Lincoln University Digital Dissertation

Selection for lean tissue growth

in Dorset Down sheep:

Responses and genetic parameters

by

James Shalaulani Nsoso

A dissertation submitted in partial fulfilment
of the requirements for the degree
of

Bachelor of Agricultural Science (Honours)
in
Animal Science

at

Lincoln University

November 1990

ABSTRACT

Performance data for Lincoln University Dorset Down sheep flock (n=1153) were available for the first five years (1985-1989) of a selection programme to improve lean tissue growth. Ewes and rams born in spring each year were run separately at pasture from late summer onwards. Animals were performance tested in autumn and winter. Measurements were made of liveweight, fat depth, and from 1988 onwards of muscle depth at each time.

Prior to 1986, only rams were selected from the base population. From the 1986 mating season (autumn) two lines were established from the base population and maintained separately thereafter. One line was a randomly selected control (C) line, and the second line was selected for lean tissue growth (LTG) on the basis of an index combining information for liveweight and fat depth measured in the winter. The aggregate breeding value was lean weight and fat weight. This index was used up to 1988 after which a new index was used into which muscle depth was incorporated. The aggregate breeding value remained the same.

Replacement ewes were selected on the same basis as rams. However at establishment of the lines mixed age ewes from the base population were randomly allocated to each line. For 1986 mating the LTG 2-T ewes selected were 0.30 index units superior to C 2-T (0.27 compared to -0.30 for 2-T C). However, the 2-T rams in the LTG were 0.62 index units superior to the 2-T C rams (0.71 compared to 0.09 for 2-T C). In 1987 the 2-T LTG rams were 0.83 index units superior (0.90 compared to 0.09 for C 2-T). Rams were used as 2-T for only one season (generation interval = 2 years) while the mean weighted age of ewes was 3.8 years (mean generation interval = 3.8 years). Data were analysed by fitting mixed models using the LMSL76 computer programme of Harvey (1977).

Non-genetic effects which significantly affected animal performance were AOD, BR, DOB, and Year. Responses to selection as indicated by the regression of the differences between lines (LTG-C) on time are shown in Table A. Heritabilities (h^2, bolded diagonal), phenotypic correlation (r_P, above bolded diagonal) and genetic correlation (r_G, below bolded diagonal) are given on Table B for rams and Table C for ewes.

Table A. Rates of response to selection

Variable	units	Rams	Ewes
Autumn liveweight	kg/yr	0.489	0.649
Winter liveweight	kg/yr	0.321	0.856
Autumn fat depth	mm/yr	-0.205	-0.114
Winter fat depth	mm/yr	-0.111	-0.284
Autumn muscle depth	mm/yr	-0.136	
Winter muscle depth	mm/yr	-0.295	

Table B. Estimates of genetic parameters for rams.
h^2 - bolded; r_p - above diagonal and r_G - below diagonal

Variable	Autumn			Winter		
	LW	FD	MD	LW	FD	MD
ALW	**0.39**	0.34	0.34	0.70	-	-
AFD	0.38	**0.21**	0.34	-	0.46	-
AMD	0.67	0.40	**0.38**	-	-	0.48
WLW	0.91	-	-	**0.52**	0.36	0.41
WFD	-	0.61	-	0.67	**0.19**	0.23
WMD	-	-	7.26	2.55	3.97	**0.01**

Table C. Estimates of genetic parameters for ewes.
h^2 - bolded; r_p - above diagonal and r_G - below diagonal

Variable	Autumn			Winter		
	LW	FD	MD	LW	FD	MD
ALW	**0.22**	0.32	0.45	0.82	-	-
AFD	0.79	**0.05**	0.33	-	0.50	-
AMD	1.51	0.44	**0.05**	-	-	0.42
WLW	0.73	-	-	**0.12**	0.30	0.52
WFD	-	0.61	-	0.80	**0.24**	0.48
WMD	-	-	NE	NE	NE	NE

NE = non-estimable

The data indicate that there has been positive responses to selection in component traits of the index, namely liveweight (an increase) and fat depth (a decrease). However, correlated responses in muscle depth have been undesirable (a possible decrease). Inclusion of muscle depth into the index currently used is expected to result in a muscle depth increase since indices containing muscle depth have been shown to result in increase in muscle depth.

The data indicate moderate heritabilities for most component traits. Heritabilities, genetic and phenotypic correlations show variation between sexes and seasons.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

INTRODUCTION

Substantial literature evidence has accumulated that consumption of sheep meat in the western countries has declined relative to that of other meats, due partly to increased consumer preference for lean meat and a market image of lamb as "fatty" (Young, 1989).

Lean carcasses can be produced by selection for increased liveweight (high growth rate) or reduced fatness independently but correlated responses are undesirable. For instance, selection for high growth rate results in increase in liveweight but also results in increase in fatness (Barlow, 1978; Bishop and Hill, 1986.) Selection for reduction in fatness results in reduced fatness but also results in reduced growth rates (Bishop, 1984 cited by Young, 1989). Both increase in fatness and reduced growth rates are undesirable outcomes. Consequently the use of selection indices is warranted whereby information on various measurable traits is combined to assess aggregate breeding value for an animal's potential to grow lean tissue rapidly (Young, 1989). However, in the sheep industry the practical use of indices is in its infancy, although early results seem to confirm theoretical predictions, more work is needed to provide unequivocal results.

Selection is normally applied to both male and female animals, although the selection differential is less in females due to their lower reproductive rate compared to males. Genetic progress from index selection depends on selection differential, heritabilities and genetic correlations of traits. However, at the moment there is little information on heritabilities, genetic and phenotypic correlations for economic important sheep traits either between sexes or within sex independently (Parratt et al., 1989) or between traits at different ages (Beatson, 1987). The few estimates that are published indicate that genetic and phenotypic parameters differ for male and female sheep (Parratt et al., 1989). Recognition of this fact should be taken when considering alternative selection strategies and the various roles sex types can play in New Zealand production systems (Parratt et al., 1989).

This project is based on data collected from a Lincoln University Dorset Down sheep flock selected since 1986 on an index combining information for liveweight (LW), fat depth (FD) and more recently (since 1988) muscle depth (MD) to improve lean tissue growth.

The objectives of this project were to analyse these data to;
1. Determine which environmental effects significantly affected variation in component traits of the index.
2. Estimate heritabilities, genetic and phenotypic of traits and between components traits in the index,
3. Determine the responses obtained after 3 years of selection.
4. Compare and contrast the results of such analyses for rams and ewes, and for autumn and winter measurements.

Chapter 2

LITERATURE REVIEW

2.1 Theory of Genetic size-scaling:

Genetic size-scaling theory provides a useful description of mammalian growth from which genetic comparisons can be made without bias due to differences in relative development. It has as it basic premise the concept of each genotype having it's own genetic size factor which operates throughout growth from embryo to adult. This factor expresses itself in many traits at various stages of growth. It is mostly clearly expressed in the fully grown adult and is estimated as adult or mature weight, A, (Taylor, 1985 & 1987). A is usually only estimated because difficulties are encountered in measuring it. For instance, A is reached when all animal tissues are mature, however, fat is likely to continue to increase in weight beyond the time when other tissues have ceased to grow and are mature (Butterfield et al., 1983). In addition, breeding stock are not necessarily allowed to grow to maturity without nutritional limitation (quality and quantity) in ideal physical environments, while their progeny, destined for meat production are killed long before they have ceased to grow (McClelland, Bonaiti and Taylor, 1976; Blaxter, Fowler and Gill, 1982; Webster et al., 1982). As a consequence, estimates of A have been based on changes in relative proportions of tissues or structures with growth terminated as soon as possible after the achievement of maturity by all tissues except fat (Butterfield et al., 1983). Taylor (1985) offers a definition of adult size,A, as body weight at a fixed body fat percentage (e.g. 20% body fat, which applies mostly to domestic stocks because feral species do not readily attain 20% body fat). Both these authors provide working definitions, but it is clear that A can not be more precisely defined or measured (Blaxter et al., 1982). Taylor (1985) assuming knowledge of A, formulated two formal genetic size-scaling rules for describing the effect of adult size (A) on performance at all growth stages as follows:

1) Treat all age and time variables in days) for the 1th genotype as proportional to $A_z^{0.27}$ where A_z is the mature body weight (in kilograms) of the zth genotype, that is:

$$\text{Time variables} \propto A^{0.27}$$

2) At ages standardized as in (1), treat all cumulated growth variables for the genotype as proportional to $A_z^{1.00}$, that is:

$$\text{Cumulated variables} \propto A^{1.00}$$

Thus rate variables are proportional to $A^{0.73}$ since they are a function of a cumulate variable divided by a time variable:

$$\text{Rate variables} \propto A^{0.73} \propto \text{cumulate/time} \propto A^{1.00} \propto A^{0.27}$$

These genetic size-scaling rules applied at the species level lead to a unified description of mammalian growth that may also apply to more closely related genetic groups. However, the easy clarity seen from species data is not always found within species (Taylor, 1985). Within species (between breeds and sex) significant differences have been demonstrated, especially in sheep even after genetic size scaling (Thonney et al., 1987 a and c). These differences have been mainly attributed to difference in maturity (U) (McClelland et al., 1976; Taylor et al., 1989). Maturity or relative maturity is the ratio of observed body weight (W) to mature weight (A) (McClelland et al., 1976). At a fixed degree of maturity, variation in body composition is not great or is very little between breeds and sex within species (McClelland et al., 1976; Taylor et al., 1989).

2.2 Use of Genetic size-scaling in the study of growth

Genetic size-scaling solves some of the problems encountered when making genetic comparison between species and breeds that differ in body size since adult size is known to affect performance traits (Taylor, 1985). Young (1989) reports that many studies based on serial slaughter experiments have shown little variation between breeds in growth and carcass composition when differences in mature size are taken care of; and deviations that do exist are either of no commercial interest (e.g.the Soay, a feral sheep which is small but exceptional lean) or benefits are offset by disadvantages (e.g. lean Texel is slow growing). Butterfield et al. (1983) working with large and small strains of merino rams, found that at the same liveweights the large size strain had a greater proportion of bone and a smaller proportion of fat than the smaller size strain because they were less mature; but at the same proportion of mature live weight (A), differences between the strains in proportional composition were reduced, and the large strain had slightly more fat. In conclusion they said that breed or strain differences in composition at the same weight may be due largely to differences in maturity. The same conclusion was reached by Taylor et al. (1989) .

Universal validity of Taylor's simple genetic size scaling rules, would imply that animal breeders should concentrate exclusively on the animals deviating from genetic size-scaled expectations (Taylor, 1985) if size itself is not commercially viable. Traits deviating from genetically size scaled mean mammalian curves (for growth, body weight, body composition, heat production, maintenance requirements, food intake, food efficiency and growth rates) can be studied, with variation independent of body size evaluated leading to identification of deviant genotypes (Taylor, 1985). For example Webster et al. (1982), using the concept of 'metabolic age' [genetically size-scaled standardisation of time (Taylor, 1985)] showed that maturation rate in Aberdeen Angus and Friesian bulls was close to a reported interspecies mean value but Hereford and Charolais bulls both matured more rapidly than expected. Also, in three breeds (Hereford, Aberdeen Angus and Charolais) the animals that achieved 0.5A at the youngest age were not much lighter than those that were slowest to mature. This suggests in these beef breeds that it may be possible to select for rapid growth without substantially affecting mature size (A) and thereby the maintenance energy cost of the parent population (Webster et al., 1982).

A major benefit of Genetic size scaling theory is that since the biochemistry of growth is similar in most mammalian species, it provides means to predict performance of genotypes we know little about from well studied genotypes, for example, experimental results on food efficiency from mice or rats to pigs or cattle (Taylor, 1985).

2.3 Appetite

Appetite can be considered to be the balance between intake (energy in) and maintenance requirements (energy lost). Appetite seems less important than genetic size scaling in explaining genotype differences in body composition, although they are examples of lean genotypes with low appetites (Wood, 1982). The percentage of fat in the body is increased when energy intake is raised to a high level relative to maintenance, although this is more noticeable in non-ruminants than in ruminants fed fibrous diets. Also the percentage of fat at a particular weight is influenced by adult size since body fat as a proportion of body weight increase as animals mature (Wood, 1982). For instance, when breeds are compared at the same immature body weight, small adult size breeds are relatively fat compared with those of large adult size because they are more mature (Wood, 1982; Butterfield et al., 1983). After accounting for mature size, remaining variation in the total fat content at constant body weight is probably small perhaps less than 10% of the whole bodyweight (Wood, 1982), and can partly be explained by variation in appetite and maintenance requirements (Wood, 1982). Generally fast growing, large adult size genotypes have higher appetites and maintenance requirements than their small counterparts because of a faster rate of protein deposition but if appetite and maintenance requirements are out of step this can have profound effect on fat deposition. The cause of this imbalance is more likely to be due to appetite than maintenance requirements (Wood, 1982). Wood (1982) from a wide range of literature concluded that breeds or strains which are leaner than would be predicted from their mature size, A (Pigs - Pietrain; sheep - Texel and cattle - Limousin), all seemed to be characterised by low appetites. The same conclusion was also reached by Whitehead and Parks (1988), working with commercial lines of broiler chickens who found that lean broiler lines had consistently low food intakes compared to fat lines.

2.4 Selection goals for meat animals

Most of the work on selection for meat animals has been for increased weight (W) at a fixed age which is equivalent to selection for growth rate (Barlow, 1978; Webster, 1982; Bishop and Hill, 1985; Hill and Bishop, 1986; Jungst et al., 1986; Kreiter et al., 1986; Parker et al., 1986; Pingel,1986;Whitehead and Parks, 1988). But increasingly selection to change body composition is becoming important. At present selection in sheep to change body composition is either against ultrasonic backfat (Fennessy, McEwan, Bain and Greer, 1989; McEwan, Fennessy, Greer, Bruce and Bain, 1989; Purchas, Abdullah and Kadim, 1989) or by use of index combining information on liveweight, fat depth and muscle depth (Simm, 1986; Simm, Smith and Thompson, 1987; Simm, Young and Beatson, 1987; Simm and Dingwall, 1989) or without muscle depth (Beatson, 1989). Selection to change body composition is becoming important

probably because of the increasing demand for lean meat in western countries (Simm, 1986; Beatson, 1987, Simm, Young and Beatson, 1987 and Simm et al., 1989) and since sheep meat is considered fatter than other meats the improvement for sheep is decrease in fat and possible increase in liveweight (Beatson, 1987; Beatson, 1989, McEwan et al., 1989).

2.5 Response to selection to change body composition

Response is affected by the heritability, selection differential and generation interval of the character selected for (Falconer, 1989). Literature estimates of genetic parameters (heritability, genetic and phenotypic correlations) for liveweight, ultrasound fat and muscle depths are presented on Tables 1 and 2. The data are variable, in part reflecting different methods of analysis used (e.g. offspring-parent regression or sib-correlations) and sampling error as experiments vary in size (Young, 1989). Under pasture grazing systems the time of the year at which measurements are taken can also influence the magnitude of heritability estimates (Beatson, 1987; Einarsson, 1987).

A notable feature of these heritabilities are the moderate to high values for carcass composition traits, strong evidence that they will respond to selection (Young, 1989). However, it must be borne in mind that selection itself can change these parameters (Falconer, 1989) and that realised heritabilities are often less, but occasionally more, than estimates from the base population (Sheridan, 1988).

Selection based on similar criteria in different genotypes within species (Sheep: Romney - McEwan et al, 1984; Coopworth - McEwan et al., 1989; South-Down - Purchas et al., 1989) and between different species independently (Sheep: McEwan et al., 1989; Soliz-Ramirez et al., 1990; Cattle: Barlow, 1978, Webster, 1982; Parker et al., 1986; Mice: Bishop and Hill, 1985; Hill and Bishop, 1986; Poultry: Whitehead et al., 1988) have generally shown similar results. Selection for growth rate has generally resulted in increases in liveweight at all ages and increase in fatness at maturity (Barlow, 1978; Jungst et al, 1986; Hill et al., 1986). Along side this, has been increases in appetite and absolute maintenance requirements (Wood, 1982).

Most selection programmes aiming to reduce fat have resulted in body fat reduction (Fennessy et al., 1989; McEwan et al., 1989). However, most of these studies do not report liveweight response.In one study Bishop (1984) cited by Young (1989) selection to reduce fatness has been reported to also result in reduced growth rate. Reductions in body fat are present throughout the growth phase of the animal and are associated with significant changes of allometric growth coefficients for some components rather than a redistribution of components within the carcass (Fennessy et al., 1989; McEwan et al., 1989). However, it is disturbing that selection pressure to reduce fat content in carcass has been less successful than towards its enhancement (McEwan et al., 1989). The few results on index selection in sheep, indicate increases in live weight with decreases in fat at constant age (Beatson, 1989; Simm et al., 1989).

Table 1: Estimates of heritability (h^2, x 100, ± SE) for liveweight, and ultrasonic fat and muscle depths from the literature.

Variable	General		Rams1		Ewes1		Reference
	h2	seh2	h2	seh2	h2	seh2	
Liveweight (general)	22	-	-	-	-	-	Rae (1984)
ditto	22	-	-	-	-	-	Parratt, Burt, Bennet, Clarke, Kirton and Rae (1987)
ditto	20	-	-	-	-	-	Parratt and Simm (1987)
ditto	24	-	-	-	-	-	Simm and Dingwall (1989)
Liveweight at 8 months (Romney)	-	-	46.2	17.3	-	-	McEwan, Fennessy, Clarke, Hichey and Knowler (1984)
Liveweight at 14 months (Romney)	-	-	48.5	18	-	-	"
Liveweight at 150 days (Suffolk)	-	-	26	10	-	-	Young (1989)
Liveweight Coopworth	-	-	21	0.5	26.0	0.5	Warmington and Beatson (1985)
Autumn liveweight	17.8	5.6	18.7	9.2	14	12.7	Einarsson (1987)
Winter liveweight	16.4	5.4	17.1	7.9	26.9	8.7	"
Ultrasonic fat depth (in vivo)	20	-	-	-	-	-	Rae (1984)
ditto	9	-	-	-	-	-	Parratt et al (1987)
ditto	16	-	-	-	-	-	Parratt and Simm (1987)
ditto	23	-	-	-	-	-	Simm and Dingwall (1989)
Ultrasonic fat depth at 8 months (Romney)	-	-	23	12.3	-	-	McEwan et al (1984)
Ultrasonic fat depth at 14 months (Romney)	-	-	45.1	17.4	-	-	"
Ultrasonic fat depth at 150 days (Suffolk)	-	-	55[*]	11	-	-	Young (1989)
Autumn fat depth (Ultrasonic)	-	-	17[*]	6	-	-	Beatson (1987)
Winter fat depth	-	-	-	34[*]	8	-	"
Spring fat depth	-	-	16	7	-	-	"
Autumn fat depth (Ultrasonic) adjusted for:							
- age	25	7.8	4.6	6.6	31.9	10.9	Einarsson (1987)
- liveweight	16.3	5.9	5.5	6.8	29.7	10.6	"
Winter fat depth (Ultrasonic) adjusted for:							
- age	23.4	7.2	17.5	9.0	30.4	10.7	"
- liveweight	26.5	7.4	23.1	10	41.6	12.4	"
Muscle depth (Ultrasonic)	22	-	-	-	-	-	Simm and Dingwall (1989)
Muscle depth at 150 days (Ultrasonic, Suffolk)	-	-	29	11	-	-	Young (1989)

* Adjusted for liveweight

Table 2: Estimates of genetic and phenotypic correlations (x100) for liveweight, ultrasonic fat and muscle depths. Associated heritabilities are also given (more heritabilities are presented in Table 1). Heritabilities on the diagonal (bold), phenotypic and genetic correlations above and below the diagonal respectively. Data are presented for relationships between liveweight (LW), autumn liveweight (ALW), Spring liveweight (SLW), Liveweight at 150 days (LW150), ultrasonic fat depth (UFD), autumn fat depth (AFD), winter fat depth (WFD), spring fat depth (SFD), fat depth at 150 days (UFD150), ultrasonic muscle depth (UMD) and ultrasonic muscle at 150 days (UMD150). The estimates of Parratt et al. (1987) are averages of values derived from different literature sources.

Variable	LW	ALW	SLW	LW150	UFD	AFD	WFD	SFD	UFD150	UMD	UMD150	Reference
LW	22	-	-	-	50	-	-	-	-	-	-	Rae (1984)
	22	-	-	-	37	-	-	-	-	-	-	Parratt et al. (1987)
	24	-	-	-	40	-	-	-	-	47	-	Simm and Dingwall (1989)
ALW	-	46.2*	30*	-	-	-	52	-	-	-	-	McEwan et al. (1984)
	-	14*	56*	-	-	-	-	-	-	-	-	Parratt, Nicholl & Alderton (1989)
	-	17	65	-	-	-	-	-	-	-	-	"
SLW	-	80*	22*	-	-	-	-	-	-	-	-	"
	-	84	27	-	-	-	-	-	-	-	-	"
LW150	-	-	-	26	-	-	-	-	40	-	40	Young (1989)
UFD	59	-	-	-	9	-	-	-	-	-	-	Parratt et al. (1987)
AFD[¶]	-	-	-	-	-	17	39	41	-	-	-	Beatson (1987)
WFD[¶]	-	-	-	-	-	83	34	38	-	-	-	"
SFD[¶]	-	-	-	-	-	69	65	16	-	-	-	"
UFD150	-	-	-	2	-	-	-	-	55	-	26	Young (1989)
UMD	-	-	-	-	15	-	-	-	-	20	-	Simm, Young and Beatson (1987)
UMD150	-	-	-	61	-	-	-	-	19	-	29	Young (1989)

¶ adjusted for liveweight

* Values for ewes, all other values were derived from rams or from both sexes

In conclusion selection for growth rate results in increased liveweight and also increased fatness, and selection for reduced fatness results in reduced fatness and also reduced growth rates. Both increase in fatness and reduced growth rates are undesirable correlated responses.Selection on index combining information for liveweight, fat and muscle depths generally results in desirable changes, increase in liveweight, decrease in fat depth and increase in muscle depth. Therefore, the way to improve lean content without undesirable correlated responses seems to selection on index. Although, they are few data reported in sheep.

2.6 Measuring response to selection

One important feature of selection experiments for sheep run at pasture is the highly variable season effects which greatly affect performance. Thus any attempt to measure response to selection should account for yearly fluctuations in performance as well as any long-term change in environmental conditions (McGuirk, Atkins, Thompson, 1986).

The most commonly used method of separating genetic and environmental changes, and so measure response to selection, is by use of two lines; a randomly selected control line and a selected line. Phenotypic means of measurable traits can be compared .This method provides a continuous measure of the effect of environment for all measured characters, from which genetic changes, both direct and correlated can be assessed (McGuirk et al, 1986). While such a control line will require considerable resources to maintain and measure, a single control can be used for more than one selection line, and control flocks have the important extra value of providing information on genetic variance and covariance without complicating effects of selection (McGuirk et al., 1986). However, over many generations, the use of a control line does not improve the precision with which the response is estimated because both selected and control lines are subjected to random genetic drift and sampling error (Falconer, 1989).

Other methods which may be used to measure response to selection are divergent lines and frozen germplasm, although they are not in wide use at present.

2.7 Measuring body composition in vivo to aid in selection

The aim of measuring body composition in vivo is to predict total tissue volume or weight in the carcass of a live animal.

In vivo estimates of body composition in farm animal species can involve both subjective and objective methods (Glodek, 1984). Subjective methods (e.g. conformation score, visual assessment of the body) are generally of poor accuracy as demonstrated by poor coefficients of determination, while objective methods are generally better with accuracy increasing with sophistication of the apparatus (Glodek, 1984). However, objective measurement of body composition on live animal in its present state may be

unsatisfactory since the measurements being made are linear but the entity to be predicted is 3-dimensional (Groenweld and Kallweit, 1984).

A range of objective methods are employed in measuring in vivo body composition especially in humans but at present, the most important in animal breeding in decreasing order of use and increasing relative accuracy are ultrasonic scanning, computed tomography (CT) and Nuclear Magnetic Spectroscopy (NMS) (Glodek, 1984; Wells, 1984; Simm, 1987).

The relatively wide spread use of ultrasonic scanning has occurred because instruments are easy to use, mobile, robust and relatively cheap and ultrasound is apparently free from hazard at the exposure level used in practice (Wells, 1984; Simm, 1987). However, ultrasound measurements are considerably less precise than those obtained from technology like CT (Simm, 1987). As a result in most farm species, it is often necessary to test, slaughter and dissect relatives to provide additional information on body composition which necessitates expensive test facilities and costly labour carcass dissection, because cheaply obtained measurements on the carcass are not sufficiently accurate (Glodek, 1984).

Commercially ultrasonic scanning measurements of fat and muscle depths have been applied with success in the pig industry. The precision achieved with cattle, and particularly sheep has been rather low (Simm, 1987). This is partly because of the dependence of pulse-echo techniques on subcutaneous fat since a lower proportion of total carcass of cattle and sheep is in the subcutaneous depose compared to that in pigs and in sheep the absolute depths of fat and muscle are lower than in cattle and pigs (Simm, 1987).

Although computed tomography (CT) has extremely high resolution, with much better tissue discrimination than ultrasonic for both muscle and fat tissues, enormous costs are still involved and the apparatus is much less mobile and so far has only been used in research. The same applies to other techniques such as NMR (Glodek, 1984; Simm, 1987). However, the higher precision in measuring in vivo body composition by methods like CT and NMR is expected to result in higher heritabilities and smaller errors in prediction of carcass composition, leading to the abandonment of slaughtering of sibs and progeny for carcass evaluation as methods of predicting breeding value. It is unclear to what extent these techniques are able to assess meat quality, which is of immense importance especially in the pig industry. Thus slaughtering of sibs and progeny may still be needed to assess this issue. In cases where abandonment of slaughtering is possible, this would lead to conversion of present progeny and sib capacity to additional performance test capacity in body composition that could be much greater than at present (Glodek, 1984; Standal, 1984). CT and NMR may be cost-effective if used in a second-stage of selection after a large population of animals has been screened by ultrasound scanning (Simm, 1987).

Chapter 3

SELECTION FOR LEAN TISSUE GROWTH IN
DORSET DOWN SHEEP

3.1 Materials and methods

3.1.1 Source and Description of data

The data used in this study are from the Lincoln University Dorset Down flock which has been selected for lean tissue growth since 1986 (Table 3). The flock was established from a common genetic base (Beatson, 1986). The selected line was established from selection for lean tissue growth index (LTG) incorporating the standard deviations of liveweight and ultrasonically-measured fat depth as described by Simm et al.(1987) cited by Beatson (1987).

The data consist of 1153 performance records of both rams and ewes measured over the period 1985 to 1989 in 2 lines (line 1 being randomly selected control to represent the whole population and line 2 animals selected on LTG) The traits measured were autumn liveweight (ALW), autumn fat depth (AFD), winter liveweight (WLW) and winter fat depth (WFD) for the whole period (1985 to 1989), and autumn and winter muscle depths (AMD and WMD respectively) were measured in 1988 and 1989. Prior to 1988, animals were selected on an index combining data for liveweight and fat depth measured in the winter, subsequently muscle depth was incorporated into the index (Logan, pers. comm). The aggregate breeding value associated with both indices used above comprised lean weight plus fat weight with positive and negative weightings respectively. The winter index was used as selection criterion (Beatson, 1986). Analyses will mostly consider selection on the basis of liveweight and fat depth .

There were fewer winter measurements in 1989 than in other years because animals were culled prior to winter that year due to feed shortages (Logan, Pers. Comm). Prior to 1986 only rams were selected from the base population but from 1986 autumn mating season onwards the lines were established and maintained separately, so that the first animals born in line were those born in spring 1986 (Beatson, 1986). After establishment of lines, the selected line has been larger than the control line (Table 4).

Replacement ewes were selected on the same basis as rams. However at establishment of the lines mixed age ewes from the base population were randomly allocated to each line. For 1986 mating the LTG 2-T ewes selected were 0.30 index units superior to C 2-T (0.27 compared to -0.30 for 2-T C). However, the 2-T rams in the LTG were 0.62 index units superior to the 2-T C rams (0.71 compared to 0.09 for 2-T C). In 1987 the 2-T LTG rams were 0.83 index units superior (0.90 compared to 0.09 for C 2-T). Rams were used as 2-T for only one season (generation interval = 2 years) while the mean weighted age of ewes was 3.8 years (mean generation interval = 3.8 years).

Table 3:   Mean Winter LTG Index values (Standard deviations) for ewes and rams in the
selection and control lines - Dorset Downs 1986. (Adapted from Beatson, 1986).

	Whole Flock	Selected Line	Control Line
Ewes	-0.04 (.65)	0.27 (0.39)	-0.03 (0.60)
Rams	-0.03 (.62)	0.71 (0.43)	0.09 (0.60)

Table 4:   Number of animals measured in each line for each measurement per year.
Line 1 = control & 2 = selected

Year	n/Line		MEASUREMENT	n/both lines
	Control	Selected		
85	252	0	ALW	252
	251	0	AFD	251
	200	0	WLW	200
	200	0	WFD	200
86	213	0	ALW	213
	161	0	WFD	161
	186	0	WLW	186
	188	0	WFD	188
87	80	131	ALW	211
	80	130	AFD	210
	78	127	WLW	205
	78	127	WFD	205
88	99	157	ALW	256
	99	157	AFD	256
	99	157	AMD	256
	84	113	WLW	197
	84	113	WFD	197
	84	113	WMD	197
89	89	132	ALW	221
	89	132	AFD	221
	89	132	AMD	221
	35	52	WLW	87
	35	52	WFD	87
	35	52	WMD	87

For the 5 years (1985 to 1989) of data used here, there were 57 sire families with an average of 19.8 progeny per sire(Table 5). In most years the age of dam ranged from 2 to 8 years old, with few younger than 2 or older than 6 years dams (Table 6). The majority of animals were born and reared as singles or twins (Tables 7 and 8). About the same number of females and males were performance tested each year (Table 9).

3.1.2 Data Sets

The traits analysed were ALW, AFD, AMD, WLW, WFD and WMD for both ewes and rams. All autumn traits (ALW, AFD and AMD) were measured in mid April (Approximately 9 months old) and winter traits (WLW, WFD and WMD) at the end of July (approximately 12 months old).

All tissue traits (AFD, WFD, AMD and WMD) were measured using a Real Time Ultrasound Scanner Model Aloka 210DIIX (Logan Pers. Comm). These were measured at the 12th rib as shown below (Figure 1). These positions were chosen because they are anatomically easy to identify (Logan, Pers. Comm).

Eight data sets were derived from the 1153 records available because not all traits were measured in both autumn and winter and for the whole period. Details of these eight data sets are shown in Table 10.

3.1.3 Data analysis

All data sets were analysed using Least Squares methodology to allow for uneven numbers of observations (progeny) in sub-groups. Mixed models were fitted using The LSML76 Computer program developed by Harvey (1977).

Model type 7 was fitted to test the significance of fixed effects (Year, line nested within year, sire nested within line and year, Age of dam, Birth and Rearing ranks) and a covariate (date of birth) for appropriate data sets. Model type 7 also gave estimates of heritability, genetic and phenotypic correlations of all traits .

The full type 7 model fitted was as follows:

$$Y_{ijklmno} = U + Year_j + Line/Year_{ij} + Sire/Line/Year_{ijk} + AOD_l + BB_m + RR_n + DOB_{ijklmno} + E_{ijklmno}$$

Figure 1. Cross-section of a carcass cut transversely at the 12th rib showing the sites at which subcutaneous fat depth (C) and depth of the longissimus dorsi (B) were measured by ultrasound.
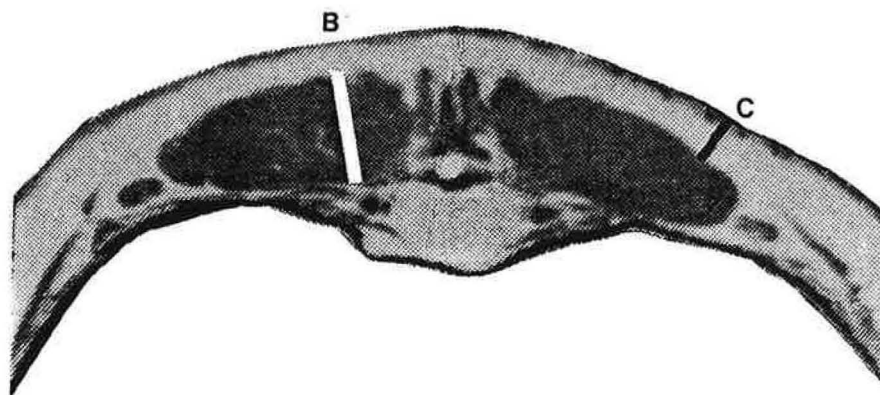
Table 5:   Number of progeny per sire.

Sire ID	Number of progeny
790013	27
790051	51
820164	1
830005	9
830008	25
830012	25
830030	15
830033	20
830036	17
830061	24
830071	18
830077	12
830141	4
830161	31
830165	11
840017	32
840020	21
840037	13
840055	37
840084	42
840101	14
840137	20
840180	7
840186	22
840196	10
840214	16
840216	15
840236	12
840239	28
840252	20
840269	20
840276	35
840307	21
840308	12
850048	14
850050	15
850053	16
850084	17
850087	19
850089	29
850149	19
850158	28
850169	22
850173	17
850193	43
850220	21
860005	11
860013	12
860033	16
860039	12
860047	17
860076	20
860108	13
860167	18
860219	21
860263	24
860271	18

Number of sire families	=	57
Mean sire family size	=	19.81
Std deviation of sire family size	=	9.39

Table 6:   Distribution of dam age groups in each year.

| | | | | AGE OF DAM (years) | | | | | | | |
Year	1	2	3	4	5	6	7	8	9	10	ALL
85	1	49	66	52	38	21	14	7	1	1	250
86	0	45	54	65	32	14	0	0	0	0	210
87	0	55	44	38	51	21	0	0	0	0	209
88	0	57	58	49	35	40	12	0	0	0	251
89	0	57	35	55	34	23	17	0	0	0	221
ALL	1	263	257	259	190	119	43	7	1	1	1141

Weighted average age of dam 3.8 years

Table 7:   Birth rank of measured animals.
            1 = SINGLE; 2 = TWINS & 3 = TRIPLETS

| Year | Birth Rank | | | |
	1	2	3	ALL
85	76	173	3	252
86	58	149	6	213
87	80	128	3	211
88	87	164	5	256
89	86	135	0	221

Table 8:   Rearing rank of measured animals.
            1 = SINGLE; 2 = TWINS & 3 = TRIPLETS

| Year | Rearing Rank | | | |
	1	2	3	ALL
85	114	138	0	252
86	90	117	3	210
87	98	111	2	211
88	100	151	5	256
89	103	117	0	220
ALL	505	634	10	1149

Table 9:   Sex distributions of animals measured.
            1 = RAMS & 2 = FEMALES

| Year | SEX | | |
	1	2	ALL
85	117	135	252
86	101	112	213
87	102	109	211
88	129	127	256
89	102	119	221
ALL	551	602	1153

Table 10: Description of the different data sets used in the analyses described in the text.

| Characteristics | IDENTIFICATION CODE | | | | | | | |
	a	b	c	d	e	f	g	h
Traits in set	ALW, AFD	ALW, AFD and AMD	ALW, AFD WLW, WFD	ALW, AFD, AMD, WLW, WFD, WMD	ALW and AFD	ALW, AFD and AMD	ALW, AFD WLW, WFD	ALW, AFD, AMD, WLW, WFD,WMD
No. of observations (n)	489	223	388	170	584	241	422	106
Sex	Rams	Rams	Rams	Rams	Ewes	Ewes	Ewes	Ewes
Years	1985-1989	1988-1989	1985-1989	1988-1989	1985-1989	1988-1989	1985-1989	1988

where:

$Y_{ijklmno}$	=	observation trait of individual specified by subscripts
U	=	population mean for that trait
$Year_i$	=	Year individuals trait was measured
$Line/Year_{ij}$	=	Line nested within year of individual
$Size/line/Year_{ijk}$	=	sire nested with year and line of individual
AOD_l	=	Age of dam of individual
BR_m	=	Birth rank of individual
RR_n	=	Rearing rank of individual
$DOB_{ijklmno}$	=	Date of birth of individual
$E_{ijklmno}$	=	random error associated with observation assumed to be normally and independently distributed with mean of zero.

Model type 3 was fitted to each data set using The LSML76 computer programme developed by Harvey (1977) to estimate the least squares means (phenotypic means) of the following effects: line nested within year, year, age of dam, birth and rearing rank and one covariate (date of birth) for all traits.

The model type 3 fitted was as follows:

$$Y_{ijklmn} = Year_i + line/Year_{ij} + AOD_k + BR_l + RR_m + DOB_{ijklmn} + E_{ijklmn}$$

where:

Y_{ijklmn}	=	observation trait of individual specified by subscripts
$Year_i$	=	Year individual's trait was measured
$Line/year_{ij}$	=	Line nested within year of individual
AOD_k	=	Age of dam of individual
BR_l	=	Birth rank of individual
RR_m	=	Rearing rank of individual
DOB_{ijklmn}	=	Date of birth of individual
E_{ijklmn}	=	random error associated with observation assumed to be normally and independently distributed with mean of zero

All reported results are based on paternal halfsibs.

3.2 Results

3.2.1 Significant fixed and covariate effects

Significant effects presented in Tables 11A and 11B were from the largest data sets (largest n) for each variable (Table 10). Year was significant ($P<0.05$) for most variables, the exception being ram AMD, ewe AMD and all ewe winter variables. The only significant interaction was LINE * YEAR for ram AFD (Table 11A).

Correction factors for statistically significant effects detailed in Table 11A are given in Table 11B. The correction factors were larger and more variable for year than for other significant fixed effects. The magnitude of the correction factors for year were larger in the ram data than in the ewe data for autumn liveweight. AOD and BR were both significant for ewe and ram ALW, and AOD was also significant for ewes WLW. DOB was significant for all rams and ewes variables except rams WFD and WMD. Ewes and rams from older ewes (3 years old and older) were heavier than those from younger ewes, while ewes and rams born as singles were heavier than twins (Table 11B). Correction factors for date of birth were similar in magnitude for ewes and rams for liveweight and fat depth (Table 11B).

3.2.2 Response to selection

In order to examine responses to selection results are presented from the largest data set of each trait. In rams most Year/line means were not significantly different within year except WFD, whereas in ewes all were significantly different except WFD (Table 12). These results are presented graphically in Figures 2A to 7.Where significant differences occurred between Year/line means (phenotypic means), the selected line was heavier and had less fat depth than control line (Figures 5A, 6A and 6B). The lack of significant differences in some phenotypic means is expected since these data are from the early stages of the selection programme, with greater divergence being expected in later stages.

Regression of the differences between line means (selected minus control) on time showed average rates of responses to selection in components traits. In rams the responses were 0.489 and 0.321 kg/year in autumn and winter for liveweight, -0.2 and -0.3 mm/year in autumn and winter for fat depth; and correlated responses were -0.1 and -0.3 mm/year in autumn and winter for muscle depth. In ewes, responses were 0.649 and 0.856 kg/year in autumn and winter for liveweight , and -0.1 and -0.3 mm/year for autumn and winter for fat depth. There is no ewe WMD because ewes were culled before winter due to feed shortages (Logan, pers.comm.).

Table 11A: Significant fixed effects and covariates for each variable.
              n = number of observations used in model.

Significant effects (P<0.05)	RAMS' MODELS						EWES' MODELS					
	ALW	AFD	AMD	WLW	WFD	WMD	ALW	AFD	AMD	WLW	WFD	WMD
	YEAR (n=489)	YEAR (n=489)		YEAR (n=388)	YEAR (n=388)	YEAR (n=170)	YEAR (n=584)	YEAR (n=584)		AOD (n=422)		
Fixed	AOD (n=489)	-	-	-		-	AOD (n=584)	-	-	-	-	-
	BR (n=489)	-	-	-	-	-	BR (n=584)	-	-	-	-	-
Covariates	DOB (n=489)	DOB (n=489)	DOB (n=223)	DOB (n=388)	-	-	DOB (n=584)	DOB (n=584)	DOB (n=241)	DOB (n=422)	DOB (n=422)	DOB (n=106)
Interaction	-	LINE X YEAR (N=489)	-	-	-	-	-	-	-	-	-	-

20

Table 11B: Correction factors for significant fixed and covariates effects for each variable (P < 0.05)
  -/+ before a number means that the number is either that magnitude below or above the "population" mean.

Significant effect		CORRECTION FACTORS FOR RAM'S MODELS						CORRECTION FACTORS FOR EWE'S MODELS					
		ALW (Kg)	AFD (mm)	AMD (mm)	WLW (Kg)	WFD (mm)	WMD (mm)	ALW (Kg)	AFD (mm)	AMD (mm)	WLW (Kg)	WFD (mm)	WMD (mm)
	YEAR												
	85	-1.97	-0.63	-	+0.40	-0.30	-	-0.14	-0.10	-	-	-	-
	86	-14.88	-2.01	-	-5.37	-0.39	-	-7.80	-1.93	-	-	-	-
Fixed	87	+3.05	+0.24	-	+4.06	+0.86	-	+2.16	+0.93	-	-	-	-
	88	+8.32	+1.37	-	+7.75	+1.78	+2.47	+2.11	+0.72	-	-	-	-
	89	+5.47	+1.04	-	-6.84	-1.95	-2.47	+3.86	-0.35	-	-	-	-
AOD 2		-0.61	-	-	-	-	-	-0.80	-	-	-1.01	-	-
3		+0.61	-	-	-	-	-	+0.80	-	-	+1.01	-	-
BR 1		+1.09	-	-	-	-	-	+0.82	-	-	-	-	-
2		-1.09	-	-	-	-	-	-0.82	-	-	-	-	-
Covariate DOB (/day)		-0.24 (linear)	-0.02 (linear)	-0.08 (linear)	-0.19 (linear)	-	-	-0.20 (linear)	-0.05 (linear)	-0.09 (linear)	-0.21 (linear)	-0.04 (linear)	-0.09 (linear)

<u>Figure 2.</u> Least squares line means (± sem) plotted against time for liveweight. Rams and ewes are compared in autumn (Figure 2A) and in winter (Figure 2B). These means are given in Table 12.

Fig 2A: Least squares means for autumn liveweight

Fig 2B: Least squares means for winter liveweight
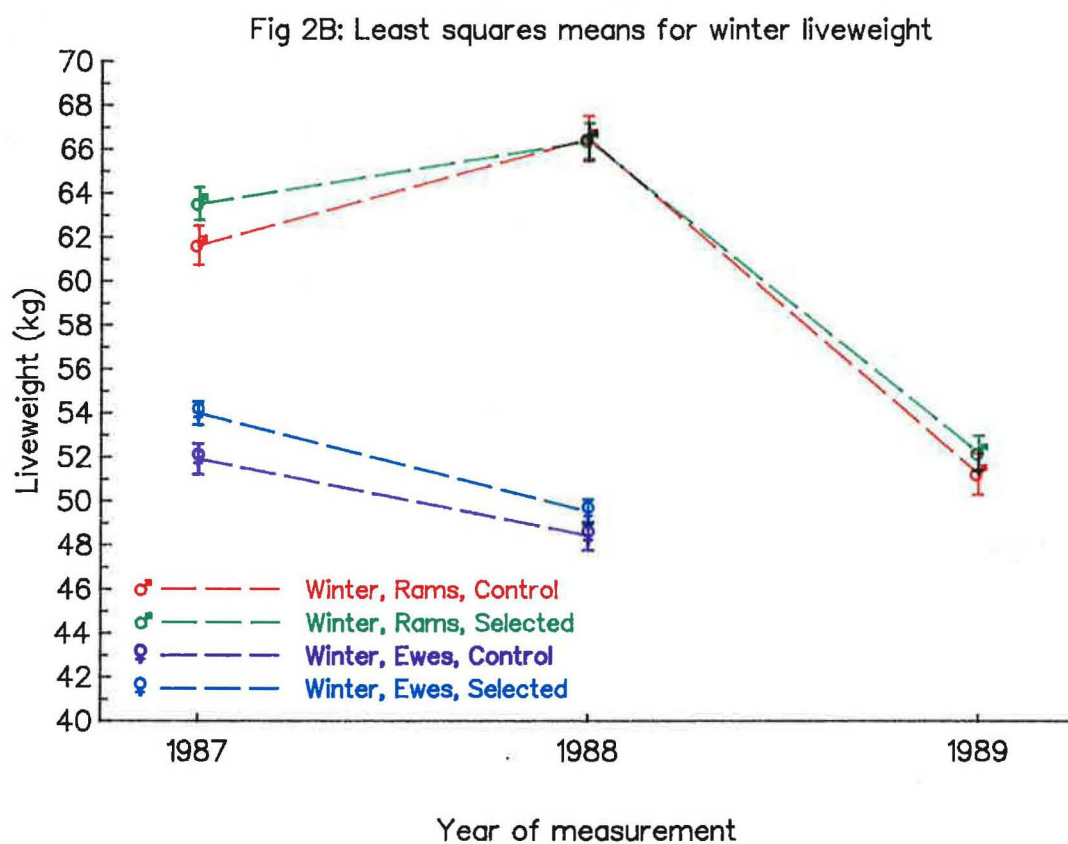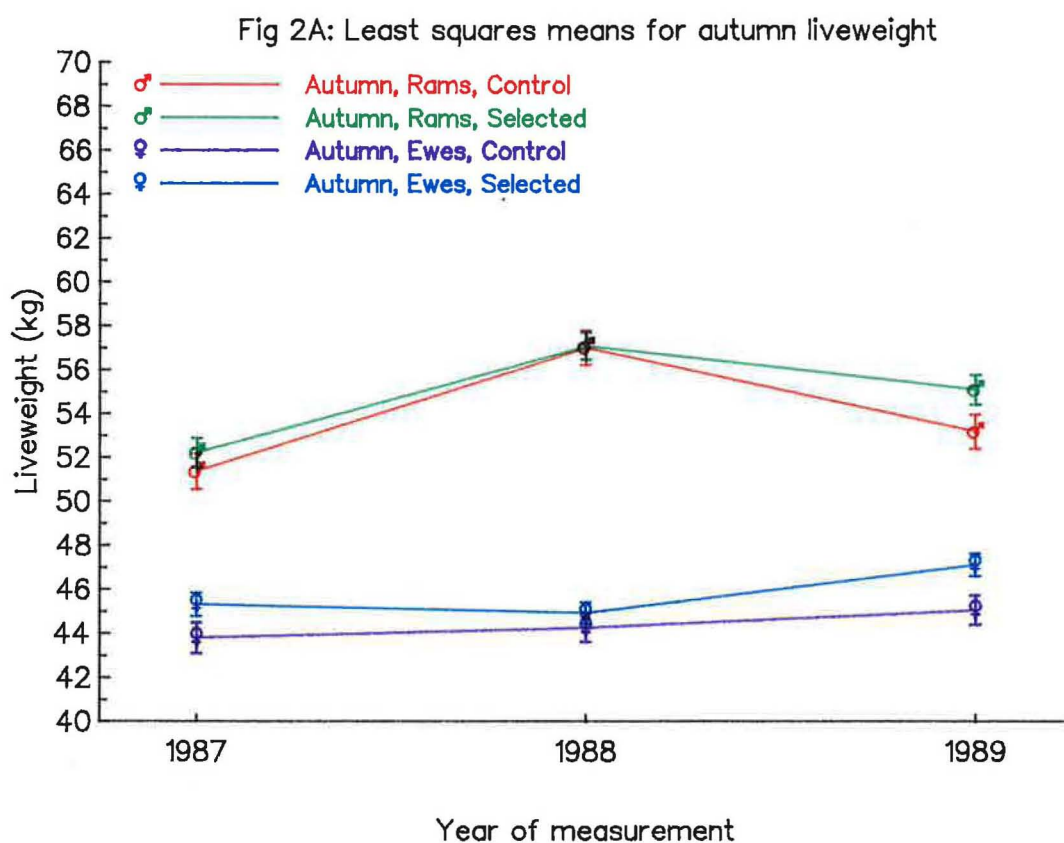
Figure 3. Least squares line means (± sem) plotted against time for fat depth. Rams and ewes are compared in autumn (Figure 3A) and in winter (Figure 3B). These means are given in Table 12.

Fig 3A: Least squares means for autumn fat depth

Fig 3B: Least squares means for winter fat depth
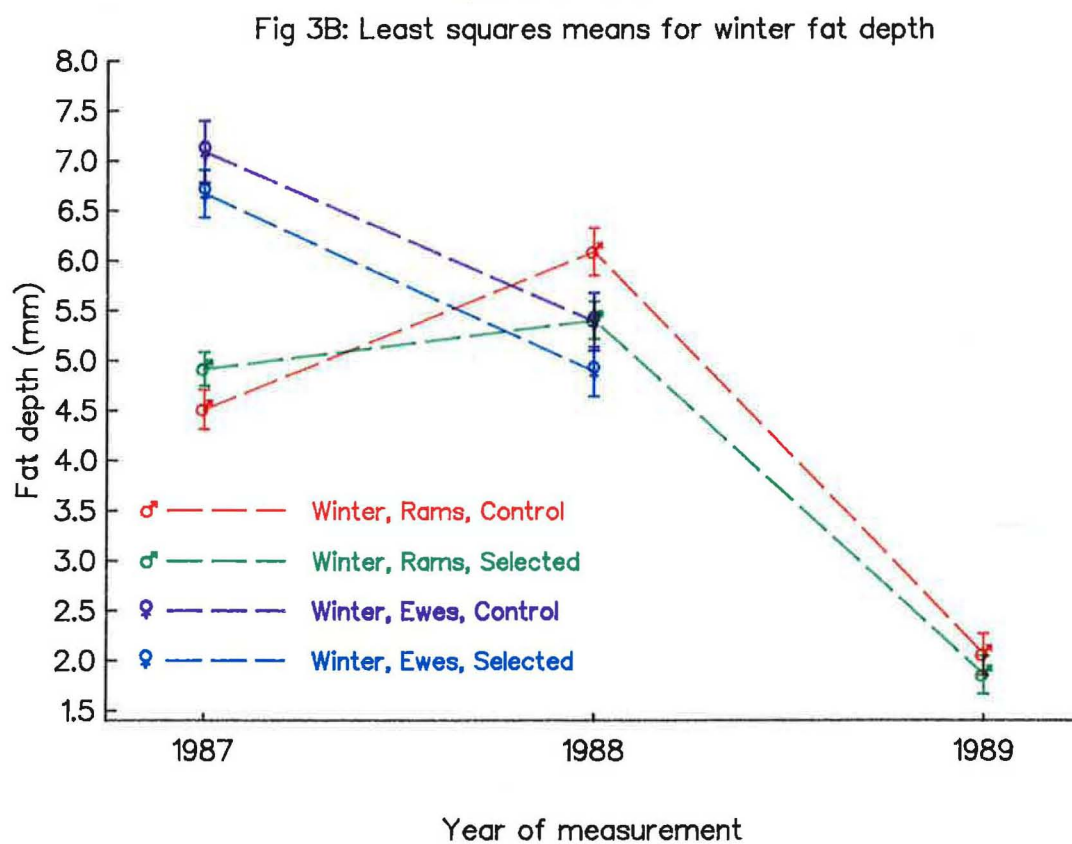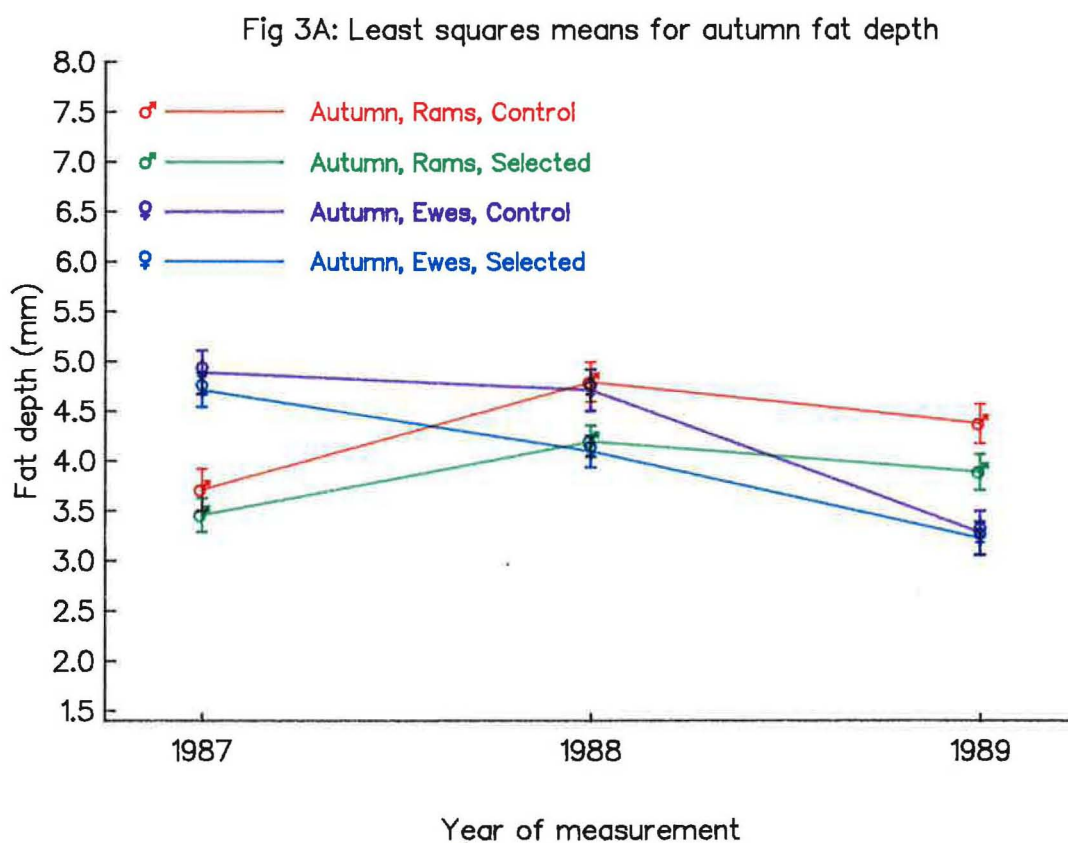
Figure 4. Least squares line means (± sem) plotted against time for muscle depth. Data are presented for rams in autumn (Figure 4A) and in winter (Figure 4B). Insufficient data were available for ewes to make a comparison. These means are given in Table 12.

Fig 4A: Least squares means for autumn muscle depth

Fig 4B: Least squares means for winter musle depth
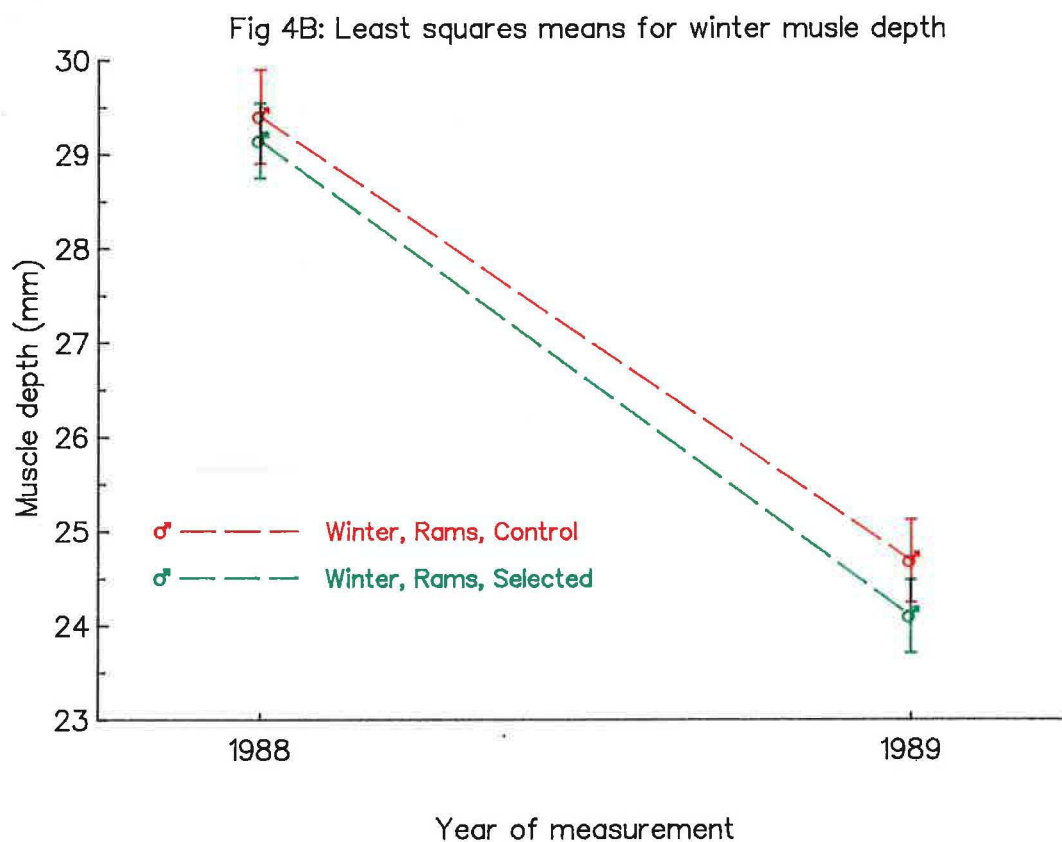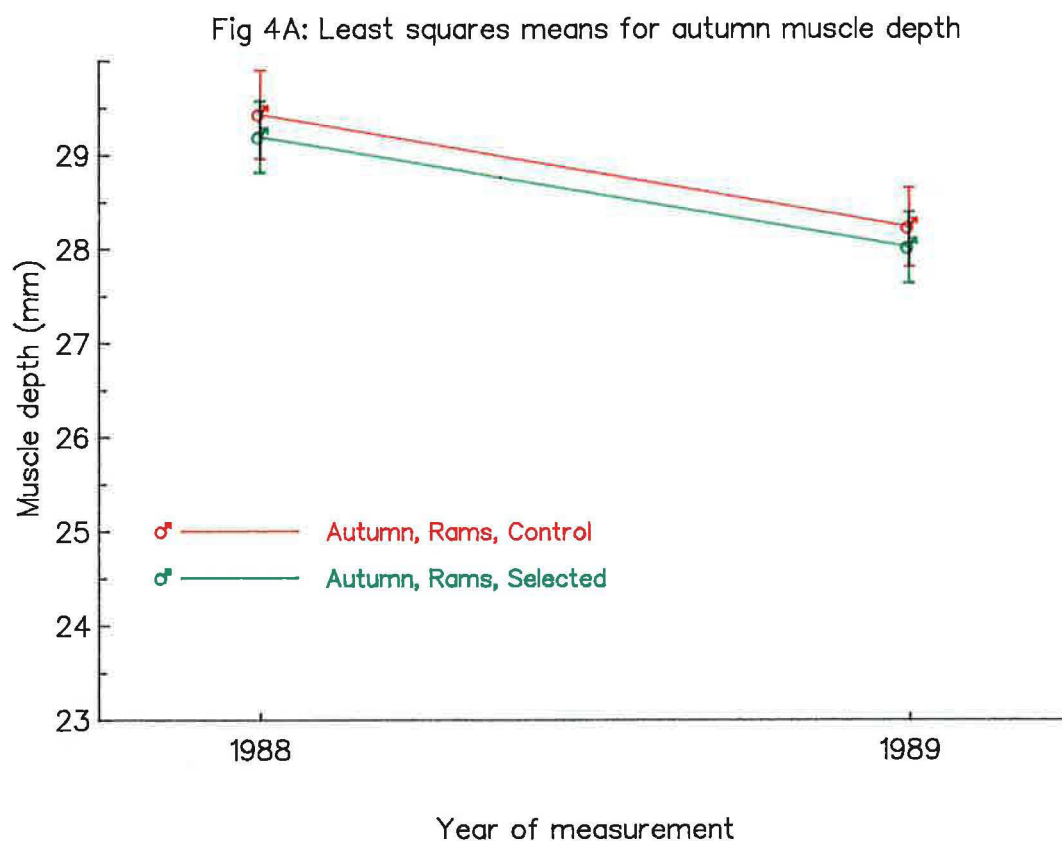
Figure 5. Least squares line means (± sem) plotted against time for liveweight. Autumn and winter data are compared for rams (Figure 5A) and for ewes (Figure 5B). These means are given in Table 12.

Fig 5A: Least squares means for liveweight — rams

♂ ——— Autumn, Rams, Control
♂ ——— Autumn, Rams, Selected
♂ ——— Winter, Rams, Control
♂ ——— Winter, Rams, Selected

Year of measurement

Fig 5B: Least squares means for liveweight — ewes

♀ ——— Autumn, Ewes, Control
♀ ——— Autumn, Ewes, Selected
♀ ——— Winter, Ewes, Control
♀ ——— Winter, Ewes, Selected

Year of measurement
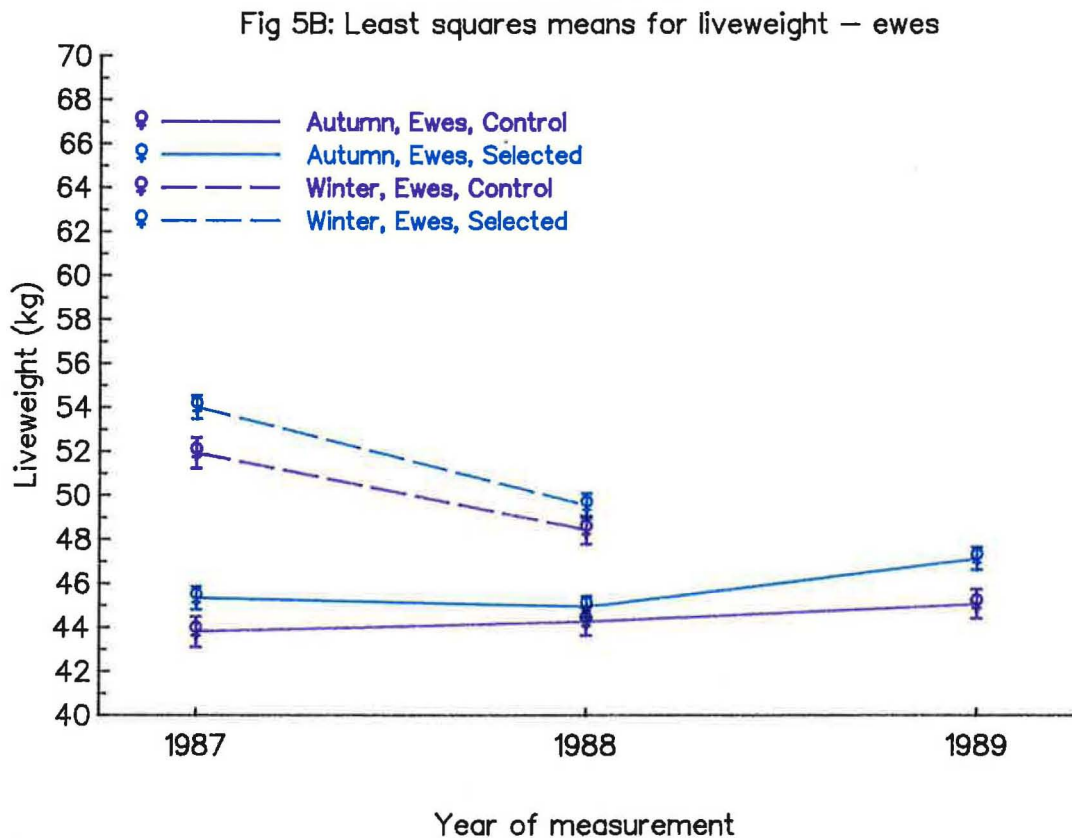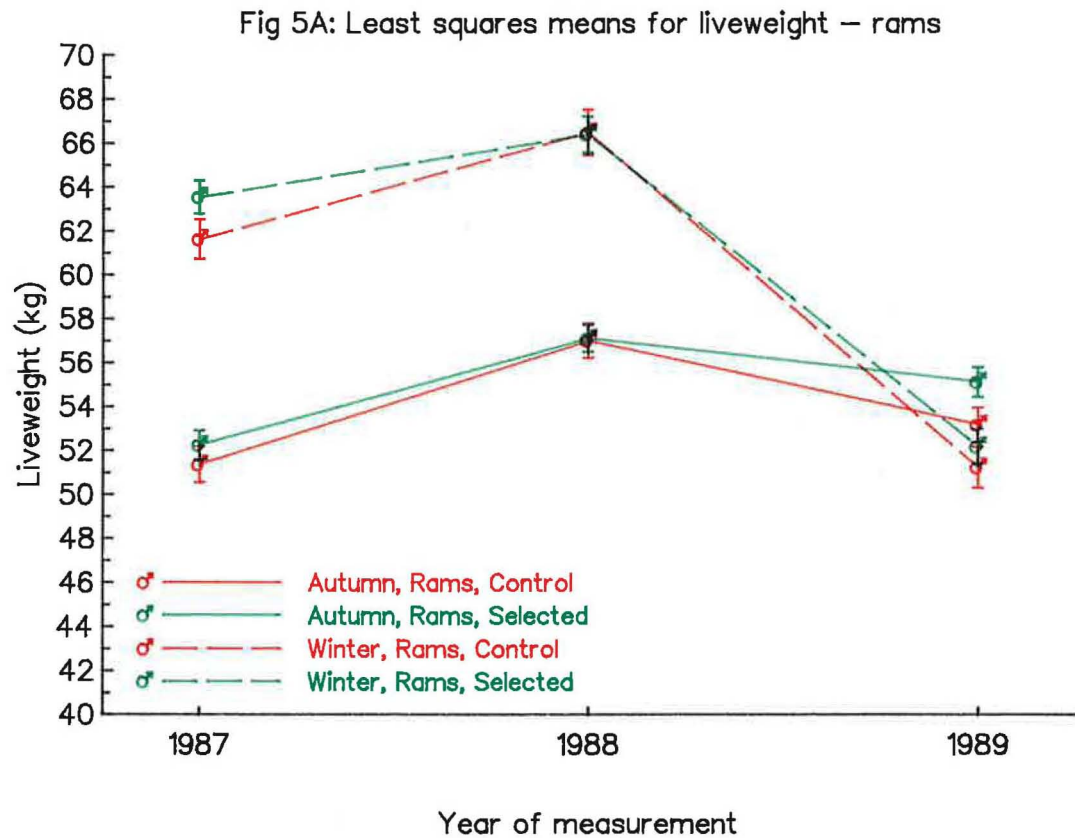
Figure 6. Least squares line means (± sem) plotted against time for fat depth. Autumn and winter data are compared for rams (Figure 6A) and for ewes (Figure 6B). These means are given in Table 12.

Fig 6A: Least squares means for fat depth — rams

Year of measurement

Fig 6B: Least squares means for fat depth —ewes

Year of measurement
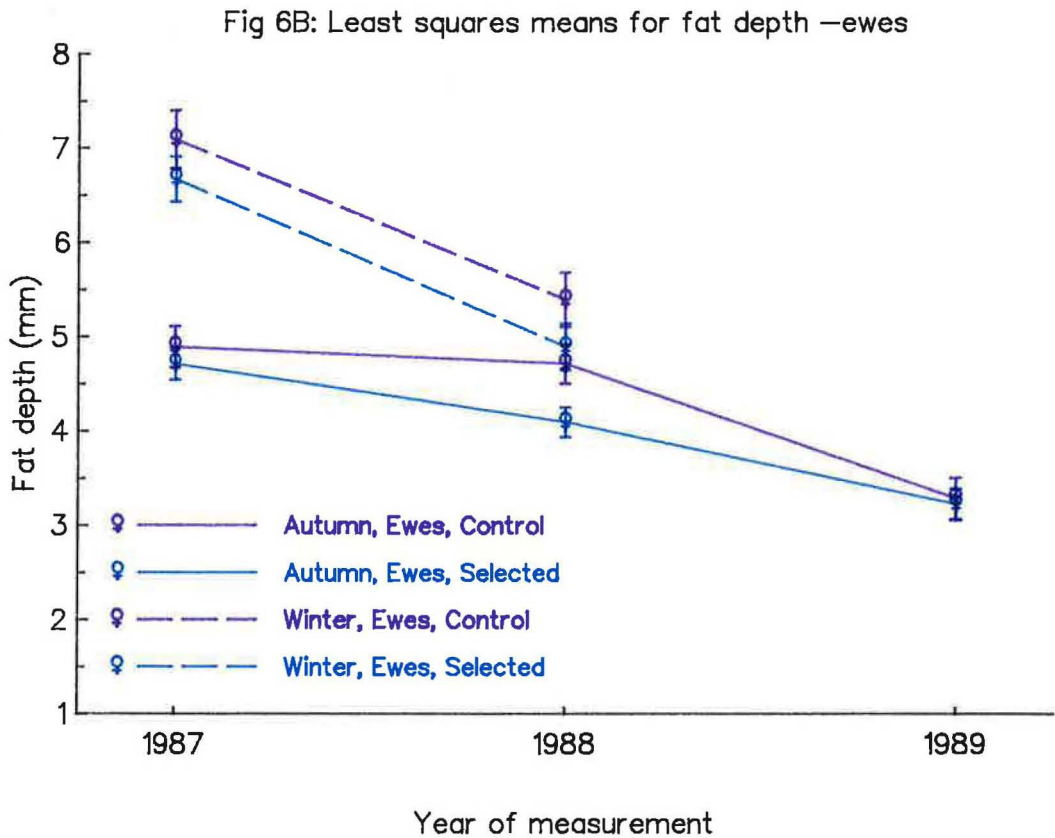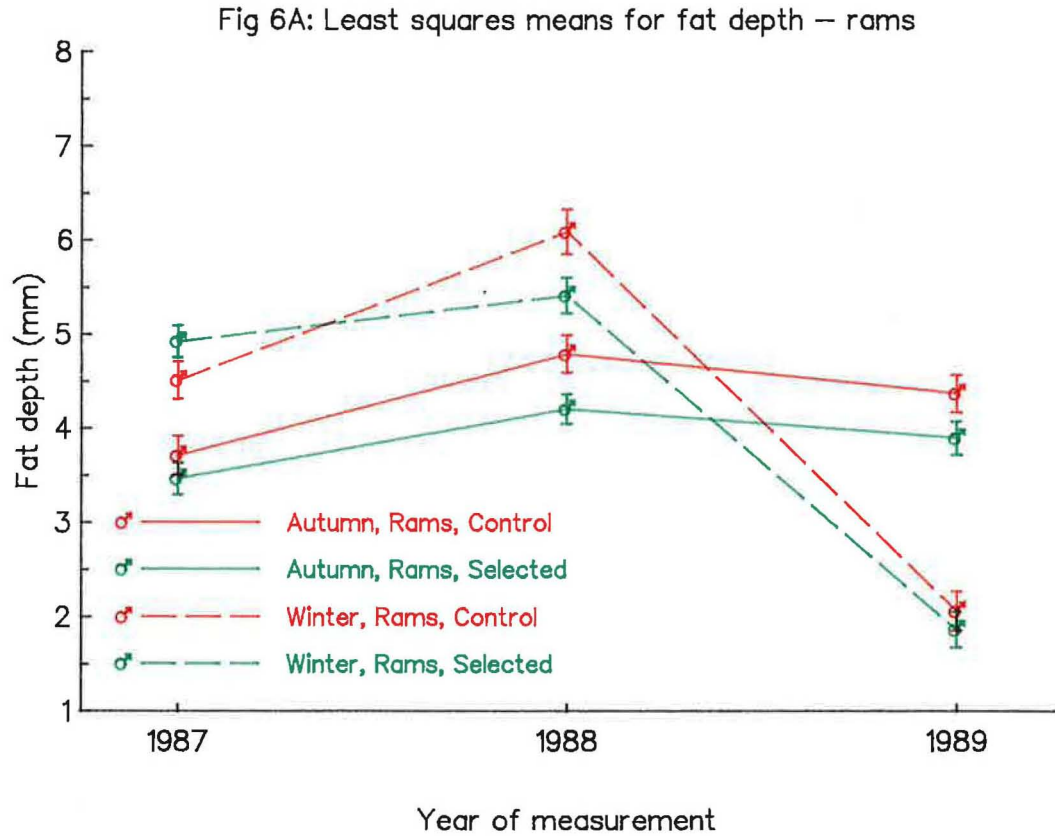
Figure 7. Least squares line means (± sem) plotted against time for muscle depth. Autumn and winter data are compared for rams only. Insufficient data were available for ewes to make the same comparison. These means are given in Table 12.

Fig 7: Least squares means for muscle depth — rams
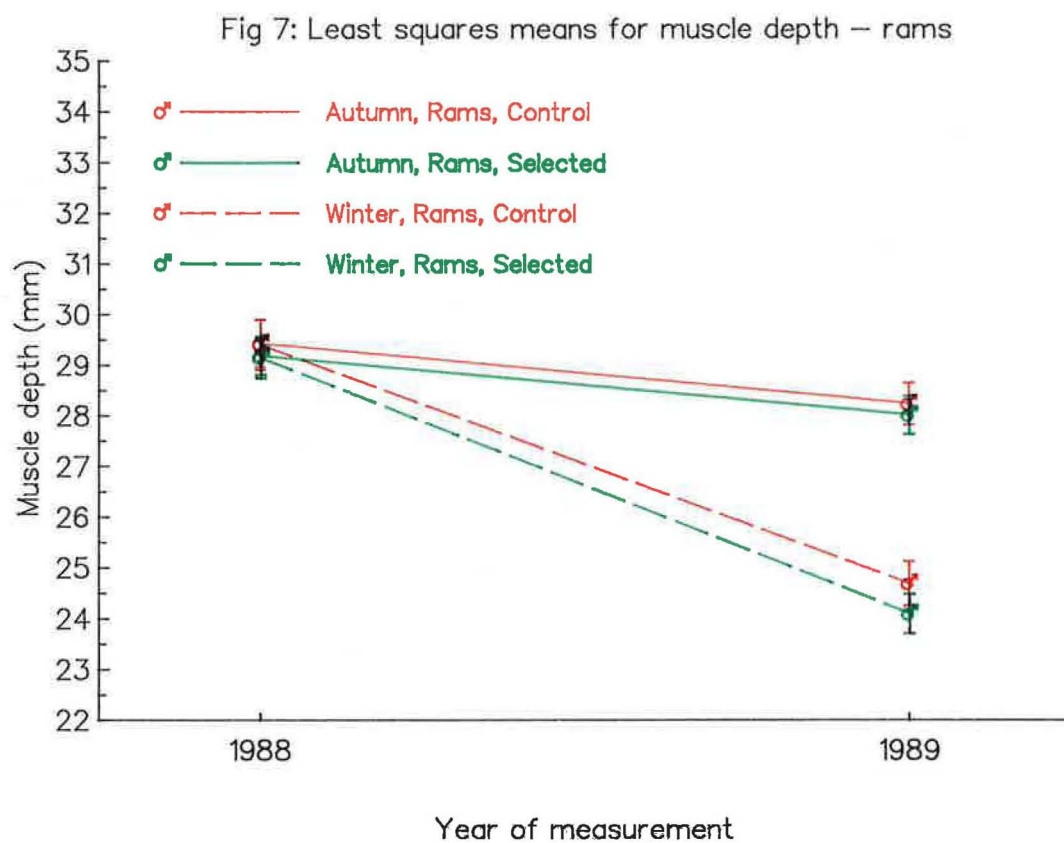
Table 12: YEAR/LINE Least Squares means (± SE). These results are also presented graphically on Figures 2A to 7

VARIABLE			RAMS		EWES	
	YEAR	LINE	LS MEANS	LINE	LS MEANS	LINE
ALW	87	1	51.36 ± 0.82 (n=41)		43.79 ± 0.70 (n=38)	
		2	52.23 ± 0.67 (n=59)		45.32 ± 0.53 (n=70)	
	88	1	57.01 ± 0.79 (n=44)	NS	44.26 ± 0.64 (n=47)	**
		2	57.10 ± 0.62 (n=78)		44.93 ± 0.49 (n=79)	
	89	1	53.18 ± 0.79 (n=42)		45.06 ± 0.67 (n=42)	
		2	55.11 ± 0.69 (n=59)		47.13 ± 0.52 (n=73)	
AFD	87	1	3.71 ± 0.21 (n=41)		4.89 ± 0.22 (n=38)	
		2	3.46 ± 0.17 (n=59)		4.71 ± 0.17 (n=70)	
	88	1	4.79 ± 0.20 (n=44)	**	4.71 ± 0.21 (n=47)	**
		2	4.20 ± 0.16 (n=78)		4.09 ± 0.16 (n=79)	
	89	1	4.37 ± 0.20 (n=42)		3.28 ± 0.22 (n=42)	
		2	3.89 ± 0.18 (n=59)		3.22 ± 0.17 (n=73)	
AMD	87	1				
		2				
	88	1	29.43 ± 0.47 (n=30)			
		2	29.19 ± 0.38 (n=54)	NS		
	89	1	28.23 ± 0.42 (n=34)			
		2	28.01 ± 0.38 (n=52)			
WLW	87	1	61.63 ± 0.90 (n=40)		51.92 ± 0.70 (n=37)	
		2	63.53 ± 0.75 (n=56)		54.00 ± 0.54 (n=70)	**
	88	1	66.50 ± 1.04 (n=30)	NS	48.42 ± 0.65 (n=47)	
		2	66.39 ± 0.82 (n=54)		49.52 ± 0.57 (n=59)	
	89	1	51.24 ± 0.94 (n=34)			
		2	52.18 ± 0.81 (n=52)			
WFD	87	1	4.51 ± 0.20 (n=40)		7.09 ± 0.31 (n=37)	
		2	4.92 ± 0.17 (n=54)		6.67 ± 0.24 (n=70)	NS
	88	1	6.09 ± 0.24 (n=30)	NS	5.39 ± 0.29 (n=47)	
		2	5.41 ± 0.19 (n=54)		4.89 ± 0.25 (n=59)	
	89	1	2.06 ± 0.21 (n=34)			
		2	1.86 ± 0.19 (n=52)			
WMD	88	1	29.40 ± 0.50 (n=30)			
	89			NS		

NS = non-estim

Rams were heavier than ewes in both autumn and winter (Figures 2A and 2B). However, fat depth data did not show clear sex differences. In 1987 ewes had more fat depth in both autumn and winter, the following year there were no difference between the sexes both in autumn and winter while in 1989 the rams had more fat depth in autumn but ewes were not performance tested in winter that year (Figures 3A and 3B). For all sex-line combinations on average animals were heavier and had greater fat depth in winter than in autumn, with the exception of rams in 1989 (Figures 5A - 6B). In 1988 the rams had similar muscle depth in autumn and winter but in 1989, autumn muscle depth was 13% more than that of winter (Figure 7). In 1989 rams lost 4.5% liveweight, with associated reductions in fat depth (53%) and muscle depth (13%) between autumn and winter (Figures 5A, 6A ,7).

3.2.3 Genetic variation

Heritabilities, genetic and phenotypic correlations for all variables varied considerably depending on the data set used, with the exception of AFD for both sexes. Heritability of AFD had less variation within sex than between sex, with ram's being the higher of the two (Table 13A and 13B). "Best" (most accurate) heritabilities, genetic and phenotypic correlations from Tables 13A and 13B are summarised in Tables 13C and 13D. These were from the largest data set for each analysis which in almost all cases had the lowest standard error .

Heritabilities were high (> 0.30) for ALW, AMD and WLW, moderate (0.10 - 0.30) for AFD and WFD and low (< 0.10) for WMD for rams (Table 13C), and were medium for ALW, AMD and WLW, low for AFD and WFD and non-estimable for WMD for ewes (Table 13D). While the heritability of liveweight and muscle depth was higher in winter than autumn for rams, the opposite was true for liveweight in ewes. Heritability of fat depth was similar for both autumn and winter within sex (Table 13C and 13D).

For both sexes all phenotypic correlations between traits within a time period were low (less than 0.50) both in autumn and winter (Tables 13C and 13D). These phenotypic correlations were of similar magnitude for rams and ewes, with exception of of those between ALW and AMD, WMD and WLW, and WMD and WFD (Tables 13C and 13D).

The only high phenotypic correlation (more than 0.60) between autumn and winter was for liveweight in both sexes, with other correlations being low. All other phenotypic correlations were of similar magnitude for most traits between autumn and winter, with the exception of ALW and WLW, ALW and AMD, WMD and AMD, and WMD and WLW (Tables 13C and 13D).

Table 13A: Heritabilities (h^2) (± SE), genotypic (r_G) (± SE) and phenotypic (r_p) correlations of variables from different data sets for rams.

VARIABLE			DATA SET			
	X	Y	a	b	c	d
h^2	ALW	-	0.39 ± 0.15	0.86 ± 0.29	0.29 ± 0.16	0.92 ± 0.33
	AFD	-	0.21 ± 0.13	0.24 ± 0.20	0.21 ± 0.25	0.26 ± 0.25
	AMD	-	-	0.38 ± 0.22	-	0.30 ± 0.25
h^2	WLW	-	-	-	0.52 ± 0.19	0.59 ± 0.29
	WFD	-	-	-	0.19 ± 0.15	0.39 ± 0.27
	WMD	-	-	-	-	0.01 ± 0.20
r_G	ALW	AFD	0.38 ± 0.33	0.52 ± 0.36	0.38 ± 0.44	0.64 ± 0.38
	ALW	AMD	-	0.67 ± 0.27	-	0.88 ± 0.33
	AFD	AMD	-	0.40 ± 0.48	-	0.93 ± 0.34
r_G	WLW	WFD	-	-	0.67 ± 0.34	0.96 ± 0.30
	WLW	WMD	-	-	-	2.55 ± 41.75
	WFD	WMD	-	-	-	3.97 ± 66.10
r_G	ALW	WLW	-	-	0.91 ± 0.13	1.06 ± 0.09
	AFD	WFD	-	-	0.61 ± 0.42	0.97 ± 0.29
	AMD	WMD	-	-	-	7.26 ± 121.75
r_p	ALW	AFD	0.34	0.36	0.37	0.39
	ALW	AMD	-	0.34	-	0.37
	AFD	AMD	-	0.34	-	0.57
r_p	WLW	WFD	-	-	0.33	0.36
	WLW	WMD	-	-	-	0.41
	WFD	WMD	-	-	-	0.23
r_p	ALW	WLW	-	-	0.70	0.72
	AFD	WFD	-	-	0.46	0.59
	AMD	WMD	-	-	-	0.48

Data set   a: n=489
            b: n=223
            c: n=388
            d: n=170

Table 13B: Heritabilities (h^2) ($\pm$ SE), genotypic (r_G) ($\pm$ SE) and phenotypic (r_P) correlations of variables from different data sets for ewes.

VARIABLES			DATA SET			
	X	Y	e	f	g	h
h^2	ALW	-	0.22 ± 0.11	0.35 ± 0.21	0.17 ± 0.13	0.46 ± 0.35
	AFD	-	0.05 ± 0.09	0.09 ± 0.15	0.06 ± 0.11	0.14 ± 0.27
	AMD	-	-	0.05 ± 0.15	-	NE
h^2	WLW	-	-	-	0.12 ± 0.12	0.19 ± 0.28
	WFD	-	-	-	0.24 ± 0.14	0.04 ± 0.24
	WMD	-	-	-	-	NE
r_G	ALW	AFD	0.79 ± 0.76	1.42 ± 1.03	0.66 ± 0.72	1.48 ± 0.93
	ALW	AMD	-	1.51 ± 1.64	-	NE
	AFD	AMD	-	0.44 ± 1.45	-	NE
r_G	WLW	WFD	-	-	0.80 ± 0.48	1.81 ± 3.96
	WLW	WMD	-	-	-	NE
	WFD	WMD	-	-	-	NE
r_G	ALW	WLW	-	-	0.73 ± 0.29	1.02 ± 0.20
	AFD	WFD	-	-	0.61 ± 0.58	2.32 ± 5.46
	AMD	WMD	-	-	-	NE
r_P	ALW	AFD	0.32	0.31	0.28	0.48
	ALW	AMD	-	0.45	-	0.37
	AFD	AMD	-	0.33	-	0.40
r_P	WLW	WFD	-	-	0.30	0.51
	WLW	WMD	-	-	-	0.52
	WFD	WMD	-	-	-	0.48
r_P	ALW	WLW	-	-	0.82	0.86
	AFD	WFD	-	-	0.50	0.61
	AMD	WMD	-	-	-	0.42

Data set
e: n=584
f: n=241
g: n=422
h: n=106
NE = non-estimable

Table 13C: "Best" heritabilities (h^2) (± SE), genetic (r_G) (± SE) and phenotypic (r_P) correlations of variables for rams.
h^2 - bolded; r_P - above diagonal   and r_G - below diagonal

VARIABLE	VARIABLE					
	ALW	AFD	AMD	WLW	WFD	WMD
ALW	**0.39 a**	0.34 a	0.34 b	0.70 c	-	-
AFD	0.38 a	**0.21 a**	0.34 b	-	0.46 c	-
AMD	0.67 b	0.40 b	**0.38 b**	-	-	0.48 d
WLW	0.91 c	-	-	**0.52 c**	0.36 d	0.41 d
WFD	-	0.61 c	-	0.67 c	**0.19 c**	0.23 d
WMD	-	-	7.26 d	2.55 d	3.97 d	**0.01 d**

a: n=489
b: n=223
c: n=388
d: n=170

Table 13D: "Best" heritabilities (h^2) (± SE), genetic (r_G) (± SE) and phenotypic (r_P) correlations of variables for ewes.
h^2 - bolded; r_P - above diagonal   and r_G - below diagonal

VARIABLE	VARIABLE					
	ALW	AFD	AMD	WLW	WFD	WMD
ALW	**0.22 e**	0.32 e	0.45 f	0.82 g	-	-
AFD	0.79 e	**0.05 e**	0.33 f	-	0.50 g	-
AMD	1.51 f	0.44 f	**0.05 f**	-	-	0.42 h
WLW	0.73 g	-	-	**0.12 g**	0.30 g	0.52 h
WFD	-	0.61 g	-	0.80 g	**0.24 g**	0.48 h
WMD	-	-	NE h	NE h	NE h	NE h

Data set   e: n=584
f: n=241
g: n=422
h: n=106
NE = NON-ESTIMABLE

For rams the only high (more than 0.60) genetic correlation in autumn was between ALW and AMD, all other correlations were low (less than 0.50). In winter the only high genetic correlation was between WLW and WFD, and all other genetic correlations were nonsensical (more than 2.50). The nonsensical genetic correlations were between muscle depth and other traits (Table 13C). For ewes, genetic correlations in autumn were high between ALW and AFD, low between AFD and AMD, and nonsensical (more than 1.50) between ALW and AMD. In winter only WLW and WFD were highly genetically correlated, and all estimable genetic correlations were low. All genetic correlations involving muscle depth were non-estimable (Table 13D). Excluding genetic correlations involving muscle depth, genetic correlations for rams and ewes were similar in autumn and in winter but differences occurred between autumn and winter. In cases where genetic correlation differences were observed, consideration of the high standard errors preludes further discussion (13C and 13D). In both sexes all genetic correlation between autumn and winter were high, with the exception of those between WMD and other traits. All genetic correlations involving WMD were either nonsensical in rams or non-estimable in ewes. Genetic correlation errors were generally larger in ewes than rams (Tables 13C and 13D).

3.3 Discussion

3.3.1 Fixed and covariate effects

Significant effects presented in Table 11A are non-genetic (environmental) effects which influence the phenotype of animals. Non-genetic effects like AOD,BR and DOB have to be corrected for in calculating genotypic values (Gregory et al., 1978 cited by Fogarty and Luff, 1985; Eikje, 1975 cited by Warmington et al., 1986). Failure to correct for these non-genetic effects will reduce genetic progress because of inaccurate estimates of genotype values and consequently reduce the selection differential (Fogarty et al., 1985; Warmington et al., 1986).

Correction factors for all significant non-genetic effects presented in Table 11B have been previously observed (Fogarty et al., 1985; Warmington et al., 1986) although year effects were not reported by these authors. The magnitude of correction factors reported here are similar to those in other studies (Fogarty et al., 1985; Warmington et al., 1986). Most studies analyse data within year. Therefore they do not estimate between years' effects.The within year analysis compares contemporaries in a similar environment whereas between years analysis compares different animals in different environments. Despite correction factors for year not being reported in the literature, Warmington et al. (1986) observed that environmental effects were not always consistent across sex and birth year classes, and differed from some of those found in other studies. From these findings, these authors suggested that flock X year X sex specific adjustments would be advantageous when numbers of animals are sufficient to allow accurate estimation of such effects. In this study only year effects varied between sexes, with other environmental effects having similar effects on component traits. Consequently the analyses in this study are equivocal in supporting the conclusions of Warmington et al.(1989).

Year significantly affected both ALW and AFD for both sexes. This is likely to be due to nutrition primarily and other unmeasured environmental effects. Nutrition would be important in autumn especially after Canterbury's characteristically dry summers.Although, year is significant for WLW for rams, the correction factors are smaller than in autumn which seems to implicate nutrition again. This is further supported by drought years like 1989 when animals liveweight was 5.47kg above average in autumn but were 6.84kg below average in winter. A similar trend was evident for fat depth.

Both AOD and BR affected only ALW for both sexes, although AOD also affected WLW in ewes. These findings are consistent with other literature reports. Widdowson (1980) cited by Butterfield et al.(1983) reports that variation in body traits produced by non-genetic factors such as parity, litter size and size of mother are likely to be maximal at birth, considerable in early

post-natal life and least at maturity. Thus these animals had probably compensated for many of the fixed effects namely significant in sheep at young ages.

The correction factors were generally larger for rams than ewes in most components traits. This is hard to explain. But seems to be due to the relative higher growth rates of rams in good years than poor. Again 1989 is a good example.

Rams were heavier than ewes as expected. Warmington et al.(1986) attributed this difference to higher potential growth rates in rams and also to preferential feeding to prepare rams for sale. In this study the observed differences are likely to be due to higher growth rates but preferential feeding was not a management policy (Logan, Pers. Comm). However, as ewes and rams were grazed separately from late summer onwards each year, it is hard to believe that nutritional differences between ewes and rams could not occur.

3.3.2 Response to selection

Very few studies to date have reported responses to index selection in fat depth during the autumn and winter. The data reported in this study show variable sex differences. In one year (1987) ewes had more fat depth in both autumn and winter but the following year there was no difference between the sexes in both autumn and winter whereas in 1989 the rams had more fat in both autumn and winter. This may be partly explained by effects of nutrition. The percentage of fat in the body is increased when energy intake is raised to a high level relative to maintenance requirements and also fat increases as animals mature, that is fat increases as maturity increases (Wood, 1982). However, under pastoral grazing systems, feed intake is likely to be a limitation both in quality and quantity terms to growth or fatness. Therefore the animals are not likely to express their genetic potential for growth or fatness.

The data do not show significant changes in muscle depth and even suggest that it might have decreased very slightly. However, selection was on an index combining information for liveweight and fat depth till 1988 when muscle depth was incorporated in the index. Therefore, there was no direct selection on muscle depth for the parents of animals tested in this study. An increase in muscle depth in rams selected on an index combining information for liveweight, fat and muscle depths over control animals has been reported (Young, 1989). A new selection index is now in use for the flock in the present study combining information for liveweight, fat and muscle depths (Logan, Pers. Comm.). This new index should result in increases in muscle depth since it is similar to that used in the study reported by Young (1989).

The winter data of 1989 is of dubious value because of the drought that year. The drought caused animals to lose liveweight (4.5%) and have reduced fat (53%) and muscle (13%) depths

between autumn and winter. The high loss in fat depth (53%) would make it quite difficult to measure fat depth. This would further reduce the already low precision achieved in sheep because of their low levels of subcutaneous fat highlighted by Simm (1987). The increase in liveweight and fat depth between autumn and winter in other years represents growth.

Consideration of year/line means (termed phenotypic means here) shows desirable changes in response to selection, namely, increase in liveweight and reduction in fat depth of selected animals compared to controls. Theoretically this is what is meant to happen but results from other similar studies have been equivocal. For instance, Young (1989) reports decrease in fat depth but not increase in liveweight in animals selected on a similar index. The results from this study concur with those of Beatson (1989) who found that early results from selection for high lean tissue deposition may result in liveweight increase and fat loss. However, it is regrettable if despite the index selection resulting in the desired changes, muscle depth (which contributes quite substantially to lean growth) was really decreasing in the selected line. If indeed muscle depth is decreasing in the selected line then an index combining information for liveweight and fat depth should incorporate muscle depth since such a three trait index has been shown to increase muscle depth (Young, 1989). It must be borne in mind that the results reported here are from the early stages of this selection programme and therefore require verification at a later stage of the programme.

Regression of the differences between line means (selected minus control) on time showed good rates of responses to index selection in components traits. Positive response to selection for either liveweight or fat depth independently are well documented in the literature. In breeding programmes, the trend is to reduce fat and increase liveweight with the hope of increasing lean tissue content since consumers discriminate against fat carcasses (Simm, 1986; Beatson, 1987; Simm et al., 1987; Young, 1989). The means of increasing lean tissue content are quite variable. For instance, selection for or against backfat has been employed in some studies (Fennessy et al., 1989; McEwan et al., 1989) or by use of indices combining information for liveweight and fat depth (Beatson, 1989) or liveweight, fat and muscle depths muscle depth (Young, 1989). Selection to reduce fatness in the body has resulted in desired changes in fatness (a decrease), but the correlated growth rate response is undesirable (a decrease) (Bishop, 1984 cited by Young, 1989) whereas index selection results in desired changes in liveweight (an increase) and fat depth (a decrease). The trends in this study concur with findings of other index selection.

3.3.3 Genetic variation

The only heritability estimates which are in good agreement with the literature estimates (Table 1) are for ALW for both ewes (0.22) and rams (0.39), and autumn (0.21) and winter (0.19) fat depths for rams. All the other heritabilities (Table 13C and 13D) are outside of the range of

literature estimates (Table 1 above). Most of these "out of range" heritabilities are those that have few reported data. For example, muscle depth has only been reported by Young (1989). This makes it hard to decide whether the estimated values are reasonable or due to high environmental influences like the 1989 drought which led to culling of ewes before they were performance tested in winter. The drought of 1989 is an environmental effect which may severely compromise accurate estimation of genetic parameters (Beatson and Young, Pers. Comm.). To find the effect of the 1989 drought on genetic parameters, genetic parameters were estimated from each year's data separately and compared. However, no conclusions could be reached since the results were very variable and had very large standard errors which were attributable to very small data sets (n ≤ 122).

For rams the heritability of liveweight was higher in winter (0.52) than autumn (0.39) whereas the opposite is true in ewes (0.12 in winter and 0.22 in autumn). There are no definite trends from the literature estimates (Table 1) to aid interpretation of this finding because there are few estimates of heritabilities for these traits in both autumn and winter. The lack of comparative literature is also highlighted by Parratt et al. (1989). The difference between autumn and winter could reflect changes in the nutrition and management priorities assigned to rams and ewes at different times of the year (Young, pers.comm.).

The heritability of ewe AFD is quite low (0.05) compared to the literature estimates (Table 1). This might reflect different data manipulations before estimation of AFD heritability. In this data no adjustments were made for liveweight whereas Einarsson (1987) to whose estimates this study estimates were compared, adjusted the data for age and liveweight independently before estimating autumn fat depth heritability. Adjusting traits for identifiable environmental effects increases heritability.

In this study, the heritability of muscle depth was either non-estimable or nonsensical (≥ 1). This probably reflects the small data sets (Table 10) utilised for estimating the heritability of this trait and also due to the effect of the 1989 drought since muscle depth was measured in 1988 and 1989 only.

The heritability of fat depth was higher in winter (0.24) than in autumn (0.05) for ewes but the heritability was quite similar in winter (0.19) and in autumn (0.21) in rams. Higher heritability of fat depth in winter than autumn has been observed for both ewes and rams (Einarsson, 1987) and for rams only (Beatson, 1987). The high heritability of fat depth in winter is likely to be due to measurement of fat depth being more precise in winter. This occurs because the accuracy of autumn measurements may be compromised by low fat levels after unfavourable summers. However, accurate spring measurements using an ultrasonic scanner are quite often difficult to achieve inspite of greater fat depths due to layers of fat being deposited during rapid spring growth (Beatson, 1987). Such layers make it difficult to resolve tissue boundaries.

High heritability for ALW and WLW, and medium for AFD in rams, and WFD in ewes provides strong evidence that they will respond to selection (Falconer, 1989). Indeed positive responses to selection are evident in this study (Figures 5A - 6B).

Estimated genetic correlations for all traits between autumn and winter except muscle depth were high (> 0.60). This is consistent with the literature estimates (Table 2 above). This might mean that selection for a trait at one time of the year will improve that trait throughout the growth phase. This is important for producers that retain a higher proportion of lambs through winter and early spring and for breeders since selection can be made at another stage of growth. Such producers and breeders require reduction in fat levels (Beatson, 1987) and increase in liveweight at various ages.

The genetic and phenotypic correlations between traits were different for the two sexes, with the exception of autumn and winter fat depth. However, when standard errors are considered the differences are generally not significant (Tables 13C and 13D). The standard errors of the genetic correlations are quite high in most cases (Table 13C and 13D). These may indicate poor estimation of genetic correlations because of small data sets (Table 10) used for analyses. However, genetic correlations are notoriously difficult to estimate accurately (Land,1985). Commonly it is assumed that genetic correlations between the same traits measured in both sexes is unity (Parratt et al., 1989). However, Parratt et al. (1989) reports that genetic correlations can vary between sexes. Results from this study tend to support this finding. Such variations could be important in determining genetic progress especially when selection is based solely on one sex or when selection indices derived from genetic parameters for one sex are applied to another. This is because genetic and phenotypic correlations between traits for each sex are important in determining correlated responses and for increasing the accuracy of predicting breeding values (Parratt et al., 1989). Although these variations appear trivial in the first instance, any marked variation between estimate may mean that different selection indices have to be used for males and females and also that selection responses could vary with sex (Parratt et al., 1989).

3.4 Conclusions

Most of the significant non-genetic effects found in this study have also been reported in the literature. Failure to correct for these effects reduces genetic progress because estimates of breeding values are less accurate and hence reduce the selection differential.

This study has shown that there have been positive responses to index selection in liveweight (an increase), and in fat depth (a decrease). The data showed relatively smaller changes in muscle depth with a very slight trend for it to decrease slightly. The inclusion of muscle depth in the selection index now used is expected to result in improvement in muscle depth as well as in liveweight and fat depth.

Analyses showed moderate heritabilities for most component traits. Heritability, genetic and phenotypic correlations generally varied between sexes and seasons. Cognizance of these facts should be taken when considering alternative selection strategies for breeding programmes or production system (Parratt et al., 1989). Estimation of these parameters may be compromised by drought and by non-significant environmental effects such as rearing rank. The environmental effects increase error in calculations of these parameters.

Errors for estimates of genetic parameters were high, particularly in ewes. Good estimates of genetic correlations are essential to develop selection indices in the future. This is because genetic parameters are important in determining correlated responses and for increasing the accuracy of predicting breeding value.

ACKNOWLEDGEMENTS

REFERENCES

Barlow, R. (1978). Biological ramification of selection for preweaning growth in cattle. A review. Animal breeding abstracts 46 : 469-491.

Beatson, P.R. (1986). Sheep Breeding Unit - Mating 1986. Lincoln College Department of Animal Science.

Beatson, P.R. (1987). The inheritance of liveweight corrected fat depth, p87-90. Proceedings of the 6th conference, Australian Association of animal breeding and Genetics, University of Western Australia, Perth, February 9-11 1987.

Beatson, P.R. (1989). Responses in Dorset Down sheep selected for Lean Tissue Growth, p48. Proceedings of the 12th Workshop on overfatness and lean meat production from sheep, June, 1989, Wellington, New Zealand.

Bishop, S.C.; Hill, W.G. (1985). Effects of selection on growth, body composition, food intake and efficiency and catabolism. Genetical Research, Cambridge 46 : 57-74.

Blaxter, K.L.; Fowler, V.R.; Gill, J.C. (1982). A study of the growth of sheep to maturity. Journal of Agricultural Science, Cambridge 98 : 405-420.

Butterfield, R.M.; Griffiths, D.A.; Thompson, J.M.; Zamora, J; 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.

Einarsson, V. (1987). A progeny test of 36 Coopworth rams. Dissertation for B. Agr. Sc. Hons., Lincoln College, New Zealand.

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

Fennessy, P.F.; Greer, G.J.; Bass, J.J. (1982). Progeny test of selected lean and fat rams. Proceedings of the New Zealand society of animal production 42 : 137-140

Fennessy, P.F.; McEwan, J.C.; Bain, W.E.; Greer, G.J. (1989). Selection of sheep for and against back thickness - The Invermay Selection Lines, p18-19. Proceedings of the 12th workshop on overfatness and lean meat production from sheep, June, 1989, Wellington, New Zealand.

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 5th conference, Australian Association of animal breeding and Genetics, University of New South Wales, Sydney, August 26-28, 1985.

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, p8-21.

Groeneveld, E.; Kallweit, E; Henning, M; Pface, 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, p84-89.

Harvey, W.R. (1977). Users Guide for LSML 76. Ohio State University, 46pp.

Hill, W.G.; Bishop, S.C. (1986). Genetic control of growth, carcass composition and food utilisation in laboratory animals. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume XI : 413-418.

Johnson, B.E.; Johnson, R.K.; Mandingo, R.W. (1986). Effect of selection and feed intake on carcass lean and fat in swine. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume XI : 413-418.

Jungst, S.B.; Kuhlers, D.L. (1986). Three generations of mass selection for growth to 70 days of age in Landrace pigs. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume XI : 425-430.

Kreiter, J.; Kalm, E. (1986). Selection for increased growth rate, feed efficiency and carcass quality taking into consideration feed intake. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume XI : 419-429.

Land, R.B. (1985). Knowledge for animal breeding. Phil. Trans. R. Soc. Lond. B310 : 243-289

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.; Fennessy, P.F.; Clarke, J.N.; Hickey, S.M.; Knowler, M.A. (1984). Selection for productive traits on back fat depth in ewe lambs. Proceedings of the New Zealand society of animal production 44 : 249-252.

McEwan, J.C.; Fennessy, P.F.; Greer, G.J.; Bruce, G.D.; Bain, W.E. (1989). Changes occurring after selection for backfat depth, p20-22. Proceedings of the 12th workshop on overfatness and lean meat production from sheep, June, 1989, Wellington, New Zealand.

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.

Olliver, L. (1986). Results of long-term selection experiment for lean tissue growth in the pig. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume XII : 168-180.

Packer, I.U.; Razook, A.G.; Trovo, J.B.F.; Bonilha, L.M.; Figueiredo, L.A.; Nascimento, J.; Pacola, L.; Candido, J.G.; Campos, B.E.S.; Machado, W.B. (1986). Selection for yearling weight in Nelore and Guzera zebu breeds: Selection applied and response. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume IX : 419-423.

Parratt, A.C.; Simm, G. (1987). Selection indices for terminal sires to improve lean meat production from sheep in the United Kingdom. Animal production 45 : 87-96.

Parratt, A.C.; Nicoll, G.B.; 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.

Pingel, H. (1986). Evaluation of (Industrial) breeding programs in waterfowl. Proceedings of the 3rd world congress on genetics applied to livestock production. Volume X : 347-359.

Purchas, R.W.; Abdullah, A.Y.; Kadim, I.T. (1989). Carcass characteristics of Southdown rams from the Massey University high and low backfat selection lines, p26-27. Proceedings of the 12th workshop on overfatness and lean meat production from sheep, June 1989, Wellington, New Zealand.

Sheridan, A.K. (1988). Agreement between estimated and realised genetic parameters. Animal breeding abstracts 56 : 877-899.

Rae, A.L. (1984). Development of selection programmes for increasing lean meat production in sheep, p3-7. Proceedings of the 4th conference of the Australian association of animal breeding and genetics, University of Adelaide, Adelaide, June 4-6 1984.

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. London: Butterworths, p125-144.

Simm, G.; Smith, C.; Thompson, R. (1987). the use of product trait such as lean growth rate as selection criteria in animal breeding. Animal production 45 : 307-316.

Simm, G.; Young, M.J.; Beatson, P.R. (1987). An economic selection index for lean meat production in New Zealand sheep. Animal production 45 : 465-475.

Simm, G.; Dingwall, W.S. (1989). Selection indices for lean meat production in sheep. Livestock production science 21 : 223-233.

Soliz-Ramirez, J.; Purchas, R.W.; Blair, H.T. (1990). Responses to divergent selection for ultrasonic backfat depth in Southdown sheep, p539-540. Proceedings of the 8th conference, Australian Association of animal breeding and genetics, Hamilton and Palmerston North, February 5-9 1990.

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, p43-51.

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, p1-12. Proceedings of the 6th conference, Australian Association of animal breeding and genetics, University of Western Australia, Perth, February 9-11 1987.

Taylor, St.C.S.; Murray, J.I.; Thonney, M.L. (1989). Breed and sex differences among equally mature sheep and goats. 4. Carcass muscle, fat and bone. Animal production 49 : 385-409.

Thonney, M.L.; Taylor, St.C.S.; McClelland, T.H. (1987). Breed and sex differences in equally mature sheep and goats. 1. Growth and food intake. Animal production 45 : 239-260.

Thonney, M.L.; Taylor, St.C.S.; Murray, J.I.; McClelland, T.H. (1987). Breed and sex differences in equally mature sheep and goats. 3. Muscle weight distribution. Animal production 45 : 227-290.

Warmington, B.G.; 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.

Webster, A.J.F. (1976). Efficiencies of energy utilisation during growth. In D. Lister, D.N. Rhodes, V.R. Fowler, M.F. Fuller (eds.). Meat animals. Growth and productivity, London: Plenum press, p89-102.

Webster, A.J.F.; Ahmed, A.A.M.; Frappell, J.P. (1982). A note on the growth rates and maturation rates in beef bulls. Animal production 35 : 281-284.

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, p25-32.

Whitehead, C.C.; Parks, J.R. (1988). the growth to maturity of lean and fat lines of broiler chickens fed diets of different protein content: Evaluation of a model to describe growth and feeding characteristics. Animal production 46 : 469-478.

Wood, J.D. (1982). Factors controlling fat deposition in meat animals. Proceedings of the New Zealand society of animal production 42 : 113-116.

Young, M.J. (1989). Responses to selection for leanness in Suffolk sheep. M.Sc. thesis, University of Edinburgh, Scotland, 60pp.