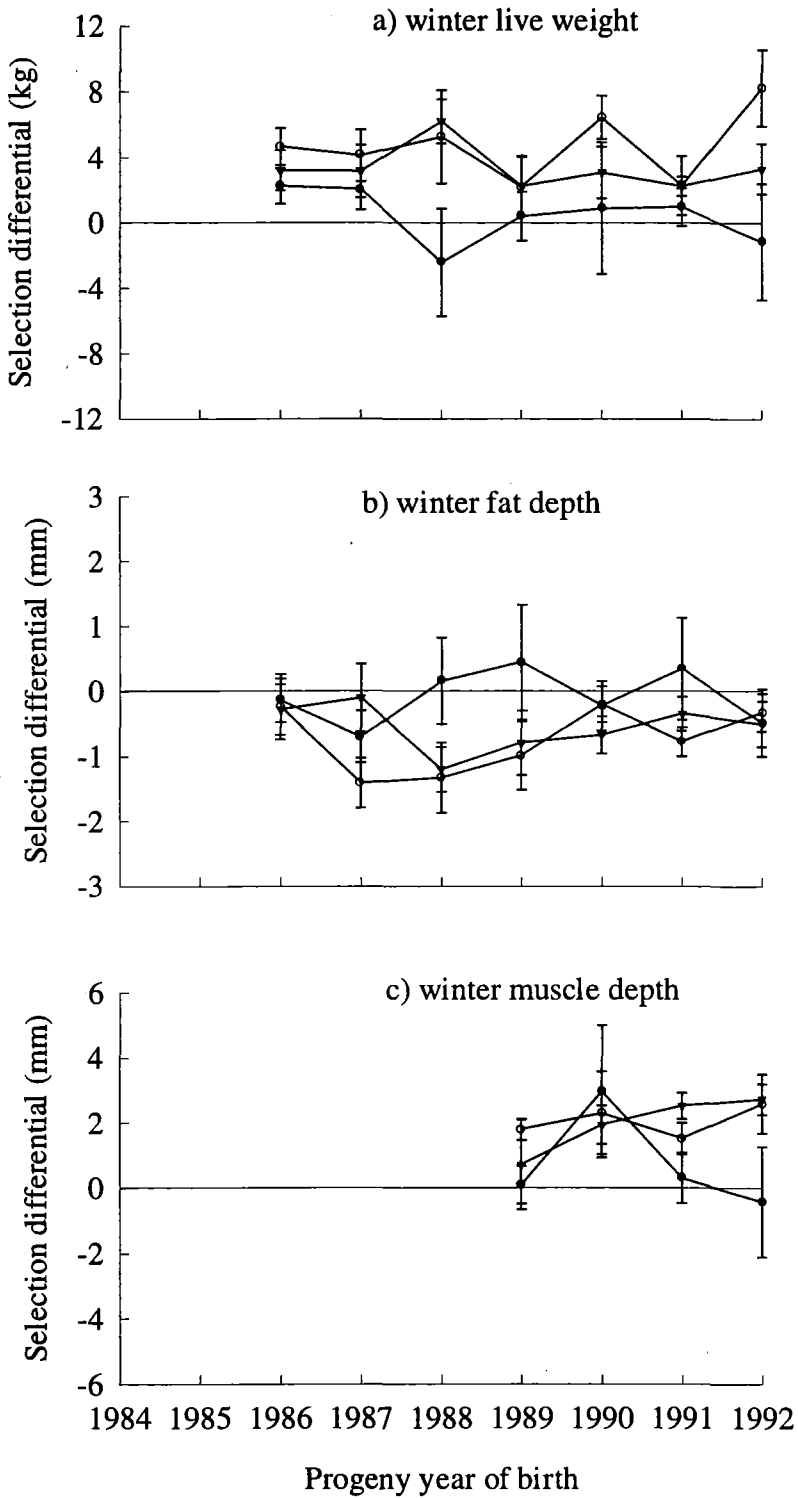


Figure 6.1: Selection differentials for index component traits for rams of the lean tissue growth rate lines for Dorset Down (O) and Border Leicester (V) plus the control line Dorset Down (●) rams. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SED. A horizontal reference line is plotted along $y=0$.

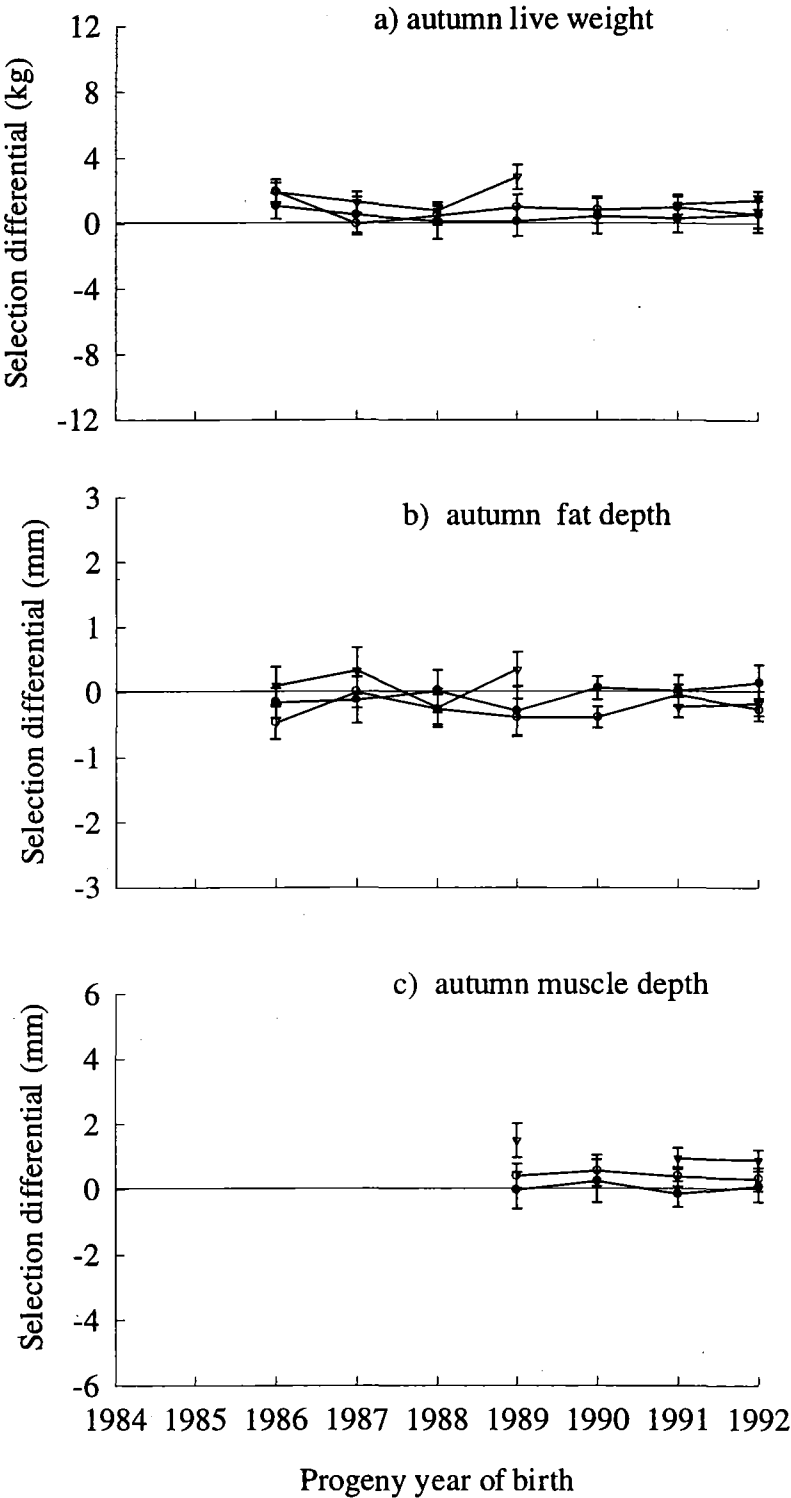


Figure 6.2: Selection differentials for index component traits for ewes of the lean tissue growth rate lines for Dorset Down (O) and Border Leicester (V) plus the control line Dorset Down (●) ewes. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SED. A horizontal reference line is plotted along $y=0$.

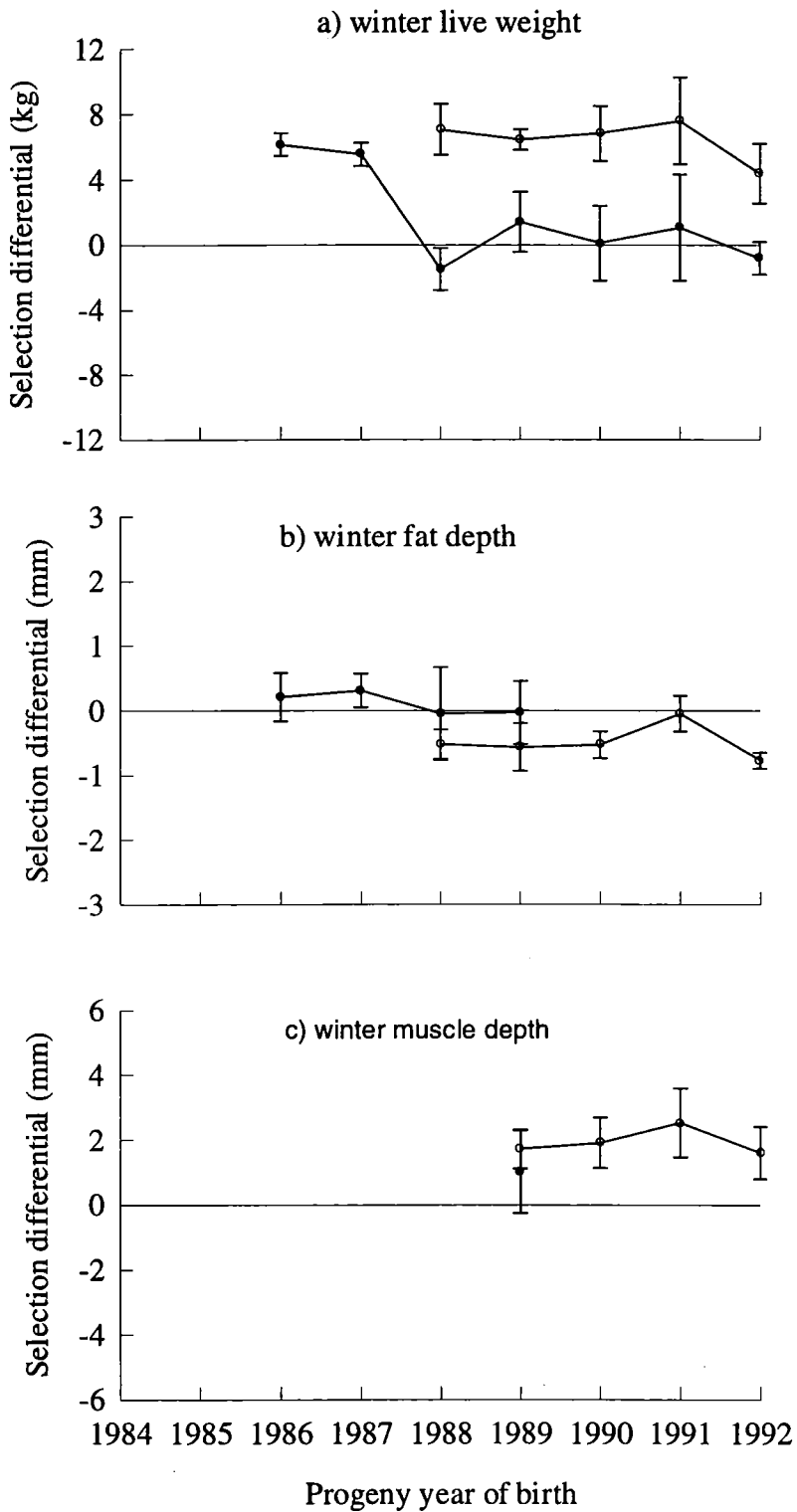


Figure 6.3: Selection differentials for index component traits in Coopworth rams of the lean tissue growth rate line (O) and the control line (●). Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SED. Rams were mated to ewes in all lines until 1988 when the lines were closed. A horizontal reference line is plotted along $y=0$.

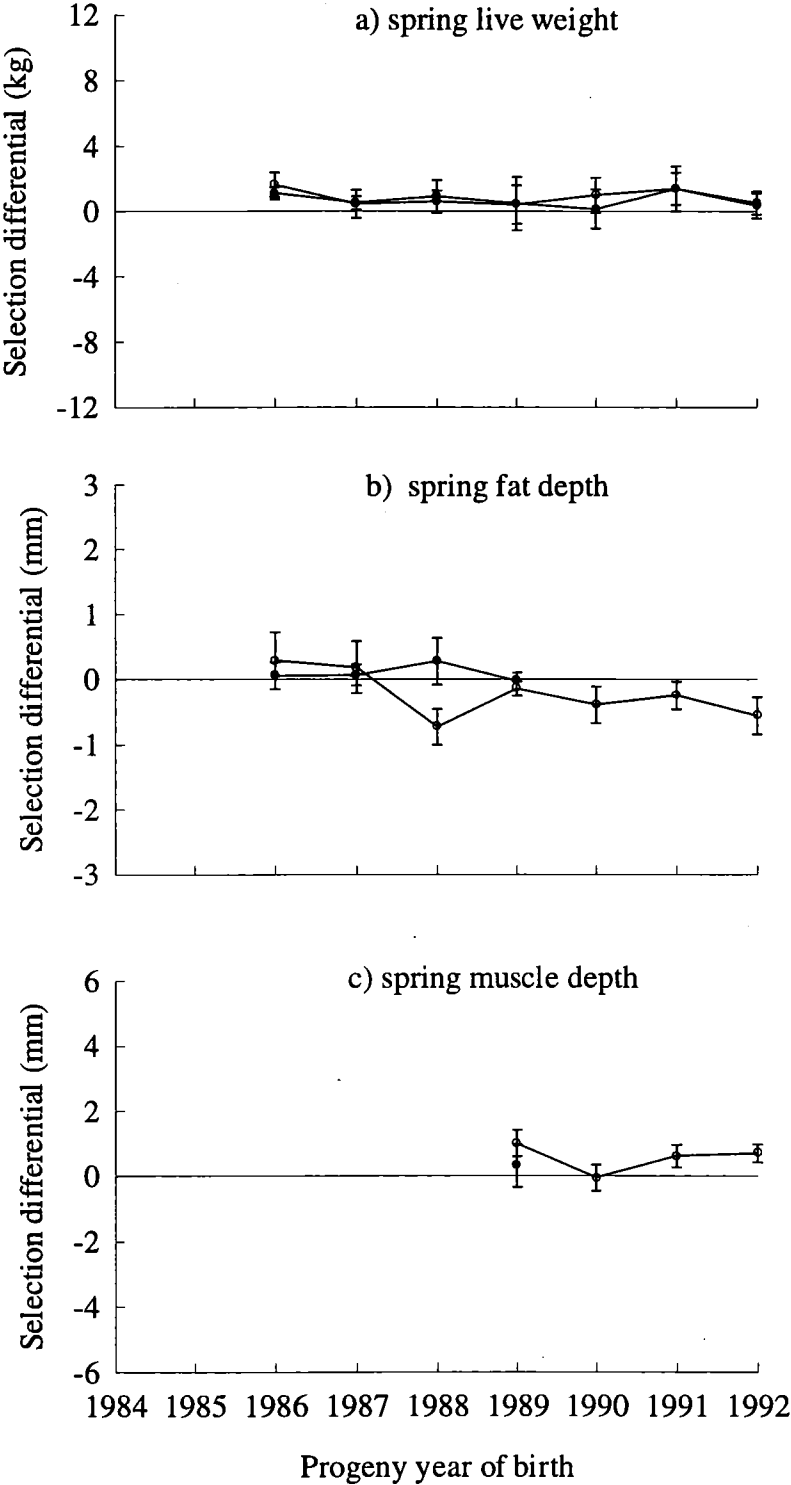


Figure 6.4: Selection differentials for index component traits in Coopworth ewes of the lean tissue growth rate line (O) and the control line (●). Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SED. A horizontal reference line is plotted along y=0.

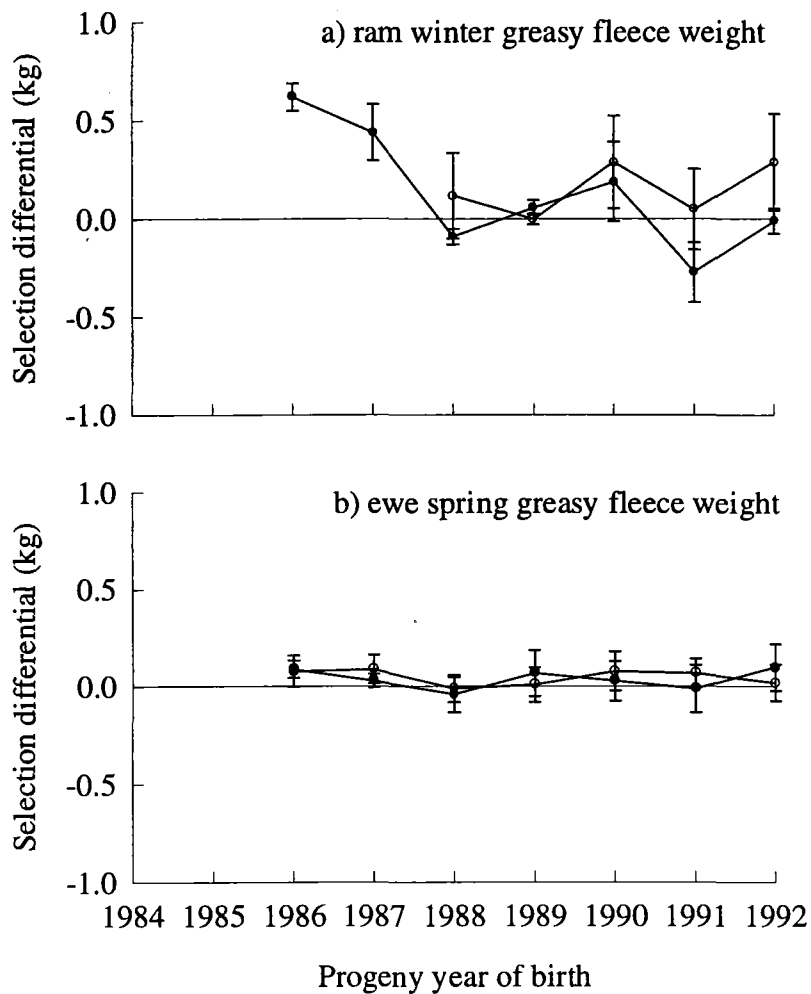


Figure 6.5: Correlated selection differentials for greasy fleece weight in Coopworth rams and ewes of the lean tissue growth rate line (O) and the control line (●). Animals born in 1989 were the first progeny from use of index 2 rams. Rams were mated to ewes in all lines until 1988 when the lines were closed. Error bar = \pm SED. A horizontal reference line is plotted along $y=0$.

Table 6.1: Average standardised selection differentials for the index (IND) and its component traits in the Border Leicester (BL), Coopworth (CP) and Dorset Down (DD) flocks. S and C are abbreviations for lean tissue growth rate selection and control lines. A dash (-) indicates trait not measured in flock. Selection intensities averaged over 7 years.

Trait	Standardised selection differential									
	BLS rams [#]	BLS ewes [*]	CPC rams [#]	CPC ewes ⁺	CPS rams [#]	CPS ewes ⁺	DDC rams [#]	DDC ewes [*]	DDS rams [#]	DDS ewes [*]
LW	0.75±0.26	0.41±0.14	0.35±0.71	0.14±0.09	1.31±0.24	0.17±0.10	0.11±0.31	0.11±0.07	0.89±0.39	0.20±0.13
FD	0.44±0.25	0.0±0.20	-	-	0.46±0.27	0.15±0.19	0.08±0.32	0.01±0.11	0.62±0.33	0.21±0.15
MD	0.89±0.46	0.46±0.06	-	-	0.85±0.12	0.27±0.20	0.23±0.50	0.01±0.07	0.96±0.22	0.20±0.04
IND	1.22±0.47	0.47±0.25	-	-	1.39±0.37	0.34±0.31	0.11±0.38	-0.02±0.14	1.35±0.18	0.43±0.12
GF	0.45±0.57	0.29±0.25	0.33±0.64	0.08±0.11	0.42±0.42	0.10±0.09	-	-	-	-

* - measured in autumn

- measured in winter

+ - measured in spring

Table 6.2: Average rams selection efficiencies for index and its components traits[§]

Traits	Selection efficiency [#]		
	Border Leicester	Dorset Down	Coopworth
Winter liveweight	0.89±0.14	2.33±3.27	1.19±0.16
Winter fat depth	0.80±0.37	0.87±0.16	0.74±0.11
Winter muscle depth	0.89±0.25	0.89±0.51	0.48±0.43
Index	0.86±0.11	0.83±0.07	0.78±0.04

§ - selection efficiencies were more than 100% in some instances because rams selected by the index within sire family had greater liveweight than those which could have been selected from mass selection in some years

- selection efficiency = selection differential for within sire family selection / selection differential for mass selection

6.2 Responses to selection

General trends in index component traits show an increase in liveweight and no visually apparent trends in fat depth across sexes and seasons for Border Leicester and Dorset Down lean tissue growth rate flocks (Figures 6.6 and 6.7). However, the changes in Coopworth ewe and ram traits show an increase in liveweight and muscle depth and a decrease in fat depth (Figures 6.8 to 6.9). Responses in all sexes and breeds appear to oscillate on a 2 year cycle *i.e* up one year and down the following year (Figures 6.6 to 6.9). For all lean tissue growth rate flocks responses in muscle depth were only apparent after 1989 when it was incorporated into the selection index (Figures 6.6 to 6.9). Patterns of change in responses for these traits closely follow those of selection differentials (Figures 6.1 to 6.4).

Correlated responses in greasy fleece weight show a marginal increase in the Coopworth lean tissue growth rate lines compare to control lines (Figures 6.10).

6.2.1 Response rates

Response rates were estimated for 2 data sets, Firstly, for animals whose parents were selected using index 1 and secondly for animals whose parents were selected using index 2. However, the resulting regression coefficients were not significantly different for the different data sets ($P > 0.05$) based on *t*-test. Therefore, data of indices 1 and 2 were combined and a single estimate produced. Due to a regular oscillating pattern of responses for liveweight and tissue depths in all lean tissue growth rate flocks (Figures 6.6 to 6.9), a founder effect was included in the regression equations. This founder effect was coded as 1 or 2 based on whether animals were born in an even or odd numbered year. This effectively grouped the 1984 born foundation rams with their sons, the 1986 born rams with their sons and so on, together as one foundation line. The other foundation line was defined in a similar way but it originated from the 1985 born foundation rams. The two lines were not genetically separate since females bred for more than one year. However, it is reasonable to suggest that a founder effect causing a difference between 1984 and 1985 foundation rams would persist as a two year cycle causing the regular oscillations observed.

The founder effect significantly ($P < 0.05$) affected regression coefficients in liveweight and fat depth for Dorset Down rams, fat depth and muscle depth in Dorset Down ewes and fat depth in Coopworth ewes and rams. The founder effect generally increased regression coefficients ($> 16\%$). Results from the combined indices data which included the founder effect are presented in Table 6.3. Regression coefficients, henceforth called response rates, generally show increases in liveweight and muscle depth

and a decrease in fat depth all flocks. There was a correlated response of increased greasy fleece weight in Border Leicester and Coopworth rams and ewes.

Although the observed response rates did not differ significantly ($P>0.05$) between sexes and same sex across breeds, they were greater for ram liveweight and muscle depth than the respective ewe traits in Border Leicester. They were greater for liveweight in Dorset Down rams than ewes. Generally, response rates were greater for liveweight and muscle depth in Dorset Down than Border Leicester data subsets. Fat depth response rates were the opposite, being greater (more negative) in ewes than rams and in Border Leicester ewe and ram data subsets than in Dorset Down ewe and ram data subsets. Increases in greasy fleece weight were higher in Border Leicester rams than ewes. In the Coopworths response rates were greater for liveweight, muscle depth and greasy fleece weight for ewes in spring than rams in winter, although this difference was not significant ($P>0.05$). The opposite was true for fat depth being greater in rams in winter than ewes in spring (Table 6.3).

Response rates were standardised to allow comparison to be made between traits and between sexes and genotypes (Table 6.4). Standardised figures were expressed as percentage changes in trait means using least squares means obtained from univariate GLM analyses presented in Tables 4.1, 4.2, 4.4, 4.5, 4.7 and 4.8. Overall, response rates were within the 1-3% per annum theoretical estimate of Smith (1984) predicted from conventional breeding programmes. Of note was the association between liveweight and fat depth whereby high response rates in fat depth were associated with low response rates in liveweight. The greatest response rates were apparent for liveweight and the least for muscle depth with fat depth being intermediate in Dorset Down flocks. However, in Border Leicester and Coopworth flocks, the greatest response rates were for fat depth and least muscle depth, with liveweight being intermediate. Relative response rates did not alter trends of the results observed in response rates between sex and between breeds within sex. Correlated response rates in greasy fleece weight were less than those of liveweight but more than those of muscle depth.

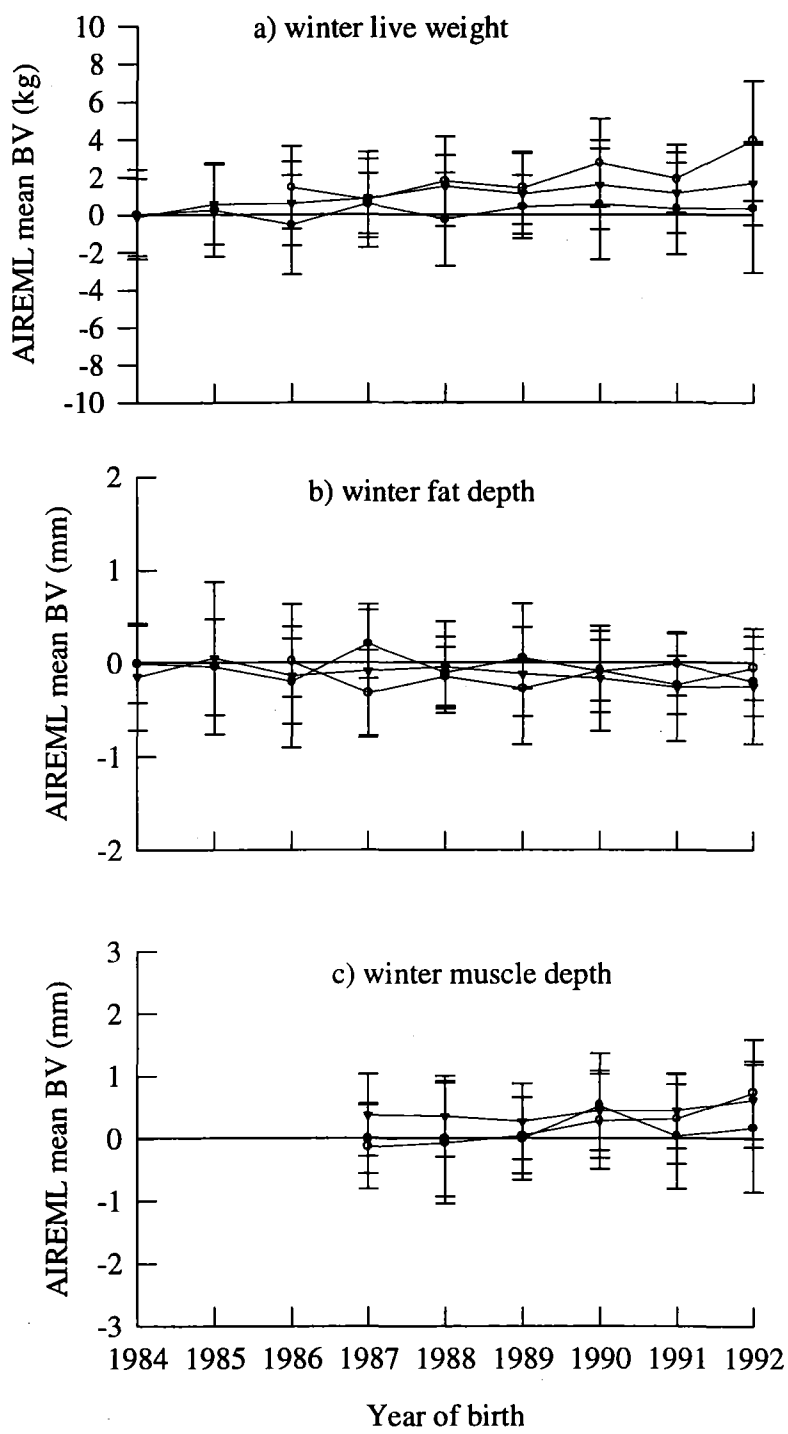


Figure 6.6: Responses to selection for index component traits for the lean tissue growth rate lines Dorset Down (O) and Border Leicester (V) plus the control line Dorset Down (●) rams. Mean breeding values (BV) output from multivariate AIREML. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SEM. A horizontal reference line is plotted along y=0.

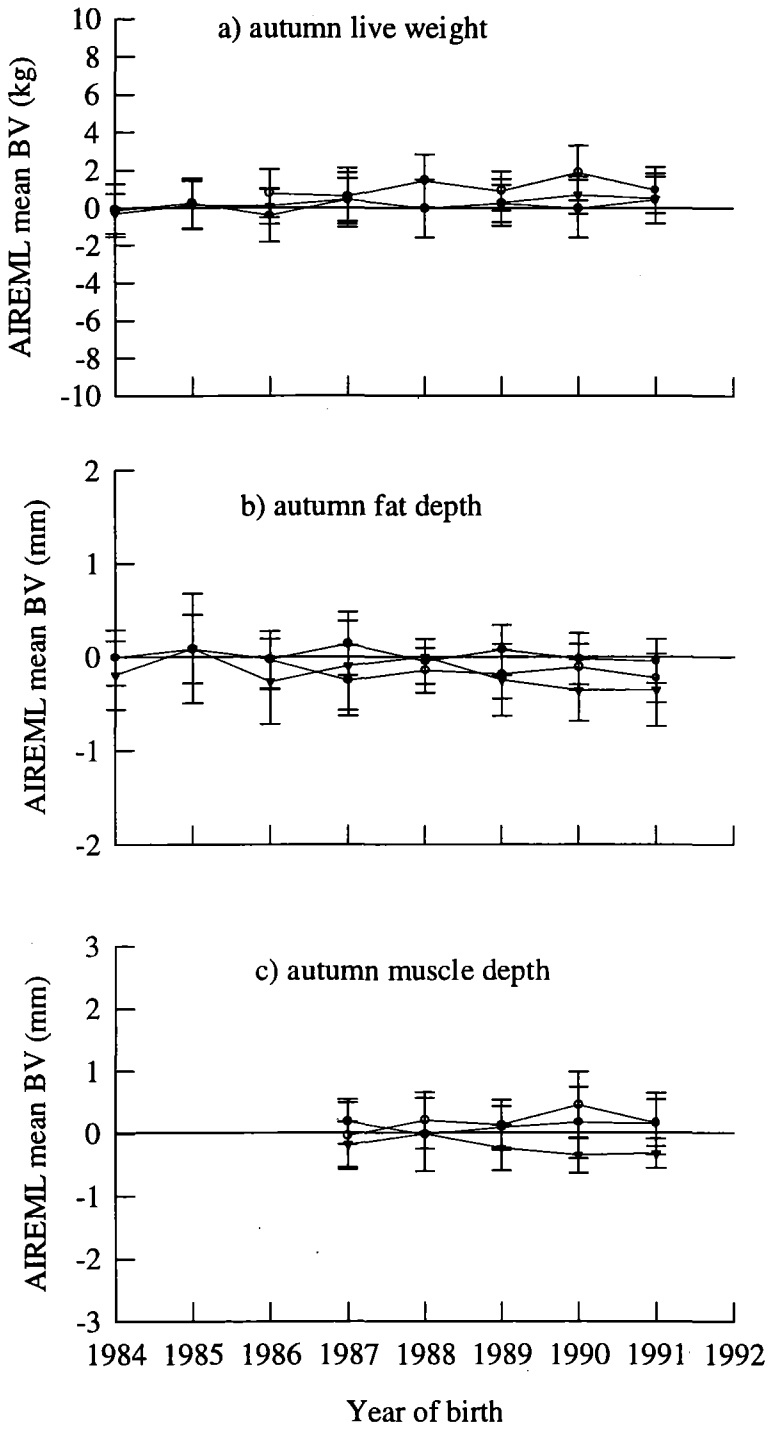


Figure 6.7: Responses to selection for index component traits for the lean tissue growth rate lines Dorset Down (O) and Border Leicester (▽) plus the control line Dorset Down (●) ewes. Mean breeding values (BV) output from multivariate AIREML. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SEM. A horizontal reference line is plotted along y=0.

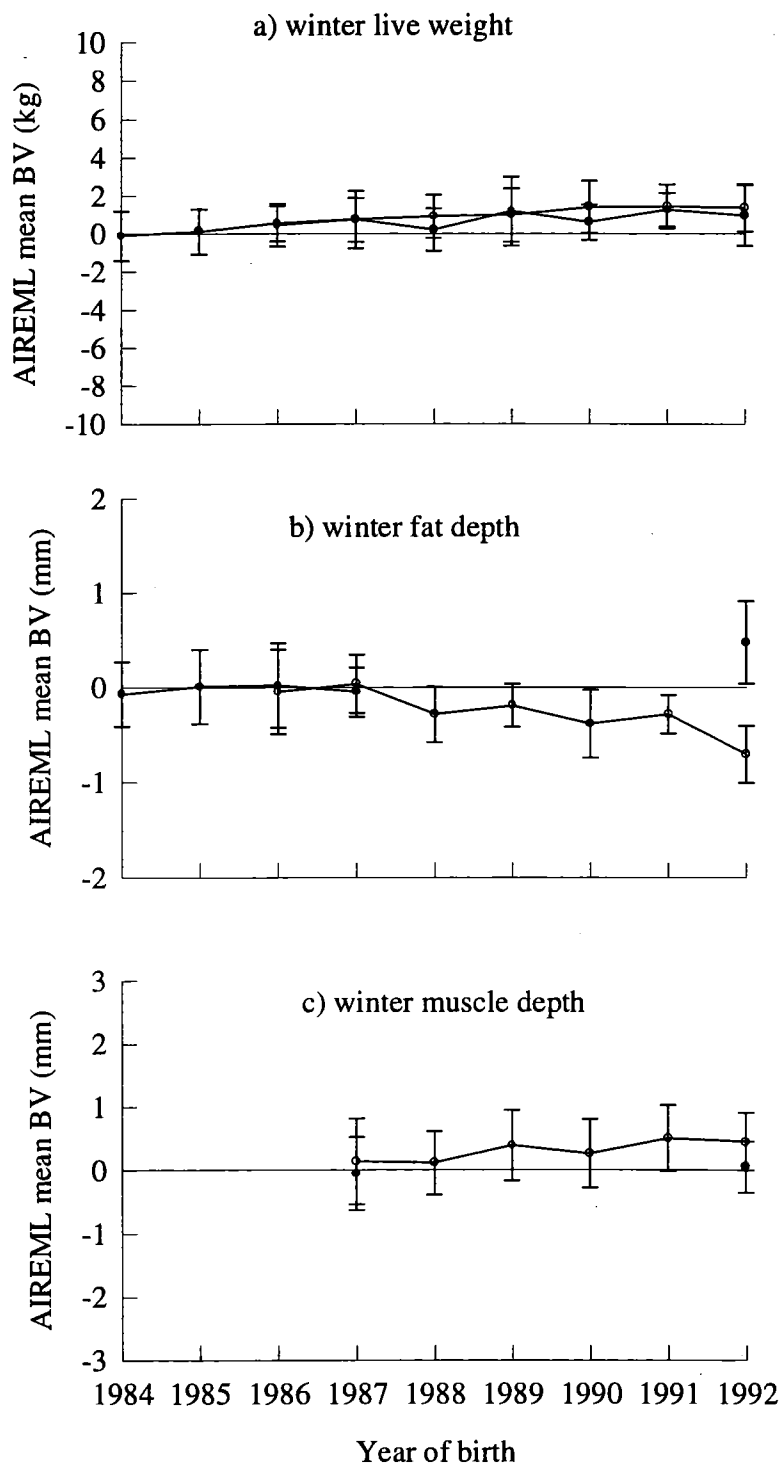


Figure 6.8: Responses to selection for index component traits for the lean tissue growth rate Coopworth line (O) and the control line (●) rams. Mean breeding values (BV) output from multivariate AIREML. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SEM. A horizontal reference line is plotted along y=0.

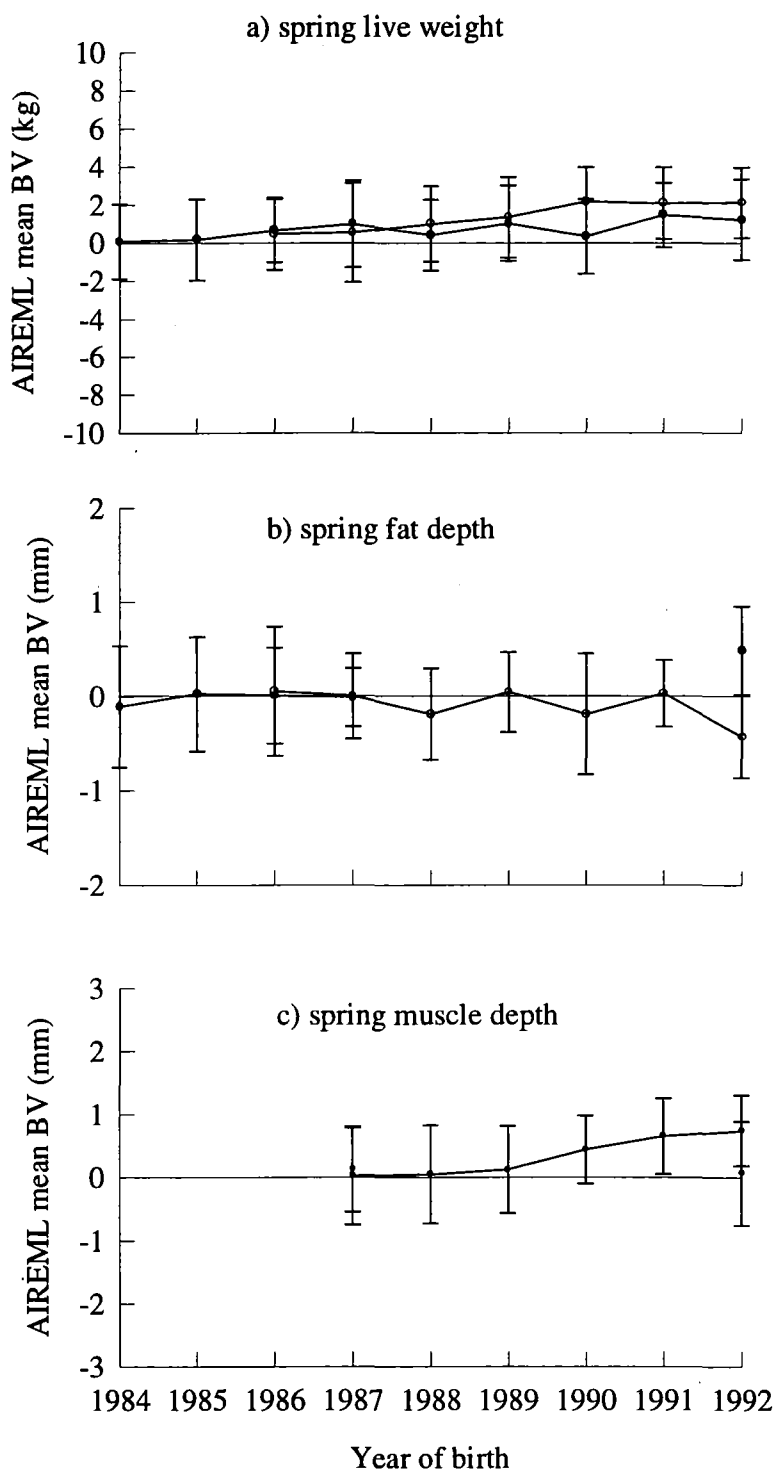


Figure 6.9. Responses to selection for index component traits for the lean tissue growth rate Coopworth line (O) and the control line (●) ewes. Mean breeding values (BV) output from multivariate AIREML. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SEM. A horizontal reference line is plotted along y=0.

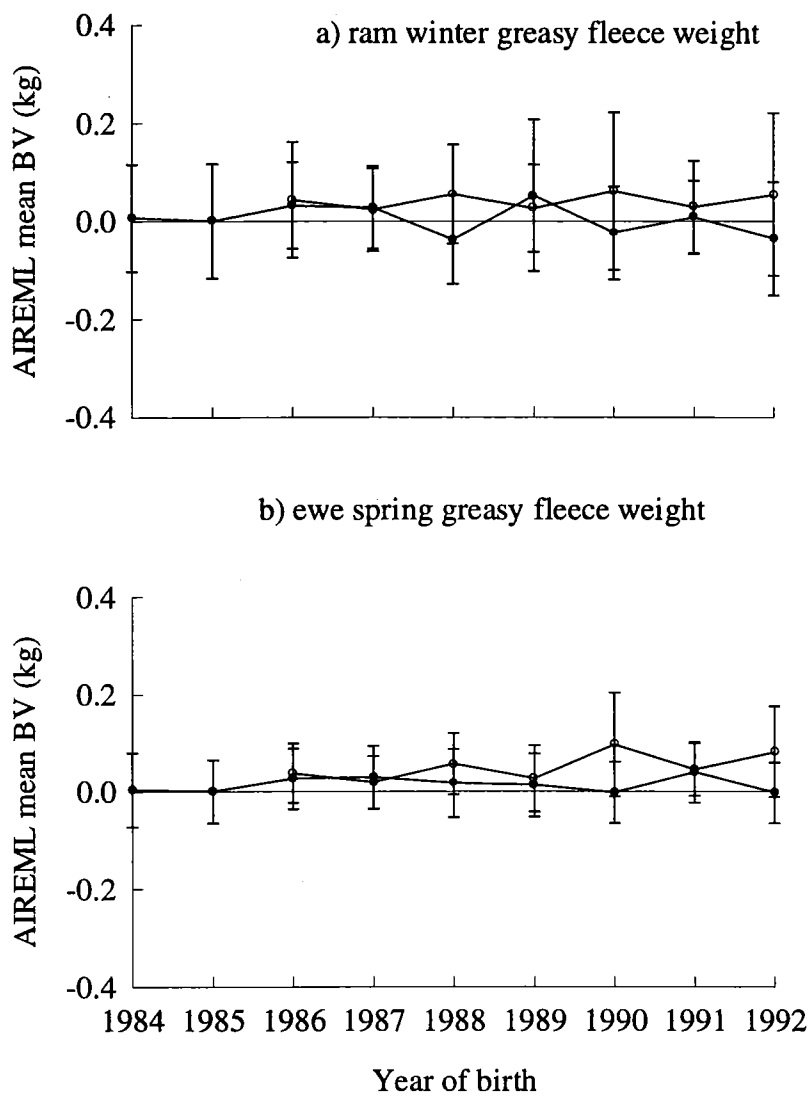


Figure 6.10: Correlated response in greasy fleece weight for the Coopworth rams and ewes. Lean tissue growth rate line (○) and the control line (●) mean breeding values (BV) output from multivariate AIREML. Animals born in 1989 were the first progeny from use of index 2 rams. Error bar = \pm SEM. A horizontal reference line is plotted along $y=0$.

Table 6.3: Rates of response from the combined indices data - regression coefficients for breeding values from AIMUL REML on time with line forced through the origin (where breeding values = 0 and years = 1984 and 1985) for liveweight and fat depth and breeding values = 0 and years = 1985 and 1986 for muscle depth). Standard deviation of regression coefficient in brackets. Autumn and spring traits are for ewes and winter traits for rams in all flocks. A dash (-) indicates the trait was not measured in that flock. Founder effect fitted in regression model.

Trait	Response rate		
	Dorset Down	Border Leicester	Coopworth
Autumn liveweight (kg/year)	+0.290(0.081)	+0.095(0.032)	-
Autumn fat depth (mm/year)	-0.001(0.01) *	-0.06(0.02)	-
Autumn muscle depth (mm/year)	+0.08(0.01) *	-0.05(0.01)	-
Winter greasy fleece weight (g/year)	-	+14.63(27.09)	-
Winter liveweight (kg/year)	+0.489(0.060) *	+0.226(0.059)	+0.168(0.017)
Winter fat depth (mm/year)	+0.01(0.01) *	-0.05(0.02)	-0.10(0.01) *
Winter muscle depth (mm/year)	+0.09(0.02)	+0.06(0.01)	+0.04(0.01)
Winter greasy fleece weight (g/year)	-	+17.01(2.20)	+7.58(2.73)
Spring liveweight (kg/year)	-	-	+0.295(0.036)
Spring fat depth (mm/year)	-	-	-0.06(0.01) *
Spring muscle depth (mm/year)	-	-	+0.09(0.02)
Spring greasy fleece weight (g/year)	-	-	+12.72(2.62)

* - founder effect significant ($P < 0.05$).

Table 6.4: Average annual response rates scaled for animal size (by dividing by least squares mean weights and tissue depths). Autumn and spring traits are for ewes and winter for rams in all flocks. A dash (-) indicates the trait was not measured in that flock.

Trait	Response rate [#]		
	Dorset Down	Border Leicester	Coopworth
Autumn liveweight (%/year)	+0.66	+0.26	-
Autumn fat depth (%/year)	-0.02	- 1.57	-
Autumn muscle depth (%/year)	+0.32	-0.22	-
Winter greasy fleece weight (%/year)	-	+0.42	-
Winter liveweight (%/year)	+0.84	+0.46	+0.37
Winter fat depth (%/year)	+0.27	-1.32	-3.25
Winter muscle depth (%/year)	+0.32	+0.23	+0.16
Winter greasy fleece weight (%/year)	-	+0.66	+0.33
Spring liveweight (%/year)	-	-	+0.67
Spring fat depth (%/year)	-	-	-1.46
Spring muscle depth (%/year)	-	-	+0.36
Spring greasy fleece weight (%/year)	-	-	+0.44

- original response rates in Table 6.3

6.3 Discussion

6.3.1 Responses to selection

Generally selection led to increases in liveweight and muscle depth with a decrease in fat depth in the present study. These trends were consistent with findings from similar studies (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). A more detailed examination of these response trends follows in terms of response rates.

Average response rates across data sets were $+0.26 \pm 0.14$ kg/year, -0.04 ± 0.04 mm/year and $+0.05 \pm 0.05$ mm/year for liveweight, fat depth and muscle depth respectively in the present study. These were less than those of Young (1989) who found changes of $+0.24$ kg/year, -0.15 mm/year and $+0.37$ mm/year for liveweight, fat depth and muscle depth respectively. Response rates from this study were also less than those of Cameron and Bracken (1992) which were $+0.22$ kg/year, -0.13 mm/year and $+0.15$ mm/year for liveweight, fat depth and muscle depth, respectively. The response rates of Cameron and Bracken (1992) reported here are half of those reported in the original paper because their selection was divergent whereas the present study and that of Young (1989) were based on unidirectional selection.

Average relative response rates (percentage of the phenotypic mean) across data sets were greatest for fat depth ($-1.23 \pm 1.26\%$ /year) and least for muscle depth ($0.20 \pm 0.19\%$ /year), with those for liveweight ($0.54 \pm 0.22\%$ /year) being intermediate. These response rates independent of the mean were generally lower than the few in the literature. Equivalent estimates for Young (1989) were; $+0.36$, -2.00 and $+1.23\%$ per year for liveweight, fat depth and muscle depth respectively. Halved response rates from the divergent selection experiment of Cameron and Bracken (1992) yielded comparative figures of $+0.44$, -2.01 and $+0.55\%$ per year for liveweight, fat depth and muscle depth respectively. Of note is the higher response rates in fat depth and muscle depth from these studies which were conducted under high energy, high protein *ad libitum* feeding than from the present study where animals were grazed at pasture.

A direct comparison of the results of the present study with those of Cameron and Bracken (1992) cannot be made since their experiment was designed to change body composition while maintaining liveweight. Care is also needed in comparing the responses rates from this study with that of Young (1989). The latter study estimated responses to selection from annual phenotypic means (selected line and control line difference) which did not correct for effects of inbreeding and linkage disequilibrium which arise because of selection (Henderson, 1988; Kennedy and Sorensen, 1988) resulting in biased parameter estimates (Meyer, 1989a; Falconer, 1989; Webb and Bampton, 1990) (although the

programme was still in its early stages) whereas the present study used breeding values estimated by individual animal model BLUP (Chapters 3). In the present study liveweight dominates response rates more than in the other similar studies (Young, 1989; Cameron and Bracken, 1992). This could be due to several effects.

Simm *et al.* (1987) predicted their index would increase lean by 59g per year and decrease fat by 18g per year based on a 2.26 year generation interval and an average selection intensity of 1.26. This index was used for selection in the present study. Actual weighted generation intervals for the flocks studied ranged between 2.74 and 2.88 years (Chapter 3), and average selection intensities were generally less than 1.26 for the index and its component traits in the lean tissue growth rate flocks (Table 6.1). Since lean and fat weights were not measured in this study, comparison of predicted and realised responses are not possible for the aggregate breeding value traits. However, a greater generation interval and lower selection intensity than anticipated would decrease response rates.

The generation interval for rams in the present study (2 years) was longer than the one year of Young (1989) and Cameron & Bracken (1992). This would decrease rates of response. Selection intensities were not greatly different in the present study from the previous studies as far as can be ascertained from published information.

Response rates in this study and that of Young (1989) could have been influenced by the changeover from a two trait index used in the early stages of the programmes to a three trait index. The two trait index used in the present study (liveweight - fat depth) was dissimilar to that used in the study of Young (1989) (liveweight + muscle depth). Subsequently, both programmes used similar 3 trait indices (liveweight - fat depth + muscle depth).

Employing an individual animal model REML to estimate breeding values is more accurate than employing traditional sire model provided all information used in selection is taken into account and the correct model is fitted (Nicholas, 1993). However, selection of animals was based on comparison of contemporaries which does not correct for inbreeding and linkage disequilibrium. However, similar studies (Young, 1989) and Cameron & Bracken (1992) also selected breeding animals based on comparison of contemporaries within sire family. Therefore, the method of parental selection should have the same effect on responses as in other studies. In this study the levels of inbreeding were generally low and increasing at a slow rate of less than 1% per annum in all flocks (Burrow, 1993) (Appendix E Table 1). Therefore, selection and inbreeding effects did not lead to biased responses.

Accuracy of selection may have been lower in the flocks in this study than in other studies. Animals of the present study which were grazed at pasture had coefficients of variation that were similar for liveweight ($10\pm4\%$ vs 9-11%) and muscle depth ($7\pm4\%$ vs 7-9%) but greater for fat depth ($30\pm12\%$ vs 18-25%) than those of Young (1989), Cameron & Bracken (1992) and Bishop (1993). The present study estimated lower response rates for tissue depths than those of Young (1989) and Cameron & Bracken (1992). The latter experiments were conducted under high energy, high protein *ad libitum* feeding to remove nutritional constraints (Cameron & Bracken, 1992) in order to maximise variation in carcass composition (Simm, Dingwall, Murphy and FitzSimons, 1990b) and thus improve discrimination between animals for *in vivo* measurements.

Young, Deaker and Logan (1992) observed higher repeatability for B muscle depth (0.77-0.95) (Palsson, 1939) than for C' fat depth (see Figure 3.1) (0.63-0.84) in animals of similar liveweight, fat depth and muscle depth to those used in this study. Low repeatability is expected for low (1-3mm) fat depths. In the present study, 30-42% of animals had low fat depth (1-3 mm) in all data sets except for Coopworth rams where these increased to 66% of the total. Animals with more than 7mm fat depth made up 5-11% of the Border Leicester and Dorset Down data sets and 2-11% in the Coopworth data sets. The ultrasound machine used in the present study can only measure tissue depths in 1 mm units. Relatively greater measurement errors for fat depth than live weight and muscle depth would mean that the breeding value of fat depth was predicted less accurately and so less selection pressure would occur on this trait. This effect is exaggerated further since low fat depth is favoured by the index.

Inadequate nutrition would adversely affect the development of fat more than any other major body tissue because fat is the tissue most prone to this environmental influence (Thorgeirsson and Thorsteinsson, 1989). The proportion of fat in an animal's body increases with stage of maturity (McClelland *et al.*, 1976). However, pasture quality and quantity decrease in late autumn and the whole of winter in Canterbury (O'Connor, Vartha and Belcher, 1968; Rickard, 1969; Rickard and Radcliffe, 1976) while animals are still growing. This may lead to animals mobilising fat to provide energy. Therefore, animals would have shallower fat depth than if feed was abundant and so may not reflect their genetic potential for fatness. This will decrease the breeding value estimates for fatness and hence reduce its impact on the index.

Use of standardised deviations rather than absolute values will put undue weight on traits with low variation. This is a problem when there may be non-genetic effects reducing the level of performance in a trait, such as level of nutrition. Normally, a reduction in mean fat depth is associated with a reduction in variance as well, from which it may be concluded that animals have not been able to express their genetic potential for fat growth. This type of effect is the reason some performance test regimes fed animals *ad libitum* on high quality

diets (*e.g.* Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). A reduction in variation provides less discrimination between individuals which will also lead to breeding values being predicted less accurately in this trait. A standardised breeding value will put undue weight on this imprecisely estimated trait and reduce emphasis on more accurately estimated traits. As a result rates of response will be reduced.

Fat depth and muscle depth generally have a positive genetic correlation (Young and Simm, 1990; Cameron and Bracken, 1992; Bishop, 1993; Chapter 5 in this study) which the index must work against. It may be that this correlation is greater than expected and that the index derived by Simm *et al.* (1987) favours liveweight more than expected. In Chapter 5 moderate (>0.40) to moderately high (>0.60) genetic correlations were reported between fat depth and muscle depth. Moderately high (>0.60) to high (>0.80) genetic correlations were calculated between liveweight and the index and muscle depth and the index. However, those between the index and fat depth were generally low (<0.30) and in some instances negative and low to moderate (-0.20 to -0.40). These genetic correlations were not derived by Simm *et al.* (1987) as they were not required for index construction. Therefore, evaluation of their impact on the predicted responses can not be undertaken.

While the index clearly favours liveweight and muscle depth, relatively smaller response rates were seen in muscle depth in the present study than other studies (Young, 1989; Cameron and Bracken, 1992). This could be due two effects.

1. The response rates from Young (1989) are from two generations of selecting on muscle depth where those of this study are for 1.3 generations. This may explain why the former study had a greater response rate in muscle depth than the current study.
2. Muscle depth was part of the two trait index of Young (1989) but not of the two trait used in the present study (index 1). In the present study a decrease in muscle depth was evident in Figures 6.6, 6.8 and 6.9 until this trait was incorporated into the selection index (index 2). This may also explain why the former study had a greater response rate in muscle depth than the current study.

Different response rates and relative responses rates between rams and ewes are not easily explained since management, sex and time of measurement were confounded. Response rates also differed between breeds within sex. Although, most heritability estimates were not significantly different between seasons, sexes and breeds, they were usually greater in the sex with greater response rates than the one with less. In part this could be because heritability estimates and breeding values were estimated together such that a higher heritability led to a higher breeding values. Higher heritability estimates could not be a statistical artefact in this study. Heritabilities were estimated from larger data sets than

those of similar studies (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993) which should produce more accurate estimates than smaller data sets (Shaw, 1987). Furthermore, heritabilities were estimated by individual animal model REML which is a more accurate estimation method than traditional sire models particularly for data arising from selection experiments (Kennedy and Sorensen, 1988; Henderson, 1990a). Thus apparently identical traits in the two sexes and between breeds are in fact different since genes affecting the trait are not all expressed by both sexes and all breeds.

Consideration of Figure 6.6 of Border Leicester and Dorset Down rams and figures 6.8 and 6.9 of Coopworth rams and ewes indicate that it is critical to include muscle depth in indices designed to improve lean tissue growth rate. Desirable responses in muscle depth only occurred after its inclusion in the index. However, in Border Leicester and Dorset Down ewes this response was not so clearcut (Figure 6.7). This may be further evidence of differences between the sexes in the genetic control of lean tissue growth rate although it is not seen in Coopworth data subsets. This may be a further indication of breed differences in genetic control of lean tissue growth rate. More data need to be collected from other breeds to provide a clear picture of this effect.

The regular, 2 year oscillation in responses for lean tissue growth rate flocks was attributed to a founder effect. In the Dorset Down, progeny descending from the 1984 cohort rams and their descendants had significantly higher responses for live weight in rams (+179%) and for muscle depth in ewes (+366%) and lower responses for fat depth in both ewes and rams (+22 and +45% respectively) than the progeny descending from the 1985 cohort rams and their descendants. However, in Coopworth, the opposite for fat depth was observed, progeny descending from the 1984 founding rams and their subsequent descendants had higher responses (+250 and +627% respectively) than those descending from the 1985 founding rams and their subsequent descending sub-population. Rams were used only once as 2-tooths. Ram selection is within sire family and the maximum number of sons kept per family is one. Therefore, these results suggest that some genetic variation between the founder ram families would be perpetuated by this type of selection. The results of the present study are consistent with genetic size scaling theory whereby selection may have led to an increase in adult size and reduction in maturity at the time of measurement.

6.3.2 Border Leicester control line

Using the Dorset Down control line as a control for the Border Leicester should not influence the results. Within sex, the breeds were run together and most environmental correction factors were not significantly different between the two breeds, except year effects in ewes. Even these do not bias estimates of breeding values since one of the desirable properties of REML is translation invariance provided all important fixed effects are fitted (Patterson and Thompson, 1971; Harville, 1977; Kennedy,

1981). These analyses fitted all identified fixed effects and covariables that significantly affected performance in index component traits and greasy fleece weight ($P < 0.10$) (Chapter 3). Therefore, use of Dorset Down control line as control for the Border Leicester selected line is valid.

6.3.3 Correlated response in greasy fleece weight

Annual response rates were an increase of 12.99 ± 4.01 g per year giving relative response rates of $0.46 \pm 0.14\%$ per year for Border Leicester and Coopworth data sets. Therefore, selection for lean tissue growth rate produced an increase in greasy fleece weight. This is an important finding given the economic importance of wool production in most New Zealand and Australian sheep farming enterprises (McEwan *et al.*, 1991). These findings require verification in other studies.

6.4 Conclusion

Three trait indices are required to produce desirable responses in all index component traits. Relative responses in these traits are affected by genetic differences between sexes and breeds and the accuracy with which measurements are made. Efforts should be made to maximise the opportunity for animals to express their genetic potential for fat growth since low fat depths have relatively high measurement errors and are favoured by index.

Responses observed indicate that animals are not partitioning protein away from other protein products (e.g. wool) but rather that they are diverting energy to protein gain away from lipid gain. The exact nature of this in terms of nutritional and metabolic processes could not be resolved in this study. Such an effect is consistent with animals being less mature at a given age and may indicate that selection has increased mature size.

CHAPTER 7

DEVELOPMENT OF OPTIMAL LEAN TISSUE GROWTH RATE SELECTION INDICES

7.0 Introduction

Earlier studies where sheep have been selected for lean tissue growth rate under *ad libitum* feeding conditions on high energy, high protein diets showed results consistent with theoretical estimates of likely responses, although realised responses for fat depth and muscle depth assessed *in vivo* were smaller in magnitude than predicted (Cameron and Bracken, 1992; Bishop, 1993). Results from the present study were similar. Generally realised responses were dominated by gains in liveweight and in fat depth. Evaluation of responses in muscle depth were probably compromised by the changeover of indices. Responses in liveweight were similar while those for fat depth and muscle depth were less than those from similar studies (see Chapter 6).

Lower realised than predicted responses could be due to inaccurate parameters used in index construction. Generally, realised genetic and phenotypic parameters for selection index component traits in the present study were greater in magnitude than those used by Simm *et al* (1987) to construct indices used for selection. Cameron and Bracken (1992), in constructing their selection index, assumed a genetic correlation of 0.15 between liveweight and the selection index. However, subsequent analysis of their own data gave an estimate of 0.67. This high correlation resulted in divergence in liveweight despite the experiment being designed to give no change in liveweight. One of the major criticisms of the use of selection indices has been that genetic and phenotypic parameters differ between breeds, strains and testing conditions. Therefore, results of the present study and that of Cameron and Bracken (1992) provide further evidence that judicious use of assumed genetic and phenotypic parameters in breeding enterprises is warranted and that as soon as data become available from the selected population, a check on consistency between assumed and derived genetic and phenotypic parameters is necessary.

Realised responses, genetic and phenotypic parameters for breeding objective traits (lean and fat weights), and similarly, correlations between aggregate breeding value traits and index components traits (liveweight, fat depth and muscle depth) were not available since these traits were not measured in the majority of animals.

7.1 Construction of more appropriate selection indices

The aim of the work presented in this section was to construct optimal indices for the populations of the present study. Alternative indices should be considered, given that this study found, (i) lower annual realised responses in index component traits compared to similar studies, (ii) response in index component traits varied between sexes and between breeds within sex and (iii) greater realised

phenotypic and genetic parameter estimates than those used by Simm *et al.* (1987) to construct the indices used for selection.

Similar lean tissue growth rate indices were constructed for each sex. The resulting index weights were critically compared with those of Simm *et al.* (1987). In addition, responses likely to be obtained from these indices were predicted and compared to those of Simm *et al.* (1987).

A general overview of index theory was covered in Chapter 2. A more detailed summary is provided here so that the way in which parameters were used is clear.

7.2 Summary of index theory

Only a brief summary of the theoretical aspects of constructing a selection index based on the works of Hazel (1943), Cunningham (1969), Yamada, Yokouchi and Nishida (1975), Lin and Allaire (1977), Falconer (1989) and Nicholas (1993) will be covered in this section. Prior to constructing a selection index, it is of critical importance to define the breeding objective(s) *i.e.* what the breeder seeks to improve (James, 1982, Smith, 1983, Land, 1985, Nicholas, 1993). The breeding or additive genetic values (Y_m) of traits in the breeding objective are then linearly combined and weighted by their economic values (v_m) to form an aggregate breeding value (T) (equation 7.1).

$$T = v_1 Y_1 + v_2 Y_2 + \dots + v_m Y_m \quad (\text{equation 7.1})$$

Using the terminology of Cunningham (1969), the information specified in the following 4 vectors and 3 matrices are involved in construction of an index and in predicting responses:

$Y = Y_1, \dots, Y_m$ is a vector of additive genetic values for the m traits included in the aggregate breeding value

$v = v_1, \dots, v_m$ is a vector of constants, usually representing the relative economic values of the m traits in Y

$X = X_1, \dots, X_n$ is a vector of phenotypic measures for the n variables or sources of information to be included in the index

$b = b_1, \dots, b_n$ is a vector of weighting factors to be used in the index

P is an $n \times n$ matrix of phenotypic covariances between the n variables in X

G is an $n \times m$ matrix of genotypic covariances of the n variables in X with m traits in Y

C is an $m \times m$ matrix of genotypic covariances between the m variables in Y

A multi-trait selection index is then constructed to maximise the correlation between the index (I) and T. The definition of an index is then a linear combination of breeding values (X_n) of traits in the selection criteria weighted by their relative importance (b_n) (equation 7.2).

$$I = b_1X_1 + b_2X_2 + \dots + b_nX_n \quad \text{(equation 7.2)}$$

The weighting factors of the index (b_n) are obtained by solving the index equations

$$Pb = Gv$$

to give $b = P^{-1}Gv$.

7.3 Materials and Methods

The Selind programme of Cunningham (1970) was used to derive index weights and other index statistics. Selection indices were constructed for both meat (Dorset Down and Border Leicester) and dual purpose breeds (Corriedale and Coopworth) using the P matrices derived for each population in Chapter 5. G matrix was modified to take account of the variable heritability in index component traits for the different data sets (Chapter 5). Part of G matrix and whole C and v vector used were those of Simm *et al.* (1987) (Table 7.1). Responses were derived for an assumed selection intensity (i) of 1.00 and an average across flock generation interval (L) of 2.84 years. Predicted responses were derived using equation 7.3.

$$R_y = ir_{AC}\sigma_A / L \quad \text{(equation 7.3 after Nicholas, 1993)}$$

where:

R_y is response per year

r_{AC} is the genetic correlation between the index and an aggregate breeding value trait

σ_A is the additive genetic standard deviation for an aggregate breeding value trait

Table 7.1: Genetic and phenotypic parameters used in index calculations by Simm *et al.* (1987). LEAN is lean weight and FAT is fat weight. Heritabilities on the diagonal (bolded), genetic correlations above diagonal and phenotypic correlations below diagonal. A dash (-) indicates the parameter is not required for index construction. The full names of abbreviations are presented in the list of abbreviations.

	LW	UFD	UMD	LEAN	FAT ⁺⁺
LW	0.24	-	-	0.70	0.73
UFD	0.40	0.23	-	0.21	0.61
UMD	0.40	0.15	0.20	0.50	0.20
LEAN	-	-	-	0.27	0.39
FAT	-	-	-	-	0.29

economic value of lean weight in the index calculation was NZ\$6.16 per standard deviation

++ economic value of fat weight in the index calculation was NZ\$-4.62 per standard deviation

7.4 Results

7.4.1 Effects of parameters on selection indices

All covariance matrices processed by Selind were positive definite.

Table 7.2 shows the index coefficients calculated for separate ram and ewe data subsets in the present study in autumn, winter or spring. Generally, compared to the coefficients from the three trait index of Simm *et al.* (1987) which were 0.25, -0.58 and 0.48 for liveweight, fat depth and muscle depth respectively, coefficients from this study were either equal or less (0.11 to 0.25) for liveweight, but higher for both fat depth (-0.72 to -1.19) and muscle depth (0.60 to 1.11). Of note are the higher coefficients for fat and muscle depth in Corriedale ram and ewe data subsets than other breed data subsets. Correlations between indices and aggregate breeding value were 4 to 65% higher than estimated by Simm *et al.* (1987). Similar results were observed for two trait indices combining liveweight with either fat depth or muscle depth, except coefficients for liveweight were greater in the liveweight-fat depth indices and equivocal *i.e.* positive in some instances and negative in others in liveweight-muscle depth indices (Tables 1 and 2 Appendix F).

Relatively higher coefficients for index component traits were observed for ram data subsets in winter in Border Leicesters and Dorset Downs than their respective ewe data subsets in autumn. However, for Coopworth data subsets, the coefficients for index component traits were higher in ewes in spring than rams in winter. There were no obvious trends in index coefficients between ram data subsets in meat and dual purpose breeds. While in ewe data subsets, the indications were for higher index coefficients in dual purpose than meat breeds (Table 7.2). Similar results were observed from two trait indices combining liveweight with either fat depth or muscle depth in Dorset Down data subsets but there were no obvious trends in other breeds data subsets (Tables 1 and 2 Appendix F).

7.4.2 Predicted responses in aggregate breeding value traits

As shown in Tables 7.3 and 7.4, desirable responses were predicted for lean weight (an increase) and fat weight (a decrease) in all indices. Compared to the adjusted predicted responses (using *i* and *L* from the present study) of Simm *et al.* (1987), predicted responses for lean weight were on average similar ($98 \pm 27\%$ per year), whereas those for fat weight were greater ($+308 \pm 92\%$ per year). Predicted responses from two trait indices combining liveweight with either fat depth or muscle depth were desirable (an increase) for lean weight, but for fat weight they were unclear *i.e.* trends in responses were not consistent for the different data sets some were desirable while others were undesirable (an increase as opposed to the desired decrease). Predicted responses in lean weight were better from two trait

indices than from the three trait indices although the unclear responses in fat weight led to lower overall predicted economic responses (Tables 3-6 Appendix F).

Generally, greater predicted responses in lean weight for three trait indices were observed in ram data subsets in winter for Border Leicesters and Dorset Downs than their respective ewe data subsets in autumn. However, the opposite was true in Coopworth and Corriedale data subsets, where ewe data subsets in spring in Coopworth and in winter in Corriedale gave greater responses than their respective ram data subsets in winter. Similar results were observed for fat weight except higher responses in lean weight were accompanied by lower predicted responses in fat weight *e.g.* Dorset Down rams had higher predicted lean weight responses than their counterpart ewes (42g vs 28g) but lower responses in fat weight (21g vs 26g). Predicted responses within sex varied without obvious trends between meat and dual purpose breeds (Tables 7.3 and 7.4).

Similar results in predicted responses in lean and fat weights to those described above were also obtained for two trait indices (Tables 3-6 Appendix F).

7.5 Discussion

Emphasis will be given to three trait indices and their predicted responses. This is because these indices consistently led to desirable predicted responses in the two component traits of aggregate breeding value.

7.5.1 Effects of parameters on selection indices

Greater relative size of coefficients for fat depth (-0.96 ± 0.19 vs -0.58) and muscle depth (0.87 ± 0.20 vs 0.48) in the three trait indices were derived in the present study than those of Simm *et al.* (1987). This could explain the low realised responses in fat depth and muscle depth obtained in the present study (see Chapter 6). While the work of Simm *et al.* (1987) which introduced three trait indices to sheep selection for lean tissue growth rate was a pioneering effort, it may not be generally useful if the parameters are incorrect. Genetic and phenotypic parameters pertaining to the population to which they are applied are necessary to derive optimal indices (Simm, 1986). These were unavailable in the mid 1980's when the work of Simm *et al.* (1987) was carried out.

Sensitivity analyses by Simm *et al.* (1987) showed that individual changes of ± 0.1 in heritabilities and ± 0.2 in genetic correlations resulted in only minor losses in index efficiency for changes in heritability (5% or less) and genetic correlation (13% or less). This led to the conclusion that large changes in genetic parameter estimates were needed to have any significant influence on index weights and predicted responses. Given that large changes are less probable they concluded that the index was relatively insensitive to changes in these parameters. What these authors failed to consider was change in more than one parameter estimate. This was found to occur in the analyses reported here. Together, these changes had a greater effect on index efficiency ($+134 \pm 23\%$) and greater responses in fat weight ($+308 \pm 92\%$ per year) than Simm *et al.* (1987) envisaged.

Relatively higher coefficients for fat depth and muscle depth obtained for Corriedale data than other data sets could be because of weaker genetic correlations between index component traits in this breed. However, genetic correlations between these traits in Corriedale data were generally similar to those of other data suggesting that this was not the case. Genetic correlations had large sampling errors relative to parameter estimates and may be the least accurately estimated compared to other parameters (*e.g.* heritabilities) (Land, 1985). Heritabilities for index component traits were generally greater in Corriedale data than other data sets. These may be an indication of true breed differences. The Corriedale is a dual purpose breed, which has had less selection pressure for meat attributes than the other breeds it is compared with in this study especially Dorset Down which have been selected and used as terminal sire breeds for many years (Eastwood, Marshall and Wickham, 1977; Warman, 1991).

Thus less selection for lean tissue growth rate like traits in Corriedale could mean that liveweight, fat depth and muscle depth are relatively more independent than in other breeds.

Greater correlations between the indices derived and the aggregate breeding value (0.31 ± 0.05 vs 0.23) in the present study than estimated by Simm *et al.* (1987) indicates that responses to selection using these indices should be greater than predicted by Simm *et al.* (1987).

7.5.2 Predicted responses in aggregate breeding value traits

Observed responses in lean and fat weight would be higher than those predicted in the present study because of the low selection intensity (1.00) used in the prediction. A constant selection intensity was necessary to allow comparison of responses based on indices derived with different parameters.

Selection intensities greater than 1.00 and closer to the 1.26 value of Simm *et al.* (1987) are likely in Border Leicester and Coopworth flocks because they have greater reproductive performances than the Dorset Down flock (see Chapter 6). Therefore, in the former flocks greater selection intensities will affect comparison of predicted responses further. However, because of within sire family selection practised in all flocks the direct impact of selection intensity on predicted responses can not be evaluated unless lean and fat weight are measured directly.

Differences in predicted responses between the sexes and between breeds within sex are readily explainable. Ewes and rams in lean tissue growth rate flocks were measured in different seasons leading to confounding by sex-season. However, the Corriedale ewe and ram data sets which were measured in winter and were the most balanced showed similar trends suggesting that other sex differences are real. The studies of Wolf *et al.* (1981) and Waldron *et al.* (1992a) have estimated parameters which are variable for lean and fat weights. Variation in such parameters may reflect sampling errors. However, the studies of (Davis, 1993; Koots *et al.*, 1994a & b) using beef cattle have shown that parameters of body composition traits vary between cattle breeds as well. Together with results of the present study, these suggest that the differences observed are real. As concluded by Parratt *et al.* (1989) and Clarke, Dobbie, Hickey, Jones, and Wrigglesworth. (1995) cognisance of such genetic differences is important in designing effective breeding programmes.

Theoretical comparisons described in this section suffer from lack of information on genetic (co)variance involving aggregate breeding value traits. The values of Simm *et al.* (1987) were used because equivalent estimates were not available for the populations studied. Such a criticism is valid but due to the fact that slaughtering of breeding animals compromises the breeding program and that there

is high cost incurred in slaughtering and dissecting carcasses of relatives this information was not collected. While slaughtering of breeding animals is possible in conjunction with using modern techniques such as oocyte *in vitro* maturation, *in vitro* fertilisation and embryo transfer, these technologies have not advanced to the stage of being viable in practice. However, the availability of a CT scanner provides the opportunity to “dissect” breeding animals and their relatives *in vivo* to measure these traits.

7.5.3 Other traits of economic importance

Failure to take into account other traits of economic importance in the present study when deriving indices for lean tissue growth rate in dual purpose sheep appear to be unwise. However, use of the lean tissue growth rate index can lead to development of unique lines within dual purpose breeds for use as terminal sires instead of traditional terminal sires such as the Dorset Down. This is consistent with the philosophical argument of Smith (1985) to select for different production traits in different lines, thereby increasing genetic diversity which will enable commercial farmers to accommodate possible changes in market conditions.

7.5.4 Decreasing generation interval to increase responses

In the present study, a decrease in average generation interval is possible if replacement ewes are mated at 7-8 months to lamb as one year hoggets and if ewes are only kept for 4 lambings. Combining these measures may lower the generation interval from 2.73-2.93 to 2.25 years as suggested by Simm *et al.* (1987). However, management implications of such policies are considerable, particularly the nutrition required to grow ewe lambs to heavier mating weights in late summer and early autumn with pastoral feeding. Canterbury suffers summer droughts and supplementary feeding of ewe lambs is not economically viable. Further reduction in average generation interval is possible, if rams are mated at 7-8 months of age. Such a policy would reduce average generation interval to 1.75 years and therefore increase rate of responses to selection. Mating rams at 7 months of age has been achieved in other studies (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993). However, selecting rams for breeding at a younger than that of the present study would further reduce accuracy of selection under pastoral feeding. Therefore, rams would have to be performance tested under high energy, high protein feeding regimes to enable accurate selection to facilitate accurate measurement of tissue depths. This is unlikely to be economically viable in the New Zealand ram breeding industry.

7.6 Conclusions

In conclusion one selection index does not suit all situations. More optimal indices derived in the present study than that used in these flocks should lead to a greater rate of reduction in fat (+308±92% per year) than originally predicted with little change in responses for lean (+98±27% per year).

Table 7.2: Index coefficients and correlations between three trait indices (liveweight, fat depth and muscle depth) and aggregate breeding value. The full names of abbreviations are presented in the list of abbreviations.

Trait	Index coefficients								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CWPE	CPWR
LW	+0.25	+0.34	+0.20	+0.14	+0.16	+0.25	+0.20	+0.25	+0.11
FD	-0.58	-0.93	-0.99	-0.72	-0.76	-1.19	-1.17	-1.14	-0.80
MD	+0.48	+0.60	+0.83	+0.65	+0.77	+1.11	+1.10	+1.08	+0.80
r_{IAB}	+0.23	+0.25	+0.32	+0.24	+0.29	+0.38	+0.37	+0.34	+0.28
$r_{IAB} : SYB \ r_{IAB}$	1.00	1.09	1.39	1.04	1.26	1.65	1.61	1.48	1.22

Table 7.3: Predicted responses in lean weight for three trait indices (liveweight, fat depth and muscle depth). σ_A is the additive genetic standard deviation for lean weight, R_y is response per year, r_{AC} is the genetic correlation between the index and an aggregate breeding value trait, I is selection intensity and L is average generation interval. The full names of other abbreviations are presented in the list of abbreviations.

Variable	Predicted responses in lean weight								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
r_{IA}	+0.19	+0.13	+0.14	+0.14	+0.21	+0.27	+0.20	+0.24	+0.16
σ_A	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567
i	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00
L	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84
R_y (g/year)	+38	+26	+28	+28	+42	+54	+40	+48	+32
$R_y : R_y SYB$	1.00	0.68	0.74	0.74	1.11	1.42	1.05	1.26	0.84

Table 7.4: Predicted responses in fat weight for three trait indices (liveweight, fat depth and muscle depth). σ_A is the additive genetic standard deviation for fat weight, R_y is response per year, r_{AC} is the genetic correlation between the index and an aggregate breeding value trait, I is selection intensity and L is average generation interval. The full names of other abbreviations are presented in the list of abbreviations.

Variable	Predicted responses in fat weight								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
r_{IA}	-0.05	-0.15	-0.23	-0.12	-0.10	-0.15	-0.23	-0.14	-0.15
σ_A	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605
i	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00
L	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84
R_y (g/ year)	-11	-32	-49	-26	-21	-32	-49	-30	-32
$R_y : R_y SYB$	1.00	2.90	4.45	2.36	1.91	2.91	4.45	2.73	2.91

CHAPTER 8

RESPONSES IN DORSET DOWN SHEEP FOR LEAN, FAT AND BONE WEIGHTS MEASURED *IN VIVO* BY COMPUTER TOMOGRAPHY

8.0 Introduction

In Chapter 6 responses in index component traits in Dorset Down sheep were described (increases in liveweight and ultrasound muscle depth with no change in ultrasound fat depth in both ewes and rams). The selection regime for these animals was reported in Chapter 3. Lean and fat weights could not be measured each year since traditional carcass evaluation techniques for measuring these entities involve slaughter (see section 2.5.5) and an accurate *in vivo* body assessing technique was not available.

Toward the end of the present work, an X-ray computer tomography (CT) scanner became available to assess lean and fat weights *in vivo*. Initial success in application of CT to measure *in vivo* body composition of farm animals is evident in the literature *e.g.* Davies, Garden, Young and Reid (1987) produced a detailed atlas of X-ray tomographical anatomy of the sheep, and a number of studies have assessed body composition *in vivo* for different farm animal species *e.g.* sheep (Sehested, 1984) and goats (Sorensen, 1984 and 1992).

The aims of this experiment were to use CT to assess fat, lean and bone weights *in vivo* in 1994 born Dorset Down ewes and rams in order to estimate:

- (i) responses in individual aggregate breeding value traits (fat and lean weights)
- (ii) correlated responses in bone.

This study was restricted to a sample of one flock due to resource limitations (time and costs of scanning and analysis). The Dorset Down flock was chosen because two lines are kept (lean tissue growth rate and control) and selection for lean tissue growth rate has been practised longer than in the Coopworth flock (9 versus 7 years). The Border Leicester flock could not be used because only one line is kept and no data were available describing differences between Border Leicester and Dorset Down for aggregate breeding value traits prior to selection.

8.1 Materials and Methods

Scanning was undertaken for 210 Dorset Down hoggets born in 1994. Each animal was scanned at four anatomically defined reference sites. The present study selected 52 of these hoggets and performed additional scans (n=20) for each animal to more accurately assess carcass composition.

8.1.1 Selection of animals

Fifty-two (52) 1994 born Dorset Down rams and ewes were randomly selected using stratified sampling of three weight groups (low, medium and high) within the rams and within the ewes (see Table 8.1). These animals comprised 26 from the lean tissue growth rate line (13 rams, 13 ewes) and 26 from the control line (13 rams, 13 ewes). Four animals were chosen at random from the low and high weight groups with five animals chosen from the medium weight group for each sex-line combination.

Table 8.1: Mean (\pm standard deviation) liveweight of rams and ewes of the control and the lean tissue growth rate (LTGR) lines. Number of animals in brackets.

Variable	Rams		Ewes	
	Control	LTGR	Control	LTGR
Average liveweight of all animals (kg)	50.2 \pm 5.5 (n=45)	54.5 \pm 4.4 (n=72)	49.3 \pm 4.2 (n=30)	49.7 \pm 5.3 (n=63)
Average liveweight of animals sampled (kg)	50.4 \pm 5.3 (n=13)	55.1 \pm 5.0 (n=13)	49.7 \pm 3.5 (n=13)	49.2 \pm 6.4 (n=13)

8.1.2 Animal restraint during scanning

Scanning was performed a minimum of 12 hours after removal from feed. Half an hour prior to scanning, each animal was given 1.0 ml (per 50kg liveweight) of 10mg/ml acepromazine ('ACEPRIL 10', Troy Laboratories, Pty, Ltd.) intramuscularly to relax the animal and minimise movement during scanning. To further minimise movement during scanning, animals were restrained in a cradle lying on their backs with forelegs strapped close to the chest and hind legs clamped at an angle of approximately 45° (see Plate 8.1).

Scanning of 26 animals of each sex occurred over five working days. Sampled animals (n=52) were scanned amongst others in the larger group (n=210). Generally, similar numbers of animals were scanned each day.

8.1.3 CT scanning approach

The Cavalieri principle (Gundersen, Bendtsen, Korbo, Marcussen, Moller, Nielsen, Nyengaard, Pakkenberg, Sorensen, Vesterby and West, 1988) was employed to measure bone, muscle and fat volumes (later converted to weights). This requires 10 to 15 slices or sections to be made at equal spacings through an object to provide an unbiased estimate of the volume of a 3-dimensional irregularly shaped object with an error (coefficient of variation) of less than 5%. The only requirement that has to be fulfilled is that the first slice be chosen at random. Shape and orientation of the object are not important.

Animals were scanned at 18-20 equally spaced sites along their long axis. The first slice was chosen at random in the neck region close to the head and subsequent slices were scanned at 55mm intervals with the last slice after the knee joint. From these, slices were selected for analyses. The first slice for analysis was in the neck region prior to the slice in which shoulders became apparent (Plate 8.2). The last slice for analysis was in the leg, after the last slice in which the thighs were apparent (Plate 8.3). A total of 15-18 slices per sheep were chosen using these criteria (Plate 8.4).

8.1.4 CT scanning procedure

A Technicare 2020 CT scanner was used to scan the sheep. All sheep were scanned with a scan circle diameter of 40cm except for one ram which was scanned with a 50cm scan circle diameter. The scan diameter was changed from 50 to 40cm to improve image resolution and therefore increase tissue differentiation. Other scanner settings were 120kV, 100mA, 5mm slice thickness, 4 second scan time, 512 x 512 image matrix resolution and a “sharp” convolver filter for image reconstruction.

8.1.5 Data transfer

CT images written by the Technicare 2020 software running on a PDP-11 computer system were archived to half-inch 1600bpi 2400' tapes (time and disk space constraints during scanning precluded archiving of duplicate copies of images). Tapes were read onto a VAX computer system using the foreign tape utility. Images were then transferred to a PC system. Due to tape transfer reading errors, partly because the tapes used were old, full data sets were recovered for only 43 Cavalieri animals. These were for 22 rams (10 control and 12 lean tissue growth rate) and 21 ewes (9 control and 12 lean tissue growth rate).

8.1.6 Image analysis

The CT image native format was converted to a standard bitmap format using a computer program called *Bitman* (Jopson, pers.comm.). Plate 8.5 shows typical tissues and organs in a bitmap image. The *Bitman* window width and window centre settings for 40 and 50cm diameter scan circles were 512/750 and 512/0 respectively. These window settings were determined through a calibration exercise (described below). CT images from the Technicare scanner are not saved as Hounsfield units (HU) for image pixels, hence the need to calibrate the ranges of bitmap values (a 256 grey-scale) corresponding to fat, muscle and bone.

Photomagic (Micrografx, 1992) was used to process bitmap images. In each image foreign materials (*e.g.* table, straps), internal organs and associated fat were removed (Plates 8.6 and 8.7). Bone marrow and spinal cord were painted white so that they could be classified as bone volume rather than fat or muscle (Plates 8.6 and 8.7). Testes (Plate 8.6) and udder (Plate 8.7) were removed from images of rams and ewes following standard carcass dressing practice in abattoirs and slaughter houses (Kempster *et al.*, 1982; Fisher and De Boer, 1994).

Individual processed (guttled) images were then “electronically” dissected into total fat, muscle and bone areas using *Autocat* (Jopson, pers.comm). *Autocat* dissection settings for fat, muscle and bone areas were 1 to 130, 131 to 250 and 251 to 255 respectively, for the 256 grey-scale bitmaps. These ranges were determined by calibration involving analysis of individual dissected fat, muscle and bone areas from three ewes and three rams images covering the neck, thoracic, abdomen and thigh regions of the body. These ranges captured more than three (3) standard deviations either side of the mean density for muscle and fat. In these bitmap images, pixel values of zero (black) corresponding to air were not counted. The wide range for bone, 200 to 1024 HU (Sehested, 1986) was collapsed by *Bitman* into a narrow range of the grey scale, since the greatest interest was in fat and muscle tissues. Processed images comprised carcass tissue plus skin.

Fat, muscle and bone areas from all slices for an animal were summed and multiplied by the distance between slices (55mm except for two rams which had distances of 45mm and 50mm respectively) to obtain tissue volumes. Volumes were converted to weight by multiplying by standard density values for carcass fat, muscle (or lean) and bone of 0.925, 1.031 and 1.549 kg/dm³ respectively (Jopson, pers.comm.).

Two types of traits were derived from the data; tissue weights (fat, lean and bone) and tissue relative sizes (fat, lean and bone). Relative size traits were derived for each animal by dividing individual tissue weight by total tissue weight (sum of fat, lean and bone weights). Relative size traits were derived in an attempt to remove the effect of size which is known to influence comparisons between traits (Smith, 1984).

Six animals (3 ewes and 3 rams) were chosen at random to estimate the effect of operator error in processing images in *Photomagic*. The first analysis was at the beginning of the experiment (after operator training on another 3 ewes and 3 rams) and the second analysis a week after all animals had been analysed.

8.1.7 Statistical analysis

Preliminary analyses using Minitab (Minitab, 1992) indicated that responses differed between the sexes. Therefore, to critically investigate the differences in responses between sexes, data were analysed in three ways; (i) as absolute traits, (ii) as percentage traits and (iii) by fitting liveweight as a covariate within sex.

Data were analysed using GLM procedures (SAS, 1991). All fixed effects (birth rank, rearing rank, age of dam, sex, line, sex-line interaction) and a covariable (age at scanning) were fitted. Subsequently, all effects not significant at the 5% significance level were dropped from the model except line and sex-line interaction (Model 1). Due to differences in latest liveweight between lines within sex (see Table 8.2), latest liveweight was nested within sex and fitted as a covariable (Model 2). In both models the sex-line interaction was fitted to allow estimation of least square means used to estimate response as the difference between the line selected for lean tissue growth rate and the control line within sex.

$$Y_{ijk} = \mu + \text{sex}_i + \text{line}_j + (\text{sex}*\text{line})_{ij} + \epsilon_{ijk}$$

Model 1

$$Y_{ijk} = \mu + \text{sex}_i + \text{line}_j + (\text{sex}*\text{line})_{ij} + \beta_i (\text{LW}_{ijk} - \text{LW}_i) + \epsilon_{ijk}$$

Model 2

where:

Y_{ijk}	=	observation of individual
μ	=	population mean
sex_i	=	sex ($i = 1, 2$)
line_j	=	line ($j = 1, 2$)
β_i	=	linear regression coefficient for LW_{ijk} deviation
LW_i	=	mean liveweight of sex
LW_{ijk}	=	liveweight deviation of individual
ϵ_{ijk}	=	random error assumed to be normally and independently distributed with mean of zero.

Significantly different ($P<0.05$) results for fixed effects, sex (across lines) and lines (across sexes) were based on *F-test*. Direct and correlated responses were assessed as differences between lines (combined sexes) and between lines within sex. Significance of differences ($P<0.05$) in responses between lines (within sex) and sex (within line) were assessed by *t-test*.

8.2 Results

Operator repeatability of analysing the same set of images for individual animal twice, was never less than 99.3% for tissue weight traits.

Averages for liveweight, age and number of scan slices analysed per animal within sex-line are presented in Table 8.2. A significant difference in liveweight occurred between rams of the lean tissue growth rate line and the control line ($5.3\pm2.4\text{kg}$). Significant differences occurred in liveweight ($5.6\pm2.4\text{kg}$) and number of scan slices (0.4 ± 0.1) between rams and ewes of the lean tissue growth rate line. Age differences at measurement significantly differed between sexes (within line) with ewes being older than rams (5.4 ± 2.4 and 7.0 ± 3.3 days for the lean tissue growth rate and the control lines respectively) (Table 8.2).

Table 8.2: Mean (\pm standard deviation) liveweight and age of animals electronically dissected and their average number of scan slices for rams and ewes for the control and the lean tissue growth rate (LTGR) lines

Variable	Rams		Ewes	
	Control	LTGR	Control	LTGR
Number of animals	10	12	9	12
Average age (days)	266.7 ± 4.5	264.6 ± 5.6	273.7 ± 8.8	270.0 ± 6.0
Average liveweight (kg)	49.8 ± 5.9	55.1 ± 5.1	49.2 ± 3.5	49.5 ± 6.5
Average no. of scan slices	16.6 ± 0.2	16.8 ± 0.2	16.4 ± 0.3	16.4 ± 0.2

8.2.1 Fixed and sex effects

Birth rank, rearing rank, age of dam, sex-line interaction and age at scanning were not significant for any trait in either model 1 or 2. In model 1, sex significantly affected all traits. Rams had heavier lean and bone weights and greater lean and bone percentages but lighter fat weight and lower fat percentage than ewes. Line only differed significantly for fat percentage, with the lean tissue growth rate line having a lower fat percentage than the control line. Coefficients of determination were highest (>0.70) for fat weight and percentages of fat, lean and bone, intermediate ($0.50 - 0.70$) for bone weight and lowest (<0.50) for lean weight.

In model 2, the covariate liveweight significantly affected the model fit for both tissue weight and relative size traits. Generally, rams had shallower slopes for all traits than ewes. Coefficients of determinations were high for all traits ($0.71 - 0.89$).

8.2.2 Responses to selection

A desirable response in fat weight was the only statistically significant difference between the lines across sexes. However, differences in other traits showed desirable trends. The responses were, decreases in fat

(weight and percentage) together with increases in lean (weight and percentage). While responses in tissue weights were greatest for lean than fat, in terms of tissue percentage they were less for lean than fat (Table 8.3).

Responses were significantly ($P < 0.05$) greater in magnitude for lean weight and less for fat weight in rams than ewes. None of the responses in relative size traits significantly differed between rams and ewes, but estimates were greater in ewes than rams (Table 8.3). None of the responses in tissue weight and relative size significantly differed between the sexes when adjusted for live weight. Nevertheless, all responses were desirable.

Generally, responses in rams and ewes were greater for lean weight but less for relative size traits and for fat weight from model 1 than 2 (Tables 8.3 and 8.4).

8.2.3 Correlated response in bone

A correlated response in bone weight was significantly ($P < 0.05$) greater in rams than ewes, paralleling responses in lean weight (Table 8.3). Between rams and ewes, bone response adjusted for liveweight and percentage was not significantly different, however, the estimate of the rams was greater than that of ewes (Table 8.4).

Bone response was greater in weight and less in bone percentage from model 1 than 2 (Tables 8.3 and 8.4).

8.3 Discussion

8.3.1 Responses to selection across sexes

There are no other reports considering responses to selection on the basis of using *in vivo* CT measurements. Selection led to an increase in lean weight and a decrease in fat weight which is consistent with theoretical predictions of Simm *et al.* (1987) and the results of Simm, Dingwall, Murphy and FitzSimons (1990b) and Cameron (1992) who used carcass dissection of crossbred progeny.

Realised response rates for lean weight (+72g per year) and fat weight (-40g per year) were higher than those predicted by Simm *et al.* (1987) of, +59g per year and -18g per year for lean and fat weights respectively, for the economic selection index used in the current study. Realised response rates of the present study were also higher than those predicted in Chapter 7; lean weight (+34 and +36g/year for autumn and winter respectively) and fat weight; (-21 and -19g/year for autumn and winter respectively). Greater responses observed than predicted could be the result of four effects.

1. Sampling errors due to sample size, scanning approach and methods of image analyses. These are described later in section 8.3.5 and are unlikely to have affected responses to selection.
2. A founder effect. Two separate ram populations founded the lean tissue growth rate line of the present study, 1984 born rams used in 1986 and 1985 born rams used in 1987. Results from the present study are for progeny of rams descending from the 1986 founder population which, relative to the 1987 ram founding population, has consistently had selection differentials that were greater for liveweight and less for ultrasonic fat depth (see Figure 6.1). This led to responses being greater in liveweight and muscle depth and less for fat depth (Figures 6.6 & 6.7) throughout this study in this group. Proof of the founder effect influencing results requires assessment of the progeny in the year following that of this study (1995) to see if results follow the patterns shown by the 1994 group.
3. Predictions of the present study (Chapter 7) were made using indices constructed using parameter estimates from the ancestral population of those animals studied and other populations, together with assumed genetic parameters involving lean and fat weights. Genetic parameters involving lean and fat weight in the population of the present study are not known. Differences between predicted and observed responses could reflect errors in estimation of these genetic parameters. It could also be that heritabilities for aggregate breeding value traits and genetic correlations between the index and aggregate breeding value are greater or that the genetic correlation between lean and fat weight are less than predicted by Simm *et al.* (1987). Recently Waldron *et al.* (1992a) reported a greater heritability for lean weight (0.37 vs 0.27) and a lower genetic correlation between lean and fat weight (0.25 vs 0.39) than those reported by Simm *et al.*

al. (1987) for animals raised at pasture. It is possible that genetic parameter estimates differ between populations, results from the present study have shown that this was the case for the index and its component traits. However, given the scarcity of the genetic parameters for aggregate traits in the literature such a hypothesis is hard to evaluate at present.

4. Differences between predicted and observed responses could reflect differences in degree of mature development. Simm *et al.* (1987) predicted responses for a 13.64kg cold carcass. Carcasses of animals from the present study were estimated to be 10.56kg heavier. Simm *et al.* (1990b) reported increases in response of +2.2 and -1.1 g/kg for lean and fat weight respectively as carcass weight increased from 16.7 to 22.3 kg in crossbred animals. However, the nature of the comparison reported by Simm *et al.* (1990b) does not allow quantitative adjustments of responses from the present study. They compared the crossbred progeny of high and low index rams. The heritability of component traits in the sire population and the degree to which heterosis may have been involved were not reported. However their work clearly shows that the magnitude of responses will increase with degree of maturity.

8.3.2 Differences in response between rams and ewes

CT data responses parallel those seen in liveweight and ultrasound measurements (see Table 6.3) in that rams showed greater response in lean (136 vs 9 g/year) and less response in fat (-3 vs -78 g/year) than ewes. Such differences between the sexes are not readily explained but could be due to three effects, (i) genetic differences, (ii) differences in developmental stage and (iii) management difference.

1. Estimates of genetic parameters for the index and its component traits of parental animals used in the present study were found to consistently differ between the sexes and the failure to reach statistical significance was attributed to large sampling errors relative to parameter estimates (see Chapter 5). Differences in genetic parameters for liveweight or body composition between rams and ewes have been reported by among others Baker *et al.* (1979), Parratt *et al.* (1989) and Maria *et al.* (1993). Such differences in genetic parameters would lead to responses differing between sexes.
2. Genetic size scaling theory is general and applies at species level, but its applicability within species and between sexes is not so clear (Taylor, 1985). A sex difference occurred whereby at the same muscle:bone ratio, ewes were fatter (7.77 ± 0.29 vs 4.68 ± 0.27 kg) than rams. Differences between the sexes could be a function of maturity (Taylor, 1985) or sexual maturity and timing of the breeding season. Adjusting for difference in size by expressing fat as a percentage of the total carcass weight still led to ewes being fatter (31.26 ± 0.84 vs $19.79 \pm 0.79\%$) at equal muscle:bone ratio. Genetic size scaling is useful in highlighting differences between sexes. In order to assess whether response rates in the sexes in this study are

interacting with stage of maturity or sex specific effect comparisons need to be made of the two sexes under the same nutritional conditions and at the same stage of equal maturity. Equal maturity could be defined as at standardised growth state *e.g.* at equal subcutaneous fat proportion (Croston *et al.*, 1987; Kempster *et al.*, 1987) to avoid problems highlighted in section 2.5.1.

3. Management differences between rams and ewes did occur (see section 4.3.2). Rams and ewes were run separately at pasture from weaning (November/December), with ewes on crop residues for 8 weeks prior to scanning while rams grazed pasture. Adjusting for sex effects removes this management influence which should produce responses less biased by management. However, if there is a genotype-environmental interaction then simple adjustments would not be appropriate. Ideally, animals should be run under the same management to allow valid comparisons of responses.

8.3.3 Responses adjusted for size

Accounting for differences in size by considering tissue proportions and by adjusting to a common liveweight within sex, did not generally alter the interpretation of responses. Comparing responses in traits independent of size is valid since this takes into account that units and means of traits may differ (Smith, 1988).

Lower responses adjusted for size in lean than fat weight are because of the part-whole relation between lean and size (Simm *et al.*, 1987). Lean is a greater proportion of the whole carcass than fat and bone, adjusting for size removes much of the difference in lean weight (see section 2.5.1).

8.3.4 Correlated response in bone

Results from the present experiment indicate an increase in carcase weight (+62g/year) which agrees with the aim of the selection experiment which was to increase lean weight in order to increase carcase weight. In the present study bone weight increased (+30g/year) as predicted by Simm *et al.* (1987). An increase in bone weight is inevitable since bone and muscle weight are functionally related and positively correlated genetically (Wolf *et al.*, 1981; Parratt, Burt, Bennett, Clarke, Kirton and Rae, 1987).

A greater correlated response in bone weight in rams than ewes reflects the greater response in lean weight in rams. A lower response in bone percent in rams than ewes could be due to differences in size of the sexes. Adjusting for size (liveweight within sex) did not alter response patterns in bone weight.

8.3.5 Scanning approach and image analysis

It is unlikely that the scanning approach and image analyses influenced the realised response found in the present study.

Fifty-two (52) animals were sampled from a whole population of 210 animals. Live weights for the sample were similar to those of the sub-populations (Table 8.1). Fortunately the 9 animals lost (leaving only 43 to be analysed) had little effect on these means (compare Tables 8.1 & 8.2). This indicates that sampling did not bias results.

Assumptions of the Cavalieri principle (Gundersen and Jensen, 1987; Gundersen *et al.*, 1988) were fulfilled. More than 15 slices were used to estimate volume (see Table 8.2) and the first slice was chosen at random and slices were equally spaced. Therefore, anatomical positioning effects are not likely to have influenced the results.

Operator error should not have biased results since repeatabilities for total fat, lean and bone weight were never less than 99.93%.

Before gutting, images were converted to bitmaps and there was concern that machine calibration (measured as water drifting over time from the calibrated value of 0 H.U.) could influence results. *Bitman* converted 512 CT values to 255 shades of grey, with zero being black and 256 white. Bitmaps were produced for a number of different window centre settings (ranging from 700-800) in which all three tissues were visible. These were electronically dissected and results compared. Provided all three tissues (fat, muscle and bone) were visible in each bitmap, the misclassification of tissues from the different *Bitman* settings was between 1% and 4%, indicating that tissue distributions were essentially non-overlapping. Therefore, machine "drift" should have had little effect on tissue dissection.

The effect of overlapping ranges of CT numbers for different tissues has been investigated by Knopp (1985). This work derived a method for allocating pixels in the overlapping range to tissues based on the relative size of the two tissues *e.g* where there is more muscle than bone more of the overlapping range is allocated to muscle than bone. *Autocat* does not do this. This would be a problem when comparing populations of animals with different tissue proportions. It should not bias the comparison of control versus selected groups within sex but could bias comparison of ewes versus rams. The nature of this bias in the latter case would be to increase differences between sexes since, according to the method of Knopp (1985) a greater proportion of overlapping range of pixels between fat and muscle should go to fat in ewes and lean in rams. However, *Autocat* allocates simply on the basis of fixed boundaries within the overlapping range. A calibration exercise indicated that the range of the two most important tissues (fat and muscle) did not overlap (described below) and bias due to this is likely to be small.

Mean *Autocat* densities (256 grey scale) were 71.6 ± 8.1 , 183.6 ± 3.3 and 254.4 ± 0.1 for fat, lean and bone tissues respectively. Within individual slices 1-4% overlap was observed between lean and bone tissues but there was no overlap between fat and muscle tissues. Fat tissue density significantly differed between rams (78.3 ± 0.9) and ewes (64.6 ± 1.0). However, muscle and bone densities did not differ significantly between rams (184.3 ± 0.7 and 254.4 for lean and bone respectively) and ewes (182.7 ± 0.7 and 254.4 for lean and bone respectively). The same density value for bone in rams and ewes is due to the truncated distribution caused when only 512 H.U. are converted to the 256 grey scale by *Bitman*. Most of the bone range in H.U. are allocated to a value of 255 on the bitmap grey scale.

Difference in fat density between rams and ewes could reflect differences in the ratio of lipid:non-lipid in adipose tissue. Hydration of adipose tissue due to fat depletion increases density *e.g.* during rutting in deer stags (Jopson, pers. comm.). It is unclear whether rams in this study were depleting fat. Both sexes were on adequate feeding which is not likely to have promoted tissue depletion in one sex and not the other. It is more likely to be a fatness effect whereby the ewes are considerably fatter overall which will lead to an increase in lipid:non-lipid ratio in the adipose tissue. Greater fatness in ewes than rams could be due to maturity, nutrition and possible sex effects.

Ewes in the present study are likely to have been more mature than rams because they had greater muscle:bone ratio than rams (3.33-3.39 vs 3.09-3.13). Muscle:bone ratio increases with increasing stage of maturity (Butterfield, 1988; Thorgeirsson and Thorsteinsson, 1989). Another indication that the two sexes were at different stages of maturity is from fat content in the body. The fat content in a carcass increases with stage of maturity (Thorgeirsson and Thorsteinsson, 1989). Ewes in the present study had higher fat content in their carcasses than rams (30.58-32.81% vs 18.51-20.06%). Therefore it is likely that the ewes had a higher lipid:non-lipid content in adipose tissue leading to lower fat density than rams. Such a hypothesis is compatible with the observation of Berg and Butterfield (1976) that the fatter an animal gets the higher will be the percent of chemical fat in each fat depot than a thinner animal.

Another possible explanation for the fat density differences between ewes and rams is that there may be genetic differences between the sexes. However, there were no data available to evaluate such a hypothesis. Nevertheless, it is not obvious why differences should occur only in fat and not in muscle density. Sehested (1986) found that in rams of the same carcass weight (21kg), a fat ram (3.6 kg fat weight) had less dense adipose tissue and less dense muscle compared to a lean ram (1.6kg fat weight). He attributed these differences in tissue densities to differences in fat composition with the fat ram having more chemical fat and less protein and water in adipose tissue. The difference in muscle density was inferred to be due to higher intramuscular fat in the fatter animal although intramuscular fat was not measured (Sehested, 1986). Since

ewes were fatter and had slightly lower muscle density (182.7 vs 184.3) than rams in the present study, the findings reported here are compatible with those of Sehested (1986).

8.4 Conclusions

Results from the present study clearly demonstrate that desirable responses occurred in aggregate breeding value traits to selection on an economic index for lean tissue growth rate. Importantly, the results suggest that responses to selection have been greater than indicated by changes in selection index components traits. Responses differed between sexes which was due in part to differences in management, or in relative maturity of the sexes. However, differences were of such a magnitude that these are unlikely to explain the differences suggesting that there were real genetic differences between the sexes, and therefore that responses have a different genetic basis in rams and ewes.

8.5 Recommendation

Responses should be predicted in descendants of 1987 founding populations to determine whether founder effects have biased results and whether any sex differences are consistent with those observed in the present study. In order to establish true sex differences, rams and ewes should be run under the same management prior to scanning and measurement and scanning should be at equal maturity.

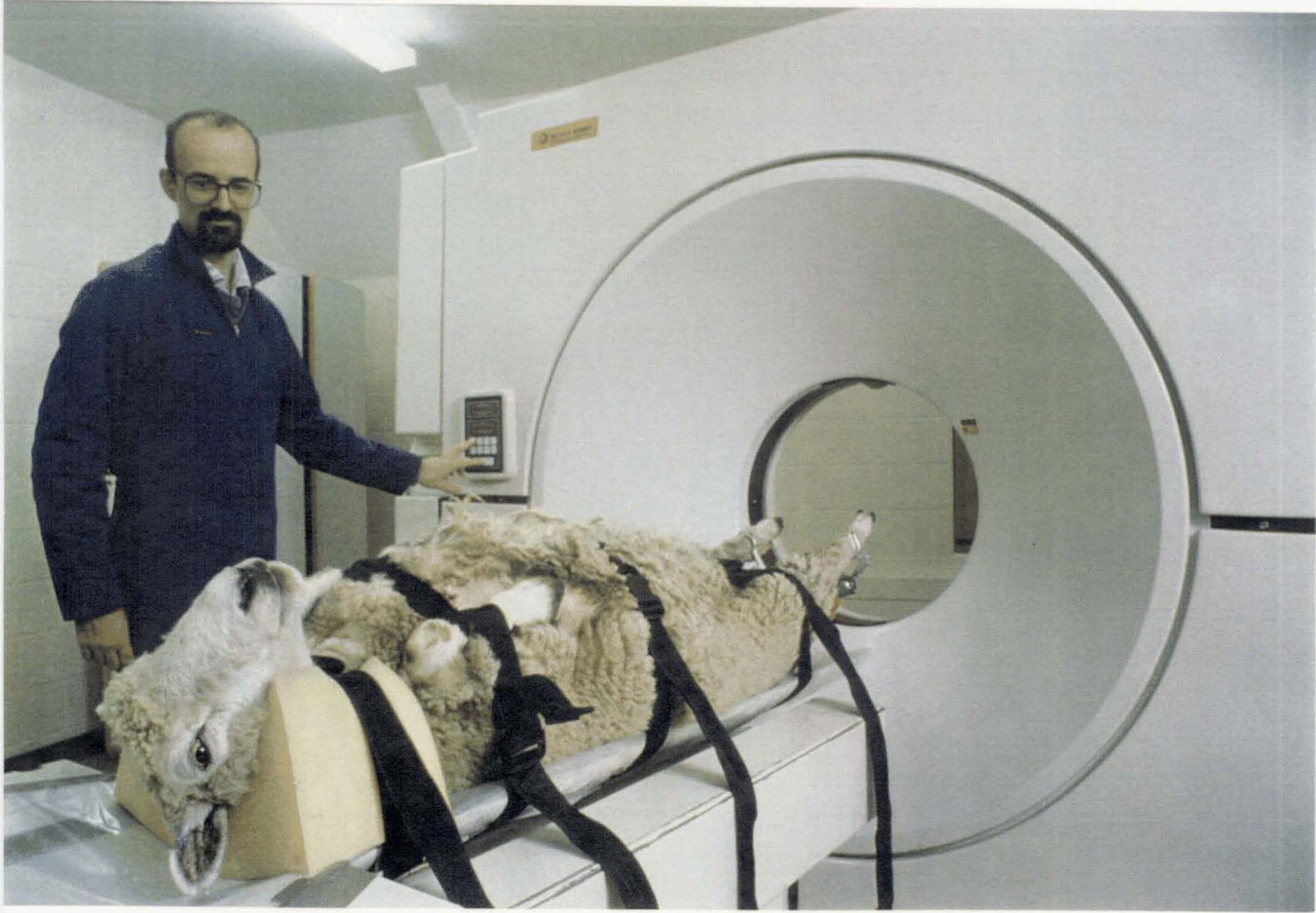


Plate 8.1: Typical restraining position: a sheep restrained with black straps in a cradle lying on its back with forelegs parallel to the spine and close to the chest and hindlegs clamped at flat angle.

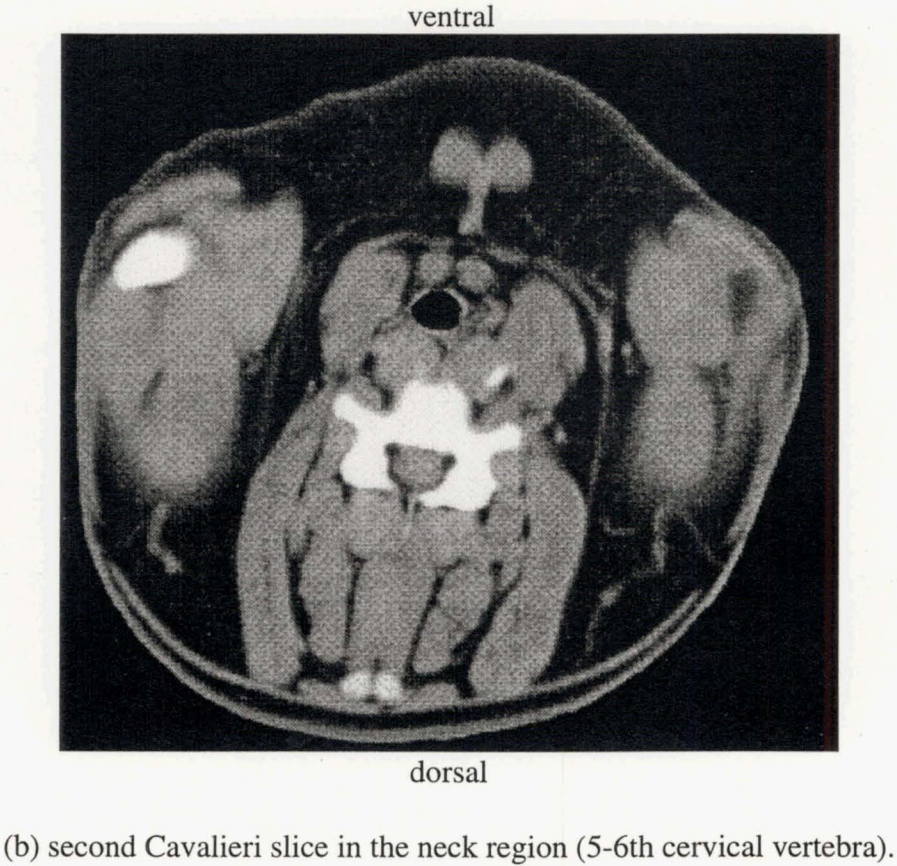
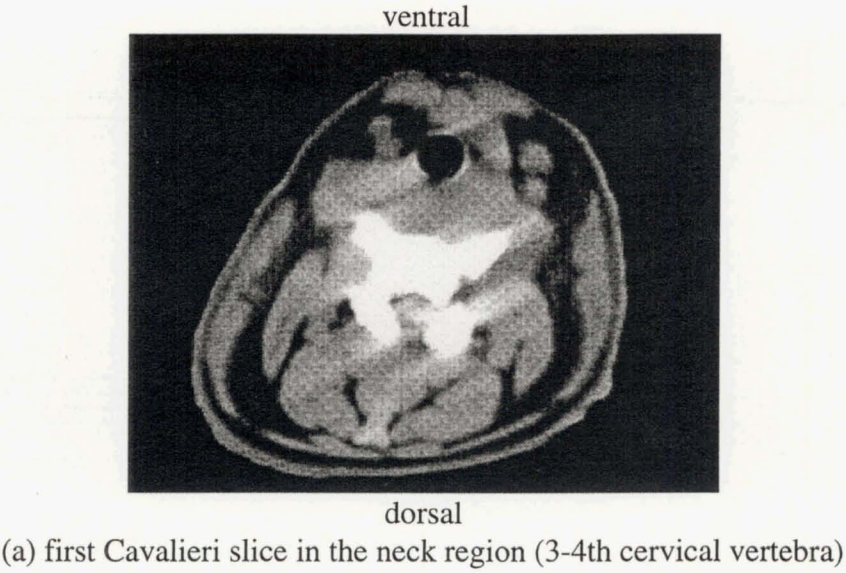
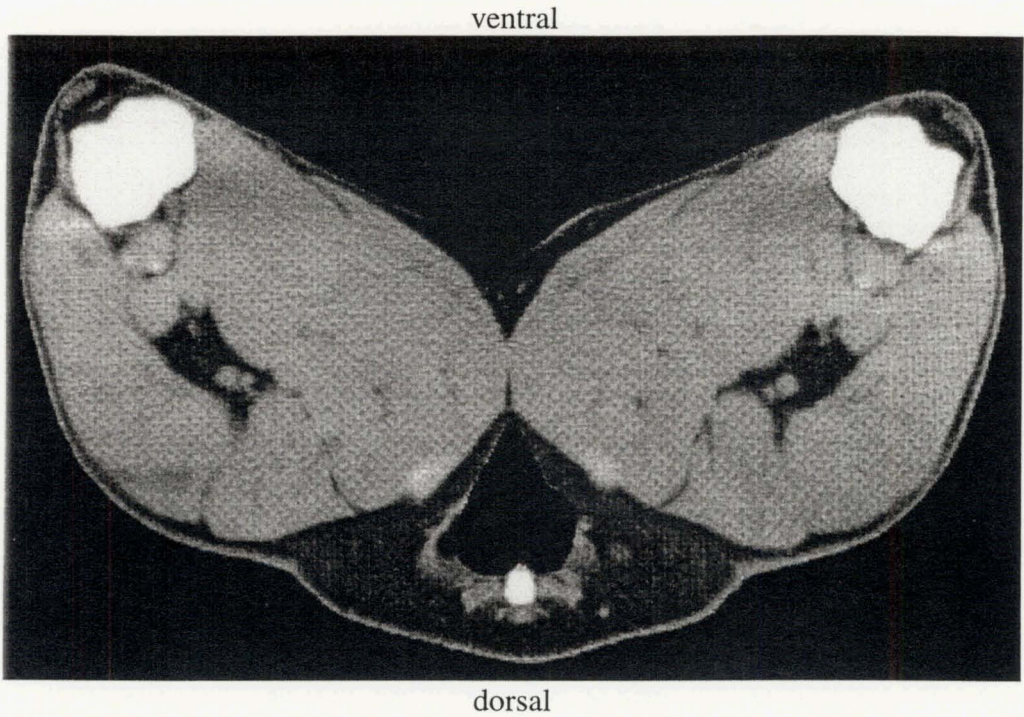
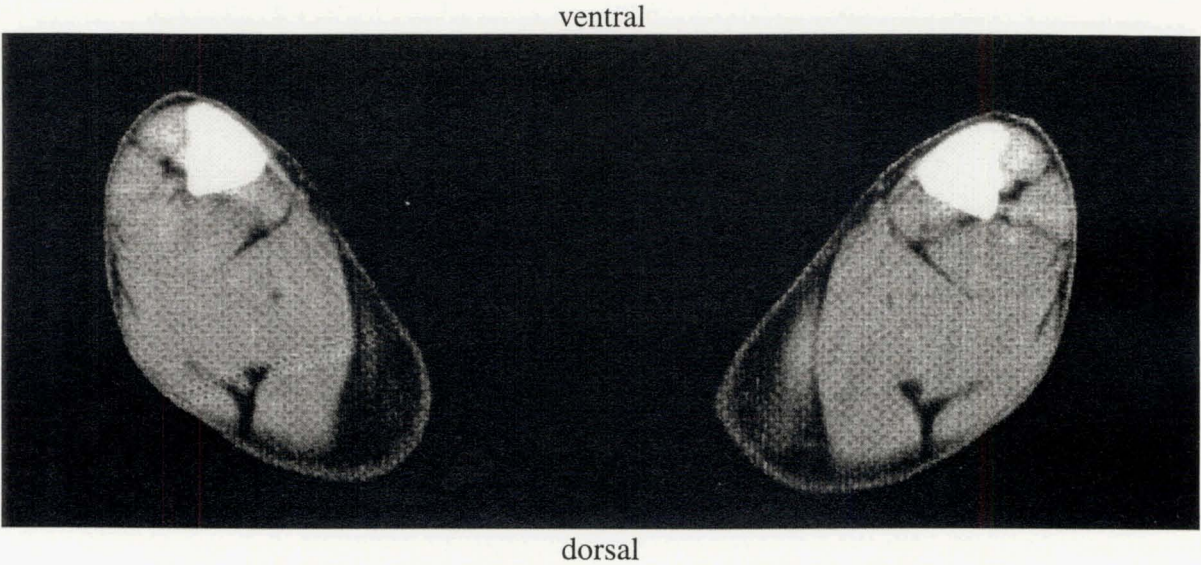


Plate 8.2: Typical first and second slices in the Cavalieri series in the neck region. Note that musculature and bone of the forelimb are not seen in (a) but are distinct in (b). Slices have been processed to remove table and other foreign material. Ventral and dorsal refer to orientation of the sheep (see Plate 8.1). Fat is dark grey, muscle light grey and bone is white.



(a) second to last Cavalieri slice in the thigh region (distal femur)

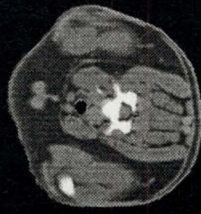


(b) last Cavalieri slice in the knee joint region (proximal tibia)

Plate 8.3: Typical second to last and last slices in the Cavalieri series in the thigh and knee joint regions respectively. Note that musculature of the thigh dominates (a) but is barely visible in (b). Slices have been processed to remove table and other foreign material. Bone marrow painted white. Ventral and dorsal refer to orientation of the sheep (see Plate 8.1). Fat is dark grey, muscle light grey and bone is white.

Plate 8.4 is on page 142

Plate 8.4: Typical slices (n=16) in the Cavalieri series from neck to leg. Slices have not been processed to remove table and other foreign material. The labels below some slices *e.g* neck, chest are on the same side as the dorsal view of the sheep (see Plate 8.1). Fat is dark grey, muscle light grey and bone is white.



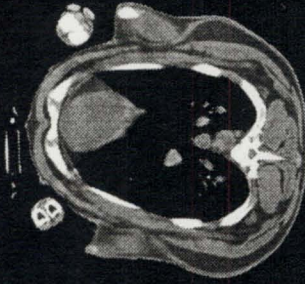
neck



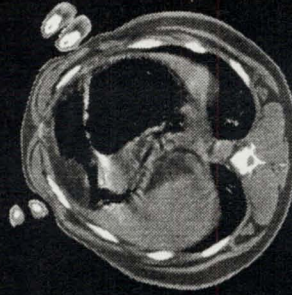
shoulder



heart



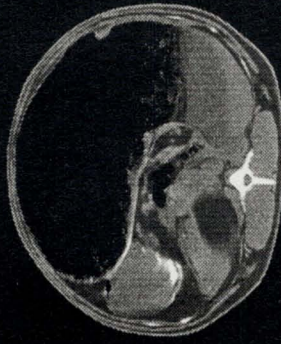
chest



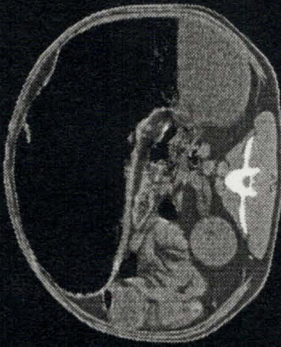
diaphragm



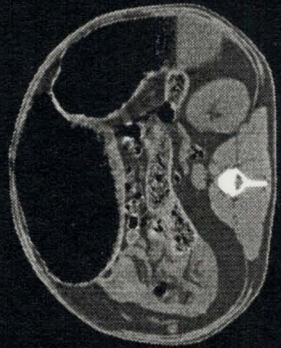
liver & spleen



right kidney



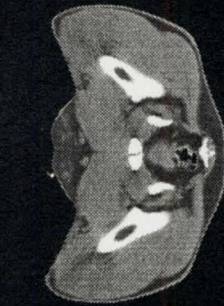
left kidney



thigh



pelvis



hip



leg

E096 - 15-MAY-95

Cavalieri scan sequence

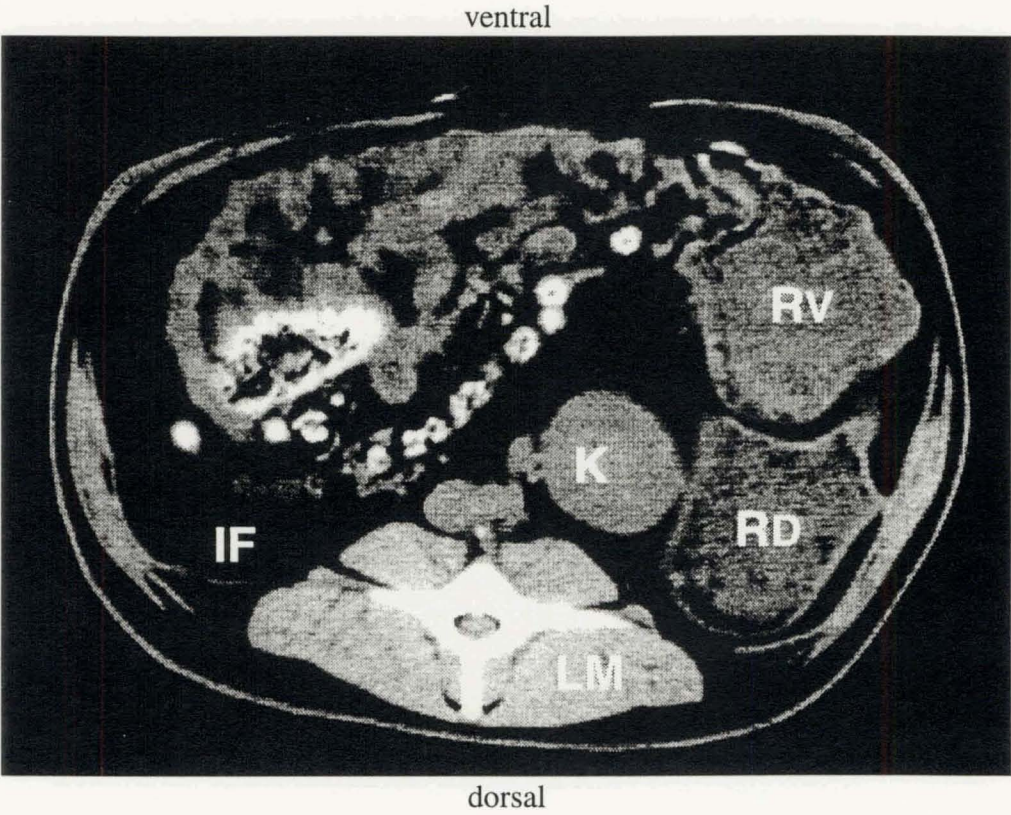
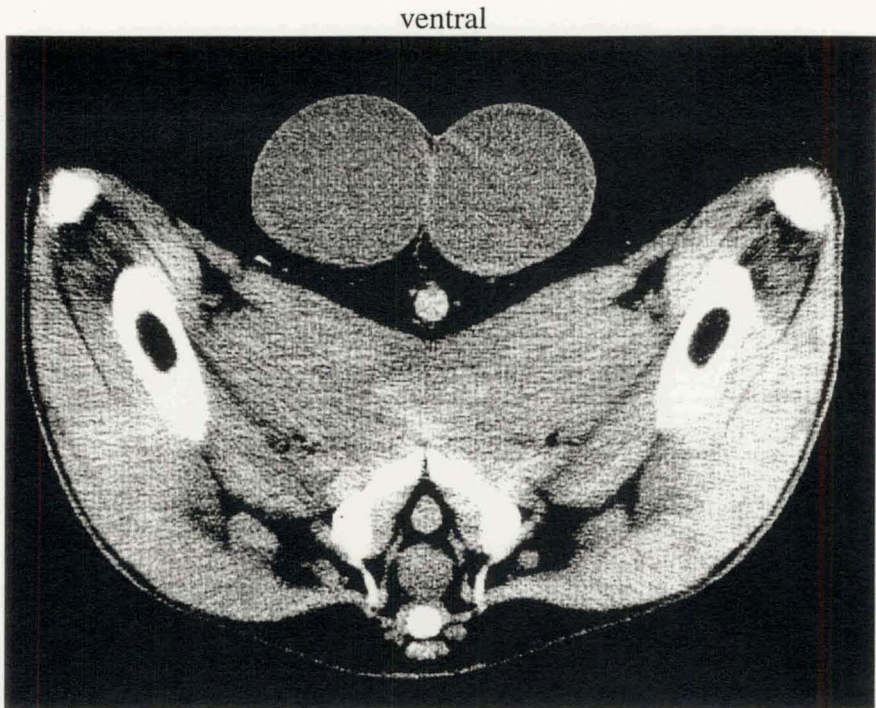
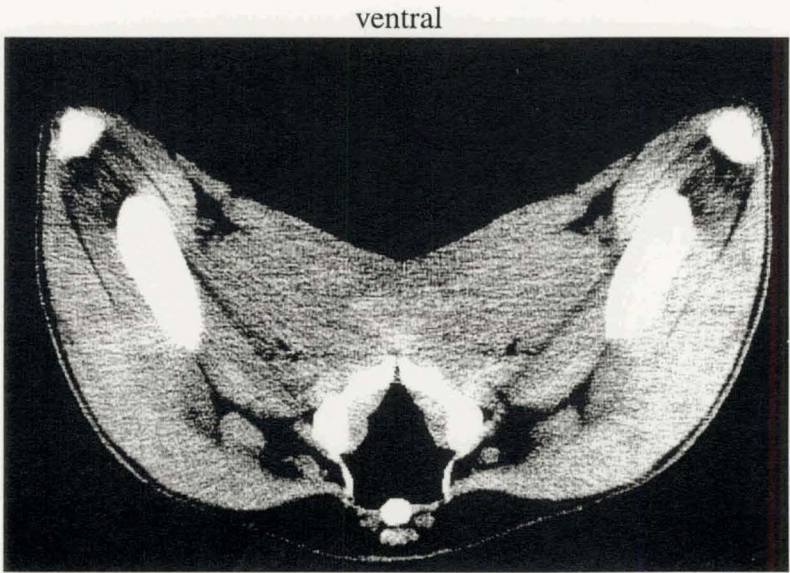


Plate 8.5: Typical CT image at the 5th lumbar vertebra, showing examples of major tissues; muscle (LM = *Longissimus dorsi*), fat (IF = internal fat) and bone (white in colour) embedded in muscle. The pale grey, outer layer is the skin, with subcutaneous fat below it. This image also shows the kidney (K) and rumen (RV and RD rumen dorsal sac and rumen ventral sac respectively). The heterogenous region in the upper left third of the slice is predominantly the intestine (small and large) and associated mesenteric fat. Material in the intestines is thought to be fine soil material (note how it highlights the loops of the intestines). Ventral and dorsal refer to orientation of the sheep (see Plate 8.1). Fat is dark grey, muscle light grey and bone is white.

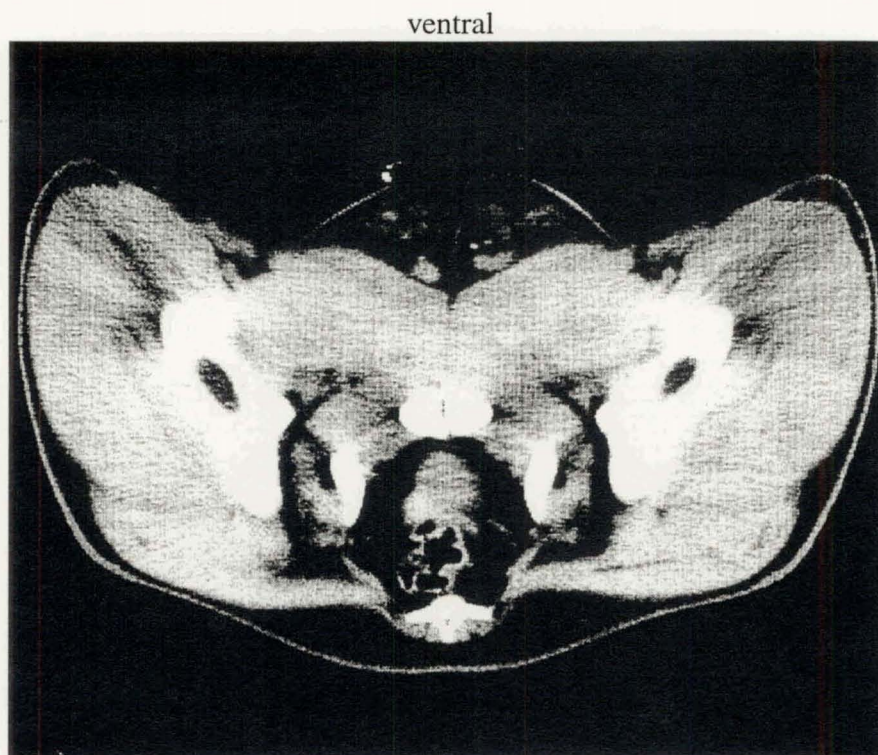


(a) Cavalieri slice in the pelvic region before gutting (mid shaft of femur)



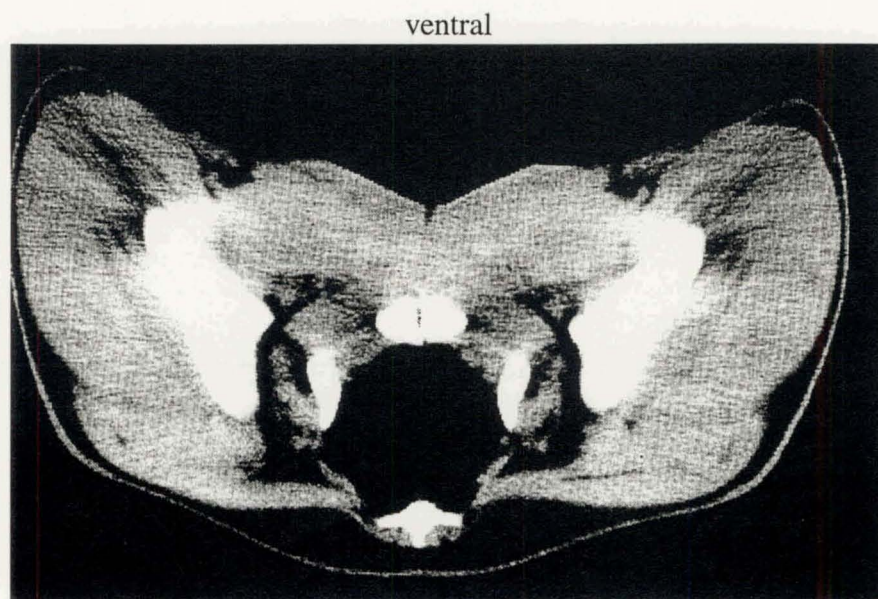
(b) Cavalieri slice in the pelvic region after gutting

Plate 8.6: An example of a ram Cavalieri slice from the pelvic region before and after gutting. Gutting involved removal of (i) testes, (ii) rectum and associated fat and (iii) painting bone marrow white. Ventral and dorsal refer to orientation of the sheep (see Plate 8.1). Fat is dark grey, muscle light grey and bone is white.



dorsal

a) Cavalieri slice in the pelvic region before gutting (mid shaft of femur)



dorsal

(b) Cavalieri slice in the pelvic region after gutting.

Plate 8.7: An example of a ewe Cavalieri slice from the pelvic region before and after gutting. Gutting involved removal of (i) udder, (ii) rectum and associated fat and (iii) painting bone marrow white. Ventral and dorsal refer to orientation of the sheep (see Plate 8.1). Fat is dark grey, muscle light grey and bone is white.

Table 8.3: Least squares mean weights (se) and percentages (se) for selected and control lines, and selected (S) - control (C) line differences (s.e.d) from Model 1. Se and s.e.d are abbreviations for least squares mean standard error and standard error of difference respectively.

SEX	LINE	TRAIT													
		Fat weight		Muscle weight		Bone weight		Total weight		Fat percent		Muscle percent		Bone percent	
		Mean (kg)	S-C (kg)	Mean (kg)	S-C (kg)	Mean (kg)	S-C (kg)	Mean (kg)	S-C (kg)	Mean (%)	S-C (%)	Mean (%)	S-C (%)	Mean (%)	S-C (%)
Rams & ewes	Control	6.42 (0.26)		13.39 (0.36)		4.11 (0.11)		23.92 (0.63)		26.43 (0.67)		56.25 (0.60)		17.32 (0.32)	
	Selected	6.06 (0.23)	-0.36 (0.08)	14.04 (0.32)	+0.65 (0.10)	4.38 (0.10)	+0.27 (0.03)	24.48 (0.56)	+0.56 (0.18)	24.55 (0.59)	-1.88 * (0.20)	57.44 (0.53)	+1.19 (0.17)	18.01 (0.28)	+0.69 (0.09)
Rams	Control	4.55 (0.36)		13.66 (0.49)		4.36 (0.15)		22.57 (0.86)		20.06 (0.92)		60.62 (0.82)		19.32 (0.44)	
	Selected	4.52 (0.32)	-0.03a (0.15)	14.88 (0.45)	+1.22a (0.20)	4.81 (0.14)	+0.45a (0.06)	24.21 (0.79)	+1.64a (0.35)	18.51 (0.84)	-1.55 (0.38)	61.55 (0.75)	+0.93 (0.34)	19.94 (0.40)	+0.62 (0.18)
Ewes	Control	8.29 (0.37)		13.12 (0.52)		3.87 (0.16)		25.28 (0.91)		32.81 (0.97)		51.89 (0.87)		15.31 (0.47)	
	Selected	7.59 (0.32)	-0.70b (0.16)	13.20 (0.45)	+0.08b (0.22)	3.96 (0.14)	+0.09b (0.07)	24.75 (0.79)	-0.53b (0.38)	30.58 (0.84)	-2.23 (0.40)	53.34 (0.75)	+1.45 (0.36)	16.08 (0.40)	+0.77 (0.19)

* = P<0.05. Least squares mean differences with different subscripts differ significantly (P<0.05) between sexes within traits

Table 8.4: Least squares mean weights (se) and percentages (se) for selected and control lines, and selected (S) - control (C) line differences (s.e.d) from Model 2. Liveweight fitted in the model as a covariate within sex. Se and s.e.d are abbreviations for least squares mean standard error and standard error of difference respectively.

SEX	LINE	TRAIT													
		Fat weight		Muscle weight		Bone weight		Total weight		Fat percent		Muscle percent		Bone percent	
		Mean (kg)	S-C (kg)	Mean (kg)	S-C (kg)	Mean (kg)	S-C (kg)	Mean (kg)	S-C (kg)	Mean (%)	S-C (%)	Mean (%)	S-C (%)	Mean (%)	S-C (%)
Rams & ewes	Control	6.67 (0.17)		13.75 (0.23)		4.21 (0.08)		24.64 (0.29)		26.68 (0.63)		56.11 (0.57)		17.21 (0.32)	
	Selected	5.91 (0.16)	-0.76 * (0.05)	13.94 (0.21)	+0.19 (0.07)	4.30 (0.07)	+0.09 (0.02)	24.16 (0.27)	-0.48 (0.09)	23.96 (0.60)	-2.72* (0.19)	58.02 (0.54)	+1.91* (0.17)	18.02 (0.31)	+0.81 (0.10)
Rams	Control	4.73 (0.23)		13.86 (0.31)		4.44 (0.11)		23.03 (0.39)		20.45 (0.87)		60.27 (0.78)		19.28 (0.44)	
	Selected	3.95 (0.24)	-0.78 (0.10)	14.24 (0.32)	+0.38 (0.13)	4.55 (0.11)	+0.11 (0.05)	22.74 (0.41)	-0.29 (0.17)	17.26 (0.90)	-3.19 (0.38)	62.65 (0.81)	+2.38 (0.34)	20.09 (0.46)	+0.81 (0.19)
Ewes	Control	8.62 (0.25)		13.64 (0.33)		3.98 (0.11)		26.25 (0.42)		32.91 (0.92)		51.95 (0.83)		15.15 (0.47)	
	Selected	7.86 (0.22)	-0.76 (0.10)	13.65 (0.28)	+0.01 (0.14)	4.06 (0.10)	+0.08 (0.05)	25.57 (0.36)	-0.68 (0.17)	30.67 (0.80)	-2.24 (0.38)	53.39 (0.72)	+1.44 (0.35)	15.94 (0.41)	+0.79 (0.20)

* = $P < 0.05$

CHAPTER 9

GENERAL DISCUSSION

9.1 Findings from the present work

Findings of this study have validated the approach put forward by Simm *et al.* (1987) to improve lean tissue growth rate in sheep under pastoral feeding conditions. Desirable responses were observed, both in index component traits and in aggregate breeding value traits. Estimates of genetic parameters derived showed some variation but generally agreed with those reported in the literature.

Responses in index component traits were similar to those previously published for liveweight but lower for fat and muscle depths (Young, 1989; Cameron and Bracken, 1992). Realised responses of these traits differed between sexes and breeds. Responses in aggregate breeding value traits measured by X-ray CT differed between sexes.

Response rates were higher (>27%) in rams for liveweight and muscle depth and lower (<19%) for fat depth than ewes in two lean tissue growth rate flocks (Border Leicester and Dorset Down) but the opposite was true for the Coopworth. Greater (11-64%) responses in the selection index and its component traits for ewes than rams were reported by Simm *et al.* (1990b). These authors did not offer an explanation for the observed differences. Differences in response rates for index component traits in the present study closely mirrored differences in genetic parameters. For example in Dorset Down and Border Leicester flocks, greater heritabilities for all traits led to greater response rates in rams than ewes except fat depth. Similar trends were evident in Coopworth flock, however, it was the ewes that had greater heritability estimates and greater response rates compared to rams. Variation in response rates for index component traits between breeds within sex, followed similar patterns to those between sexes within breed in that higher parameter estimates generally led to higher responses.

Responses in aggregate breeding value traits were desirable but differed between sexes. Dorset Down rams had higher (>100%) and lower (<10%) responses in lean and fat weight respectively than Dorset Down ewes. This effect was mirrored by observed responses in index component traits where rams had higher responses in liveweight (+127%) and lower responses in fat depth (<100%) than ewes. That this was a basic difference between the sexes was further evidenced by response predictions based on parameter estimates derived in this study. These predicted response rates were higher (+150%) for lean and lower for fat weight (+81%) in rams than ewes.

Differences between sexes and breeds in parameter estimates, index component trait responses and aggregate breeding value trait responses observed could be due to several effects.

1. Seasonal effect. Earlier work at Lincoln has shown that in rams heritability for fat depth was greater in winter (0.34 ± 0.08) than either autumn (0.17 ± 0.06) or spring (0.16 ± 0.09) leading to greater predicted response per generation in winter (0.58mm) than either autumn (0.22mm) or spring (0.50mm) (Beatson, 1987). Results for heritability estimates from Border Leicester and Dorset Down flocks support this conclusion. However, those of the Coopworth do not, since in spring higher heritabilities and higher responses were seen than in winter for this breed. Coopworth ewes were required to be performance tested in spring as part of a sire reference breeding scheme this breed was involved in. These data suggest a possible increase in additive genetic variance relative to environmental variance with season. This could be due to the decreasing importance of maternal effects, a reduction in environmental variance in winter/spring, catch-up growth reducing variation between animals due to stage of maturity or a developmental effect whereby animals have more opportunity to exhibit their genotype as they mature.
2. Genotype by environment interaction. Border Leicester and Dorset Down rams were occasionally preferentially fed. This could have led to higher parameter estimates and responses to selection if it increased additive genetic variance because animals had greater opportunity to express their genetic make-up. However, preferential feeding did not occur in Coopworth ewes. It is concluded that this effect did not have bias results.
3. Bias in environmental effects that was not corrected for. Maternal effects are the most likely effects to bias such results (Ch'ang and Rae, 1970). However, the evidence from DFREML univariate analyses was that these were generally small (2-5%). Therefore maternal effects are unlikely to have influenced results.
4. Relative maturity of animals. Simm *et al.* (1990b) demonstrated that relative responses in lean and fat weights increase with degree of maturity. While there are no similar studies reporting such phenomena in index component traits, they should also increase with degree of maturity. Confounding in the present data sets does not allow evaluation of such a hypothesis.
5. Random sampling effects. Data sets used in this study were larger than those of similar studies (Young, 1989; Cameron and Bracken, 1992 and Bishop, 1993). Together with the extra precision of multivariate individual animal model REML used in analysis to estimate parameter estimates and BLUP breeding values, random sampling error effects are unlikely to have had much influence.

6. True sex differences. The Corriedale data sets for rams and ewes measured in winter showed differences in parameter estimates between sexes suggesting that differences between sexes in other breeds do exist. Responses in the aggregate breeding value traits of Dorset Down ewes and rams both measured in autumn followed those of index component traits for ewes in autumn and rams in winter, supporting the argument that differences between sexes were real. This implies that separate selection indices should be derived for rams and ewes.
7. True breed differences. Differences occurred in parameter estimates and in responses of index component traits for the Border Leicester and Dorset Down breeds which were run together as single mobs within sex. In part this association may be because responses and genetic parameters were derived from the same REML analyses. Other data sets can not help elucidate this issue because of confounding between breed and mob management. Whether breed differences are real is hard to resolve. However, similar studies, each conducted with only one breed (Young, 1989; Cameron and Bracken, 1992 and Bishop, 1993) have shown variability in the magnitude of parameter estimates and of responses to selection similar to that seen in the present study. This could suggest that while not always statistically significant, results of the present study point towards the existence of real differences in responses to selection and parameter estimates between breeds. This may suggest that breed specific selection indices are more appropriate.

The present work has shown that performance in index component traits is affected by systematic environmental effects such as birth rank, age of dam and year. The magnitude of correction factors for these non-genetic effects varies between seasons, sexes and breeds. Examination of previously published estimates of environmental correction factors led to the following observations. Firstly, estimates were variable between sexes (Warmington and Beatson, 1986), seasons (Eikje, 1971, Baker *et al.*, 1974) and breeds (Eikje, 1971). Secondly, estimates from experiments which were designed to minimise these by feeding high energy, high protein diets *ad libitum* were significant and variable (Young, 1989, Cameron and Bracken, 1992, Bishop, 1993). While differences in literature estimates may reflect unidentified sampling errors due to variation between experiments *e.g* in size, management, nutrition and method of analysis, results of the present study support the conclusion that they are real and difficult to minimise through intensive feeding. Therefore, it is desirable to estimate correction factors within flock, within sex and within year when this can be done accurately.

Correlated response to selection for lean tissue growth rate occurred in bone weight. This verified the prediction that an increase in lean would be accompanied by an increase in bone (Simm *et al.*, 1987) due to the positive genetic correlation between these traits (Wolf *et al.*, 1981; Parratt *et al.*, 1987). Together with increase in lean and fat weights, this suggests selected animals are less mature at a given age. On the basis of genetic size scaling theory, this indicates that mature size is increasing. This is not

desirable in dual purpose breeds where it will affect efficiency of the ewe flock but probably not important in terminal sire breeds.

Greasy fleece weight showed a desirable, positive correlated response for lean tissue growth rate. Therefore, selection using the economic index of the present work should increase wool production as well as lean tissue growth rate. Together with responses seen in index component traits and aggregate breeding value traits, these suggest animals are partitioning relatively more energy towards protein metabolism and relatively less towards fat metabolism.

9.2 Technology use

For ongoing selection programmes where the focus is genetic improvement, traditional carcass assessment techniques which necessitate slaughtering and dissection cannot be employed (Sehested, 1986 and Sehested and Vangen, 1989). While it is possible to evaluate crossbred progeny of the selected and control animals, resources are not always available to meet this and the effects of heterosis and genotype by environmental interaction complicate such comparisons. This study has shown that X-ray computer tomography (CT) can be used to estimate fat and lean weights *in vivo* for the population under selection to overcome such problems. Data obtained in this study using CT, are the first of their kind applied to this situation and demonstrate the potential this technology has to offer to animal breeding research. CT can provide further opportunities for selection as it allows novel traits such as internal fat and total bone weight *in vivo* to be measured.

Use of CT can allow rapid genetic improvement when used in a two stage selection programme. First stage mass screening using ultrasound technology can be combined with a second stage using CT scanning to aid in final selection (Simm, 1987). Following identification of superior genotypes, use of artificial insemination will enhance spread of the benefits of superior genetic material (Allen, 1990).

9.3 Conclusions

Lean tissue growth rate can be improved through index selection and responses observed under pastoral feeding conditions are similar to those under intensive feeding conditions. While responses under pastoral feeding were smaller, this is simply due to lower rates of growth in an environment with a lower average level of nutrition.

Variation occurs between genotypes (sex and breed) for genetic parameters and this lead to variation in responses to selection for lean tissue growth rate.

CT has been shown to be an exciting tool in experimental animal breeding and has the potential to make an important contribution to commercial breeding programmes.

9.4 Recommendations

1. Lean tissue growth rate economic indices should be separately derived for each sex and breed to maximise efficiency of selection.
2. Further investigation is needed to determine whether selection for lean tissue growth rate increases adult size. This is of great significance in dual purpose sheep.
3. These experiments should be more carefully controlled to minimise confounding. In order to advance our knowledge of the genetic control of lean tissue growth rate, differences between breeds, sexes and seasons in terms of genetic parameters and responses should be characterised more accurately. Due to confounding of effects in the present work such differences could only be partly characterised, with a degree of difficulty. Comprehensive characterisation of such differences is possible through experiments carried out under standardised conditions for clearly defined periods of time with clearly defined objectives which must be adhered to. Paramount among the objectives of such a study would be the need to characterise genetic and phenotypic parameters for lean and fat weight as well as for index component traits, together with assessment of responses in ewes and rams of different breeds measured together at several times of the year (autumn, winter and spring).
4. Use of CT employing a similar approach to that used in this study would allow characterisation of responses in aggregate breeding value traits. Analyses of data from such measurements would help elucidate the nature of differences observed between seasons, sexes and breeds and therefore, should lead to derivation of effective commercial breeding strategies. Furthermore, correlated responses in economically important traits should be monitored to ensure that they do not occur.

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REFERENCES

- Allden, W.G.** (1970). The effects of nutritional deprivation on the subsequent productivity of sheep and cattle. *Nutritional abstracts and reviews* **40**: 1167-1184.
- Allen, P.** (1990). New Approaches to Measuring Body Composition in Live Animals. In J.D. Wood and A.V. Fisher (eds.). *Reducing Fat in Meat Animals*. London: Elsevier Applied Science Publishers; 201-254.
- Alliston, J.C.** (1983). Evaluation of carcass quality in the live animal . In W. Haresign (ed.). *Sheep Production*. Butterworths, London; 75-95.
- Anon** (1977). *Breeds of sheep registered with the New Zealand sheepbreeders association as recorded in the New Zealand Flock Book*. Whitcoulls, Christchurch, New Zealand. 31pp.
- Anon** (1993). *Financial Budget Manual 1993*. In P.H. Fleming and E.S. Burt (eds.). Farm Management Department, Lincoln University, Canterbury, New Zealand; A3-A20.
- Baker, R.L., Clarke, J.N., Carter, A.H.** (1974). Sources of variation for wool, body weight and oestrus characters in Romney hoggets. *Proceedings of the New Zealand Society of Animal Production* **34**: 19-22.
- Baker, R.L., Clarke, J.N., Carter, A.H. and Diprose, G.D.** (1979). Genetic and phenotypic parameters in New Zealand Romney Sheep. 1. Body weights, fleece weights, and oestrus activity. *New Zealand Journal of Agricultural Research* **22**: 9-21.
- Banks, D.B., Mao, I.L., Walter, J.P.** (1985). Robustness of the Maximum Likelihood estimator derived under normality as applied to data with skewed distribution. *Journal of Dairy Science* **68**: 1785-1792.
- Barlow, R.** (1978). Biological ramification of selection for preweaning growth in cattle. A review. *Animal breeding abstracts* **46** : 469-491.
- Barlow, R.** (1984). Selection for growth and size in ruminants: is it time for a moratorium? *Proceedings of the 2nd World Congress on Sheep and Beef cattle Breeding, 16-19 April, Pretoria South Africa*; 421-432.
- Barnicoat, C.R., Logan, A.G. and Grant, A.I** (1949). Milk secretion studies with New Zealand Romney ewes. Parts I and II. *Journal of Agricultural; Science Cambridge* **39**: 44-55.
- Beatson, P.R.** (1987). The inheritance of live weight corrected fat depth. *Proceedings of the Australian Association of animal breeding and Genetics* **6**: 87-90.
- Becker, W.A.** (1992). *Manual of Quantitative Genetics* (4th edition). Academic Enterprises, Pullman, Washington, USA; 189pp.
- Bennett, G.L.** (1990). Selection for growth and carcass composition in sheep. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*, Vol. **XV**: 27-36.
- Bennet, G.L., Meyer, H.H. and Kirton, A.H.** (1988). Effects of selection for divergent ultrasound fat depth in rams on progeny fatness. *Animal Production* **47**: 379-386.
- Berg, R.T. and Butterfield, R.M.** (1976). *New concepts of cattle growth*. Sydney University Press Sydney; 240pp.

- Berg, R.T. and Butterfield, R.M.** (1985). New and improved types of meat animals. In R. Lawrie (ed.). *Development in Meat Science* 3. Elsevier Applied Science Publishers London; 1-23.
- Berg, R.T and Walters, L.E.** (1983). The meat animal: changes and challenges. *Journal of Animal Science* 57 (suppl. 2): 133-146.
- Bichard, M.** (1988). Changes in quantitative genetic technology in animal breeding. In B.S. Weir, E.J. Eisen, M.M. Goodman and G. Namkoong (eds.). *Proceedings of 2nd International Conference on Quantitative Genetics*. Sinauer, Sunderland, Massachusetts; 145-149.
- Bishop, S.C.** (1993). Selection for predicted carcass lean content in Scottish Blackface sheep. *Animal Production* 56: 379-386.
- Black, J.L.** (1983). Growth and development of lamb. In W. Haresign (ed.). *Sheep Production*. Butterworths, London; 21-58.
- Brash, L.D., Fogarty, N.M., Gilmour, A.R. and Luff, A.F.** (1992). Genetic parameters for live weight and ultrasonic fat depth in Australian meat and dual purpose sheep breeds. *Australian Journal of Agricultural Research* 43: 831-841.
- Burrow, H.M.** (1993). The effects of inbreeding in beef cattle. *Animal breeding abstracts* 61(11) : 737-751.
- Busk, H.** (1984). Improved Danscanner for cattle, pigs and sheep. In D. Lister (ed). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 8-21.
- Butterfield, R.M.** (1988). *New concepts of sheep growth*. Sydney: University of Sydney Press; 168pp.
- Butterfield, R.M., Griffiths, D.A., Thompson, J.M., Zamora, J. and James, A.M.** (1983). Changes in body composition relative to weight and maturity in large and small strains of Australian Merino rams. 1. Muscle, bone and fat. *Animal production* 36: 29-37.
- Cameron, N.D.** (1992). Correlated responses in slaughter and carcass traits of crossbred progeny to selection for carcass lean content in sheep. *Animal Production* 54: 379-388.
- Cameron, N.D. and Bracken, J.** (1992). Selection for carcass lean content in terminal sire breeds of sheep. *Animal Production* 54: 367-377.
- Carroll, M.A. and Coniffe, D.** (1967). Beef carcass evaluation: fat, lean and bone. In G. A. Lodge and G.E. Lamming (eds.). *Growth and development of mammals*, London: Butterworths and Co. publisher; 389-399.
- Ch'ang, T.S. and Rae, A.L.** (1970). The genetic basis of growth, reproduction, and maternal environment in Romney ewes. 1. Genetic variation in hogget characters and fertility of the ewe. *Australian Journal of Agricultural Research* 21: 115-129.
- Clarke, J.N., Dobbie, J.L., Hickey, S.M., Jones, K.R. and Wrigglesworth, A.L.** (1995). Genetic parameters for lifetime wool production. *Proceedings of the New Zealand Society of Animal Production* 55: 268-271.
- Clarke, J.N. and Johnson, D.L.** (1993). Lessons from New Zealand sheep selection experiments. In H.T. Blair and S.N. McCutcheon (eds.). *Proceedings of the A.L. Rae Symposium on Animal Breeding and Genetics*. Massey University, New Zealand; 52-68.

Clarke, J.N. and Rae, A.L. (1991). Selection for lean and against fat in sheep. *Proceedings of the New Zealand Society of Animal Production* **51**: 401-404.

Clarke, J.N.; Waldron, D.F. and Rae, A.L. (1991). Selection objectives and criteria for terminal lamb sires. *Proceedings of the Australian Association of Animal Breeding and Genetics* **9**: 265-271.

Conington, J., Bishop, S., Waterhouse, A. and Simm, G. (1995). A genetic analysis of early growth and ultrasound measurements in hill sheep. *Animal Science* **61**: 85- 93.

Croston, D., Kempster, A.J., Guy, D.R. and Jones, D.W. (1987). Carcase composition of crossbred lambs by ten sire breeds compared at the same fat proportion. *Animal Production* **44**: 99-106.

Cunningham, E.P. (1969). The relative efficiencies of selection index. *Acta Agriculture Scandinavica* **19**: 45-48.

Cunningham, E.P. (1970). *Selind: a Fortran computer program for genetic selection indexes*. An Foras Taluntais, Dunsinea, Eire (Mimeograph).

Dalton, D.C. (1985). *An introduction to practical animal breeding (2nd edition)*. BSP Professional Books, Oxford. 182pp

Davies, A.S., Garden, K.L., Young, M.J. and Reid, G.S. (1987). *An Atlas of X-ray tomographical anatomy of the sheep*. Wellington: Science Information Publishing Centre, DSIR; 118pp.

Davis, G.P. (1993). Genetic parameters for tropical beef cattle in Northern Australia: A review. *Australian Journal of Agricultural Research* **44**: 179-198.

De Boer, H., Dumont, B.L., Pomeroy, R.W. and Weniger, J.H. (1974). Manual on E.A.A.P.reference methods for the assessment of carcase characteristics in cattle. *Livestock Production Science* **1**: 151-164.

Dempfle, L. (1988). Estimation of breeding values. In B.S. Weir, E.J. Eisen, M.M. Goodman and G. Namkoong (eds.). *Proceedings of 2nd International Conference on Quantitative Genetics*. Sinauer, Sunderland. Massachusetts; 145-149.

Dransfield, E., Nute, G.R., Hogg, B.W. and Walters, B. (1990). Carcass and eating quality of rams, castrated rams and ewe lambs. *Animal Production* **50**: 291-299.

Eastwood, K., Marshall, P. and Wickham, G. (1977). *Sheep breeds in New Zealand*. Ministry of Agriculture and Fisheries Bulletin No.414. Wellington; 50pp.

Eikje, E. (1971). Studies on Sheep Production Records. I. Effect of Environmental factors on Weight of lambs. *Acta Agriculture Scandinavia* **21**: 26-32.

Eikje, E. (1974). Studies on Sheep Production Records. IV. Genetic, phenotypic and Environmental parameters for weight of lambs. *Acta Agriculture Scandinavia* **24**: 291-298.

Falconer, D.S. (1989). *Introduction to quantitative genetics* (3rd edition). London: Longman; 438pp.

Fennessy, P.F., Bain, W.E., Greer, G.J. and Johnstone, P.D. (1992). Carcass characteristics of progeny from ram lamb selected for high or low ultrasonic backfat thickness. *New Zealand Journal of Agricultural Research* **35**: 177-183.

- Fennessy, P.F., Greer, G.J. and Bass, J.J.** (1982). Progeny test of selected lean and fat rams. *Proceedings of the New Zealand society of Animal Production* **42** : 137-140.
- Fisher, A.V.** (1990). New approaches to measuring fat in the carcass of meat animals. In J.D. Wood and A.V. Fisher (eds.). *Reducing Fat in Meat Animals*. London: Elsevier Applied Science Publishers; 255-342.
- Fisher, A.V. and De Boer, H.** (1994). The EAAP standard method of sheep carcass assessment. Carcass measurements and dissection procedures. Report of the EAAP Working Group on carcass evaluation, in cooperation with the CIHEAM Instituto Agronomico Mediterraneo of Zaragoza and the CEC Directorate General for Agriculture in Brussels. *Livestock Production* **38**: 149-159.
- Fogarty, N.M.** (1995). Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. *Animal Breeding Abstracts* **63**(3): 101-143.
- Fogarty, N.M.; Luff, A.F.** (1985). Non-genetic adjustments to growth rate in a performance testing scheme for terminal meat sheep sires. *Proceedings of the Australian Association of Animal Breeding and Genetic* **5**: 26-28.
- Foulley, J.L.** (1990). Genetic parameter estimation: introduction. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*, Vol. **XIII**: 403-406.
- Fowler, V.R., Bichard, M. and Peace, A.** (1976). Objectives in pig breeding. *Animal Production* **23**: 365-387.
- Frazer, A.E.** (1976). Tighter grading for lamb fatness in coming season. *The New Meat Producer*, **4**(10): 1.
- Frazer, A.E.** (1983). The quantities and types of sheep meat requirement. *Proceedings of Ruakura Farmers conference* **35**: 7-10.
- Geenty, K.G. and Jagusch, K.T.** (1974). A comparison of the performance of Dorset, Corriedale and Romney sheep during lactation. *Proceedings of the New Zealand Society of Animal Production* **34**: 14-18.
- Geenty, K.G. and Sykes, A.R.** (1983). Feed requirement of the ewe and lamb between birth and weaning. In A.S. Familton (ed.). *Lamb growth*. Animal Industries Workshop Lincoln College. Technical Handbook. 95-104pp.
- Glimp, H.A. and Snowden, D.G.** (1989). Production methods to increase lean and reduce fat in lamb: a review. *SID Research Journal* **5**(3): 18-27.
- Glodek, P.** (1984). The measurement of body composition-opportunities and requirements in animal production. In D. Lister (ed). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 8-21.
- Grant, A.L. and Helferich, W.G.** (1991). An overview of growth. In A.M. Pearson and T.R. Dutson (eds.). *Growth and regulation in farm animals. Advances in meat research volume 7*, London: Elsevier applied Science publishers; 1-16.
- Graser, H.U., Smith, S.P. and Tier, B.** (1987). A derivative-free approach for estimating variance components in animal models by Restricted Maximum Likelihood. *Journal of Animal Science* **64**: 1362-1370.

- Groeneveld, E., Kallweit, E., Henning, M. and Pfau, A.** (1984). Evaluation of body composition of live animals by x-ray and NMR computed tomography. In D. Lister (ed). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 84-89.
- Gundersen, H.J.G., Bendtsen, T.F., Korbo, L., Marcussen, N., Moller, A., Nielsen, K., Nyengaard, J.R., Pakkenberg, B., Sorensen, F.B., Vesterby, A. and West, M.J.** (1988). Some new, simple and efficient stereological methods and their use in pathological research and diagnosis. *APMIS* **96**: 379-394.
- Gundersen, H.J. G. and Jensen, E.B.** (1987). The efficiency of systematic sampling in stereology and its prediction. *Journal of Microscopy* **147**: 229-263.
- Hammond, J., Mason, I.L. and Robinson, T.J.** (1971) (4th edition). *Hammond's farm animals*. London; Edward Arnold publishers ltd; 293pp.
- Harper, J.M.M. and Buttery, P.J.** (1992). Muscle growth. In P.J. Buttery, K.N. Böorman and D.B. Lindsay (eds.). *The control of fat and lean deposition*. Butterworth, London. ;27-58.
- Harrington, G. and Kempster, A.J.** (1989). Improving lamb carcass composition to meet modern consumer demand. In O.R. Dyrmondsson and S. Thorgeirsson (eds.). *Reproduction, Growth and Nutrition in sheep*. Dr. Halldor Palsson Memorial Publication. Agricultural Research Institute and Agricultural Society, Reykjavik, Iceland; 79-90.
- Harvey, W.R.** (1985). *Users Guide for LSM76*. Ohio State University, 46pp
- Harville, D.A.** (1977). Maximum likelihood approaches to variance component estimation and to related problems. *Journal of American Statistics Association* **72**: 320-338.
- Hazel, L.N.** (1943). The genetic basis for constructing selection indices. *Genetics* **28**: 476 -490.
- Hazel, L.N. and Lush, J.L.** (1942). The efficiency of three methods of selection. *The Journal of Heredity* **33**: 393-399.
- Henderson, C.R.** (1949). Estimation of changes in herd environment. *Journal of Dairy Science* **32**:706.
- Henderson, C.R.** (1973). Sire evaluation and genetic trends. In Anon. (ed.). *Animal breeding and genetics*. (Proceedings of Symposium in honour of Dr. J.L. Lush). American Society of Animal Science, and American Dairy Science Association campaign, Illinois; 10-41.
- Henderson, C.R.** (1980). Best Linear Unbiased Prediction populations that have undergone selection. *Proceedings of the World Congress on Sheep and Beef cattle Breeding Technical Volume 1*: 191-200.
- Henderson, C.R.** (1984). *Application of Linear Models in Animal Breeding*. Canada: Canadian Cataloguing in Publication Data; 426.
- Henderson, C.R.** (1986). Estimation Variances in Animal Model and Restricted Animal Model for single traits and single records. *Journal of Dairy Science* **69**: 1394-1402.
- Henderson, C.R.** (1988). Progress in statistical methods applied to quantitative genetics since 1976. In B.S. Weir, E.J. Eisen, M.M. Goodman and G. Namkoong (eds.). *Proceedings of 2nd International Conference on Quantitative Genetics*. Sinauer, Sunderland. Massachusetts; 85-90.

- Henderson, C.R.** (1990a). Statistical methods in animal improvement: historical overview. In D. Gianola and K. Hammond (Eds.). *Advances in Statistical Method for Genetic Improvement for Livestock*. Springer-Verlag Berlin, Heidelberg, New York: Springer-Verlag; 1-14.
- Henderson, C.R.** (1990b). Accounting for selection and mating biases in genetic evaluation. In D. Gianola and K. Hammond (Eds.). *Advances in Statistical Method for Genetic Improvement for Livestock*. Springer-Verlag Berlin, Heidelberg, New York: Springer-Verlag; 413-437.
- Hight, K.G. and Jury, K.E.** (1971). Hill country sheep production. III. Sources of variation in Romney and Border Leicester x Romney lambs and hoggets. *New Zealand Journal of Agricultural Research* **14**: 669-686.
- Hill, W.G.** (1972a). Estimation of realised heritability from selection experiments. I. Divergent Selection. *Biometrics* **28**: 747-765.
- Hill, W.G.** (1972b). Estimation of realised heritability from selection experiments. II. Selection in one direction. *Biometrics* **28**: 767-780.
- Hill, W.G.** (1972c). Estimation of genetic change. I. General theory and design of control populations. *Animal Breeding Abstracts* **40**(1): 1-15.
- Hill, W.G.** (1972d). Estimation of genetic change. I. Experimental evaluation of control population. *Animal Breeding Abstracts* **40**(2): 193-213.
- Hill, W.G. and Meyer, K.** (1988). Developments in methods for breeding value and parameter estimation in livestock. In *Animal Breeding Opportunities*. British Society of Animal Production Occasional publication no.12. 81-91.
- James, J.W.** (1982). Economics aspects of developing breeding objectives: general considerations. In J.S. Barker, K. Hammond and A.E. McClintok (Eds.). *Future developments in the genetic improvement of animals*. Academic Press, London; 107-116.
- James, J.W.** (1991). Effect using an incorrect model in animal model REML estimation of heritability. *Proceedings of the Australian Association of Animal Breeding and Genetics* **9**: 477-479.
- Johnson, D.L. and Thompson, R.** (1995). Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. *Journal of Dairy Science* **78**: 449-456.
- Johnson, M.H.** (1977). Development in mammals. In M.H. Johnson (ed.). *Development in mammals*. Volume 1, Amsterdam: North-Holland publishing company; 1-4.
- Kadim, I.T., Purchas, R.W., Rae, A.L. and Barton, R.A.** (1988). The distribution and partitioning of fat in Southdown sheep selected for high and low fat depths in backfat. *Proceedings of the 34th international congress of meat science and technology (part A)*: 65 -67.
- Kadim, I.T., Purchas, R.W., Rae, A.L. and Barton, R.A.** (1989). Carcass characteristics of Southdown rams from high and low backfat selection lines. *New Zealand Journal of Agricultural Research* **32**: 181-191.
- Kempster, A.J.** (1983). Carcass quality and its measurement in sheep. In W. Haresign (ed.). *Sheep Production*. Butterworths, London; 493-514.

- Kempster, A.J.** (1984). Cost-benefit analysis of *in vivo* estimates of body composition in meat animals. In D. Lister (ed). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 8-21.
- Kempster, A.J.** (1986). Carcass and meat quality research to meet market. *Animal Production* **48**: 483-496.
- Kempster, A.J.** (1989). Correlation between indirect and direct measurements of body composition. *Proceedings of the Nutrition Society* **45**: 55-62.
- Kempster, A.J.** (1990). Marketing procedures to change carcass composition. In J.D. Wood and A.V. Fisher (eds.). *Reducing Fat in Meat Animals*. London: Elsevier Applied Science Publishers; 255-342.
- Kempster, A.J., Cook, G.L. and Grantley-Smith, M.** (1986). National estimates of the body composition of British cattle, sheep and pigs with special reference to trends in fatness. A review. *Meat Science* **17**: 107-138.
- Kempster, A.J., Croston, D., Guy, D.R. and Jones, D.W.** (1987). Growth and carcase characteristics of crossbred lambs by ten sire breeds, compared at the same estimated carcase subcutaneous fat proportion. *Animal Production* **44**: 83-98.
- Kempster, A.J., Cuthbertson, A. and Harrington, G.** (1982). *Carcass Evaluation in Livestock Breeding, Production and Marketing*. London: Granada Publishing Limited; 306pp.
- Kennedy, B.W.** (1981). Variance component estimation and prediction of breeding values. *Canadian Journal of Genetic cytology* **23**: 565-578.
- Kennedy, B.W. and Sorensen, D.A.** (1988). Properties of mixed-model methods for prediction of genetic merit. In B.S. Weir, E.J. Eisen, M.M. Goodman and G. Namkoong (eds.). *Proceedings of 2nd International Conference on Quantitative Genetics*. Sinauer, Sunderland. Massachusetts; 91-103.
- Kirton, A.H.** (1989). Current methods of on-line carcass evaluation. *Journal of Animal Science* **67**: 2155-2163.
- Kirton, A.H., Clarke, J.N. and Cater, A.H.** (1967). Effect of pre-slaughter fasting on live weight, carcass weight, and carcass composition of Southdown ram lambs. *New Zealand Journal of agricultural research* **10**: 43-55.
- Kirton, A.H. and Johnson, D.L.** (1979). Interrelationships between GR and other lamb carcass fatness measurements. *Proceedings of the New Zealand Society of Animal Production* **39**: 194-201.
- Kirton, A.H., Sinclair, D.P. and Dobbie, J.L.** (1978). Overfat lambs-significance, GR measurement and management strategies. *Proceedings of Ruakura Farmers Conference* **FPP155**; 4.
- Klassen, D.J. and Smith, S.P.** (1990). Animal model estimation using simulated REML. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*, Vol. **XIII**: 472-475.
- Knopp, T.C.** (1985). Quantitative analysis of computer tomograph images. *M. Sc Thesis, University of Otago. New Zealand*.
- Koots, K.R., Gibson, J.P., Smith, C. and Wilton, J.W.** (1994a). Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Animal breeding abstracts* **62(5)** : 309-338.

- Koots, K.R., Gibson, J.P. and Wilton, J.W. (1994b).** Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. *Animal breeding abstracts* **62(11)** : 825-853.
- Land, R.B. (1985).** Knowledge for animal breeding. *Phil. Trans. R. Soc. Lond.* **B310**: 243-289.
- Large, R.V. (1970).** The biological efficiency of meat production in sheep. *Animal Production* **12**: 393-401.
- Lasley, J.F. (1978).** *Genetics of livestock improvement* (3rd edition). Prentice-Hall, Englewood Cliffs, New Jersey. 492pp.
- Lawes Agricultural Trust (1990).** *Genstat 5 Release 2.2 a general statistical program*. Numerical Algorithm Group Limited.
- Lin, C.Y and Allaire, F.R. (1977).** Heritability of a linear combination of traits. *Theoretical Applied Genetics* **51**: 1-3.
- Little, T.M. and Hills, F.J. (1978).** *Agriculture Experimentation: Design and Analysis*. John Wiley and Sons, Inc. New York, USA; 350pp.
- Madsen, P., Jensen, J. and Thompson, R. (1994).** Estimation of (co)variance components by REML in multivariate mixed linear models using average of observed and expected information. *Proceedings of the 5th world congress on genetics applied to livestock production*. Volume **22**: 19-22.
- Maria, G.A., Boldman, K.G. and van Vleck, L.D. (1993).** A note on heritability estimates for growth traits in males and female Romanov sheep. *Animal Production* **57**: 326-328.
- McClelland, T.H., Bonaiti, B., Taylor, St. C.S. (1976).** Breed differences in body composition of equally mature sheep. *Animal production* **23**: 281-293.
- McEwan, J.C., Dodds, K.G., Davis, G.H., Fennessy, P.F. and Hishon, M. (1991).** Heritability of ultrasonic fat and muscle depths in sheep and their correlation with production traits. *Proceedings of the Australian Association of Animal Breeding and Genetics* **9**: 276 -279.
- McGuirk, B.J., Atkins, K.D., Thompson, R. (1986).** Long term selection experiment with sheep. *Proceedings of the 3rd world congress on genetics applied to livestock production*. Volume **XII** : 181-195.
- Meat and Livestock Commission (1987).** *Sheep Yearbook*. Meat and Livestock Commission, Bletchley, Milton Keynes; 39-42.
- Meyer, K. (1989a).** Estimation of genetic and phenotypic parameters. In W.G. Hill and T.F.M. McKay (eds.). *Evolution and Animal Breeding. Reviews on molecular and quantitative approaches in Honour of A. Robertson*; 161-167.
- Meyer, K. (1989b).** Restricted Maximum Likelihood to estimate variance components for animal models with several random effects using a derivative-free approach algorithm. *Genetical Selection Evolution* **21**: 317-340.
- Meyer, K. (1990).** Present status of knowledge about statistical procedures and algorithms available to estimate variance and covariance components. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*, Vol. **XIII**: 407-418.

Meyer, K. (1991a). Estimating variance components for multivariate animal models by Restricted Maximum Likelihood. *Genetical Selection Evolution* **23**: 67-83.

Meyer, K. (1991b). *Derivative Free Maximum Likelihood User Notes*. Version 2.0. 84pp.

Meyer, K. (1993). *Derivative Free Maximum Likelihood User Notes*. Version 2.1. 101pp.

Meyer, K. and Hill, W.G. (1992). Approximation of sampling variances and confidence intervals for maximum likelihood estimates of variance components. *Journal of Animal Breeding Genetics* **109**: 264-280.

Micrografx (1992). *Photomagic user's guide*. Micrografx Inc.

Minitab (1992). *Minitab Statistical software, standard version Release 9.1*. Minitab Inc.

Misztal, I. (1994). Comparison of software packages in animal breeding. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production*. Volume **22**: 3-10.

Moav, R. (1973). Economic evaluation of genetic differences. In: T. Moav (ed.). *Agricultural Genetics. Selected topic*. John Wiley and Sons, New York; 319-352.

Nelder, J.A. and Mead, R. (1965). A simplex method for function minimization. *Computer Journal* **7**: 147-151.

New Zealand Meat Producer (1992a). *The New Zealand Meat Producers Board*. Volume **21** (1): 4.

New Zealand Meat Producer (1992b). *Annual Report*. Published by The New Zealand Meat Producers Board; Wellington. New Zealand, 33p.

New Zealand Meat Producer (1993a). *The New Zealand Meat Producers Board*. Volume **21** (4):3-6.

New Zealand Meat Producer (1993b). *Annual Report*. Published by The New Zealand Meat Producers Board; Wellington. New Zealand, 33p.

New Zealand Meat Producer (1994). *The New Zealand Meat Producers Board*. Volume **22** (2): 4.

Nicholas, F.W. (1993). *Veterinary Genetics*. Oxford Science Publications. U.K. 580pp.

Nicoll, G.B. and Morris, C.A. (1993). Lessons from New Zealand beef cattle selection experiments. In H.T. Blair and S.N. McCutcheon (eds.). *Proceedings of the A.L. Rae Symposium on Animal Breeding and Genetics*. Massey University, New Zealand; 69-87.

O'Connor, K.F., Vartha, E.W. and Belcher, R.A. (1968). Seasonal and annual variation in pasture production in Canterbury and Otago. *Proceedings of the New Zealand Grassland Association* **30**: 50-63.

Olesen, I. and Husabo, J.O. (1994). Effects of using ultrasonic muscle depth and fat depth on the accuracy of predicted phenotypic and genetic values of carcass traits on live ram. *Acta Agriculture Scandinavica* **44**: 65-72.

Palsson, H.D. (1939). Meat quality in sheep with special reference to Scottish breeds and crosses. *Journal of agricultural science, Cambridge* **29**: 544-626.

- Parratt, A.C., Burt, C.M., Bennett, G.L., Clarke, J.N., Kirton, A.H. and Rae, A.L.** (1987). Heritabilities, genetic and phenotypic correlations for carcass traits and ultrasonic fat depth in sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* 6: 76-78.
- Parratt, A.C., Nicoll, G.B. and Alderton, M.J.** (1989). Romney male and female heritabilities and genetic correlations for weaning, autumn and spring body weights and hogget fleece weights. *Proceedings of the New Zealand society of Animal Production* 49: 191-195.
- Parratt, A.C. and Simm, G.** (1987). Selection indices for terminal sires to improve lean meat production from sheep in the United Kingdom. *Animal production* 45: 87-96.
- Patterson, L.D. and Thompson, R.** (1971). Recovery of inter-block information when block sizes are unequal. *Biometrika* 58: 545-554.
- Purchas, R.W., Davies, A.S. and Abdullah, A.Y.** (1991). An objective measure of muscularity: Changes with animal growth and differences between genetic lines in the Southdown sheep. *Meat Science* 30: 81-94.
- Rae, A.L.** (1984). Development of selection programmes for increasing lean meat production in sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* 4: 3-7.
- Rickard, D.S.** (1969). Climate, pasture production and irrigation. *Proceedings of the New Zealand Grassland Association* 30: 81-93.
- Rickard, D.S. and Radcliffe, J.E.** (1976). Seasonal distribution of pasture production in New Zealand. XII Winchmore, Canterbury Plains dryland and irrigated pastures. *New Zealand Journal of Experimental Agriculture* 4: 329-335.
- Robertson, A.** (1977). The effect of selection on the estimation of genetic parameters. *Z. Tierzuchtg. Zuchtgsbioll* 94: 131-135.
- SAS** (1991). *SAS Procedures Guide version 6.08 edition*. Cary, NC. SAS Institute Inc.
- Scholtz, M.M. and Roux, C.Z.** (1984). Correlated responses to selection for growth, size and efficiency. *Proceedings of the 2nd World Congress on Sheep and Beef cattle Breeding, 16-19 April, Pretoria South Africa*; 433-441.
- Searle, S.R.** (1989). Variance components-some history and a summary account of estimation methods. *Journal of Animal Breeding Genetics* 106: 1- 29.
- Sehested, E.** (1984). Computerised tomography of sheep. In D. Lister (ed.). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 67-74.
- Sehested, E.** (1986). In vivo prediction of lamb carcass composition by Computerised Tomography. *Ph.D. Thesis, Agricultural University of Norway, Norway*; 81pp.
- Sehested, E. and Vangen, O.** (1989). Computer tomography, a non-destructive method of carcass evaluation. In E. Kallwett, M. Henning and E. Groeneveld (eds.). *Application of NMR techniques on the body composition of live animals*. London: Elsevier Applied Science; 98 -102.
- Shaw, R. G.** (1987). Maximum-likelihood approaches applied to quantitative genetics of natural populations. *Evolution* 41: 812-826.

- Sheridan, A.K.** (1988). Agreement between estimated and realised genetic parameters. *Animal breeding abstracts* **56**: 877-899.
- Simm, G.** (1986). Economic selection indices for lean meat production in sheep. *Proceedings of the 3rd world congress on genetics applied to livestock production*. Volume **IX**: 541-546.
- Simm, G.** (1987). Carcass evaluation in sheep breeding programmes. In I.F.M. Marai, J.B. Owen (eds.). *New Techniques in Sheep Production*. London: Butterworths; 125-144.
- Simm, G.** (1989). Current and possible future application of *in vivo* assessment in sheep breeding programmes. In E. Kallwett, M. Henning and E. Grooeneveld (eds.). *Application of NMR techniques on the body composition of live animals*. London: Elsevier Applied Science; 149-158.
- Simm, G.** (1992). Selection for Lean Meat Production in Sheep. In A.W. Speedy (ed.). *Progress in Sheep and Goat Research*. CAB International; 193-215.
- Simm, G. and Dingwall, W.S.** (1989). Selection indices for lean meat production in sheep. *Livestock production science* **21**: 223-233.
- Simm, G., Dingwall, W.S., Murphy, S.V. and Brown, W.R.** (1990a). Selection for improved composition in terminal sire sheep breeds. In C.F.R. Slade and T.J.L. Lawrence (eds.). *New Developments in Sheep Production*. British Society of Animal Production Occasional Publication no. **14**. 166-168.
- Simm, G., Dingwall, W.S., Murphy, S.V. and FitzSimons, J.** (1990b). Selection for improved carcass composition in Suffolk sheep. *Proceedings of the 4th world congress on genetics applied to livestock production*. Volume **XV**: 100-103.
- Simm, G., Young, M.J. and Beatson, P.R.** (1987). An economic selection index for lean meat production in New Zealand sheep. *Animal Production* **45**: 465-475.
- Skjervold, H., Gronseth, K., Vangen, O. and Evensen, A.** (1981). *In vivo* estimation of body composition by computerised tomography. *Z. Tierzuchtg Zuchtgsbiol* **98**: 77-79.
- Smith, C.** (1983). Effects of changes in economic weights on the efficiency of index. *Journal of Animal Science* **56**: 1057-1064.
- Smith, C.** (1984). Rates of genetic change in farm livestock. *Research and Development in Agriculture* **1**: 79-85.
- Smith, C.** (1985). Scope for selecting many breeding stocks of possible economic value in the future. *Animal Production* **41**: 403-412.
- Smith, C.** (1988). Potential for animal breeding, current and future. In B.S. Weir, E.J. Eisen, M.M. Goodman and G. Namkoong (eds.). *Proceedings of 2nd International Conference on Quantitative Genetics*. Sinauer, Sunderland. Massachusetts; 150-160.
- Smith, S.P. and Graser, H.U.** (1986). Estimating variance components in a class of mixed models by Restricted Maximum Likelihood. *Journal of Dairy Science* **69**: 1156-1165.
- Snedecor, G.W. and Cockran, W.G.** (1980). *Statistical methods (7th edition)*. Iowa State University Press, Iowa, U.S.A; 507p.

- Sorensen, M.T.** (1984). Computerised tomography of goats during pregnancy and lactation. In D. Lister (ed.). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 43-51.
- Sorensen, M.T.** (1992). *In vivo* prediction of goat body composition by computer tomography. *Animal Production* **54**: 67-73.
- Standal, N.** (1984). Establishment of CT facility for farm animals. In D. Lister (ed.). *In vivo measurement of body composition in meat animals*. London: Elsevier applied science publishers; 43-51.
- Taylor, St. C.S.** (1985). Use of genetic size-scaling in evaluation of animal growth. *Journal of Animal Science* **61** (Supplement 2): 118-143.
- Taylor, St. C.S.** (1987). An evaluation of genetic size-scaling in breed and sex comparisons of growth, food and body composition. *Proceedings of the Australian Association of animal breeding and genetic* **6**: 1-12.
- Thatcher, L.P. and Couchman, R.C.** (1983). Determining consumer requirements for lamb loin chops-preliminary study. *Review of marketing and agricultural economics* **51**:(2) 170-176.
- Thompson, J.M., Butterfield, R.M. and Perry, D.** (1985). Food intake, growth and body composition in Australian Merino sheep selected for high and low weaning weight. 2. Chemical and dissectible body composition. *Animal Production* **40**: 71-84.
- Thonney, M.L., Taylor, St. C.S. and McClelland, T.H.** (1987). Breed and sex differences in equally mature sheep and goats. 1. Growth and food intake. *Animal production* **45**: 239-260.
- Thorgeirsson, S. and Thorsteinsson, S.S.** (1989). Growth, development and carcass characteristics. In O.R. Dyrmondsson and S. Thorgeirsson (eds.). *Reproduction, Growth and Nutrition in sheep. Dr. Halldor Palsson Memorial Publication*. Agricultural Research Institute and Agricultural Society, Reykjavik, Iceland; 169-204.
- Villanueva, B., Wray, N.R. and Thompson, R.** (1993). Prediction of asymptotic rates of responses from selection on multiple traits using univariate and multivariate best linear unbiased predictors. *Animal Production* **57**: 1-13.
- Waldron, D.F., Clarke, J.N. and Rae, A.L.** (1991). Analysis of lamb schedules and relative economic values of lean and fat. *Proceedings of the New Zealand Society of Animal Production* **51**: 405-409.
- Waldron, D.F., Clarke, J.N., Rae, A.L., Kirton, A.H. and Bennett, G.L.** (1992a). Genetic and phenotypic parameter estimates for selection to improve lamb carcass traits. *New Zealand Journal of Agricultural Research* **35**: 287-298.
- Waldron, D.F., Clarke, J.N., Rae, A.L. and Woods, E.G.** (1992b). Selected responses in carcass composition to selection for muscularity in sheep. *Proceedings of the New Zealand Society of Animal Production* **52**: 29-31.
- Warman, M.** (1991). *What sheep is that? New Zeland's most popular sheep breeds*. GP publications LTD. Wellington; 64pp.
- Warmington, B.G. and Beatson, P.R.** (1986). Genetic and environmental sources of variation in hogget fleece weight and live weight in Coopworth sheep. *Proceedings of the New Zealand society of Animal Production* **46**: 87-91.

- Warwick, E.J. and Legates, J.E.** (1979). *Breeding and improvement of farm animals* (7th edition). McGraw-Hill Publication in the Agricultural Sciences. New York; 624pp.
- Webb, A. J. and Bampton, P.R.** (1990). Impact of the new statistical technology on pig improvement. In C.F.R. Slade and T.J.L. Lawrence (eds.). *New Developments in Sheep Production*. British Society of Animal Production Occasional Publication no. 14. 166-168.
- Webster, A.J.F.** (1989). Bioenergetics, bioengineering and growth. *Animal Production* 48: 249-269.
- Wells, P.N.T.** (1984). Introduction to imaging technology. In D. Lister (ed.). *In vivo measurement of body composition in meat animals*, London: Elsevier applied science publishers, 25-32.
- Westfall, P.H.** (1987). A comparison of variance component estimates for arbitrary underlying distributions. *Journal of American Statistical Association* 82: 866-874.
- Widdowson, M.E.** (1980). Definitions of growth. In T.L.J. Lawrence (eds.). *Growth in animals*, London: Butterworths and Co. publisher; 1-9.
- Wills, M.B.** (1991). *Dalton's Introduction to practical animal breeding* (3rd edition). Blackwell Scientific publications; London; 159pp.
- Wolf, B.T. and Smith, C.** (1983). Selection for carcass quality. In W. Haresign (ed.). *Sheep Production*. Butterworths, London; 493 -514.
- Wolf, B.T., Smith, C., King, J.W.B. and Nicholson, D.** (1981). Genetic parameters of growth and carcass composition in the crossbred progeny of six terminal sire breeds of sheep. *Animal Production* 32: 1-7.
- Wood, J.D.** (1982). Factors controlling fat deposition in meat animals. *Proceedings of the New Zealand society of Animal Production* 42: 113-116.
- Wood, J.D.** (1990). Consequences for meat quality of reducing carcass fatness. In J.D. Wood and A.V. Fisher (eds.). *Reducing Fat in Meat Animals*. London: Elsevier Applied Science Publishers; 344-397.
- Wood, J.D. and Fisher, A.V.** (1990). Improving the quality of lamb meat-taste, fatness and consumer appeal. In C.F.R. Slade and T.J.L. Lawrence (eds.). *New Developments in Sheep Production*. British Society of Animal Production Occasional Publication no. 14. 166-168.
- Wood, J.D., MacFie, H.J.M., Pomeroy, R.W. and Twinn, D.J.** (1980). Carcass composition in four sheep breeds: The importance of type of breeds and stage of maturity. *Animal Production* 30: 135-152.
- Wood, J.D. and Warriss, P.D.** (1992). The influence of the manipulation of carcass composition on eating quality. In P.J. Buttery, K.N. Boorman and D.B. Lindsay (eds.). *The control of fat and lean deposition*. Butterworth, London; 331-353.
- Woolaston, R.R.** (1984). Relative efficiency of selection for fasted body weight in merinos. *Proceedings of the Australian Association of Animal Breeding and Genetics* 4: 207-208..
- Yamada, Y., Yokouchi, K. and Nishida, A.** (1975). Selection index when genetic gains of individual traits are of primary concern. *Japan Journal of Genetics* 50(1): 33-41.
- Young, M.J.** (1989). Responses to selection for leanness in Suffolk. *M. Sc Thesis, University of Edinburgh, Scotland*; 60pp.

Young, M.J. and Deaker, J.M. (1994). Ultrasound measurements predict fat and muscle depth better than carcass measurements. *Proceedings of the New Zealand Society of Animal Production* **54** : 215-217.

Young, M.J., Deaker, J.M. and Logan, C.M. (1992). Factors affecting repeatability of tissue depth determination by real-time ultrasound in sheep. *Proceedings of the New Zealand Society of Animal Production* **52**: 37-39.

Young, M.J. and Simm, G. (1990). Genetic parameters for in vivo body measurements in Suffolk sheep. *Proceedings of the New Zealand Society of Animal Production* **50**: 403-406.

Appendix A: Description of performance data

Table 1: Number of progeny surviving to measurement per sire in Border Leicester flock. Ewe progeny were not performance tested in autumn in 1988 and 1992 but were tested in spring and winter respectively

Sire ID	Number of progeny
770050	7
790117	25
790519	22
800097	22
820034	24
820084	1
830026	18
830035	26
830128	16
830384	2
830566	7
840415	25
840419	24
840431	29
840457	33
840467	30
840473	22
840486	26
840495	32
840526	20
840538	29
840563	27
840575	33
840612	29
850440	2
850471	24
850481	23
850482	1
850535	21
850582	29
850585	19
850652	27
860436	10
860454	5
860473	4
860504	9
860527	8
860532	4
870360	28

Table 1 cont...

870398	27
870406	28
870447	29
870521	25
870532	26
880351	29
880417	35
880419	30
880421	29
880546	33
890365	27
890381	34
890385	27
890493	30
890522	36
900323	21
900366	29
900392	30
900412	27
900442	39
<hr/>	
Number of sire families	= 59
Mean family size	= 22.6
Standard deviation of family size	= 10.0
<hr/>	

Table 2: Frequency of birth rank for animals surviving to measurement each year in Border Leicester flock. Ewe progeny were not performance tested in autumn in 1988 and 1992 but were tested in spring and winter respectively

Year of birth	Frequency of birth rank		
	Singles	Twins	Triplets
1984	48	99	14
1985	39	145	8
1986	51	111	14
1987	32	87	26
1988	7	31	3
1989	28	106	29
1990	38	105	13
1991	34	102	18
1992	32	103	11
<hr/>			
Total	309	889	136
<hr/>			

Table 3: Frequency of rearing rank for animals surviving to measurement each year in Border Leicester flock.

Year of birth	Frequency of rearing Rank		
	Singles	Twins	Triplets
1984	70	88	3
1985	57	127	6
1986	68	107	1
1987	36	90	19
1988	10	30	1
1989	36	98	29
1990	42	106	8
1991	38	108	8
1992	56	84	6
Total	413	840	81

Table 4: Number of rams and ewes surviving to measurement in Border Leicester flock. A dash (-) indicates that ewe progeny were not performance tested in autumn.

Year of birth	Sex [#]	
	Rams	Ewes
1984	47	114
1985	95	97
1986	89	87
1987	39	106
1988	41	-
1989	75	88
1990	73	83
1991	82	72
1992	67	-
Total	608	647

- rams performance tested in winter and ewes in autumn

Table 5: Frequency of age of dam for animals surviving to measurement each year in Border Leicester flock. Ewe progeny were not performance tested in autumn in 1988 and 1992 but were tested in spring and winter respectively

Year	Age of dam at birth of offspring (years)					
	2	3	4	5	6	7
1984	45	65	22	23	6	0
1985	67	66	59	0	0	0
1986	46	55	34	41	0	0
1987	35	30	29	27	24	0
1988	7	16	4	9	5	0
1989	45	40	39	18	18	3
1990	40	46	33	22	10	5
1991	40	29	46	23	16	0
1992	41	35	35	18	12	1
Total	366	382	301	181	91	13

Table 6: Number of progeny surviving to measurement per sire in Coopworth flock in autumn

Sire ID	Number of progeny
200	55
201	53
202	52
203	57
204	54
206	50
209	54
213	52
214	56
780079	48
790974	9
791338	51
810018	104
810276	55
810855	63
811195	60
814518	5
815269	51
820180	58
820215	40
820265	55
820280	65
820290	49
820381	45
820601	46
820674	101
820711	51
820865	48
820943	51
820950	47
825290	21
826354	4
830241	45
830397	47
830463	51
830599	59
830693	63
830949	49
831268	67
834579	16
840013	28
840056	33
840085	18
840171	16
840185	13
840197	23

Table 6 cont...

840407	14
840480	38
840502	11
840527	35
840536	20
840623	20
840780	13
840891	20
841155	13
841454	10
850041	19
850081	11
850083	20
850141	15
850290	18
850575	17
850611	13
850619	18
850689	19
850843	15
850861	17
851063	17
851115	12
851160	13
851171	19
851319	15

Number of sire families	=	72
Mean family size	=	36.0
Standard deviation of family size	=	22.0

Table 7: Frequency of birth rank for animals surviving to measurement in autumn each year in Coopworth flock.

Year of birth	Frequency of birth Rank					
	Singles		Twins	Triplets	Quadruplets	Total
1984	86	628	253	7		974
1985	68	633	218	14		933
1986	43	236	47	2		328
1987	53	240	62	0		355
Total	250	1737	580	23		2590

Table 8: Number of rams and ewes surviving to measurement in autumn each year in Coopworth flock.

Year of birth	Sex		
	Rams	Ewes	Total
1984	451	523	974
1985	406	527	933
1986	152	176	328
1987	174	181	355
Total	1183	1407	2590

Table 9: Frequency of age of dam for animals surviving to measurement in autumn each year in Coopworth flock.

Year	Age of dam at birth of offspring (years)							
	2	3	4	5	6	7	8	9
1984	244	203	227	148	89	48	15	0
1985	217	252	164	146	86	36	18	14
1986	150	44	67	35	27	5	0	0
1987	154	105	37	36	18	3	2	0
Total	765	604	495	365	220	92	35	14

Table 10: Number of progeny surviving to measurement per sire in Coopworth flock in winter and spring.

Sire ID	Number of progeny
200	54
201	52
202	50
203	56
204	54
206	50
209	53
213	52
214	54
780079	48
790974	8
791338	48
810018	91
810276	55
810855	62
811195	57
814518	5
815269	51
820180	54
820215	39
820265	54
820280	59
820290	45
820381	45
820601	48
820674	97
820711	49
820865	43
820943	47
820950	41
825290	18
825354	1
826354	3
830241	41
830397	45
830463	53
830599	61
830693	60
830949	45
831268	65
834579	16
840013	25
840056	32
840085	17
840171	20

Table 10 cont...

840185	11
840197	23
840407	14
840480	35
840502	12
840527	34
840536	19
840623	21
840780	14
840891	20
841155	14
841454	12
850041	19
850081	11
850083	21
850141	15
850290	16
850575	17
850611	11
850619	18
850689	17
850843	14
850861	17
851063	18
851115	12
851160	13
851171	19
851319	15
860086	15
860100	21
860438	31
860605	22
860628	11
860771	24
860773	18
860814	5
860835	25
860942	2
860976	27
861007	13
861203	15
870001	8
870132	30
870252	11
870380	6
870535	16
870579	8
870750	27
870822	30

Table 10 cont...

870958	23
871330	13
871360	36
871515	26
880191	24
880285	35
880522	40
880579	44
880670	34
880722	17
880786	16
880865	15
881014	36
881119	20
890486	18
890567	37
890711	16
890716	41
890739	17
890744	41
890818	35
890825	16
891113	39
891142	14
900576	16
900588	14
900596	15
900645	32
900654	15
900773	30
900820	22
900874	30
900897	34
900933	12
<hr/>	
Number of sire families	= 128
Mean family size	= 29.24
Standard deviation of family size	= 18.24
<hr/>	

Table 11: Frequency of birth rank for progeny surviving to measurement in winter and spring each year in Coopworth flock.

Year of birth	Frequency of birth Rank			
	Singles	Twins	Triplets	Quadruplets
1984	83	606	243	7
1985	67	605	209	13
1986	43	242	45	2
1987	49	232	59	0
1988	26	176	27	0
1989	24	176	33	1
1990	30	174	72	5
1991	32	157	82	3
1992	27	159	34	0
Total	381	2527	804	31

Table 12: Frequency of age of dam for progeny lambs surviving to measurement in winter and spring each year in Coopworth flock.

Year	Age of dam at birth of offspring (years)							
	2	3	4	5	6	7	8	9
1984	34	198	215	145	86	45	16	0
1985	205	242	152	142	85	38	17	13
1986	151	43	68	38	27	5	0	0
1987	147	99	37	37	15	3	2	0
1988	47	93	56	16	14	3	0	0
1989	50	73	58	42	7	4	0	0
1990	86	71	53	48	14	9	0	0
1991	71	65	63	40	20	15	0	0
1992	75	54	56	21	12	2	0	0
Total	1066	938	758	529	280	124	35	13

Table 13: Number of rams performance tested in winter each year in Coopworth flock. Rams performance tested in 1984 and 1985 were treated as controls. A dash (-) indicates years when there was no lean tissue growth rate flock.

Year of Birth	Number of rams available for selection	
	Control line	Lean Tissue Growth line
1984	437	-
1985	378	-
1986	57	93
1987	64	106
1988	19	78
1989	19	89
1990	32	96
1991	29	93
1992	43	78
Total	1078	633

Table 14: Number of rams and ewes surviving to measurement in Coopworth flock.

Year of birth	Sex [#]	
	Rams	Ewes
1984	437	502
1985	378	516
1986	150	182
1987	170	170
1988	97	132
1989	108	126
1990	128	153
1991	122	152
1992	121	99
Total	1711	2032

- rams were measured in winter and ewes in spring

Table 15: Number of progeny surviving to measurement per sire in Dorset Down flock

Sire ID	Number of progeny
790013	20
790051	41
830001	19
830002	16
830005	8
830008	23
830030	13
830033	17
830036	13
830061	21
830077	10
830141	4
830161	28
830165	10
840017	31
840020	21
840037	13
840055	35
840084	36
840101	14
840137	17
840180	7
840186	18
840196	10
840214	15
840216	15
840236	11
840239	28
840252	16
840269	21
840276	33
840307	22
840308	12
850048	14
850050	12
850053	12
850084	14
850087	16
850089	25
850149	16
850158	24
850169	21
850173	15
850193	37
850220	20
860005	10

Table 15 cont...

860013	11
860033	13
860039	9
860047	16
860076	17
860108	13
860167	17
860219	20
860263	24
860271	17
870025	29
870041	20
870073	12
870107	12
870150	19
870184	23
870213	15
870228	4
870257	33
870271	23
870273	16
870309	31
880006	26
880037	18
880048	17
880061	28
880126	21
880168	14
880203	28
880226	15
880238	26
880261	16
890023	21
890032	35
890054	22
890158	3
890182	25
890186	20
890215	33
890220	16
890272	20
890289	15
900030	7
900047	11
900075	6
900104	7
900115	6
900152	2
900173	8

Table 15 cont...

900204		7
900224		12
900259		10
<hr/>		
Number of sire families	=	98
Mean family size	=	17.8
Standard deviation of family size	=	8.3
<hr/>		

Table 16: Frequency of birth rank for animals surviving to measurement each year in Dorset Down flock.

Year of birth	Frequency of birth Rank		
	Singles	Twins	Triplets
1984	65	140	3
1985	47	130	6
1986	81	125	3
1987	71	135	4
1988	80	121	0
1989	73	158	6
1990	85	120	4
1991	74	135	1
1992	33	43	0
Total	609	1107	27

Table 17: Frequency of rearing rank for animals surviving to measurement each year in Dorset Down flock.

Year of birth	Frequency of rearing Rank		
	Singles	Twins	Triplets
1984	95	113	0
1985	76	104	3
1986	99	108	2
1987	83	123	4
1988	97	104	0
1989	82	152	3
1990	93	113	3
1991	84	126	0
1992	53	23	0
Total	762	966	15

Table 18: Number of rams and ewes surviving to measurement in Dorset Down flock. A dash (-) indicates that ewe progeny were not performance tested in autumn.

Year of birth	Sex [#]	
	Rams	Ewes
1984	80	128
1985	83	100
1986	100	109
1987	84	126
1988	86	115
1989	120	117
1990	99	110
1991	92	118
1992	76	-
Total	820	923

- rams lambs were performance tested in winter and ewes in autumn

Table 19: Frequency of age of dam for animals surviving to measurement each year in Dorset Down flock.

Year	Age of dam at birth of offspring (years)								
	2	3	4	5	6	7	8	9	10
1984	44	52	43	31	18	12	6	1	1
1985	37	49	57	27	13	0	0	0	0
1986	53	44	39	53	20	0	0	0	0
1987	44	49	42	32	32	11	0	0	0
1988	52	31	49	31	22	16	0	0	0
1989	61	73	39	31	21	12	0	0	0
1990	43	50	61	30	15	10	0	0	0
1991	48	59	48	36	18	1	0	0	0
1992	25	27	12	6	6	0	0	0	0
Total	407	434	390	277	165	62	6	1	1

Table 20: Number of rams performance tested each year. Rams performance tested in 1984 and 1985 were treated as controls. A dash (-) indicates years when there was no lean tissue growth rate flock.

Year of Birth	Number of rams available for selection	
	Control line	Lean Tissue Growth line
1984	80	-
1985	83	-
1986	42	58
1987	30	54
1988	34	52
1989	41	79
1990	38	61
1991	31	61
1992	28	48
Total	407	413

Table 21: Number of progeny surviving to measurement per sire in Corriedale flock

Sire ID	Number of progeny
850584	27
860118	31
860417	34
860433	24
870010	30
870044	30
870069	27
870127	40
870421	37
870568	33
870599	34
870710	31
870730	33
870757	31
870783	24
870788	26
880007	28
880015	38
880048	33
880083	24
880136	28
880162	27
880174	27
880184	24
880419	30
880554	30
880643	30
880851	25
880975	29
890017	32
890023	36
890042	33
890070	39
890094	22
890146	29
890154	33
890219	29
890291	27
890309	32
890409	30
890649	12
890844	19
900001	21
900063	26

Table 21 cont...

900116	21
900203	28
900205	17
900349	25
900405	29
900423	27
900480	29
900493	23
900596	11
<hr/>	
Number of sire families	= 53
Mean family size	= 28.2
Standard deviation	= 5.9
<hr/>	

Table 22: Frequency of birth rank for animals surviving to measurement each year in Corriedale flock.

Year of birth	Frequency of birth Rank		
	Singles	Twins	Triplets
1989	88	290	35
1990	125	275	6
1991	85	292	16
1992	91	188	4
<hr/>			
Total	389	1045	61
<hr/>			

Table 23: Frequency of rearing rank for animals surviving to measurement each year in Corriedale flock.

Year of birth	Frequency of rearing Rank		
	Singles	Twins	Triplets
1989	110	280	23
1990	135	268	3
1991	104	279	10
1992	125	155	3
<hr/>			
Total	474	982	39
<hr/>			

Table 24: Number of rams and ewes surviving to measurement in Corriedale flock.

Year of birth	Sex	
	Rams	Ewes
1989	192	221
1990	205	201
1991	206	187
1992	119	164
Total	722	773

Table 25: Frequency of age of dam for animals surviving to measurement each year in Corriedale flock.

Year	Age of dam at birth of offspring (years)					
	2	3	4	5	6	7
1989	100	101	97	66	47	2
1990	75	95	88	91	38	19
1991	90	69	94	79	44	17
1992	60	67	59	51	26	20
Total	325	332	338	287	155	58

Appendix B: Number of observations for performance traits

Table 1: Number of observations for traits jointly analysed by AIREML for Border Leicester rams.

	ALW	AFD	AMD	WLW	WFD	WMD	GFWT
ALW	394						
AFD	393	397					
AMD	123	123	123				
WLW	301	304	80	608			
WFD	303	306	80	608	613		
WMD	80	80	80	377	377	377	
GFWT	300	303	80	604	606	376	607

Table 2: Number of observations for traits jointly analysed by AIREML for Border Leicester ewes.

	ALW	AFD	AMD	WLW	WFD	WMD	GFWT
ALW	647						
AFD	617	621					
AMD	349	349	349				
WLW	386	369	130	462			
WFD	339	322	84	415	415		
WMD	84	84	84	155	155	155	
GFWT	343	327	127	382	337	117	382

Table 3: Number of observations for traits jointly analysed by AIREML for combined sexes Border Leicester.

	ALW	AFD	AMD	WLW	WFD	WMD	GFWT
ALW	1041						
AFD	1010	1018					
AMD	472	672	472				
WLW	687	673	210	1070			
WFD	642	628	164	1032	1028		
WMD	164	164	164	532	532	532	
GFWT	643	630	207	986	943	493	989

Table 4: Number of observations for traits jointly analysed by AIREML for Coopworth rams.

	ALW	AFD	AMD	WLW	WFD	WMD	GFWT
ALW	1183						
AFD	673	686					
AMD	174	174	174				
WLW	1109	669	170	1711			
WFD	1028	668	170	1518	1525		
WMD	170	170	170	645	645	645	
GFWT	1087	657	170	1680	1498	645	1696

Table 5: Number of observations for traits jointly analysed by AIREML for Coopworth ewes.

	ALW	AFD	AMD	SLW	SFD	SMD	GFWT
ALW	1407						
AFD	726	728					
AMD	180	180	180				
SLW	1334	693	161	2021			
SFD	1066	696	159	1475	1516		
SMD	159	159	159	562	598	598	
GFWT	1334	690	161	1998	1479	592	2024

Table 6: Number of observations for traits jointly analysed by AIREML for combined sexes Coopworth.

	ALW	AFD	AMD	GFWT
ALW	2590			
AFD	1399	1414		
AMD	354	354	354	
GFWT	2422	1347	331	3720

Table 7: Number of observations for traits jointly analysed by AIREML for Dorset Down rams.

	ALW	AFD	AMD	WLW	WFD	WMD
ALW	513					
AFD	512	514				
AMD	223	223	223			
WLW	422	422	170	820		
WFD	421	421	170	819	819	
WMD	170	170	170	557	557	557

Table 8: Number of observations for traits jointly analysed by AIREML for Dorset Down ewes.

	ALW	AFD	AMD	WLW	WFD	WMD
ALW	923					
AFD	922	925				
AMD	586	586	586			
WLW	509	512	190	607		
WFD	427	430	106	523	525	
WMD	106	106	106	201	201	201

Table 9: Number of observations for traits jointly analysed by AIREML for combined sexes Dorset Down.

	ALW	AFD	AMD	WLW	WFD	WMD
ALW	1439					
AFD	1434	1439				
AMD	809	809	809			
WLW	931	934	360	1427		
WFD	848	851	276	1342	1344	
WMD	276	276	276	758	758	758

Table 10: Number of observations for traits jointly analysed by AIREML for combined sexes and breeds Border Leicester and Dorset Down.

	ALW	AFD	AMD	WLW	WFD	WMD
ALW	2477					
AFD	2444	2457				
AMD	1281	1281	1281			
WLW	1618	1607	570	2497		
WFD	1490	1479	440	2365	2372	
WMD	440	440	440	1290	1290	1290

Table 11: Number of observations for traits jointly analysed by AIREML for Corriedale rams.

	WLW	WFD	WMD	GFWT
WLW	721			
WFD	721	722		
WMD	721	722	722	
GFWT	721	722	722	722

Table 12: Number of observations for traits jointly analysed by AIREML for Corriedale ewes.

	WLW	WFD	WMD	GFWT
WLW	773			
WFD	773	773		
WMD	773	773	773	
GFWT	771	771	771	772

Table 13: Number of observations for traits jointly analysed by AIREML for combined sexes Corriedale.

	WLW	WFD	WMD	GFWT
WLW	1494			
WFD	1494	1495		
WMD	1494	1495	1495	
GFWT	1492	1493	1493	1494

Appendix C: Finding the most appropriate analytical method

1.0 Development of analytical approach

The objectives of this section were those of the first paragraph of section 3.6.1.

1.2 Data sets for analyses

Performance data sets of Dorset Down breed became available earlier than those of other breeds hence they were used for most of the developmental work. Tables 1 and 2 show the number of observations involved in each analysis for univariate SAS (SAS, 1991) and Genstat (Lawes Agricultural Trust, 1990) and also multivariate SAS. The number of observations used in DFREML and AI-REML are shown in Appendix B. Generally the number of observations in the different data sets were comparable with those from similar studies (Young, 1989; Cameron and Bracken, 1992; Bishop, 1993) and were of adequate size based on the criteria of Koots *et al.* (1994a) (see section 3.6.3). Therefore, developmental analyses were carried out as described below.

Table 1: Number of observations for Dorset Down data subsets

Traits	Rams		Ewes	
	No. of observations	No. of sires	No. of observations	No. of sires
ALW	513	53	922	79
AFD	514	53	922	79
AMD	223	23	586	49
WLW	742	88	509	52
WFD	742	88	428	42
WMD	480	88	106	12

Table 2: Number of observations for Corriedale data subsets

Trait	Rams		Ewes	
	No. of observations	No. of sires	No. of observations	No. of sires
WLW	597	42	614	42
WFD	597	42	614	42
WMD	597	42	614	42
GFWT	597	42	614	42

1.3 Univariate analyses

Exploratory data analyses were conducted using Minitab (Minitab, 1992) and SAS (SAS, 1991) statistical packages. Analyses were performed first for sexes combined within breed and within season but most of the least squares means were not estimable for Dorset Down data because the data were unbalanced, since ewes were mostly performance tested in autumn with very few data points for winter, while the opposite was true for rams (Table 1). Rams were performance tested in winter because earlier work at Lincoln has shown that heritability for fat depth and predicted responses were higher in winter

than either autumn or spring as described in Chapter 3. Due to the non-estimable least squares means analyses in Dorset Down a decision was made to perform separate analyses for the two sexes. This analytic approach was also employed in analysing Corriedale progeny test data sets. These data sets were chosen because they were balanced and had similar observations for ewes and rams in winter (Table 2). Since these data sets were balanced, analyses were also done for sexes combined.

1.3.1 Univariate SAS GLM

1.3.1.1 Materials and Methods

Fixed and covariate effects to be fitted in models were identified as described in detail in Chapter 3. Briefly, a sire model was fitted in univariate SAS GLM (SAS, 1991). All main effects, birth rank, rearing rank, age of dam, year and age were fitted. In addition, all two factor interactions were fitted. All non-significant ($P>0.10$) two way interactions and main effects were dropped from the model.

Data analyses were performed using univariate SAS GLM procedures (SAS, 1991) to obtain heritability estimates. Variance components were estimated fitting a sire model, with sire nested within year and line for Dorset Down and nested within year only for Corriedale data sets.

1.3.1.2 Results and Discussion

Generally heritabilities for most traits were estimable, and of moderate (>0.10) to high (>0.30) magnitudes. However, in Dorset Down data subsets, heritability estimates differed across sexes and seasons, with greater estimates in rams than ewes and also for autumn season than winter (Table 3). Of note was the negative heritability estimate for autumn muscle depth in Dorset Down ewes, which was predominantly a function of small data size ($n=106$). Comparatively, there were no clear cut trends in heritability estimates across sexes in Corriedale data subsets (Table 4). Across breeds same sex and season comparison, heritability estimates were generally greater in Corriedale ram and ewe data subsets than the respective traits for Dorset Down in winter (Tables 3 and 4). Heritability estimates for combined sexes were intermediate those of across sexes in Corriedale (Table 5).

Due to the variable heritability estimates across seasons and sexes, no firm conclusions could be reached, since data sets were not balanced across seasons and sexes especially for Dorset Down breed. Data were also from selection experiments as briefly described previously and in detail in Chapter 3.

In order to get more reliable heritability estimates VARCOMP procedure employing REML (SAS, 1991) and Genstat REML (Lawes Agricultural Trust, 1990) were used, fitting a sire model. This was because of the desirable features of REML described in Chapter 2. However, REML in these instances would not remove effects of selection but it would give better estimates since one of its desirable feature

is handling analyses from unbalanced data sets better than ANOVA and related procedures (see Chapter 2).

Table 3: Estimates of genetic and residual variances and heritability from univariate SAS GLM for Dorset Down data subsets

Trait	Rams			Ewes		
	V_a	V_e	h^2	V_a	V_e	h^2
ALW	14.02	24.999	0.49	2.780	17.621	0.15
AFD	0.324	1.636	0.19	0.216	1.570	0.13
AMD	2.970	5.698	0.46	0.307	4.980	0.06
WLW	6.949	26.565	0.24	2.610	20.804	0.12
WFD	0.338	1.286	0.25	0.598	3.245	0.18
WMD	0.642	4.840	0.13	-0.179	3.749	-0.05

Table 4: Estimates of genetic and residual variances and heritability from univariate SAS GLM for Corriedale data subsets

Trait	Rams			Ewes		
	V_a	V_e	h^2	V_a	V_e	h^2
WLW	6.680	25.876	0.24	8.300	20.307	0.37
WFD	1.058	1.285	0.68	1.070	1.747	0.53
WMD	2.435	4.238	0.50	1.429	4.261	0.31
GFWT	0.091	0.152	0.52	0.138	0.167	0.69

Table 5: Estimates of genetic and residual variances and heritability from univariate SAS GLM for sexes combined Corriedale

Trait	Sexes combined Corriedale		
	V_a	V_e	h^2
WLW	5.738	23.750	0.23
WFD	0.722	1.596	0.41
WMD	1.716	4.302	0.36
GFWT	0.104	0.163	0.55

1.3.2 Univariate SAS VARCOMP and Genstat

Superior features of REML compared to ANOVA and related type *e.g* GLM were discussed in Chapter 2. Therefore, heritability estimates from REML based methods were considered to be provide better estimates than those of GLM. To test such a hypothesis REML methods were used to analyse data analysed by GLM in section 1.3.1.1.

1.3.2.1 Materials and Methods

Similar models as in section 1.3.1.1 were fitted. Analyses were performed for Dorset Down data subsets only because of variable estimates obtained from GLM.

Procedure VARCOMP does not allow fitting covariables (SAS, 1991), therefore, traits were corrected for age using regression coefficients from univariate SAS GLM where age significantly affected performance in a trait ($P < 0.10$).

13.2.2 Results and Discussion

Similar estimates were obtained from both univariate SAS VARCOMP REML and Genstat REML procedures for Dorset Down ram data subset. Comparatively for ewes the estimates were consistently greater from SAS VARCOMP REML than Genstat 5 REML (Tables 6 and 7). Compared to univariate SAS GLM, the estimates were generally the same for Dorset Down ram data subsets. However, for the ewe data subset, the estimates were less from SAS GLM than VARCOMP REML and although most of the estimates were the same for SAS GLM and Genstat REML where different there were greater for SAS GLM than Genstat REML (Tables 3, 6 and 7).

Differences in heritability estimates from statistical packages fitting the same model to the same data subset for autumn traits in Dorset Down ewe data subset were of concern. Therefore, analyses were carried out using DFUNI REML of Meyer (1991b & 1993) and AIUNI REML of Johnson and Thompson (1995). Advantages and disadvantages of DFREML and AIREML methods were described in Chapter 2.

1.3.3 DFUNI REML and AIUNI REML

DFUNI REML and AIUNI REML, fitting an individual animal model which takes into account all relationships between animals which reduces bias due to selection hence provides less biased heritability estimates (see Chapter 2). Therefore, individual animal models using DFUNI REML and AIUNI REML were fitted to autumn data subset Dorset Down ewes. The aim was to evaluate the effects of selection in heritability estimates which had been observed to vary with method of analyses above.

1.3.3.1 Materials and Methods

An individual animal model was fitted to autumn data subset Dorset Down ewes. Animal was the only random effect together with significant fixed and covariable effects as described in section 1.3.1.1.

1.3.3.2 Results and Discussion

Although, heritability estimates from DFUNI REML did not differ significantly ($P>0.05$) from those of AIUNI REML, they were slightly greater and generally had larger sampling errors (Table 8). Comparatively, although none of the estimates of DFUNI were significantly different ($P>0.05$) from those of SAS GLM, VARCOMP REML and Genstat REML, estimates from the former method were consistently greater than those of the latter methods. Similar conclusions were also evident between estimate of AIUNI and other methods except there were no trends in heritability estimates between AIUNI and VARCOMP REML (Tables 3, 4, 6-8). Therefore, methods which take into account unbalanced nature of data and selection were considered to be appropriate for selection experiments.

1.3.4 Overall conclusions on univariate analyses

Based on all univariate results, conclusions were that variability in heritability estimates between sexes, seasons and breeds could be real. These results were consistent with other studies in sheep experiments and beef cattle (Chapter 2). Therefore, multivariate analyses were carried out to estimates genetic and phenotypic correlations which are important in multi-trait selection experiments. Genetic parameters were also to be used to derive breeding values to estimate responses to selection for lean tissue growth rate.

Table 6: Estimates of genetic and residual variances and heritability from univariate SAS VARCOMP procedure using REML method for Dorset Down data subsets

Trait	Rams			Ewes		
	V_a	V_e	h^2	V_a	V_e	h^2
ALW	13.880	24.750	0.49	3.248	17.413	0.18
AFD	0.336	1.630	0.20	0.289	1.559	0.18
AMD	3.040	5.650	0.47	0.480	4.923	0.10
WLW	7.960	26.260	0.28	4.432	20.206	0.21
WFD	0.328	1.290	0.24	0.788	3.219	0.23
WMD	0.648	4.838	0.13	NE	NE	NE

NE - non-estimable

Table 7: Estimates of genetic and residual variances and heritability from univariate REML Genstat 5 for Dorset Down data subsets

Trait	Rams			Ewes		
	V_a	V_e	h^2	V_a	V_e	h^2
ALW	14.096	24.910	0.50	2.871	17.770	0.16
AFD	0.336	1.632	0.20	0.156	1.590	0.10
AMD	2.974	5.680	0.46	0.307	5.128	0.06
WLW	8.440	26.690	0.29	2.570	20.730	0.12
WFD	0.331	1.290	0.24	0.457	3.272	0.13
WMD	0.648	4.842	0.13	NE	NE	NE

NE - non-estimable

Table 8: Estimates of genetic and residual variances and heritability from DF and AI REML method for Dorset Down ewe data subset in autumn. Standard error of estimate in brackets.

Trait	DFUNI DFREML			AIUNI AI-REML		
	V _a	V _e	h ²	V _a	V _e	h ²
ALW	4.587	14.167	0.24 (0.07)	4.052	15.070	0.21 (0.07)
AFD	0.340	1.266	0.21 (0.07)	0.274	1.355	0.17 (0.06)
AMD	0.437	4.381	0.09 (0.07)	0.356	4.811	0.07 (0.04)

1.3.5 Multivariate SAS GLM analyses

As described above the objectives of fitting multivariate models were to estimate genetic and phenotypic parameters in autumn and winter in separate sexes and use heritability estimates to help derive breeding values.

1.3.5.1 Materials and Methods

Only Dorset Down data subsets were analysed because rams and ewes were performance tested in both autumn and winter, although one sex had more measurement in one season than the other.

Multivariate SAS GLM was used for analyses (SAS, 1991). The data sets and models of analyses were the same as in section 1.3.1.1. Multivariate SAS GLM only utilises observations from animals with measurements in all traits included in the model. This meant that including muscle depth which was measured later than fat depth and liveweight in models with liveweight and fat depth reduced the number of animals to about half or even less than that for liveweight and fat depth. Therefore, to reduce bias in parameter estimates, bivariate models were employed for analyses involving liveweight and fat depth both within and between autumn and winter.

1.3.5.2 Results and Discussion

Trends in heritability estimates seen in univariate analyses were still evident in multivariate analyses. Generally, ram estimates were greater than those from ewe data subset (Tables 9 and 10). Estimates of phenotypic parameter estimates were similar between the data subsets for the two sexes. Most of the genetic correlations were of different magnitudes between the sexes, although there were no trends apparent *i.e.* neither rams nor ewes genetic correlation were consistently greater or less. Furthermore, some estimates of genetic correlations from the ewe data subset were non-estimable or nonsensical (>1.00).(Tables 9 and 10).

Due to nonsensical genetic correlation estimates, it was suspected that there was a possibility that heritability and phenotypic parameters were not well estimated too. Furthermore, the effects of selection and unbalanced nature of data were thought to further undermine estimates of GLM. Therefore, a search was begun for better statistical method(s) of estimation than multivariate SAS GLM in the literature.

Table 9: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from multivariate SAS GLM for Dorset Down ewe data subset.

Variable		Genetic [#] (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
ALW	ALW	1.960	19.245	0.10	-
ALW	AFD	-0.176	2.010	-0.27	0.35
ALW	AMD	0.824	4.316	1.16	0.45
ALW	WLW	1.884	13.977	0.66	0.73
AFD	AFD	0.216	1.560	0.13	-
AFD	AMD	-0.009	1.124	-0.03	0.42
AFD	WFD	0.568	1.477	1.12	0.61
AMD	AMD	0.308	4.980	0.06	-
WLW	WLW	2.468	21.237	0.11	-
WLW	WFD	0.900	2.926	0.68	0.37
WLW	WMD	NE	NE	NE	NE
WFD	WFD	0.716	3.221	0.21	-
WFD	WMD	NE	NE	NE	NE
WMD	WMD	NE	NE	NE	NE

[#] characterised as sire variance multiplied by four; NE - non-estimable

Table 10: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from multivariate SAS GLM for Dorset Down ram data subset.

Variable		Genetic [#] (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
ALW	ALW	14.200	24.788	0.50	-
ALW	AFD	0.660	2.090	0.31	0.32
ALW	AMD	4.532	3.775	0.61	0.38
ALW	WLW	10.718	18.955	0.88	0.75
AFD	AFD	0.310	1.641	0.18	-
AFD	AMD	0.354	1.000	0.31	0.31
AFD	WFD	0.340	0.751	0.89	0.53
AMD	AMD	2.728	5.720	0.43	-
WLW	WLW	7.884	26.171	0.28	-
WLW	WFD	0.992	1.830	0.61	0.33
WLW	WMD	1.328	5.114	0.62	0.47
WFD	WFD	0.338	1.286	0.25	-
WFD	WMD	0.174	0.584	0.38	0.27
WMD	WMD	0.692	4.860	0.14	-

characterised as sire variance multiplied by four

1.3.6 A search for better methods of analyses

This search highlighted that method(s) of analyses in selection experiments should also include numerator relationships to minimise bias in genetic and phenotypic parameter estimates due to selection *i.e* to remove bias from selection data. The effects of selection on genetic and phenotypic parameters estimates are discussed in Chapter 2. The most popular method fitting these criterion at that time was DFREML of Meyer (1991b). However, there were other methods available and some in development.

1.3.7 DFMUW REML

In June 1993 DFREML version 2.0 of Meyer (1991b) was sourced. Many problems were encountered trying to compile and run DFMUW program, partly because of the lack of a good Fortran Compiler (Bell, pers. comm.) and also because of possible errors in the program which were later corrected in DFREML version 2.1 by Meyer (1993). From DFREML version 2.0 DFMUV and DFUNI were run successfully. DFMUV is the multivariate analyses for equal design while DFMUW is more general than DFMUV and allows different models to be fitted for individual traits, differing in both fixed and random effects (Meyer, 1991b & 1993). Therefore, compared to DFMUV, DFMUW was deemed to be more suitable for analysis since the number of observations differed for most traits as shown in Tables 1 and 2.

1.3.7.1 Problems encountered with DFREML

DFREML version 2.1 was last updated in September 1993 (Meyer, 1993). DFREML version 2.1 was sourced in November 1993. Problems were also encountered when compiling this version. Joint analysis of three traits for separate sexes were successful but not for four or more traits. Joint analysis of four or more traits were necessary where greasy fleece was included in the analysis of liveweight, fat and muscle depths or when genetic correlations between sexes and seasons data sets were desirable. Increasing array dimensions to cope with unbalanced data sets was unsuccessful. The main problem was in the ordering step which never worked with all options given by Meyer (1993).

1.3.7.2 Materials and Methods

Only the Dorset Down ewe data subset described in section 1.3.1.1 was analysed using DFMUW. The aim being to compare estimates from DFMUW with those from multivariate SAS GLM. This data set was chosen because of the unsatisfactory estimates obtained above. As discussed in Chapter 2, DFREML method can give unbiased estimates from data which is unbalanced and from selection

experiments provided all information contained in the data set and used in selection is included in analysis.

An individual animal model was fitted with animal being the only random effect and year the only fixed effect. All other significant ($P < 0.10$) fixed effects (birth rank and age of dam) and covariable (age at measurement) were corrected for because they were not consistently significant across traits. In retrospect fixed and covariable effects could have been coded as a constant in traits where there were non-significant. Fitting all significant fixed and covariables is important to make the analyses translation invariant *i.e.* remove bias due to fitting these effects (Harville, 1977; Kennedy, 1981).

1.3.7.3 Results and Discussion

Heritability estimates were greater from DFMUW than multivariate SAS GLM. In addition, genetic correlations from DFMUW were within theoretical limits (between -1.00 and 1.00) *i.e.* none were nonsensical. Phenotypic correlations were generally similar for the two methods (Table 9 and 11).

Based on these findings a conclusion was reached that DFMUW was a better method of analyses than multivariate SAS GLM. Therefore, more data subsets from Border Leicester, Dorset Down and Corriedale flocks were analysed. Data manipulation and the model of analyses were similar to those of Dorset Down ewe data subset described above.

The results of these analyses are shown in Tables 11 to 16. Basically, all genetic and phenotypic parameters were within their theoretical limits.

Table 11: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from DFMUW DFREML for Dorset Down ewe data subset in autumn. A dash (-) indicates parameter not tabulated.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	4.698	14.072	0.25	-
LW	FD	0.146	1.876	0.11	0.37
LW	MD	0.678	4.318	0.52	0.52
LW	GFWT	-	-	-	-
FD	FD	0.344	1.263	0.21	-
FD	MD	-0.009	1.045	-0.03	0.40
FD	GFWT	-	-	-	-
MD	MD	0.448	4.373	0.09	-
MD	GFWT	-	-	-	-
GFWT	GFWT	-	-	-	-

Table 12: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from DFMUW DFREML for Border Leicester ewe data subset in autumn. A dash (-) indicates parameter not tabulated.

Variable		Genetic [#] (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	3.422	11.117	0.24	-
LW	FD	0.263	2.472	0.27	0.49
LW	MD	1.373	4.460	0.60	0.61
LW	GFWT	0.115	0.364	0.23	0.35
FD	FD	0.280	1.859	0.13	-
FD	MD	-0.105	1.645	-1.00	0.52
FD	GFWT	0.002	0.059	0.01	0.11
MD	MD	0.782	4.759	0.14	-
MD	GFWT	0.146	-0.016	0.67	0.15
GFWT	GFWT	0.100	0.064	0.61	-

Table 13: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from DFMUW DFREML for Border Leicester ram data subset in winter. A dash (-) indicates parameter not tabulated.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	5.455	18.367	0.23	-
LW	FD	0.987	1.370	0.63	0.35
LW	MD	1.073	4.729	0.41	0.51
LW	GFWT	0.201	0.621	0.39	0.41
FD	FD	0.445	1.431	0.24	-
FD	MD	0.123	0.844	0.16	0.37
FD	GFWT	0.056	0.071	0.32	0.26
MD	MD	1.006	3.909	0.20	-
MD	GFWT	-0.055	0.262	-0.29	0.24
GFWT	GFWT	0.049	0.119	0.29	-

Table 14: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from DFMUW DFREML for Dorset Down ram data subset in winter. A dash (-) indicates parameter not tabulated.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	12.946	19.881	0.39	-
LW	FD	0.664	1.415	0.29	0.31
LW	MD	3.274	2.907	0.75	0.47
LW	GFWT	-	-	-	-
FD	FD	0.415	0.931	0.31	-
FD	MD	0.381	0.281	0.55	0.29
FD	GFWT	-	-	-	-
MD	MD	1.352	3.750	0.27	-
MD	GFWT	-	-	-	-
GFWT	GFWT	-	-	-	-

Table 15: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from DFMUW DFREML for Corriedale ewe data subset in winter. A dash (-) indicates parameter not tabulated.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	10.616	7.974	0.57	-
LW	FD	2.008	0.701	0.64	0.46
LW	MD	3.468	1.016	0.79	0.47
LW	GFWT	0.787	0.082	0.64	0.40
FD	FD	0.902	0.978	0.48	-
FD	MD	0.877	0.518	0.72	0.48
FD	GFWT	0.063	0.082	0.19	0.21
MD	MD	1.624	2.903	0.37	-
MD	GFWT	0.110	0.278	0.24	0.37
GFWT	GFWT	0.124	0.124	0.50	-

Table 16: Estimates of genetic and residual (co)variances and heritability (h^2), genetic correlation (r_G) and phenotypic correlation (r_P) from DFMUW DFREML for Corriedale ram data subset in winter. A dash (-) indicates parameter not tabulated.

Variable		Genetic (co)variance	Residual (co)variance	h^2 or r_G	r_P
X	Y				
LW	LW	6.636	26.809	0.20	-
LW	FD	1.326	2.446	0.62	0.52
LW	MD	0.780	6.277	0.23	0.55
LW	GFWT	0.174	0.706	0.25	0.40
FD	FD	0.716	0.888	0.45	-
FD	MD	0.555	0.724	0.48	0.46
FD	GFWT	-0.035	0.103	-0.15	0.14
MD	MD	1.661	3.193	0.34	-
MD	GFWT	-0.103	0.230	-0.31	0.15
GFWT	GFWT	0.075	0.073	0.51	-

1.3.8 Deficiencies of DF based REML

Deficiencies of DF based REML as discussed in Chapter 2 were of concern and failure to successfully compile DFMUW with increased array dimension to cope up with some of the large data sets (2000 or more animals) led to a further search for a “better” method in the literature.

1.3.9 AIMUL AI-REML

In February 1994, AI-REML programmes of Johnson and Thompson (1995) and Johnson (pers. comm.) were recommended by D.J. Garrick (Garrick, pers. comm.). The salient features of AI based REML methods are their higher speed and higher efficiency in utilising computer time as discussed in Chapter 2 than DF based methods. AI-REML programmes were sourced in June 1994 together with univariate AI-REML of Johnson and Thompson (1995). These programmes were still in developmental stage at that time. A Fortran compiler was sourced and AI-REML were compiled successful (Bell, pers. comm.).

1.3.9.1 Materials and Methods

Similar to analyses in DFMUW fixed and covariable effects were identified using univariate SAS GLM procedure. However, in contrast to DFMUW none of the significant fixed and age effects were corrected for. These were included in AIMUL AI-REML analyses to make genetic and phenotypic parameters translation invariant as described before.

1.3.9.2 Results and Discussion

Genetic and phenotypic parameters from AIMUL AI-REML are presented in Chapter 5. Comparison of estimates from DFMUW and AIMUL showed that generally the estimates were similar. In conclusion because of the desirable features as described in Chapter 2 of AI-REML, this method was used for the bulk of the analyses and estimation of breeding values as described in Chapter 3.

Appendix D: Method of calculating genetic and residual (co)variances between index and component traits (after Young, 1989).

The indices used were a linear combination of two and three traits respectively. The former being a combination of liveweight (LW) and fat depth (FD) and the latter also incorporating muscle depth (MD) (Simm *et al.*, 1987). Thus the covariances between the index and any one component trait is a linear combination of the covariances between that component trait and each of the component traits using the index coefficients as weights (Young, 1989), as shown below. Coefficients used were +0.25, -0.58 and +0.48 for liveweight, fat and muscle depths respectively from the three-traits index (I).

$$\begin{aligned}
 \text{COV}_{I,LW} &= b_{LW} \text{COV}_{LW,LW} & + & b_{FD} \text{COV}_{LW,FD} & + & b_{MD} \text{COV}_{LW,MD} \\
 \text{COV}_{I,FD} &= b_{LW} \text{COV}_{FD,LW} & + & b_{FD} \text{COV}_{FD,FD} & + & b_{MD} \text{COV}_{FD,MD} \\
 \text{COV}_{I,MD} &= b_{LW} \text{COV}_{MD,LW} & + & b_{FD} \text{COV}_{MD,FD} & + & b_{MD} \text{COV}_{MD,MD} \\
 \text{COV}_{I,I} &= b_{LW} \text{COV}_{I,LW} & + & b_{FD} \text{COV}_{I,FD} & + & b_{MD} \text{COV}_{I,MD}
 \end{aligned}$$

Appendix E: Inbreeding

Table 1: Degree of inbreeding for progeny of Border Leicester (BL), Coopworth (CPW) and Dorset Down (DD) flocks. The mean annual inbreeding coefficient (I) was derived by univariate DFREML (Meyer, 1993). Degree of inbreeding calculated as $[(I-1.0)*100]$ (Young, 1989). LTGR is abbreviation for lean tissue growth rate. A dash (-) indicates years when there were no LTGR flocks.

Year	Degree of inbreeding (%)				
	BL LTGR	CPW control	CPW LTGR	DD control	DD LTGR
1984	0.00	0.00	-	0.00	-
1985	0.00	0.00	-	0.00	-
1986	0.30	0.10	0.18	0.27	0.34
1987	0.35	0.35	0.34	0.12	0.24
1988	0.73	0.63	0.68	1.28	1.24
1989	1.03	0.38	0.32	1.02	1.12
1990	1.39	1.34	0.93	1.65	0.60
1991	1.89	1.20	1.51	1.23	1.50
1992	1.82	1.69	1.56	2.92	1.45
Average	0.83±0.74	0.63±0.63	0.79±0.57	0.94±0.97	0.93±0.53

Appendix F: Coefficients and predicted responses for two-trait indices

Table 1: Index coefficients and correlations between two trait indices (liveweight and fat depth) and aggregate breeding value.

Trait	Index coefficients								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
LW	+0.44	+0.58	+0.55	+0.43	+0.48	+0.78	+0.68	+0.51	+0.40
FD	-0.58	-0.71	-0.76	-0.54	-0.63	-0.91	-0.91	-0.65	-0.57
r_{IAB}	+0.18	+0.20	+0.24	+0.17	+0.21	+0.27	+0.25	+0.20	+0.18

Table 2: Index coefficients and correlations between two trait indices (liveweight and muscle depth) and aggregate breeding value.

Trait	Index coefficients								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
LW	+0.01	+0.09	+0.004	-0.003	-0.02	-0.10	-0.25	+0.02	-0.07
MD	+0.49	+0.21	+0.52	+0.41	+0.62	+0.76	+0.81	+0.56	+0.55
r_{IAB}	+0.15	+0.09	+0.16	+0.13	+0.19	+0.22	+0.20	+0.18	+0.16

Table 3: Predicted responses in lean weight for liveweight and fat depth indices. σ_A is the additive genetic standard deviation for lean weight, R_y is response per year, r_{AC} is the genetic correlation between the index and an aggregate breeding value trait, I is selection intensity and L is average generation interval. The full names of other abbreviations are presented in the list of abbreviations

Variable	Predicted responses in lean weight								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
r_{IA}	+0.16	+0.21	+0.18	+0.19	+0.22	+0.37	+0.12	+0.21	+0.12
σ_A	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567
i	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00
L	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84
R_y (g)	+32	+42	+36	+38	+44	+74	+24	+42	+24
$R_y : R_y SYB$	1.00	1.31	1.13	1.19	1.38	2.31	0.75	1.31	0.75

Table 4: Predicted responses in fat weight for liveweight and fat depth indices. σ_A is the additive genetic standard deviation for fat weight, R_y is response per year, r_{AC} is the genetic correlation between the index and an aggregate breeding value trait, I is selection intensity and L is average generation interval. The full names of other abbreviations are presented in the list of abbreviations

Variable	Predicted responses in fat weight								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
r_{IA}	-0.02	+0.01	-0.07	+0.03	+0.02	+0.12	-0.16	+0.01	-0.08
σ_A	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605
i	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00
L	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84
R_y (g)	-4	+2	-15	+6	+4	+26	-34	+2	-17
$R_y : R_y SYB$	1.00	-0.50	3.75	-1.50	-1.00	-6.50	8.50	-0.50	4.25

Table 5: Predicted responses in lean weight for liveweight and muscle depth indices. σ_A is the additive genetic standard deviation for lean weight, R_y is response per year, r_{AC} is the genetic correlation between the index and an aggregate breeding value trait, I is selection intensity and L is average generation interval. The full names of other abbreviations are presented in the list of abbreviations

Variable	Predicted responses in lean weight								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
r_{IA}	+0.23	+0.22	+0.24	+0.19	+0.27	+0.26	+0.23	+0.27	+0.21
σ_A	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567	+0.567
i	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00
L	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84
R_y (g)	+46	+44	+48	+38	+54	+52	+46	+54	+42
$R_y : R_ySYB$	1.00	0.96	1.04	0.83	1.17	1.13	1.00	1.17	0.91

Table 6: Predicted responses in fat weight for liveweight and muscle depth indices. σ_A is the additive genetic standard deviation for fat weight, R_y is response per year, r_{AC} is the genetic correlation between the index and an aggregate breeding value trait, I is selection intensity and L is average generation interval. The full names of other abbreviations are presented in the list of abbreviations

Variable	Predicted responses in fat weight								
	SYB	BLE	BLR	DDE	DDR	CORE	CORR	CPWE	CPWR
r_{IA}	+0.10	+0.16	+0.10	+0.07	+0.10	+0.05	+0.02	+0.12	+0.06
σ_A	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605	+0.605
i	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00	+1.00
L	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84	+2.84
R_y (g)	+21	+34	+21	+15	+21	+11	+4	+26	+13
$R_y : R_ySYB$	1.00	1.62	1.00	0.71	1.00	0.52	0.19	1.24	0.62