DIRECT AND CORRELATED RESPONSES TO SELECTION

FOR HIGH OR LOW ULTRASONIC BACKFAT DEPTH IN

SOUTHDOWN SHEEP

A thesis presented in partial fulfilment

of the requirements for the degree of

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ABSTRACT

Divergent selection was employed to establish high and low lines for liveweight-adjusted backfat depth (LABF) assessed ultrasonically in Southdown sheep. The selection lines were initially constituted from several sources with stock brought-in during the first three years of the experiment (1976-1978). These first years were used to evaluate ultrasonic equipment for measuring backfat depth. The lines were closed in 1979. Data analysed in this study were collected over 8 years (1979-1986) representing, approximately 2.66 generations.

Selection was practised in two stages, with a preliminary selection based on the first LABF on the rams and ewes, and a final selection based on an average of all measurements assessed throughout the year for the rams only.

Direct selection for high or low backfat depth resulted in the 1986 born animals in the high line having about 1.69mm (59.6%DEV) and 2.00mm (49.57%DEV) thicker backfat than the low line in the rams and the ewes, respectively. The responses to selection per unit of cumulated selection differential were in most cases high. Due to prior selection and difficulties in assessing the selection pressure, it was concluded that these regressions poorly represented the selection process.

Correlated responses to selection for and against backfat depth were generally small. However, consistent positive correlated response were observed in liveweight-adjusted height and length (LAH

and LAL) over the selection period. These responses imply a negative genetic correlation between these traits and backfat depth. This finding was in agreement with the published literature.

Phenotypic correlations were calculated within-trait between-days and between-traits within-days. Correlations were pooled within-trait following tests of homogeneity. The within trait values were generally moderate to high and they were in agreement with the values reported in the literature. The between-traits correlation values were generally low, but were consistently negative for LABF-LAH and LABF-LAL, and consistently positive for LAL-LAH. Repeatability estimates, using the within-trait combinations, were also in agreement with the literature and suggested a moderate to high repeatability for LABF and LAH. Repeatability estimates for LAL were low to moderate and they were slightly smaller than the values reported in the literature.

Estimates of the heritability of LABF varied with method used. The paternal half-sib method resulted in low values (0.14 to 0.19) while dam/offspring method gave moderate values (0.29 to 0.43). Corresponding heritability estimates for LAH and LAL were about 0.31 and -0.14, respectively. These values were smaller than other results quoted in the literature. It was concluded that truncation selection on LABF reduced the genetic variability of these traits, although not to the same extent as for LABF.

It was concluded that divergent selection for LABF was effective, resulting in lines with significantly different backfat depth at the same liveweight. Furthermore, selection for low LABF led to significantly longer and taller animals.

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CHAPTER ONE. INTRODUCTION.

In planning genetic improvement schemes decisions must be made about the choice of selection objectives and selection criteria. In meat-animals, a prime objective is the economic production of lean meat which can be achieved by: improving the efficiency of conversion of feed into meat; improving the lean to bone ratio; improving the lean to fat ratio, or by modifying the fat partitioning and distribution.

The level of fatness in sheep meat is a factor taken into account in the carcass grading system and by consumers. Incentives to produce lean meat indicate the increase in demand for this product. A major problem with the production of carcasses with optimum fat content is that of identifying live animals that are capable of producing such carcasses, either directly or through their offspring (Shelton et al, 1977; Gooden et al, 1980). Backfat depth in the live animal has been found to be positively correlated with the total fat content in the carcass (Jensen et al, 1967; Wolf et at, 1981; Gooden et al, 1980). Over the years there have been a number of attempts to estimate backfat depths from measurements made on the live animal. The early use of probing devices (Hazel and Kline, 1952) has been largely superceded by ultrasonic techniques. According to Kempster et al(1982), ultrasonic techniques have the greatest practical value of various objective methods presently available for predicting carcass composition in live animals. In addition, ultrasonic techniques cause neither pain to the animal nor damage to the hide and have the added advantage of providing information on tissues lying below the most superficial layers of the

body (Russel and Wright, 1982).

The Southdown breed was used in this study, because it was a numerically important breed in New Zealand at the time of trial initiation, and has also contributed to the development of most Down breeds. The Southdown breed accounted for 30% of all registered Down-type ewes, and approximately 90% of all terminal Down sires prior to 1960, when the market demanded small and well-finished carcasses (Clarke and Meyer, 1982). However, the change to a demand for lean and heavy carcasses, has significatively reduced the Southdown breed population since 1977, and favoured the larger Down breeds. An additional reason for using this breed was the greater variation in fatness compared with other breed types. Therefore, the Southdown breed provided good material to study the genetic and physiological basis of fatness in sheep.

The main objectives of this study were to use eight year's liveweight-adjusted data (expressed as percent deviations) available from a divergent selection experiment based on backfat depth in Southdown sheep to:

a) estimate direct responses to selection for liveweight-adjusted backfat depth assessed ultrasonically,

b) estimate correlated responses in birth weight, pre- and post-weaning growth rate and in shoulder height and body length to selection for liveweight-adjusted backfat depth, and

c) estimate genetic parameters for liveweight-adjusted backfat, shoulder height and body length.

CHAPTER TWO   REVIEW OF LITERATURE

CHAPTER TWO.   REVIEW OF LITERATURE

2.1 Introduction

Responses to selection and estimation of realized genetic parameters from selection experiments involving characteristics of importance to meat production are well documented in laboratory animals (e.g. Falconer, 1960, 1973; Lang and Legates, 1969; Sutherland et al, 1974; McPhee and Neil, 1976; Eisen and Bandy, 1977 and Roberts, 1979), but few such experiments have been undertaken with farm animals. However, results from experiments in poultry, sheep and pigs have been published from Australia, New Zealand, United Kingdom and United States of America. Cattle have played a less important role and because of their long generation interval and the large expense of individual animals, therefore there is little published work available.

This review summarises the theoretical approach to the analysis of selection experiments in the first instance, followed by a review of direct and correlated response in selection experiments involving characteristics related to meat production.

2.2 Selection experiments.

2.2.1 Objectives of selection experiments

Hill(1980) pointed out that the best selection experiment design for quantitative traits depends on the objectives of the experiment. Despite the multiplicity of specific objectives in establishing selection experiments, the measurement of selection response, from which the estimation of genetic parameters can be made, is a common point for all selection experiments (McGuirk et al, 1986).

Hill(1980) distinguished between two groups of selection experiments. The first group comprised short term experiments (five years or less) and were essentially used to estimate parameters or test hypotheses on the base population from which the selection lines were obtained, but they were not able to effectively measure rate of response or parameters which derived from alterations in gene frequencies and variances caused by the selection itself. In contrast, long-term experiments were concerned with measuring and/or utilizing rates of response over time.

McGuirk et al(1986) listed six main points for the usefulness of selection experiments: 1) to provide an

experimental check on theoretical predictions of progress in both selected and correlated traits, 2) to determine how long predicted or initial rates of response are maintained, 3) to measure the symmetry of direct and correlated responses, 4) to compare alternative selection programs, 5) to study genotype-environment interaction, and 6) to provide information on possible correlations between the trait under selection and other traits, where there is no prior information on the genetic correlation.

2.2.2 Design and parameter estimation in selection experiments.

Selection experiments can be used to estimate the heritability of a trait or other genetic parameters in a population and to compare responses under alternative selection schemes (Hill 1971, 1972c). Hill(1971, 1972a, b, c, d) discussed the general theory, design and efficiency of selection experiments, as will be pointed out in the following sections.

The estimator of a parameter is a random variable and as such, has an expected value and a variance (Sellier, 1980). He pointed out that an estimator will be said to be best or more efficient if it is both: a) Unbiased (i.e., the estimator is equal to the parameter) and b) Precise (i.e., small sampling variance). In selection experiments, the precision of these parameters is influenced by the design of the experiment, by the

size of the selection flocks, the number of replications, the intensity of selection, the duration of the experiment and the procedure used to measure responses (McGuirk et al, 1986).

On statistical grounds, a properly designed experiment aims to achieve minimal bias and low sampling error. However, in selection trials genetic sampling may affect the expected theoretical results, because the selection of parents of the next generation is made after the measurements, and the gene frequencies among these selected individuals are different from what they were in the unselected population. The genetic sampling or genetic drift and the direct change due to selection are the two phenomena that affect the gene frequency in any selection programme (Robertson, 1960). This means that year or generation averages may fluctuate through the generations, irrespective of environmental fluctuations.

Avery and Hill(1977) pointed out that accurate predictions of genetic parameters in the base population cannot be made from single selection lines results, because of the large variance in successive generations, caused by genetic sampling. One technique to estimate this variance is by the replication of the selection lines (Falconer, 1973). In addition to the replication of selection lines, it may be advisable to also replicate the control lines to (Dalton and Baker, 1980), in order to evaluate the accuracy of genetic sampling in these lines.

In selection experiments, as in any animal breeding

study, one of the basic problems has been the separation of environmental and genetic effects. Meaningful comparisons within any generation may be made between treatments without the use of a control, providing the treatments are applied to the same population and all of the material has been bred in the same experiment. However, in selection experiments, some method of control is necessary in order that this partition may be made (Hohenboken, 1985).

2.2.2.1 Selection in one direction with a control.

To overcome the problem of measurement of genetic change in selection experiments, the usual practice is to maintain an unselected control population in order to assess environmental fluctuations, maintain genetic constancy over a period of time and determine the cumulative change in the selected population as a deviation from the control (Gowe et al, 1959a; Hill, 1971). However, the usefulness of control populations to estimate the genetic change which has ocurred in a selected population is compromised by four possible sources of error: a) random genetic drift in the control, b) genetic changes in the control due to natural selection, c) differential response of control and selected lines to environmental changes (genotype-environment interaction), and d) error of estimation of the genetic mean from the phenotypic mean in both populations (Hill, 1972d).

Gowe et al(1959b) noted that there are several methods of setting up a control population to measure the efficiency of selection, but pointed out that two requisites must be evaluated. First, their efficiency in maintaining genetic constancy over a period of time and secondly, the cost and labour necesary to maintain each at a given level of genetic efficiency. McGuirk et al(1986) added that because of the considerable resources required, a single control can be used for more than one selection line. In addition, control flocks provide information on genetic variances and covariances, without the complicating effects of selection. They pointed out that often the control flock will be larger than the selection flocks, or will use more sires for mating, to reduce genetic drift. However, this means that different rates of inbreeding in the selected and control populations may result. Therefore, adjustment for inbreeding will be necessary.

Hill(1972c) noted that there were two types of control population in non-inbreeding populations in which breeding individuals were choosen at random and were subjected to genetic sampling (drift) variance. First, where the control and the selected line were taken from the same base population at generation zero, so the initial mean was known without error. Secondly, where they have a different base and there was error of estimation of the initial mean. Although some genotype-environment interaction is more likely in the latter case it is usually assumed there is none and that the

genetic parameters are the same in each population (Hill, 1972c).

One of the problems associated with control populations is directional genetic drift (Hill, 1972c). Therefore, control populations must be as large as possible to minimize changes in their genetic structure from sampling or genetic drift (Hill, 1972c). To ensure that the error associated with random genetic drift is minimized, the effective population number (Ne), must be maximized. It can be calculated for random mating and discrete generations as follows (Hill, 1972c):

$$1/N_e = 1/16M \ [\ 2 + G_{mm} + 2M/F \ COV_{(mm,mf)} + (M/F) \ G_{mf} \ ]$$

$$+ \ 1/16F \ [\ 2 + (F/M) \ G_{fm} + 2F/M \ COV_{(fm,ff)} + G_{ff} \ ]$$

where, M = number of males,

F = number of females,

G_{mm} = variance in the numbers of male progeny
from male parents,

G_{mf} = variance in the numbers of female progeny

from male parents, and

$COV_{(mm,mf)}$ = covariance of numbers of male and
female progeny from male parents.
Similarly from female parents are
G_{fm}, G_{ff} and $COV_{(fm,ff)}$.

Hill(1972c) also pointed out that the above formula can be the same for random mating and overlapping generations if the number of animals entering the flock each year and the age distribution of individuals in the flock remain constant, or at least show little variation. Similarly, the age distribution of parents of individuals born in any year should be stable. Under these circunstances, the N_e calculation can be reduced to:

$$N_e = 1/4N_m + 1/4N_f .$$

Goodwin et al(1960) and Hohenboken(1985) listed three limitations of using a control group. First, natural selection may cause genetic change (ΔG_n) in the control population such that:

$$\Delta P_c = \Delta E_c + \Delta G_n ,$$

where: ΔP_c = phenotypic change in the control population, and

ΔE_c = environmental change in the control population.

However, If it can be assumed that the direction and strength of natural selection are the same in selected and control population, the unselected control technique is still effective since:

$$\Delta G_s = \Delta P_s - \Delta P_c$$
$$= (\Delta G_s + \Delta E_s + \Delta G_n) - (\Delta E_c + \Delta G_n)$$
$$= \Delta G_s \ ,$$

where: $\underline{s}$ denotes selected and $\underline{c}$ control
populations.

Secondly, the control and selection lines will become genetically distinct after several generations of selection and it is possible that they will respond differently to environmental effects, leading to biased estimates of genetic change. Thirdly, for livestock populations the most serious limitation in using this form of control is generally the cost.

2.2.2.2 Modified controls.

a)Genotype storage. The possibility of long-term storage of embryos from the base genetic material is potentially a good technique for the conservation of genotypes as an alternative to control groups (Land, 1977; Hill, 1972c). However, it has not widely used due to concerns of viability, the need for highly qualified labour and costs. When an estimate of the genetic response is required, a proportion of the stored embryos are allowed to develop, producing a group of animals against which the selected animals could be compared.

b)Gamete storage. Frozen semen is a convenient method for storing genes and for measuring genetic trends in performance traits, both in commercial and experimental populations of large farm animals. An estimate of one half of the average annual genetic change occurring over a given period of time can be obtained by inseminating females from the current selected population with frozen semen from a group of sires (base population) and comparing their progeny with that of sires (selected population) in current use. However, this comparison should take into account that the dams from the selected population has been exposed to some degree of imbreeding and that when these females are inseminated with semen of sires from the base population, would be expected some degree of heterosis, which in turn will bias the genetic

change. Sellier(1980) pointed out that because of the number of animals needed to achieve the same precision in the estimate of annual genetic change, discontinous testing (one comparison at the end of the period) is up to three times more efficient than continuous testing (yearly comparisons over the whole period).

c)Repeat matings procedure. Goodwin et al(1955) defined repeat mating as the replication in adjacent years of generations of progeny from the same parents, they proposed this design to enable the estimation of genetic gain in poultry, without maintaining a control line. Brinks et al(1965) and Benson et al(1972) used this method of control to determine environmental trends in cattle over a period of 26 and 8 years, respectively. However, this method has not been widely used in selection experiments.

Smith(1962) pointed out that this sort of control has two main limitations. First, the number of sires to get a substantial number of repeat mating for adjacent years. This limitation implies that the repeat use of sires for several years will extent the generation interval, reducing the genetic gain per year. Secondly, any selection or progressive culling of sires would throw doubt on estimates of the genetic parameters. In addition, progeny from the repeat matings will have been raised by dams differing in age. Hohenboken (1985)proposed that records be adjusted for age of dam effects before full-sib comparisons are made.

d)<u>Inbred lines</u>. This type of control is essentially equivalent to the storage of individuals, Hill(1972c). Several highly inbred lines or their hybrid progeny can be used as a control group, Cassuto <u>et al</u>(1970). This method overcomes the problems of genetic drift and natural selection, but highly inbred lines of animals are subjected to reproductive difficulties (Falconer, 1981). This sort of control has been used more widely in laboratory experiments than in farm animals.

e)<u>Best linear unbiased prediction (BLUP)</u>. This technique has been widely used in the dairy industry (Henderson, 1973), but can also be used in other animal industries (e.g., sheep), Blair and Pollack(1984). The BLUP technique enables the separation of genetic and environmental effects when predicting breeding values from records taken in different years (Henderson <u>et al</u>, 1959).

Blair and Pollack(1984) evaluated genetic trends in a single trait selection experiment with and without control. They stressed that Henderson's technique is a viable alternative for the analysis of selection experiments without control, but noted some limitations.

2.2.2.3 Divergent selection.

The relative accuracy of the response measured by the use of a control can be improved if the control is not an unselected population but is selected in the opposite direction. This is known as two-way selection or divergent selection, Soller and Genizi(1967), Hill(1971, 1972a, c), Falconer(1981).

There are two approaches to establishing a divergent selection experiment: first, the animals could be randomly assigned to 2 lines fromn a commom base population (high and low). Alternatively, animals could be screened on the basis of high or low performance into the high or low lines, respectively in subsequent generations, two separate populations are maintained, selected in opposite directions. With divergent selection, the common environmental effects are assummed to be removed during the subtraction of the low line mean from the high line mean, Richardson et al(1968);

Hill(1971) pointed out that if the animals in the lines of selection are reared at the same time, then common environmental effects are eliminated. Phenotypic changes in the upward and downward selection lines, respectively, are:

$$\Delta P_u = \Delta G_u + \Delta E_u,$$

and $\qquad \Delta P_d = -\Delta G_d + \Delta E_d,$

then $\qquad \Delta P_u - \Delta P_d = (\Delta G_u + \Delta E_u) - (-\Delta G_d + \Delta E_d),$

now, if $\qquad \Delta G_u + \Delta G_d = 2\Delta G,$

and if $\qquad \Delta E_u = \Delta E_d$

then $\qquad \Delta P_u - \Delta P_d = 2\Delta G,$

and $\qquad \Delta G = (\Delta P_u - \Delta P_d)/\ 2\ ,$

and finally $\qquad \Delta G = 1/2\ \Delta P,$

where: ΔP is the phenotypic change,

ΔG is the genetic change, and

ΔE is the environmental change.

The subscripts $\underline{d}$ and $\underline{u}$ are for upward and downward selection lines.

This shows that half of the phenotypic divergence estimates the genetic change. Providing both lines respond equally to selection, i.e response is symmetrical.

Falconer(1953), when selecting for large and small size in mice, noted that progress was more rapid in the line selected for small size than in the line selected for large size. Furthermore, Falconer (1954) noted that the selection for increased body weight was only one third as effective as the selection for decreased body weight. These asymmetrical responses observed by Falconer, make the prediction of genetic response from divergent selection more complex. In this case,

a control group will help in the detection of asymmetrical responses (McGuirk et al, 1986) with a consequential loss in the efficiency of the divergent design.

Hill(1972b) noted that when the variance of common environmental effects remains zero, the efficiency of divergent selection and selection in one direction without a control were very similar. But when the variance becomes positive, selection in one direction without a control becomes less efficient in genetic terms. He also indicated that including a control group from the original population to calculate the effect of the common environmental effect, was less efficient than a divergent selection design. However, Blair(1981) pointed out that if the control group was already present for some other purpose, then equality of efficiency may be retained.

2.2.3 Selection experiments involving meat production.

2.2.3.1 Introduction.

Long-term selection experiments in sheep have involved a variety of traits: wool weight, weaning weight cannon bone length and fleece characteristics (Turner, 1977; Pattie, 1965a, b; Purser, 1982; Blair, 1986). In general, rates of gain have been 1-3% per annum depending of the trait involved (Purser, 1982).

The increase in demand for leaner meat has given impetus to the development of breeding programmes for lean lamb production. The preference of consumers for leaner cuts of sheep meat has caused more emphasis to be placed on the carcass merit (Robison et al, 1960; Beatson, 1987). This move has been aided by sophisticated techniques enabling the in vivo measurement of body tissues becoming available to sheep breeders.

Meat from lamb carcases is often perceived as too fatty and this is usually given as one of the reasons for the decreasing consumption of lamb in some countries (Kirton, 1983). In addition, the production of fat in excess of consumer requirements is wasteful for two reasons (Allen and

MaCarthy, 1980). First, fatty tissue is energetically more expensive to deposit than lean, thereby reducing the efficiency of meat production. Secondly, excess fat must be trimmed from the carcass, thereby reducing the percentage yield of lean meat. Therefore, the main long-term objective of any selection improvement programme for meat-breeds of sheep should be the efficient production of lean lamb (Fortin and Sherestha, 1986).

The effectiveness of improving carcass quality by selecting for a quantitative character such as backfat depth depends on both the heritability of the character and its genetic correlation with carcass merit. Therefore, estimates of these genetic parameters are of interest.

The availability of ultrasonic devices has reduced the problem of identifying animals with high genetic merit for lean carcasses (Kirton, 1975; Gooden et al, 1980; Wolf et al, 1981). However, it is expected that future research in this area will improve the accuracy by more precisely showing when and where to measure backfat depth. Meyer(1981) indicated that the optimal age for ultrasonic backfat depth measurement may depend upon the growth pattern of animals to be measured. Variation in body weight and fatness at weaning is largely due to maternal environmental effects which diminish as lambs grow older. Therefore, measurements taken later in life should be more indicative of the animals own genetic merit for leanness.

2.2.3.2 Selection for/against liveweight.

Liveweight adjusted for age is an important characteristic in meat production and it has been used as a selection criterion by many workers (e.g. Pattie, 1964; Pym and Nicholls, 1979; Allen and McCarthy, 1980 and Davies, 1987). It has also been demonstrated to respond to selection, and has a moderate to high heritability depending on the age of selection (Table 2.1).

One of the most intensively studied selection experiments for sheep body weight (Pattie, 1964, 1965a, b) involved divergent selection for weaning weight for eleven years (4 generations) in the Australian Merino. A clear trend was shown and strong genetic relationship was shown between the age-corrected weaning weight and age-uncorrected 17-month body weight (Pattie, 1965b). Based on the estimates of genetic parameters and costs of correcting for weaning weight, it was concluded that selection for uncorrected 17-month body weight offered an alternative to selection based on corrected weaning weight. But this would necessitate that all animals

Table 2.1. Heritability estimates for liveweight at various ages in some farm animals.

Character[1]	Heritability	Method[3]	Author	Animal
Weaning Wt	0.23	Realized h^2	Pattie,1964.	Merino sheep
Weaning Wt	0.20 to 0.55		Dalton,1980	Beef cattle
Weaning Wt	0.17±0.03	Realized h^2	Lasslo et al,1985	Targhee sheep
Weaning Wt	0.10 to 0.40		Dalton,1980	Sheep
Weaning Wt	0.08		Dalton,1980	Pigs
Weaning Wt	0.31	β_{cr-csd}	Pattie,1964.	Merino ewes
Weaning Wt	0.19	β_{cr-csd}	Pattie,1964.	Merino rams
Weaning Wt	0.18±0.05	β_{cr-csd}	Davies,1987.	Merino sheep
Weaning Wt	0.07±0.13	PHS	Vesely and Robison,1970	Ramboullet rams
Weaning Wt	0.06±0.12	PHS	Vesely and Robison,1970	Ramboullet ewes
120-d Wt	0.40±0.17	PHS	Osman and Bradford,1965	Targhee sheep
50-d Wt	0.30±0.03	PHS	Shrestha et al,1986	Ramboullet rams
100-d Wt	0.47±0.04	PHS	Shrestha et al,1986	Ramboullet ewes
10-mths Wt	0.35		Dalton,1980	Sheep
18-mths Wt	0.30 to 0.55		Dalton,1980	Beef cattle
Hogget Wt	0.23±0.05	Realized h^2	Johnson,1981.	Romney sheep
Final Wt	0.23±0.15	PHS	Vesely and Robison,1970	Ramboullet rams
Final Wt	0.30±0.15	PHS	Vesely and Robison,1970	Ramboullet ewes
Final Wt	0.50 to 0.60		Dalton,1980	Beef cattle

[1], d=days and mths=months of age, Wt=Weight.

[3], β_{cr-csd}=Regression of cumulated selection differential on cumulative response,

PHS=Paternal half sibs analysis.

be carried to 17 months of age, whereas selection on weaning weight would necessitate carrying only the selected animals and would allow mating at 6-8 months of age, thereby reducing the generation interval.

Further analysis of Pattie's animals showed that selecting for size, whether directly or indirectly,resulted in animals of different mature size but similar body composition at maturity. Thompson(1985) also pointed out that at the same body weight the larger breed or strain would have less fat, which is consistent with results from most breed comparisons. Furthermore, varying the age of selection for body weight may provide an indirect means by which total body fat may be manipulated (Thompson, 1982, 1985). Selection for high or low weaning weight resulted in an increase and decrease, respectively, in the total weight of fat in the body of mature animals. However, the differences in fat partitioning were very small when the comparisons were at the same stage of maturity (Thompson et al, 1987). They also pointed out that the production of a leaner carcass at the same body weight can be achieved through an increase in mature size. However, they warned that in a self-replacing flock this increase in mature size is associated with an increase in food intake and may result in a decline in the biological efficiency of meat production.

Davies(1987) noted that selecting for high weaning weight in Merino sheep resulted in a slight decrease in the

unadjusted backfat depth, relative to the low weaning weight selection group. Pattie(1965b) also noted changes in the number of twins selected. In the low weaning weight line, there were 20% more twin ewes and 100% more twin rams joined than in the high line. He found there were no significant differences between lines in reproductive performance but that a positive genetic correlation between weaning weight and multiple births possibly existed. Moreover, adequate corrections for twins in any selection programme based on weaning weight should be considered.

Recently, Atkins(1986) pointed out that effective genetic improvement of litter size will result as a consequence of indirect selection for 18 month body weight. He noted that selection on body weight applied at ages younger than 18 months would be less efficient at increasing litter size, because the heritability and genetic correlations are lower.

Selection for weaning weight has shown little effect on lamb mortality in sheep (Pattie, 1965b). Pattie and Trimmer(1964) pointed out that selection for high weaning weight increased milk production without reducing its nutritive value (Pattie and Trimmer, 1964). However, the correlated response in mature size (Thompson, 1985) indicates also an increase in the general frame of the ewe, and an increase in twining rate (Pattie, 1965b), which in turn reduced the chance of dystokia.

In pigs, England et al(1954) reported that a program to develop a breed of anatomically and physiologically normal, miniature, pig for use in medical and other laboratory research was undertaken in 1949. They showed that selection for small body size was effective and that after three generations the average 154-day body weight decline from 52 to 20 kgs. Later, Dettmers et al(1965) indicated that body size in miniature pigs at 140 days of age had been reduced by at least 29% over a period of 11 years. They reported a heritabilities for 56- and 140-day weight of 0.41 and 0.11, respectively. They also noted that some reduction in birth and 56-day weight had accompanied selection for reduced 140-day weight.

In cattle, Newman et al(1973) studied yearling weight from a selection experiment with two replicate herds of Beef Shorthorns. They reported that selection for increased yearling weight was effective, the realised heritability estimates being 0.50 and 0.39 for males and females, respectively.

In another selection experiment, selection response was studied in three lines of Hereford selected for weaning weight, yearling weight or index of yearling weight and muscling score (Koch et al, 1974). The lines showed the greatest degree of response in whatever trait was under direct selection. The weaning weight selection line showed the highest response in weaning weight, for instance. But the

lines also showed positive correlated responses in associated traits. For example, the weaning weight selection line showed the highest correlated response in pre-weaning growth rate, and the yearling weight selection line showed the highest correlated response in post-weaning growth rate. These correlated responses, together with the high heritability values previously reported, suggested that improvement in all these traits can be carried out under the same programme (Koch et al, 1974).

In poultry, it has been demonstrated that body weight adjusted for age under direct selection is very responsive: in turkeys (e.g. Nestor, 1984; Nestor et al, 1985; Nestor et al, 1987b), in chickens (e.g. Siegel, 1962; Marks, 1983, 1987; Renden, 1987)and in quail (e.g., Nestor et al, 1982, 1987a).

In turkeys, Nestor(1984) selected for increased 16-week body weight and noted that genetic gains continued throughout 11 generations of selection. However, in generations 12, 13 and 14 there appeared to be a cesation of response, but in generation 15 and 16 responses returned to the expected levels of gain. They explained this slight (non-significant) curvilinear trend, as a genotype-environment interaction when in generations 12, 13 and 14 the animals were transferred to a different environment and in generations 15 and 16 the animals were taken back to the same environment. He estimated an average realized heritability across sexes of

0.26 for the whole period of 16 generations and an estimation up to 11 generations of 0.30.

Selection for 16-week body weight in turkeys resulted in large increases in body weight at 8, 20 and 24 weeks of age and at maturity. Therefore, the genetic correlations between 16-week body weight and body weight at all other ages measured were large and positive (Nestor, 1984). Nestor et al(1985) also reported strong correlated responses in leg problems, walking ability and egg production. But when selection was for increased leg width, an increase in shank width resulted, which was accompanied by an improvement in walking ability (Nestor et al, 1987b).

In chickens, Siegel(1962) showed that one generation of divergent selection for 8-week body weight resulted in highly significant differences between lines for the selected trait. These differences became progressively larger with each successive generation of selection. The realized heritabilities across sexes were 0.22, 0.32, 0.31 and 0.30 for the four generations, respectively.

Marks(1983) after developing two different chicken populations for size (dwarf and normal), selected during four generations for 8-week body weight in both populations. He indicated that selection progress for increased weight in the pure dwarf lines was similar to that of normal lines originating from the same non-selected base population.

Reproductive performance of dwarf and normal lines were comparable. Further analysis by Marks(1987) showed that selection for 8-week body weight of normal and dwarf birds across four generations under two different salty environments resulted in different response rates. Body weight was greater under the low salt environment than under the high salt environment. Following correction for environmental variation, the increase in body weight was greater in dwarf lines than in normal lines.

In quail (Coturnix coturnix japonica), Nestor et al(1982) selected for body weight and yolk precursor in quail. Both up and down lines were responsive to selection, with the total gain and total gain per generation being greatest in the low weight strain, due to the larger selection differentials. The realized heritability values were 0.37 for the high line and 0.44 for the low line. Later, Nestor et al(1987a) noted that response to selection for high 4-week body weight in quail was linear until generation 6-7, but appeared to decline in later generations. Therefore, an apparent selection plateau existed in the response over generations. Realized heritabilities in the high and low body weight lines were 0.38 and 0.32 respectively.

Siegel(1962) provided a summary of heritability estimations of body weight in poultry obtained at ages ranging from 6 to 12 weeks. McCarthy and Siegel(1983) provided a review of genetic and physiological effects of selection in

meat-type poultry.They pointed out that the genetic variation
in body size is large resulting in a high heritability.
Therefore, growth rate between fixed ages and body weight at a
given age are traits easily changed by individual phenotypic
selection. It was also pointed out that the variety of
estimates obtained in different experiments may reflect
variation in the genetic constitution of the founder
populations and/or effects of population size.

McCarthy and Siegel(1983) noted from published
experiments with poultry, that selection for increased body
weight is associated with increases in feed consumption, with
a pronounced increase during the first week posthatching.
They suggested that selection for increased body weight of
fowls may affect the sensitivity of the higher nerve centers
involved with the termination of food intake.

Allen and McCarthy(1980), after selecting for high
and low body weight in mice, pointed out that the high line
showed a significant correlated response in the kidney and
gonadal fat depots. They also noted that the high body weight
line showed a greater rate of total fat deposition but were
relatively leaner at weights less than 20 grams. They
concluded that the selection lines had different fat
distributions at fixed ages, at fixed body weight and at fixed
weights of fat. Earlier, Hayes and McCarthy(1976) noted that
selection for increased body weight resulted in fatness at
older ages in the high lines, so that the proportion of fat

deposited prior to age of selection remained similar in high and unselected lines, but the proportion of fat in high lines at later ages was greatly increased in comparison with unselected lines.

In general, the evidence suggests that selection for liveweight in farm animals has been effective. Furthermore, it has been accompanied by correlated responses in liveweights at other ages, reproductive traits, increases in food intake and reduction in the efficiency of meat production. However, body composition at mature weight from sheep selected for high and low body weight appears to be similar.

2.2.3.3 Selection for/against growth rate and efficiency of growth.

Animal growth, when defined as a change in size or mass, is a very superficial concept because as the animal grows it also experiences developmental changes in body proportions, shape and composition, Purchas(1986). Growth is most commomly considered in terms of liveweight changes although other measurements, such as length, height and girth of the body, may also be used. These latter measurements could be important if they are highly related to body weight and composition, but they may also be useful in describing differences or changes in body shape.

In general, growth rate has been used widely as an selection criterion to increase meat production. Selection experiments based on growth rate have been reported mainly for laboratory animals (Roberts, 1979), although some relevant studies have been published for farm animals (Krider et al, 1946; Hess et al, 1962; Swiger et al, 1962). Table 2.2 presents a summary of heritability estimates for various assessments of growth rate. Most heritability values are moderate to high, suggesting that reasonable genetic progress should be achieved using growth rates between fixed weights.

Robertson(1982), after reviewing several studies, pointed out that lines selected for high early growth rate in mice were larger at maturity and took slightly longer to reach half mature weight. On the other hand, they were fatter at a given age and the increased fatness remained at maturity. Females from large lines become sexually mature somewhat earlier than the small females. He also noted that at a given absolute weight, the animals in the lines selected for high growth rate would be physiologically less mature than the control animals (or those selected for low growth rate), and would therefore be leaner. Robertson(1982) stressed that the total variation in growth rate might be split up into that due to intake and that due to efficiency of growth at a particular level of intake. Animals capable of higher protein deposition at a particular intake would have a higher overall growth, because water content of the muscular tissue is higher than that of fat and would also be more desirable in terms of

Table 2.2. Heritability estimates for various assessments of growth rate.

Character[1]	Heritability	Method[3]	Author	Animal
PrGR	0.21±0.13	PHS	McKay and Garnett,1986	Pigs
50-100d ADG	0.47±0.04	PHS	Shrestha et al,1985	Suffolk
50-100d ADG	0.50±0.04	PHS	Shrestha et al,1986	Sheep
ADG(25kg-100kg)	0.14±0.04	Henderson's 3	Merks,1987	Dutch Yorkshire pigs
ADG(25kg-100kg)	0.22±0.05	Henderson's 3	Merks,1987	Dutch Landrace pigs
Birth to slaughter growth rate.	0.10±0.06	PHS	Wolf et al,1981	Sheep
PoGR	-0.07 to 0.40		Hetzer and Miller,1972a	Pigs
PoGR	0.17±0.04	β_{o-mp}	Hetzer and Miller,1972a	Duroc pigs
PoGR	0.33±0.04	β_{o-mp}	Hetzer and Miller,1972a	Hampshire pigs
PoGR	0.19±0.02	Henderson's 3	Merks,1988	Dutch Yorkshire pigs
PoGR	0.13±0.02	Henderson's 3	Merks,1988	Dutch Landrace pigs
PoGR	0.58±0.33	PHS	McKay and Garnett,1986	Pigs
PoGR	-0.014±0.09	β_{o-p}	Gregory et al,1978	Sheep
PoGR	0.05±0.03	β_{o-mp}	Edwards and Omtvedt,1971	Pigs
PoGR	0.20±0.023	Realized h[2]	Rahnefeld and Garnett,1976	Pigs
PoGR	0.28±0.16	PHS	Vesely and Robison,1970	Ramboullet rams
Total ADG	0.24±0.09	PHS	Botkin et al,1969	Sheep
Total ADG	0.38±0.34	β_{o-p}	Botkin et al,1969	Sheep
Total ADG	0.27±0.16	PHS	Vesely and Robison,1970	Ramboullet rams
Total ADG	0.15±0.13	PHS	Vesely and Robison,1970	Ramboullet ewes
Wt Gain	0.37±0.15	PHS	Hundley and Carter,1956	Hampshire lambs
Wt gain	0.04±0.14	PHS	Hundley and Carter,1956	Southdown lambs
Total gain	0.16±0.13	PHS	Vesely and Robison,1970	Ramboullet ewes
Lean wt/d-age	0.23±0.11	PHS	Wolf et al,1981	Sheep
Ccwt/d-age	0.35±0.11	PHS	Botkin et al,1969	Sheep
Ccwt/d-age	0.58±0.33	β_{o-p}	Botkin et al,1969	Sheep

[1], PoGR=Post-weaning growth rate, ADG=Average daily gain, 50-100d-age ADG=ADG from 50 to 100 days of age, Wt gain=Weight gain,PrGR=Preweaning growth rate, Lean wt/d-age=Lean weight/day of age, Ccwt/Dd-age=Carcass weight/day of age.

[3], β_{o-mp}=Regression of offspring on mid-parent, B_{o-p}=Regression of offspring on parent. PHS=Paternal Half-sibs analysis.

saleability, because of their better body condition.

In pigs, Krider et al(1946) selected for high and slow growth rate in Hampshire pigs. They showed that from a common base population, selection for a rapid growing line and for a slow growing line had been successful in separating lines for growth. They reported an average heritability, within line, of 0.17 and 0.19 for growth rate up to 150 and 180 days, respectively, while the estimates across lines were 0.29 and 0.33, respectively.

Dickerson and Grimes(1947) studying food conversion efficiency, reported the results of 5 generations of selection for either high or low feed utilization efficiency. They found that pigs from the high food utilization efficiency line ate less, grew faster, and were heavier and fatter than pigs of the low line at the same age. They concluded that selection based on rate of gain would be just as effective in improving economy of gain as selection based on individual feed, records and considerably more effective in improving rate of gain. However, Vogt et al(1963) and Park(1965) both reported a low genetic correlation between efficiency and rate of gain, and suggested that selection on gain would not increase significantly food utilization efficiency, especially in a time constant feeding test.

Fowler and Esminger(1960), studying the effect of nutrition on rate of gain and food utilization efficiency,

selected for rate of gain from weaning to 68 kgs body weight.
They noted that selection for growth rate over that period was
effective in high- or low-plane of nutrition, and that there
was a highly significant difference of 200 grs in favor of the
high-plane pigs, which would be expected since they were full
feed while the low-plane pigs were limited to 70% of full
feed. This difference in growth rate also suggested that at
the same age the low plane pigs were with lower liveweight.
However, when the increase per generation was expressed as a
percentage of the initial average growth rate at generation 1,
the progress under the high-plane line was 3.57% per
generation compared with 4.69% under the low-plane line. They
reported a realized heritability for growth rate of 0.52 and
0.49 under the high- and low-planes of nutrition,
respectively. Furthermore, Fowler and Esminger (1960),
regarding to food utilization efficiency speculated that the
differences in efficiency among pigs were largely due to the
differences in the composition (muscle vs fat) of weight
gains. They therefore selected under both restricted and ad
libitum regimes. They noted that pigs on the restricted
feeding regime were more efficient and less fat than those on
ad libitum feeding regimes, which suggest that the efficiency
of conversion to muscle is higher than that to fat. They also
suggested that the pigs selected for superior rate of gain
under restricted feeding were actually selected for superior
efficiency of food utilization.

Biswas et al(1966) reported that efficiency of feed

utilization, expressed as the ratio of average daily gain to average daily feed consumption, was significantly positively correlated (0.24) with gain but negatively correlated(-0.54) with feed consumption in a feeding test. The correlation was still negative when food consumption was adjusted for initial weight. They concluded that pigs with faster growth rate were more efficient than slow growing pigs.

Fredeen and Mikani(1986) reported that selection for high growth rate in pigs at the same age was effective. They pointed out that as the experiment progressed the high growth rate line became less fat at the same age relative to the control. They estimated a realized heritability for growth rate of 0.20±0.03 and a realized genetic correlation between growth rate and liveweight-adjusted backfat depth of -0.51.

In Hereford cattle, Irgang et al(1985) found that direct selection for post-weaning growth rate was more effective in changing post-weaning growth rate than was selection for weaning weight. Furthermore, the correlated response in weaning weight, following post-weaning growth rate selection, was also higher than the direct selection on that trait. They calculated a realized heritability for growth rate of 0.31±0.13 in bulls and 0.04±0.08 in heifers.

Swiger et al(1962)studying economic aspects of gain in cattle, suggested that selection for incresed weaning weight and post-weaning growth rate would be effective in

improving the efficiency of food utilization. However, Koch et al(1963) suggested that selection for food consumption would result in improved daily gain, but would not improve food utilization efficiency other than that attributable to a smaller portion of the intake being used for body maintenance. They indicated that food utilization efficiency would be best improved by selection for rate of gain adjusted for differences in food consumption.

In poultry, Hess et al(1962)showed that selection for fast or slow growth rates on a methionine deficient diet led to the development of two lines of chickens with significantly different body weights at 3-week of age. However, they found that the response to selection was rapid for the first two generations, but negligible thereafter. Cunningham et al(1987) noted similar results when selecting for 21-day body weight gain of chicks fed on a purified selenium deficient diet. It was observed that a large initial response declined after the first generation, and was negligible after the third generation. They proposed that the lack of response to selection observed in the third generation may have resulted from a rapid reduction in additive genetic variance associated with the selection process for this trait.

Pym and Nicholls(1979), working with broilers in a selection experiment for food conversion efficiency, established 3 separate lines: 1) selected for 5 to 9 week weight gain, 2) selected for increased food consumption, and

3) selected for food consumption ratio. They noted that the selection line for weight gain showed fast weight gain, moderate food consumption and poor efficiency compared with the control line. The correlated responses indicated that selection for 9-week weight alone should substantially increase 9-week weight and slightly increase feed consumption.

Efficiency in meat production has been a controversial topic in nutrition, genetics and physiological studies, particularly when it was related to body composition of the animal. Some authors have found that chickens with poor food conversion efficiency were fatter than a corresponding group from the same strain with superior conversion efficiency (see Pym and Solvyns, 1979 for a review). Proudman et al(1970) selected chickens for feed utilization efficiency in fast and slow growing lines. They noted that the greater growth attained by the high growth line with restricted feed reflected an inherent ability of those birds to utilise feed more efficiently than birds of the slow growth line. They commented that since the high line birds maintained a larger body size throughout most of the experiment period, their better growth and efficiency were probably attained by utilizing a larger proportion of their diet for maintenance.

Wethli and Wessels(1973a) found that feed intake and body mass gain, feed intake and final body mass, and body mass gain and final body mass were all highly positively

correlated, while feed conversion ratio (feed intake/mass gain) was strongly negative correlated with feed intake, mass gain and final mass in chickens. They concluded that there was a trend for chickens exhibiting superior feed conversion to have a low thyroid activity, large gain in body mass, to be heavier and have a high feed intake. In a subsequent paper, Wethli and Wessels(1973b) added that a bird with the above characteristics will also have a high body fat content.

Other experiments in chickens (e.g., Pym and Solvyns, 1979) found that selection for improved food conversion efficiency alone, resulted in a decrease in carcass fatness and an increase in protein and water, when measured at either a given age or body weight. This means that highly efficient lines would store more protein and less fat than low-efficiency lines (Brody, 1935).

McCarthy and Siegel(1983) suggested that selection for body weight in poultry may affect feed efficiency by reducing some or all of the components of the relative maintenance cost, but this did not necessarily implicate a change in body composition. They pointed out that genetic variation in feed efficiency may result from differences in body composition, because feed efficiency (gain/food) is negatively correlated and feed conversion (food/gain) positively correlated, with the proportion of fat in the weight gain. They stated that an increase in efficiency may be most easily explained in terms of changes in the relative

amounts of energy expended on weight gain and maintenance. An increase in efficiency will occur if more energy is used for weight gain relative to that used for maintenance. This could be achieved by: a) the amount of metabolizable energy available for gain relative to maintenance energy cost being increased, if intake per unit body weight were increased and/or if the ability to digest food were increased; b) a proportionate reduction in the cost of maintenance per unit of body weight, or c) the composition of weight gain, and therefore the energy cost, being altered after selection.

Soller and Eitan(1984) proposed a model to explain the effect of selection for liveweight gain on fat deposition. They showed that selection for weight gain should act to: increase food intake (or appetite), decrease maintenance requirements, and to increase the lean:fat partition coefficient. While selection for appetite alone should result in a greater degree of fatness than selection for weight gain. They concluded that selection for efficiency in mice, if manifested primarily on maintenance requirements, need not necessarily result in decreased body fat, and may even induce a relative increase. Furthermore, in poultry the presence of significant genetic variation in the lean:fat partition coefficient may enable reduced fat deposition after selection for feed efficiency.

The literature reviewed in this section indicates that selection for growth rate or liveweight between two fixed

weights or ages, and the efficiency of food utilization are moderate to highly heritable in farm animals. In addition, multiple correlated responses to selection for/against growth rate have been pointed out. It does seems that selection for increased growth rate is likely to increase food intake, reduce feed efficiency and increase body fat. Whereas, selection for increased feed efficiency is likely to increase the ability of the animals to utilise feed more efficiently, resulting in an increase in protein and water deposition at the same age or weight. Furthermore, selection for increase feed efficiency should result in a decrease in food intake, decrease in body fat and a decrease in growth rate. However, as Fowler and Esminger(1960) noted, the point of comparison is important in order to determine the best alternative. Therefore, selection for feed efficiency should be more reliable in economic terms.

2.2.3.4 Selection for/against skeletal size.

There are few selection experiments for characteristics related to skeletal size in the live animal. However, some studies have been reported (Purser, 1980a, b, 1982; Hetzer and Miller, 1972b). Table 2.3 shows heritability estimates for cannon bone length, body length and shoulder height. These values indicate that selection for body dimentions should result in moderate responses.

Table 2.3. Heritability estimates for measurements of skeletal size.

Character	Heritability	Method[1]	Author	Animal
Length Cannon bone	0.36 ± 0.03	PHS	Purser, 1980b	Sheep
Short cannon bone	0.30 ± 0.03	PHS	Purser, 1980b	Sheep
Cannon bone length	0.50 ± 0.03	β_{cr-csd}	Purser 1980b	Sheep
Body length	0.29 to 0.68	β_{o-mp}	Hetzer and Miller, 1972b	Pigs
Body length	0.34 ± 0.04	β_{o-mp}	Hetzer and Miller, 1972b	Duroc pigs
Body length	0.58 ± 0.04	β_{o-mp}	Hetzer and Miller, 1972b	Yorkshire pigs
Shoulder height	0.20 to 0.64	β_{o-mp}	Hetzer and Miller, 1972b	Pigs
Shoulder height	0.29 ± 0.04	β_{o-mp}	Hetzer and Miller, 1972b	Duroc pigs
Shoulder height	0.57 ± 0.04	β_{o-mp}	Hetzer and Miller, 1972b	Yorkshire pigs

[1], For additional abbreviations see Table 2.1 and 2.2.

A selective breeding programme in Scottish Blackface sheep based on the cannon bone length (adjusted for body weight) of eight weeks old lambs was started at the Animal Breeding Research Organization (ABRO) between 1952-1955, Purser(1980b). The responses to selection in the high and low selection lines showed a strong degree of symmetry. Furthermore, Purser(1980a) noted that relative to control ewes, the long cannon bone ewes produced 20% more lambs and their crossbred lambs were 3% heavier in carcass weight at a constant bodyweight. As a consequence, the lamb meat production by the long cannon bone ewes was almost twice that from short cannon bone ewes. He added that the resultant higher prolificacy in the long cannon bone line should have led to higher mortality due to the increase in birth weight and litter size rather than the lower mortality experienced in the long cannon bone line, which can be explained by the increase also in ewe mature size. Further analysis on lamb mortality showed that selection for cannon bone length did not have any significant effects on lamb mortality (Cue, 1983).

From experience gained during handling the lambs, Purser(1980a) pointed out that different fattening rates had become established within the first two generations of selection. He also noted that short cannon bone lambs at weaning were generally at least half a point better in condition score than long cannon bone lambs, but differences were less evident in the adult sheep. He concluded that selection for longer cannon bone has resulted in a more

productive, though ungainly looking, sheep with higher twinning rate and better lamb survival.

Purser(1980a, 1982) also noted that the cannon bone length selection lines exhibited some common characteristics with other breeds. For instance, Finnish Landrace have long, thin bones, high fertility and low lamb mortality and Down breeds have short thick bones, fatten early, with good carcass quality, but low reproductive performance. These characteristics correspond to the long and short cannon bone selection lines, respectively. In addition, selection for more prolific ewes in several breeds has apparently resulted in a tendency to produce longer-legged animal(Purser, 1982). Whether there is a common cause for these genetic effects is not known, but it is believed by Purser(1982) that variation in pituitary function is involved, since pituitary gonadotropins affect both bone and gonad development.

Atkins and Thompson(1986) reported that selection for increased weight-adjusted cannon bone length at 8 weeks of age in sheep resulted in the following correlated responses: 1) increased body weights at all ages of growth from birth to maturity, 2) increased reproduction rate, mainly through litter size, but with smaller increases in the proportion of ewes lambing and the survival rate of lambs, and 3) increased numbers of adult ewes arising from fewer deaths and necessary culling. They reported correlations of 0.12 and 0.17 between adjusted cannon bone length and litter size and body weight,

respectively, and a correlation of 0.66 between body weight and litter size.

Selection for tall animals results in moderate to rapid progress. Furthermore, this change is accompanied by increases in the total productivity of larger and taller animals.

2.2.3.5 Selection for/against fatness.

Fat is the most variable tissue in the body, both in total amount and its partition within the body (Thompson, 1985). The total amount of fat in the body at any particular weight may be manipulated by the use of large or small maturing breeds. High heritability estimates for the level of fatness in carcass would suggest the possibility of manipulation within breeds (Thompson, 1982; Hood, 1983). However, heritability estimates in the live animal are not of the same magnitude as estimates based on carcass data. Table 2.4 shows some examples of heritabilities in sheep and pigs for both carcass and live animal fatness traits. In general, the heritability of carcass derived traits is from moderate to high and this indicates that appropriate selection should result in rapid genetic improvements in carcass composition in any desired direction.

Table 2.4. Heritability estimates for various assessment of fatness either in the live animal or from carcass data.

Character[1]	Heritability	Method[1]	Author	Animal
LABF	0.09	Henderson's 3	Parrat et al,1987	Sheep
8UBF	0.23±0.12	PHS	McEwan et al,1984	Romney sheep
14UBF	0.45±0.17	PHS	McEwan et al,1984	Romney sheep
7UBF	0.17±0.06	PHS	Beatson,1987	Coopworth sheep
10UBF	0.34±0.08	PHS	Beatson,1987	Coopworth sheep
13UBF	0.13±0.09	PHS	Beatson,1987	Coopworth sheep
UBF	0.26±0.07	Henderson's 3	Merks,1987	Dutch Landrace pigs
UBF	0.29±0.07	Henderson's 3	Merks,1987	Dutch Yorkshire pigs
LABF	0.39±0.04	Henderson's 3	Merks,1988	Dutch Landrace pigs
LABF	0.27±0.03	Henderson's 3	Merks,1988	Dutch Yorshire pigs
PERCENT FAT	0.36	Henderson's 3	Parrat et al,1987	Sheep
PERCENT FAT	0.34±0.22	β_{o-p}	Botkin et al,1969	Sheep
PERCENT FAT	0.21(sd=1.4%)	PHS	Bennett et al,1982	Southdown sheep
CCBFD	0.28(sd=0.5mm)	PHS	Bennett et al,1982	Southdown sheep
CCBFD	0.20	PHS	Clevelland et al,1988	Pigs
CCBFD	0.32±0.08	PHS	Thorsteinsson and Bjornsson,1982	Sheep
ADJUST-CCBF	0.28	PHS	Olson et al,1976	Sheep
CCBF	0.21±0.11	PHS	Wolf et al,1981	Sheep
PROBE-BF	0.30±0.06	β_{o-mp}	Edwards and Omtvedt,1971	Sheep
BF	0.39 to 0.66	β_{o-mp}	Hetzer and Miller,1972a	Pigs
BF	0.56±0.04	β_{o-mp}	Hetzer and Miller,1972a	Duroc pigs
BF	0.50±0.05	β_{o-mp}	Hetzer and Miller,1972a	Yorkshire pigs
BF	0.45		Dalton,1980	Beef cattle
BF	0.62 to 0.65		Dalton,1980	Pigs
BF	0.51±0.13	PHS	Botkin et al,1969	Sheep
BF	0.15±0.22	β_{o-p}	Botkin et al,1969	Sheep

[1], BF=Backfat depth, UBF=Ultrasonic BF, 7UBF= 7 months UBF(or 8, 10, 13, 14 months),

   CCBF=Carcass backfat depth, Adjust-CCBF=Carcass fat depth adjusted for skinning variation,

   PROBE-BF=Probe backfat depth. For additional abbreviations see Tables 2.1 and 2.2.

Selection against fatness at one carcass site may not be as beneficial as anticipated in reducing total carcass fatness (Wolf et al, 1981; Meyer et al, 1982). Therefore, if live animal predictors of fatness are based on the subcutaneous fat depot, selection may result in a change in only this depot, rather than total body fat, (Thompson, 1982). However, Olson et al(1976) and Wolf et al(1981) showed that the genetic correlation between most fat depots are high and positive suggesting that direct selection for a change in one depot should result in similar changes in other depots within the body. Therefore, genetically reducing fat at different subcutaneous positions could be expected to decrease total fat in sheep (Bennett et al, 1982). Furthermore, Kadim(1988) in a study of carcass composition and meat quality in Southdown sheep reported that selection against liveweight-adjusted backfat depth will be effective in reducing other body fat depots, without deterioration in muscle quality.

Olson et al(1976) also reported higher phenotypic correlations between carcass traits indicative of fatness (at 22-33 weeks of age) and pre-weaning gain (0.2 to 0.4) than with gains closer to slaughter age (-0.3 to 0.2). Because, the genetic correlation between post-weaning average daily gain and backfat depth adjusted by skinning variation tended to be near zero, it was suggested that selection for post-weaning gain to an average of 25 weeks would not increase subcutaneous fat depths. However, an increase in kidney fat (weight of kidney fat/carcass weight) could occur, because of

the negative genetic correlation between backfat depth and kidney fat and the positive genetic correlation between post-weaning growth rate and kidney fat. This would be of less importance since this fat is easily removed, the only undesirable effect being to slightly reduced the killing-out percentage.

In live animals, visual and tactile assessment, together with body weight and breed are the most important sources of information for estimation of body composition for commercial purposes. For commercial breeding and research work an increasing use of ultrasonic machines has occurred over the last decade. In pigs and cattle breeding, in particular, ultrasonic equipment has been used for many years in many countries. The equipment available ranges from small portable A-mode instruments giving only fat depth to complex B-mode scanners capable of producing two dimensional pictures of cross-sections through parts of the body (Alliston, 1983). Ultrasonic machines have the greatest practical value of various objective methods presently available for predicting carcass composition in live animals. The principles of the use of ultrasonic machines have been described by several authors (e.g., Andersen, 1975; Kempster et al, 1982; Alliston, 1983; Simm, 1983)). Briefly, This technique is based on the principle that high frequency sound will transmit through the tissues of the body, but when an interface between two tissues is encountered some sound is reflected back. A pulse generator transmits electric pulses which are converted

into sound signals in the transmiter. These signals are then passed through the tissues until reflected at an interface. The reflected signals are then picked up by the received and can be amplified and shown in a visual form by an oscilloscope. Variations in the time taken for the reflected signals to return to the transmiter-receiver are used to measure variations in the distance of boundaries between tissues.

The accuracy of ultrasonic assessments on the live animal depends on: the repeatability of several measurements on the same animal over time (Purchas et al, 1982); the repeatability of measurement between different operators (Rehben, 1981; Purchas et al, 1981a); the ultrasonic machine model (Andersen et al, 1981); the relationship between live animal and carcass measurements (Gooden et al, 1980), and on the animal species (Kempster et al, 1982).

Sheep have been the most controversial species with regard to the usefulness of ultrasonic measurements for breeding purposes. Kempster et al(1982) pointed out that ultrasonic measurements have not been as successful with sheep as with pigs and cattle. The primary reasons for this are first, to the smaller backfat depths and secondly, the greater mobility of the skin on the layer of fat under the skin. However, Moody et al(1965), Meyer et al(1966), Jensen(1977), Kemspter et al (1977), Gooden et al(1980) and McEwan et al(1987) have shown the feasibility of using ultrasonic

instruments in backfat depth assessments in live sheep, although caution was recommended. Fortin(1980) and Cameron and Smith(1985) reported unsatisfactory results of backfat depth measurements using ultrasonic instruments. They argued that the poor results obtained were due to the restricted or small range of liveweights and a small magnitude of backfat depth in sheep. They indicated that estimates of fatness or leanness could improve by measuring sheep at heavier liveweights as backfat depth will be greater and differences may be easier to detect.

Backfat depth measurements taken above m.longissimus (the 'eye muscle') in the region of the last rib, whether on the live animal or on the carcass, have usually been found to be more precise predictors of carcass lean content than other indirect measurements (Wood and MacFie, 1980). Gooden et al(1980) carried out an experiment to compare the relationship between each of ultrasonic measurements on live animals and the direct carcass measurements of subcutaneous backfat depth, and total carcass fat percent. Correlation coefficients of 0.76 and 0.80 between total carcass fat percent and ultrasonic fat depth, and total carcass fat percent and carcass backfat at the 'C' position respectively, indicated similar accuracies. Earlier, Moody et al(1965)also found that backfat depth and m.longissimus area of live lambs can be ultrasonically measured with acceptable accuracy.

In New Zealand, Bennett et al(1983b) crossed

ninety-three sires of the Romney, Dorset, Border Leicester and Coopworth breeds with Romney ewes at Wiremu, Wairakei and Rotomahana Research Stations. They found that longer carcasses adjusted for weight were genetically associated with less subcutaneous fat (ultrasound and carcass) and total carcass fat. However, actual backfat depths were more indicative of total fat than was length.

Bennett et al(1984), analysing data from sheep at the Ruakura Animal Research Station, noted that subcutaneous fat depth at equal stocking rate and birth-rearing status decreased as a consequence of selection for twining rate. In addition, the lambs of the high fertility selected line appeared to deposit less subcutaneous fat per kilogram of increase in carcass weight when the increases were caused by nutritional levels.

A preliminary report of a selection experiment for high or low weight-adjusted ultrasonic backfat depth in Coopworth sheep, has pointed out that selection for this trait was relatively successful (Fennessy et al, 1987). However, They indicated that after several years of selection the high and low lines diverged 0.8 and 2.3 standard deviations, respectively, from the control line, suggesting that response may be asymetric. They also pointed out that the low selection line had higher birth weights, and that the ewes had apparently higher ovulation rates. But the lines did not show differences in growth rate. This was not surprising since fat

depths were liveweight adjusted.

Selection against fatness in sheep usually employs individual selection based on one record. An alternative is to pick rams (progeny test) on the basis of differences between progeny groups in live animals or after slaughter (Rae, 1984). He pointed out that the use young rams in of progeny test could improve the rate of genetic gain by up to 50%. Kirton(1975) pointed out the two main difficulties of progeny testing for carcass characteristics were first, the high cost and secondly, the difficulty in collecting carcass data through slaughtering houses. However, Barton et al (1986) proposed a method in which these difficulties could be overcome using a progeny testing programme involving commercial breeders.

In pigs, direct selection for backfat depth has been carried out within and between breeds (Zoeller et al, 1964; Hetzer and Harvey, 1967; Gray et al, 1968; Hetzer and Miller, 1970; Berruecos et al, 1970). Zoeller et al(1964) reported that selection was effective in reducing weight-adjusted backfat depth and that the realized heritability was 0.74. They noted that a decrease in average daily gain took place along with the the decrease in backfat depth, but that productivity was not affected by selection. Later, Gray et al(1968) and Berruecos et al(1970) also selected against weight-adjusted backfat depth. Gray et al(1968) pointed out that much of the selection response

apparently occurred in the first two generations. They reported a realized heritability for average backfat depth of 0.32 and that the genetic correlation between backfat probes at shoulder, loin and ham ranged from 0.59 to 0.82 suggesting that many of the same genes affect backfat at different sites. Berruecos et al(1970) reported a realized heritability of 0.27 for low weight-adjusted backfat depth.

In one of the more important studies in pigs, Hetzer and Harvey (1967) and showed fatness in pigs was highly responsive to both upward and downward selection. They noted that after 10 generations of selection for backfat depth, the Duroc line selected for high fatness differed from the line selected for low fatness by 2.6 cm or 68% of the initial mean, at a liveweight of 79.4 kgs. Later, the difference in fatness between the high and low lines after 13 generations of selection amounted to 92% of the initial mean, while in Yorkshires after 11 generations the corresponding value was 73%. Additional heritability estimates for the trait are given in Table 2.4.

Further studies by Hetzer and Miller(1970, 1972a, b) noted also some correlated responses to selection for/against backfat depth. Hetzer and Miller(1970) reported that there was no clear indication of a consistent decline in reproductive performance due to the selection for/against backfat depth. Later, Hetzer and Miller(1972a) found that in Durocs both the pre- and post-weaning weights appear to be

negatively genetically correlated with liveweight-adjusted
backfat depth, but this was not the case to the same extent
with the Yorkshire. They concluded that if growth rate in
different breeds responded differently to selection against
backfat depth, then the way to produce leaner pigs most
effectively could vary depending on the way in which backfat
depth is genetically correlated with growth rate in the breed
in question. In the same experiment, they noted that moderate
to high negative genetic correlations obtained between some of
the body measures and backfat depth in Durocs and Yorkshires
suggested that selection based on length and height measures
could be effective in breeding for leaner pigs. However, they
stressed that simultaneous selection for any of these measures
along with selection against backfat depth should be more
effective in breeding meatier pigs than selection for either
of the two groups of traits alone (Hetzer and Miller, 1972b).

Fredeen and Mikani(1986) reported that selection for
low liveweight-adjusted backfat depth in pigs, measured using
the scalpel probe technique, was effective. The realized
heritability for this trait was 0.28 ± 0.04. They also pointed
out that the selection line for low liveweight-adjusted
backfat depth did not show any significant difference in
growth rate relative to the control line ($r_g=0.02$).

In poultry, results of selection for fatness are well
documented (i.e.Becker et al, 1978; Leclercq et al, 1980;
Griffin and Whitehead, 1982). Becker et al(1978)pointed out

that selection for abdominal fat to body weight ratio should decrease fat in other locations without changing the fat-free weight. Leclercq et al(1980) selected divergently for low and high abdominal fat in broilers and reported realized heritability estimates up to the second generation of 0.37 and 0.67 for the low and high lines, respectively. They noted that the food consumption of the fatty line was lower than that of the the lean line. Since the growth rate of the fatty line was also less, the food conversion ratio of both lines were not different. However, a better food conversion ratio in males of the lean line was found.

Griffin and Whitehead(1982) pointed out that selecting for very low density lipoprotein (VLDL) concentration in plasma can be used for predicting fatness in live birds. Later, Whitehead and Griffin(1984) selecting for or against plasma VLDL concentration during three generations found a high realized heritability for VLDL (0.50±0.08), and several correlated responses. Selection for decreased VLDL caused a relative decrease in abdominal fat and total body lipid and an increase in body protein, together with improvements in the conversion efficiencies of food and dietary protein. They concluded that selective breeding could result in leaner chickens and that the plasma VLDL selection method could be applied on a commercial scale. Thereby providing an alternative to the expensive nutritional methods of controlling excessive fat deposition in broilers. Garwood(1987) stated that the findings of Griffin and

Whitehead(1982) and Whitehead and Griffin(1984) agreed with his own and that VLDL had a high positive correlation with body lipid content. However, this method is unlikely to be successful with mammals because of the physiological differences between birds and mammals in the synthesis and transport of lipids (Hood and Pym, 1982; Hood, 1983; Cameron and Smith, 1985)). In birds, the fatty acids are synthesised in the liver and transported by the blood stream to the fat depots, but in mammals the synthesis occurs is in the fat depots (adipocyte cells) themselves.

In conclusion, selection to modify fatness traits in farm animals has been successful and resulted in several desirable correlated responses in skeletal size, reproductive performance rate, feed intake and the efficiency of feed utilization. However, the use of objective measurements of fatness and leanness in the live animal on commercial farms is still limited. Rae(1984) suggested using progeny testing to improve the rate of genetic gain and Barton et al(1986) suggested a method of overcoming the difficulties associated with progeny testing in sheep. Therefore, it is likely in the near future with the help of ultrasonic equipment and efficient breeding plans that rapid genetic gains towards the objective of leaner sheep should be achieved.

CHAPTER THREE   MATERIALS AND METHODS

CHAPTER THREE. MATERIALS AND METHODS

3.1 The sheep and their environment.

Details of the Southdown base flock have previously been given by Barton(1981) and Purchas et al(1981b, 1982). Briefly, stock came from several sources and were chosen to represent a range of types with regard to fatness and meatiness or muscling. After being assessed ultrasonically in 1976, ewes were allocated to either the fat or meaty flock on the basis of percent fat depth deviations (see section 3.2). The ultrasonic information was used in the initial allocation of the sheep to these flocks, but not at the time of their purchase from various commercial flocks.

The data analysed in the present investigation comes from the descendants of the above animals that were born in years 1979 to 1986, inclusive. Data were used from 1979 onwards only because: prior to 1979 the ultrasonic equipment was in the development phase, the selection lines were closed in 1979, and the ultrasonic backfat depth (UBF) assessments were more regularly assessed from that year. Ultrasonic assessments were made using equipment similar to that described by Gooden et al(1980); model AIDD(3).

The flocks were run on the Terrace Block of The Sheep and Beef Research Unit, at Massey University, Palmerston North., N.Z.

Both flocks were run together on pasture with no supplementary feeding, and were managed under commercial conditions wherever possible.

The breeding ewes were separated only for the mating period however, every effort was made to maintain similar conditions across the flocks. The mating season varied slightly between years, starting between 14 and 25 March each year. The ewes remained with the sires for approximately eight weeks. The allocation of the ewes to each sire was at random within each flock, except that rams were not mated to their dams or sibs.

Lambing took place during August and September. The ewes were observed daily and new lambs were weighed, tagged and sexed. The birth rank, date of birth and dam tag number was recorded. Lambs were tailed at about 4 weeks of age and weaned and weighed in late November or early December. Males and females were separated at weaning.

At about 6-9 months of age, UBF measurements were assesed on the ram and ewe hoggets. Approximately 20 ewe hoggets were chosen to enter each flock based on this measurement. About 20 ram hoggets were also chosen based on this first UBF assessment. Remaining animals were culled. Table 3.1 shows the number of hoggets available for selection, and the number selected, each year. Several more measurements were taken on the rams only, up to 19-20 months of age. These measurements were averaged to enable the final selection of two-tooth replacement rams for each flock.

Table 3.1. Availability of hoggets for selection each year from 1980 to 1986.

YEAR	BACKFAT SELECTION LINE	EWES		RAMS	
		NO.MEASURED	NO.SELECTED IN THE FIRST STAGE	NO.MEASURED	NO.SELECTED IN THE FIRST STAGE.
1979	High9	36	19	30	18
	Low9	43	24	32	22
1980	High	27	27	19	19
	Low	22	22	21	21
1981	High	39	23	38	22
	Low	18	14	20	15
1982	High	30	20	36	20
	Low	31	20	41	20
1983	High	39	20	42	21
	Low	33	20	28	20
1984	High	31	21	31	19
	Low	24	20	28	18
1985	High	30	20	38	22
	Low	38	19	40	21
1986	High	34	22	38	24
	Low	45	24	47	24

9, Abbreviations are defined in Table 3.3.

To arrive at a final selection decision, the weight and physical condition of replacement rams were also taken into account. Two reserve rams for each flock were chosen following the same procedure. In some years a reserve sire was used when one of the originally selected rams was unavailable for mating (i.e. injuries, infertility or dead). The sires were replaced each year. Ewes were culled for barrenness. Some ewes were culled due to poor condition of their teeth. Table 3.2 shows the size and age composition of the ewe mating flocks.

3.2 Traits investigated.

All measurements were liveweight-adjusted prior to analysis, except for birth weight, pre- and post-weaning growth rates. The traits regularly assessed were UBF, body length (L), shoulder height (H), pre-weaning growth rate (PrGR) and post-weaning growth rate (PoGR). Table 3.3 shows the most common abbreviations used in the text.

Ultrasonic backfat depth was assessed on live sheep (Gooden et al, 1980). Backfat depth in this study was measured at the C position, which is defined as the thickness of backfat over the deepest part of the 'eye muscle' (M.longissimus) over the last rib (Palsson, 1939; Dodd et al, 1986). The distance of the C site from the midline varies with the liveweight of the sheep (Purchas et al, 1981a). Table 3.4 shows the guidelines presented by

Table 3.2. Size of the ewe flocks at mating and their age composition by line and by year.

YEAR	HIGH LINE								LOW LINE								LINES TOTAL
	2	3	4	5	6	7	8	total	2	3	4	5	6	7	8	total	
1979	22	1	8	22	2	–	–	55	16	–	12	25	–	–	–	53	108
1980	1	17	–	5	18	–	–	41	4	10	–	9	13	–	–	36	77
1981	17	8	25	1	2	–	1	54	16	4	9	–	1	–	–	30	84
1982	5	19	5	18	–	1	–	48	13	19	6	12	1	2	1	54	102
1983	12	13	22	6	13	–	–	66	5	12	20	5	4	–	–	46	112
1984	8	12	13	14	2	1	–	50	9	13	10	12	4	–	–	48	98
1985	9	10	14	13	8	1	–	55	10	11	9	12	17	3	–	62	117
1986	8	15	11	18	10	4	–	66	11	13	16	10	8	8	–	66	132

9, Abbreviations are defined in Table 3.3.

TABLE 3.3. Common abbreviations used in the text.

%DEV	Percent deviation unit
High	High backfat selection line
Low	Low backfat selection line
UBF	Ultrasonic backfat depth
LABF	Liveweight-adjusted backfat depth
LAL	Liveweight-adjusted body length
LAH	Liveweight-adjusted shoulder height
h^2	Heritability
t	Repeatability
r_g	Genetic correlation
r_p	Phenotypic correlation
PrGR	Pre-weaning growth rate
PoGR	Post-weaning growth rate
ADG	Average daily gain
CSD	Cumulative selection differential
YR	Yearly response
CYR	Cumulative yearly response
GASD	Group-Average selection differential
Dam age	Age of dam (2yo=2 years old, 3-5yo=3 to 5 years old and 6+yo= 6 or more years old)
BRK	Birth rank
LSM±SE	Least square means and their standard errors
OVLSM	Overall LSM

Purchas et al(1981a). The distance varied slightly, depending on the shape of the individual animals. Measurements were taken in both sides and the average was recorded.

After transforming UBF and liveweight to logarithmic values, a simple linear regression was fitted to adjust UBF by liveweight, resulting in a liveweight-adjusted backfat depth (LABF). This was undertaken within each sex and time of measurement. The individual deviations from the regression line were expressed as either positive or negative percent deviations (%DEV) using the equation:

$$\%DEV = \left[10^{(Y_i - \hat{Y}_i)} - 1.0)\right] 100 ,$$

where: Y_i = The observed value, and

$\hat{Y}_i$ = The predicted value from the regression line.

Table 3.4. Guideline distances from the midline to take UBF measurements in sheep (Purchas et al, 1981).

LIVEWEIGHT (KG)	DISTANCES FROM THE MIDLINE (mm)
lighter than 35	35
between 35 to 45	40
between 45 to 55	45
heavier than 55	50

Shoulder height was measured over the forelegs from the base of the hoof to the top of the shoulder. Body length was measured as the distance from the brisket (cranial end of the sternum) to the pin bones (tuber ischii) (Purchas et al, 1981b). Shoulder height and body length were adjusted by liveweight and expressed as percent deviations (LAH and LAL, respectively) as explained for LABF.

Pre-weaning growth rate was calculated by subtraction of the birth-weight from the weaning weight and dividing by the number of days from birth to weaning. The result was expressed in grams per day.

Post-weaning growth rate was divided into three phases: a) pre-selection growth rate which was calculated from weaning to the first UBF measurement for ram and ewe hoggets; b) periodical growth-rate, whereby growth rates for several periods, within a year, were calculated using several measurements (from 2 to 8) for rams only, and c) periods within b), excluding the pre-selection stage, were reduced to two periods (winter and spring) and a total period from weaning to the last UBF measurement (W, S and WW-UBF, respectively) within each year, to facilitate interpretation and comparisons between periods and years. These periods are defined in Appendix 7.1. For LABF, LAH and LAL, each trait was divided into three periods within year, and analysed separately in a similar way to PoGR. These periods are defined in Appendices 7.2, 7.3 and 7.4, for LABF, LAH and LAL, respectively.

3.3 Statistical methods.

3.3.1 Linear models.

Birth weight, pre- and post-weaning growth rate, LABF,
LAH and LAL were analysed using a general linear model which
included birth rank, line of selection, dam age, sire and
interaction effects. All analyses were carried out within sex,
except for birth weight and pre-weaning growth rate, because they
were run together in the pre-weaning stage. Date of birth was
included also in the general model as a covariate, because of
possible effect of differences in lamb age on the response
variable. The analyses was carried out within year (this being
the year in which animals were born) using a Generalized Linear
Model Computer Program, Gilmour(1985). The general linear model
was:

$$Y_{ijklmn} = \mu + D_i + BRK_j + SEX_k + G_l + S_{lm} +$$

$$(SEX_k)(BRK_j) + (S_m)(BRK_J) + (D_i)(G_l) + (G_l)(BRK_j) +$$

$$(D_i)(BRK_j) + \beta(x_{ijklmn}) + E_{ijklmn}$$

where: Y_{ijklmn} = an observation on the nth animal

being in the ith dam class age, j^{th} birth rank

of the kth sex, sired by the mth sire in

the lth selection line,

μ= the general mean,

D_i= the fixed effect of the ith dam class

age(i = 1, 2, 3),

BRK_j= the fixed effect of the jth birth

rank(j = 1, 2),

SEX_k= the fixed effect of the kth sex (k = 1,2),

G_l= the fixed effect of the lth selection

line (l = 1, 2),

S_{lm} = the random effect of the mth sire nested

in the lth selection line (m = 1, 2),

$(S_m)(BRK_j)$= the interaction between the random

effect of the mth sire and the jth birth rank,

$(D_i)(G_l)$ = the interaction between the fixed effects of

the ith dam class age and the lth selection line,

$(BRK_j)(SEX_k)$ = the interaction between the fixed

effects of the jth birth rank and the kth sex.

$(BRK_j)(G_l)$ = the interaction between the fixed effects

of the jth birth rank and the lth selection line,

$(D_i)(BRK_j)$ = the interaction between the fixed

effects of the ith dam class age and the

j^{th} birth rank,

$(D_i)(G_l)$ = the interaction between the fixed

effect of the ith dam class age and

the lth selection line,

$(BRK_j)(G_l)$ = the interaction between the fixed

effect of the jth birth rank and the lth

selection line,

β= the regression coefficient of the Y_{ijklmn}

(birth weight, PrGR, PoGR, LABF, LAH or LAL)

on the covariate X_{ijklmn} (date of birth or DB),

$x_{ijklmn} = (X_{ijklmn} - \bar{X})$, $\bar{X}$ being the overall

mean of the covariate X_{ijklmn}, (DB), and

E_{ijklmn} = the random effect of the error associated

with an observation on the nth animal being in

the i^{th}dam class age, in the jth birth

rank, in the kth sex, sired by the mth sire being used

in the kth selection line.

Residual effects were assumed to have a normal and independent distribution with mean=0, and variance=σ_e^2. The sire effects were assumed also to have a normal and independent distribution with mean = 0 and variance = σ_s^2.

Prelimiary analyses were undertaken to identify non-significant factors for each of the traits under investigation. Non-significant effects (except for selection line) were dropped from the final model.

3.3.2 Generation interval.

The generation interval(GI) was estimated as the average age of parents when their offspring born (Turner and Young, 1969). In the case of sires, the GI was two years because they were replaced each year. For dams, the calculation of GI was more complicated because several ewe-age-groups were run representing different generations. To overcome this problem, each age-group was weighted by the number of dams in each age-group in a particular year. The GI in the $\underline{i}$ year was calculated as:

$$GI_i = 1/2 \left[GI_{i-dams} + GI_{i-sires} \right] ,$$

where: $GI_{i-sires}$ = 2 years, and

$$GI_{i-dams} = \sum_{j=2}^{a} D_j n_{ij} \bigg/ \sum_{j=2}^{a} D_j$$

where: D_j = the jth ewe age (a = 2,...,8), and

n_{ij} = number of ewes in the jth ewe-age-group in the ith year.

3.3.3 Direct responses to selection.

Direct responses to selection for or against LABF were evaluated in two ways. First, as the difference between successive years within selection line, this will be called yearly response. Secondly, as the divergence between selection lines within years, this will be called divergence. The cumulated responses to selection were calculated as either the cumulated yearly response (obtained by adding the previous year responses to the current year), or the cumulated divergence.

For ram hoggets, responses to selection were based on either the first LABF assessment alone or the average of all measurements. Response in the ewe hoggets was based on the first LABF measurement only.

3.3.4 Correlated responses to selection.

The correlated responses to selection were calculated as the divergence between the high and low backfat depth selection lines for birth weight, PrGR, PoGR, LAH AND LAL. Correlated responses were expressed in terms of change in the trait (in original units of measurement) resulting from the application of one unit of selection pressure on LABF.

3.3.5 Selection differential.

The selection differential is the difference between the mean phenotypic value of the individuals selected as parents and the unselected population mean (Falconer, 1981). Selection differentials are used to provide an estimate of the selection pressure applied to obtain the measured selection response in the selection experiment. This allows fair comparisons of selection responses in different selection experiments. The selection differential for parents in the first years was set to zero.

Several selection differentials were calculated in order to describe the selection intensity applied at different levels. First, a simple selection differential was calculated as the difference between the selected sires and unselected population means for each selection line. This was calculated based on the first LABF assessment for males only (S1), Figure 3.1. This was done even though selection of the sires was based on the average of several measurements throughout the year, because not all animals were present at the final selection (Table 3.1). This is likely to represent an underestimate of the actual selection differential.

In an attempt to examine the degree to which the selection differential based on the first LABF measurement alone underestimated the actual selection differential a combined selection differential was calculated (S2), Figure 3.1. This

comprised the selection differential based on the first selection (S3) plus the selection differential based on the second selection (S4), Figure 3.1. The S3 was calculated for the ram and ewe hoggets, but S4 was calculated on the ram hoggets only.

A linear regression of S1 on S2 was calculated to examine the functional dependency of the two estimates of selection pressure, within each selection line. If the distribution of LABF after culling on first measurement was to be the same as the distribution of the average of all measurements, then a regression coefficient of 1 would be expected.

Because the physical condition and liveweight of rams was included in the selection of breeding rams, there was some loss of selection efficiency. This loss was examined by calculating selection differentials for the top 2 rams and the two sires for each selection line.

The calculation of cumulated selection differential was complicated by overlapping generations in the ewes. To overcome this, a group-average selection differential (GASD) which included the selection differential for each dam-age-group and the two sires was calculated within sex and within line of selection. The GASD was calculated as the average selection differential of the dam-age-groups and the two sires weighted by the number of offspring. The selection differentials for parents

(a)
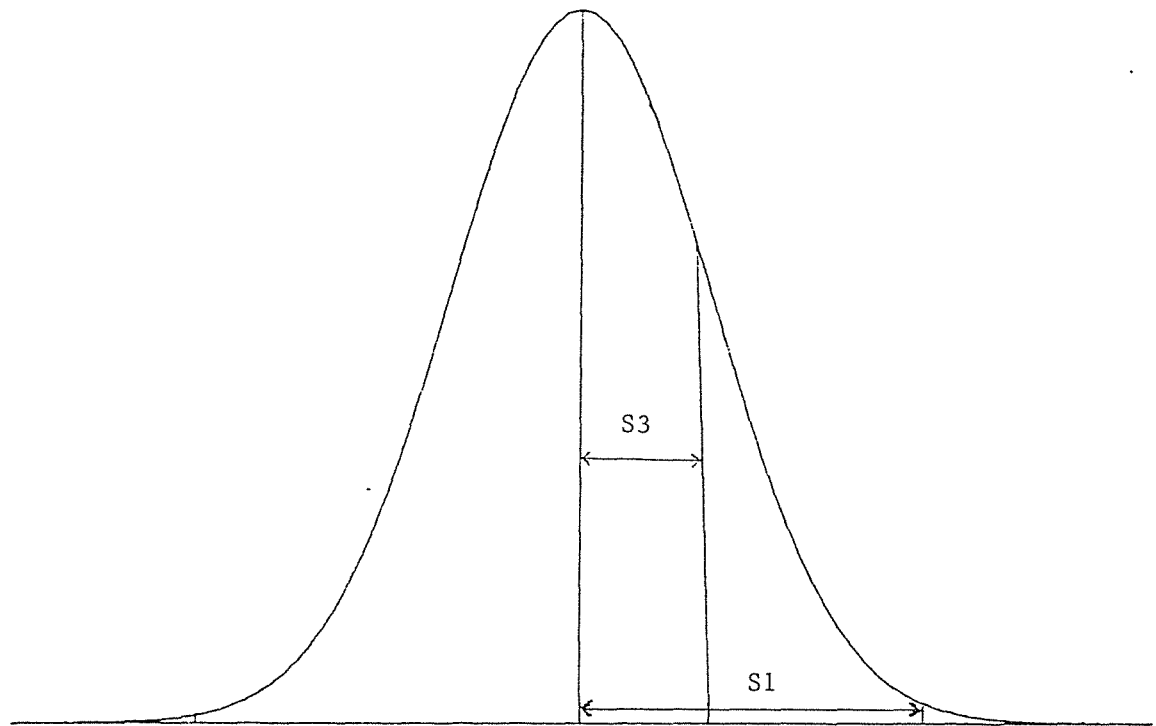
(b)
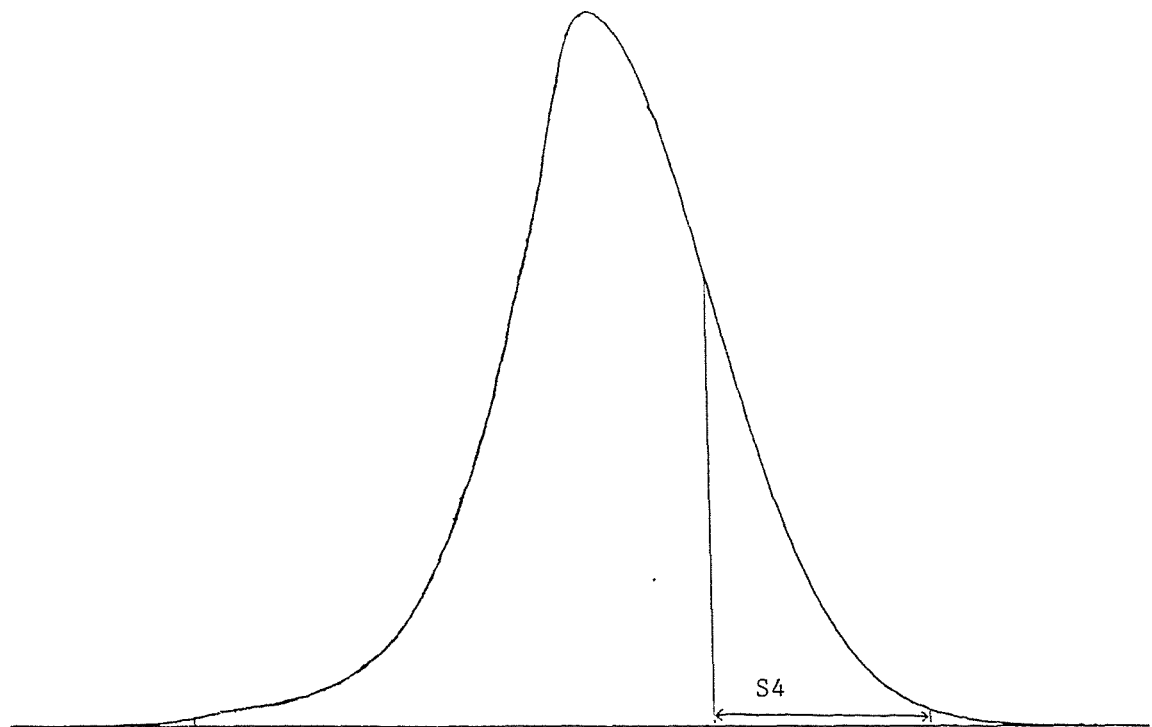
$$S2 \quad = \quad S3 \ + \ S4$$

Figure 3.1   Diagrams of the selection differentials (S1, S2, S3 and S4) based on: (a) the first LABF measurement, and (b) the average of all LABF measurements.   See text for a description of the selection differentials.

in the first years was set to zero. The GASD for each sex within selection line in year $\underline{i}$ is given by:

$$GASD_i = \left\{ \left[\sum_{j=1}^{a} (S_{ij}(n_{ij}/N_i))/a \right] + \left[\sum_{j=2}^{b} (S_{ij'}(n_{ij'}/N_i))/b \right] \right\} /2 \ ,$$

where: i = the hogget birth year or year of analysis ($i = 1,\ldots,8$),

S_{ij} = the simple selection differential for the jth sire ($a = 1, 2$; sometimes 3 if a reserve sire used),

$S_{j'}$ = the simple selection differential for the j'^{th} dam-age-group($b = 2,\ldots, 8$),

n_{ij} = the number of lambs for the jth sire in the ith year,

N_i = total number of lambs in the ith year, and

$n_{ij'}$ = the number of lambs by the j'^{th}

dam-age-group in the ith year,

The cumulated selection differential (CSD) for each
selection line, in each year and sex, was calculated by adding
the average of the parental CSD to the group-average selection
differential. The CSD for year $\underline{i}$ is given by:

$$CSD_i = GASD_i + \left\{ CSD_{i-2} + \left[\sum_{j=2}^{b} CSD_{i-j'}(n_{ij'}/N_i) \right] \right\} / 2 ,$$

where: CSD_i = the cumulated selection differential

in the ith year,

$GASD_i$ and b = defined as before,

CSD_{i-2} = the sires' CSD of the

progeny born in the ith year of analysis,

$CSD_{i-j'}$ is the CSD of the respective j'^{th}

dams-age-group of the offspring born in

the ith year of analysis,

$n_{ij'}$ = the number of dams in the

j'^{th} dam-age-group in the ith year, and

N_i = total number of dams in the ith year.

.

An estimation of the selection response per unit of selection pressure applied was calculated using simple linear regression. This regression was considered to be the realized heritability of the trait by Falconer (1981). However, because of selection having been applied prior to 1979 the term realized heritability is not strictly aplicable in this study. This approach was used for both of the techniques named in section 3.3.3 for estimating response to selection. First, the regression of the CSD on the cumulated yearly response and secondly, the regression of the CSD on divergences between lines in LABF. In the first case, regressions were calculated for each sex and line combination but in the the second case regression estimates were within sex only. The standard error of the regression coefficient was used also as the standard error of the realized heritability (Falconer, 1981).

3.3.6 Phenotypic correlations.

Product-moment correlations between all pairs of combinations of variables (LABF, LAH and LAL) were calculated. Correlations between consecutive measurements were calculated within trait.

The pooled product-moment correlations (pooled phenotypic correlations) within and between variables were calculated after first testing the hypothesis that the various correlation coefficients were from the same bivariate population, using the Z transformation (Snedecor, 1956; Steel and Torrie, 1981). If the hypothesis was accepted, it was concluded that the correlation coefficients were homogeneous and from the same population. By converting a weighted mean Z value back to a correlation coefficient, a pooled value of the several coefficients was obtained.

3.3.7 Genetic parameters.

3.3.7.1 Heritability.

Heritability estimates were calculated using several approaches for LABF trait across and within lines, using data obtained prior to the first culling. Heritability estimates for LAH and LAL were calculated only using nested design. The approaches were:

1) Dam-offspring correlation. This method was used on the LABF without correction for any non-genetic effects (other than for liveweight). The standard error was calculated as twice the standard error of the correlation coefficient.

2) Dam-offspring regression. An intrasire regression was calculated for LABF without any corrections other than liveweight. This was to examine whether using a selected population of dams inflated the heritability obtained from the first method. The standard error was calculated as twice the standard error of the regression coefficient.

3) Henderson's method 3. Estimation of variance

components in this approach was undertaken by fitting a model including sire as the only independent variable (Henderson, 1953). Variance components were calculated as detailed by Becker(1984). The standard error was calculated using the approach of Swiger et al(1964).

4) <u>Nested design.</u> A heritability estimate was based on a two-way nested design following Henderson's method 2 (Henderson, 1953). The general procedure was divided in two parts:

4.1) <u>First model.</u> The liveweight-adjusted data for backfat depth, shoulder height and body length was adjusted for all fixed effects and the covariate date of birth. The model was:

$$Y_{ijklmn} = \mu + A_i + D_j + BRK_k + SEX_l +$$
$$G_{im} + \beta(x_{ijklmn}) + E_{ijklmn},$$

where: Y_{ijklmn} = an observation on the

n^{th} animal, being of the jth dam

class, the kth birth rank,

from the lth sex, from the mth selection

line within the ith year,

A_i = the fixed effect of the ith
year $(i = 1, \ldots, 7)$,

SEX_l = the fixed effect of the lth
sex $(l = 1, 2)$,

G_{im} = the fixed effect of the mth
selection line within the ith
year $(m = 1, 2)$,

E_{ijklmn} = the random effect of the
error associated with the $ijklmn^{th}$
observation.

Factors μ, D_j, BRK_k, β and $x_{ijklmno}$
are defined in section 3.3.1.

4.2) <u>Second model.</u> Once the data for LABF, LAH and LAL were adjusted for the first model, an estimation of the sum of squares within sire was calculated on the residuals and then pooled across sires to obtain the sum of squares due to sires. The model was:

$$Y_{ij} = \mu + S_i + E_{ij}$$

where: S_i = the random effect of the ith sire, and μ and E_{ij} defined in similar way that in section 3.3.1.

Variance components were calculated as detailed by Becker(1984). Residual effects were assumed to have a normal and independent distribution with mean = 0 and variance= σ_e^2. The sire effects were assumed also to have a normal and independent distribution with mean = 0 and variance = σ_s^2.

All the standard errors estimations were calculated using the approach of Swiger et al(1964), unless otherwise stated.

Three periods for LABF, LAL and LAH were formed (Appendices 7.2, 7.3 and 7.4, repectively.). The first period pertained to the unselected population, only in the case of the LABF. Data from this period for LABF were analysed as previously described. Because of the interest in obtaining heritability estimates for LAH and LAL in the three periods and LABF in the second two periods, Henderson's method 2 was also used.

3.3.7.2 Repeatability.

The repeatability of the traits (LABF, LAH and LAL) was assesed as the intraclass correlation of the trait (Snedecor, 1956; Becker, 1984). All the information available within year for each trait was analysed across and within flocks.

3.3.7.3 Genetic correlation.

The genetic correlations considering the offspring-dam relationships were calculated for all pairs of combinations among LABF, LAH and LAL. The general equation to calculate the genetic correlation was derived as:

$$r_{p1-2} = 1/2(r_{g1-2} \; h_1 \; h_2), \text{ then}$$

$$r_{g1-2} = 2r_{p1-2}/h_1 \cdot h_2,$$

where: r_{p1-2} = phenotypic correlation between character 1 and character 2,

r_{g1-2} = genetic correlation between character 1 and character 2,

h_1 = root square of the heritability of character 1, and

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h_2 = root square of the heritability of character 2.

CHAPTER   FOUR   RESULTS

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CHAPTER FOUR. RESULTS.

4.1 Non-genetic effects.

The contribution of various non-genetic effects in the

various traits studied will be presented in sequence from animal

birth to sire selection. In all cases, preliminary analysis were

run to allow the removal of non-signififcant factors from the model.

However, because in most years birth rank, sex and age of dam were

significant, they were always included. Selection line was always

included to enable the examination of selection line differences in

the traits investigated.

4.1.1 Birth weight.

Table 4.1 shows the least square means and standard

errors (LSM±SE), the overall LSM (OVLSM) and levels of

significance for the factors affecting birth weight. In all

years, birth rank was the most important factor affecting birth

weight. Singles weighed between 0.51 kg (14%) and 0.93 kg

(28.4%) more than twins at birth. Ram lambs were significantly

heavier than ewe lambs in most years, with the advantage being

between 0.18 kg (5%) and 0.29 kg (8%). In spite of the

non-significant difference between sexes in 1980 and 1986, the

ram lambs were approximately 3% heavier than the ewes. In most

years, age of dam also significantly affected birth

Table 4.1. Least square means (LSM±SE) for birth weight (kg) within various non-genetic classes and for each selection line.

YEAR		1980	1981	1982	1983	1984	1985	1986
No.of lambs		159	146	193	182	162	164	174
SEX:	Ram	3.94±0.08	3.98±0.07	3.78±0.08	3.95±0.07	3.57±0.09	3.53±0.06	3.57±0.07
	Ewe	3.82±0.07	3.78±0.09 *	3.60±0.09 *	3.66±0.09 **	3.33±0.09 *	3.27±0.07 **	3.46±0.07
BRK[1]:	Single	4.13±.10	4.25±0.10	4.0±0.10	4.27±0.09	3.77±0.10	3.67±0.80	3.84±0.09
	Twin	3.62±0.05 **	3.50±0.07 **	3.39±0.08 **	3.34±0.07 **	3.14±0.08 **	3.13±0.06 **	3.18±0.05 **
LINE:	High	3.74±0.07	3.81±0.07	3.59±0.09	3.73±0.07	3.42±0.09	3.43±0.07	3.50±0.07
	Low	4.02±0.07 *	3.94±0.09	3.79±0.08 *	3.89±0.09	3.48±0.09	3.38±0.07	3.53±0.07
DAM AGE[1]:2yo		3.73±0.12	3.59±0.07	3.38±0.10	3.45±0.13	3.20±0.11	3.35±0.10	3.23±0.11
	3-5yo	3.86±0.07	4.11±0.07	3.78±0.05	3.95±0.06	3.66±0.06	3.45±0.06	3.61±0.06
	6+yo	4.06±0.08 *	3.92±0.17 *	3.92±0.20 *	4.00±0.13	3.50±0.19 **	3.41±0.09	3.70±0.09 **
OVLSM[1]		3.88±0.06	3.87±0.07	3.70±0.07	3.80±0.06	3.45±0.08	3.40±3.51	3.51±0.05

[1], Abbreviations are defined in Table 3.3, *P≤0.05, **P≤0.01

weight. Generally, 2-year-old (2yo) ewes produced significantly lighter lambs than 3- to 5-year-old (3-5yo) ewes, with the difference being between 0.13 kg (3.5%) and 0.52 kg (14.5%). The difference between 3-5yo ewes and 6- or more-years-old (6+yo) ewes were inconsistent and in most years the differences were non-significant.

4.1.2 Pre-weaning growth rate.

Table 4.2 shows LSM±SE, levels of significance, and birth weight regression coefficients for factors affecting pre-weaning growth rate. Birth rank and sex were the most important factors affecting pre-weaning growth rate. The effect of birth rank was significant in all years with singles growing between 9 g/day (5.4%) and 36 g/day (22.6%) faster than twins. Ram lambs grew significantly faster than ewe lambs in all years with the advantage being between 12 g/day (6%) and 23 g/day (13.8%).

In 1980, 1982, 1984 and 1985 age of dam showed significant effects. The effect of ewe age on pre-weaning average daily gain (PrGR) was inconsistent, although 3-5yo ewes generally provided the fastest growth rates and there was generally little difference between 2yo and 6+yo ewes.

Table 4.2. Least square means (LSM±SE)[1] for pre-weaning average daily gain (g/day) for various non-genetic classes and for each selection line.

Year	1980	1981	1982	1983	1984	1985	1986
No.of lambs	159	146	193	182	162	164	174
SEX: Ram	155.31±4.13	210.43±4.50	211.52±3.89	169.11±4.88	187.38±5.83	198.27±3.50	206.68±4.36
Ewe	142.72±3.52 **	198.46±5.22 *	194.12±4.25 **	157.30±5.43 *	164.79±5.50 **	185.09±3.91 **	192.04±4.09 **
BRK[1]: Single	160.31±5.33	213.77±6.32	215.55±4.77	167.51±6.70	193.93±6.44	198.51±4.54 .	207.07±5.78
Twin	137.73±2.79 **	195.12±4.02 **	190.09±3.77 **	158.90±4.83 **	158.25±5.42 **	184.85±3.34 **	191.65±3.44 **
LINE: High	150.26±3.78	206.48±4.28	202.26±4.19	161.64±4.51	172.25±5.72	188.47±3.86	199.46±4.26
Low	147.77±3.78	202.41±5.43	203.37±3.95	164.78±5.72	179.92±5.56	194.89±3.58	199.26±4.16
DAM AGE[1]:2yo	142.84±6.14	206.25±4.21	205.40±4.60	167.68±8.16	163.06±7.19	192.19±5.61	203.73±6.77
3-5yo	158.75±3.62	211.96±4.61	219.01±2.56	159.73±4.19	189.89±3.83	197.13±3.42	204.17±3.65
6+yo	145.46±4.20 *	195.13±9.51	184.05±9.16 **	162.21±8.27	175.32±11.58 **	185.71±4.74 *	190.18±5.50 *
β_{bwt}(g/kg)	3.83	10.36 *	13.10 **	12.10	5.67	16.30 **	13.38 **
OVLSM[1]	149.02±3.09	204.45±4.00	202.82±3.56	163.21±4.16	176.09±4.75	191.78±2.75	199.36±3.37

[1], β_{bwt} = regression of birth weight on PrGR. For additional abbreviations see Table 3.3., *P≤0.05, **P≤0.01.

The regression coefficient of birth weight on PrGR was significant and positive for most years indicating that lambs with higher birth weight grew significantly faster.

4.1.3 Post-weaning growth rate.

The ewe and ram lambs were run separately after weaning, therefore the analysis for post-weaning growth rate (PoGR) pre-selection was carried out within sex. Table 4.3 shows the LSM±SE for PoGR up to the time of first selection and their level of significance for ram hoggets. Birth rank continued to be the most important factor affecting growth rate. Birth rank was significant in four of the seven years with twins growing between 14 g/day (25%) and 17 g/day (31%) faster than singles. As with pre-weaning growth rate, 3 to 5 years old ewes provided the fastest growth in 1982 and 1983, but this was inconsistent across years.

Table 4.4 shows the LSM±SE and the level of significance for PoGR of ewe hoggets. The effect of birth rank was significant in most of the years with twins growing between 9 g/day (18.4%) and 20 g/day (23.5%) faster than singles. The age of dam factor did not significantly affect growth rate in the ewe hoggets.

Table 4.3. Least square means (LSM±SE) for post-weaning ADG[1] within various non-genetic classes and for each selection line in the unselected population of ram hoggets.

	YEAR						
	1980	1981	1982	1983	1984	1985	1986
No.HOGGETS	40	58	77	70	59	78	85
BRK[1]:Single	80±10	56±5	75±5	99±5	52±6	80±5	75±6
Twin	86±7	70±3	91±5	116±5	68±5	90±4	84±3
		**	**	*	*		
LINE:High	84±9	66±3	94±6	108±4	60±5	85±4	82±5
Low	81±8	60±5	73±5	107±6	60±5	85±4	77±4
DAM AGE[1]:2yo	89±21	64±4	71±7	108±7	69±8	82±6	84±7
3-5yo	77±5	64±4	94±3	115±4	53±4	82±4	78±3
6+yo	83±5	62±7	86±10	100±7	59±10	92±6	78±6
			**	*			
OVLSM[1]	83±8	63±3	84±4	108±4	60±4	85±3	80±5

[1], Abbreviations are defined in Table 3.3., *P≤0.05, **P≤0.01.

Table 4.4. Least square means (LSM±SE) for post-weaning ADG within various non-genetic classes and for each selection line in the unselected ewe hogget population.

YEAR		1980	1981	1982	1983	1984	1985	1986
No.HOGGETS		49	57	61	72	55	68	79
BRK[1]:	Single	40±4	58±6	57±7	85±7	49±4	52±4	81±5
	Twin	53±3 **	65±4	65±6	105±7 **	58±4 *	63±3 *	94±3 **
LINE:	High	48±3	60±4	63±6	97±6	55±4	59±4	86±4
	Low	45±3	63±5	59±6	94±7	52±4	57±3	89±4
DAM AGE[1]:2yo		46±7	65±4	57±5	94±13	57±4	62±6	90±6
	3-5yo	48±3	59±3	58±3	98±4	52±2	53±2	84±3
	6+yo	46±4	59±10	67±16	95±12	51±9	59±4	88±5
OVLSM		47±3	61±4	61±6	96±6	53±3	58±3	88±3

[1], Abbreviations are defined in Table 3.3., *$P \leq 0.05$, **$P \leq 0.01$.

The LSM±SE of ADG over the winter and spring periods (periods W and S, respectively, see section 3.2) in the selected ram hoggets are shown in Table 4.5, post-weaning growth rate prior to winter were presented in Tables 4.3 and 4.4 for the unselected ram and ewe hoggets, respectively.

The analysis of PoGR for periods W and S showed significant factors affecting growth rate in 1982 and 1983 only. In the analysis of the ADG over the total period (period WW-UBF) for 1983, the birth rank effect was significant with twins growing 8 g/day (9%) faster than singles. Date of birth was found to be significant in 1982 and 1983 for both periods W and WW-UBF. The regression coefficient indicated that ram hoggets born late in the season grew between 0.8 g/day and 1.3 g/day faster than ram hoggets born earlier, in both periods W and WW-UBF in 1982 and 1983.

Table 4.5. Least square means (LSM±SE) for post-weaning average daily gain for selected ram hoggets from 1980 to 1986.

YEAR	1980	1981	1982	1983	1984	1985	1986
No.HGTS	37	37	40	41	38	43	48
Period W[1]	–	137±11	74±6	87±4	49±5	59±2	145±5
Period S	94±4	113±9	118±7	–	207±12	215±11	77±9
Period WW-UBF	90±4	95±2	89±4	93±3	60±2	86±2	106±3

[1], Period W is winter; Period S is spring; Period WW-UBF is from weaning date to the last UBF. The period dates are in Appendix 7.2.

4.1.4 Liveweight-adjusted backfat depth (LABF).

The analysis for LABF was carried out in a similar manner to that of post-weaning growth rate (see Appendix 7.2 for the period dates). Therefore, the models were fitted on the data for the ewe hoggets up to the first LABF assessment (unselected population) only. For ram hoggets, the models were fitted for the first (unselected population) and two later periods throughout the year, (periods I, II and III, respectively).

Table 4.6 shows the LSM±SE and levels of significance for LABF from 1980 to 1986 in the unselected population of ram and ewe hoggets. The non-genetic effects were generally unimportant in controlling variation in LABF. Thus, only the LSM±SE for each selection line within ram and ewe hoggets is presented in table 4.7.

Table 4.6. Least square means(LSM±SE) for LABF within various non-genetic classes and for each selection line, in the
unselected population of ram   and ewe hoggets.

YEAR	Dam age			Birth rank		Line of selection		Date of birth
	2yo	3-5yo	6+yo	Single	Twin	High	low	
1980								
Ram	0.33±24.90	10.59±6.50	11.31±6.30	20.76±11.5	-5.94±9.23	34.58±15.16	-19.76±15.90	-0.53±0.44
					**		**	
Ewe	3.78±15.55	12.73±6.45	-9.17±8.18	7.18±8.72	-2.30±7.28	25.57±7.79	-20.69±7.57	-0.33±0.51
							**	
1981								
Ram	-2.44±5.64	-1.59±5.52	3.22±11.93	-0.43±7.11	-0.11±5.12	21.61±7.91	-22.15±9.10	0.24±0.30
							**	
Ewe	-1.33±6.54	-3.56±5.64	10.97±17.16	1.88±9.45	2.16±6.42	18.91±7.00	-14.86±8.96	0.11±0.28
							**	
1982								
Ram	-4.28±7.94	3.71±3.60	14.1±11.76	-5.2±6.22	14.22±5.53	23.65±6.60	-14.64±5.10	-0.47±0.40
		**			*		**	
Ewe	21.34±12.19	7.07±5.77	3.96±34.80	13.19±14.5	8.39±12.55	34.44±13.74	-12.86±12.7	-1.52±0.63
							**	*
1983								
Ram	1.77±6.70	4.21±3.96	-12.23±6.44	-7.25±4.52	3.08±4.61	14.26±3.95	-18.44±4.95	-0.97±0.43
							**	*
Ewe	30.55±12.10	-0.43±3.13	23.13±10.67	17.84±6.16	17.66±6.37	30.11±5.69	5.39±6.59	-1.21±0.37
		**					**	**
1984								
Ram	-3.49±9.40	3.04±4.45	22.47±11.99	6.37±7.1	8.31±5.87	27.75±6.19	-13.1±6.56	-0.39±0.35
		*					**	
Ewe	-9.48±9.56	6.69±4.86	8.12±18.49	9.72±8.78	-6.18±7.73	18.52±8.14	-14.97±8.39	0.18±0.37
							**	
1985								
Ram	3.25±8.14	10.92±5.77	0.87±7.51	-1.14±6.54	11.18±5.28	24.85±5.84	-14.81±5.68	0.10±0.37
							**	
Ewe	25.37±10.84	8.84±4.24	6.53±6.79	16.41±6.39	10.76±5.10	37.22±5.95	-10.05±5.47	-0.24±0.34
		**			*		**	
1986								
Ram	15.54±8.33	7.95±4.20	4.72±7.26	6.06±6.69	12.76±4.12	40.45±5.59	-21.64±4.87	0.14±0.37
Ewe	6.58±8.36	10.68±4.42	3.77±6.29	4.20±6.27	3.82±4.12	28.42±4.88	-20.39±5.24	-0.88±0.37
							**	

¹, Abbreviations are defined in Table 3.3, * P≤0.05 , ** P≤0.01

In the next two periods through the year (period II and III) a few isolated effects of birth rank, age of dam and date of birth were found to be significant. However, the non-genetic effects were generally unimportant.

4.1.5 Liveweight-adjusted shoulder height (LAH).

Because LAH was not assessed in the pre-selection stage, the models were fitted for the three periods in the selected population of ram hoggets. The period dates are defined in Appendix 7.3. Table 4.7 shows the LSM±SE for LAH adjusted by birth rank and age of dam in the selection lines for the whole period of selection.

The effects of birth rank and age of dam were significant on an irregular basis. The effect of birth rank was significant in period I for 1983, in period II for 1982 and 1983, and in period III for 1981; for all the cases twins were significantly shorter than single hoggets, with the difference being between 1.17 and 2.24%DEV. Furthermore, age of dam indicated that 3-5yo ewes was significantly shorter than age of dam 2yo and 6+yo ewes in 1986 (period II) with the differences being 1.58 and 1.28%DEV, respectively. In periods II and III in 1986, 3-5yo ewes showed significantly greater height than 2yo and 6+yo ewes with the differences being between 1.73 and 1.71%DEV, and between 1.94 and 2.86%DEV, respectively.

4.1.6 Liveweight-adjusted body length (LAL).

Liveweight-adjusted length was not assessed in the pre-selection stage, therefore the three periods considered were in the selected population of ram hoggets only. Table 4.7 shows the LSM±SE for liveweight-adjusted length (LAL) adjusted for age of dam and birth rank in the selection lines for the whole period of selection. The non-genetic factors affecting LAL were age of dam in period III of 1981 and date of birth in period I of 1985. In 1981, 3-5yo ewes provided hoggets with longer frames with an advantage of 0.9 and 2.51%DEV, on 2yo and 6+yo, respectively. In 1985, the regression coefficient of date of birth on LAL (-0.08±0.04) indicated that hoggets born late in lambing season were shorter in length than hoggets born early in the season.

Table 4.7. Least square means (LSM±SE)[1] for liveweight-adjusted backfat depth (LABF), shoulder height (LAH) and body length (LAL) of the ram hoggets in the high and low backfat depth selection lines.

YEAR	LABF		LAH		LAL	
	High	Low	High	Low	High	Low
1980[3]						
I	——	——.	——	——	——	——
II	——	——	——	——	——	——
III	22.84±8.12	-9.49±7.46	——	——	——	——
1981						
I	——	——	——	——	——	——
II	23.62±5.19	-32.00±7.20	-1.27±0.57	2.68±0.79	-1.33±0.52	1.86±0.71
III	21.21±5.80	-27.73±8.03	-0.79±0.41	2.02±0.57	-1.82±0.46	1.77±0.64
1982						
I	——	——	-0.54±0.60	0.49±0.57	-0.54±0.60	0.49±0.57
II	43.69±6.83	-22.43±6.43	-0.99±0.55	0.45±0.52	——	——
III	13.32±6.48	-15.01±6.12	——	——	——	——
1983						
I	——	——	-1.51±0.47	0.50±0.52	——	——
II	32.18±4.80	-20.87±5.26	-1.26±0.51	0.90±0.56	-1.61±0.49	1.48±0.53
III	——	——	——	——	——	——
1984						
I	——	——	-1.01±0.67	1.29±0.72	-1.01±0.67	1.29±0.72
II	28.11±5.10	-17.92±5.13	——	——	——	——
III	26.70±4.63	-0.72±4.66	——	——	——	——
1985						
I ·	——	——	-1.66±0.48	1.37±0.46	-1.26±0.54	1.87±0.51
II	39.26±5.35	-24.09±5.07	-2.18±0.74	1.48±0.70	-1.28±0.45	1.13±0.43
III	34.98±5.08	-23.18±4.81	——	——	——	——
1986						
I	——	——	-2.45±0.67	1.54±0.66	-1.72±0.62	2.30±0.61
II	48.45±7.30	-27.89±7.10	-2.06±0.90	1.10±0.88	-1.81±0.55	1.42±0.53
III	47.09±8.40	-23.27±8.22	-2.88±0.72	1.35±0.71	-2.58±0.62	2.10±0.60

[1], All the values are significantly different between lines ($P \leq 0.01$);

[2], Abbreviations are defined in Table 3.3;

[3], Dates for Periods I, II and III are defined in Appendices 7.2, 7.3, 7.4.

4.2 Direct responses to selection.

4.2.1 Introduction.

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After several years of selection for high and low backfat depth in the Southdown flock at Massey University, clear trends in both lines have been observed. Table 4.8 shows the least square means (LSM±SE) for actual and the liveweight-adjusted values for backfat, body length and shoulder height and level of significance for the first and last sets of measurements taken in the last year of selection reported in this investigation in both the ram and ewe hoggets.

Because of the difficulty involving the two selection stages (section 3.3.3) in the ram hoggets, the direct responses to selection for high LABF or low LABF will be presented for the first LABF measurement and then for all LABF measurements. The ewe hoggets were only measured once, therefore they will be mentioned only in that stage.

4.2.2 Generation interval.

The generation interval estimated by the procedure in section 3.3.2 was 3.01 years. Therefore, over the 8 years of selection, reported in this study, there would have been approximately 2.66 generations.

4.2.3 Selection differentials.

The selection procedure for the replacement sires involved two cullings, one based on the first LABF measurements, and one based on an average from all LABF measurements. The replacement ewes were selected based on the first LABF measurement only. Therefore, two main selection differentials were calculated in the ram hoggets involving the sires, but only one in the ewe hoggets.

First, a simple selection differential was obtained by difference between the mean of the two selected sires and the mean of the unselected population of ram hoggets based on the first LABF measurement (S1), Figure 3.1. The yearly means for the selected sires and the unselected population are plotted in Figure 4.1. Secondly, a combined selection differential (S2) was calculated based on the selection differential from the first measurement (S3) plus the selection differential based on the

Table 4.8. Least square means (LSM±SE) and level of significance for a group of traits measured on ram and ewe hoggets for the first and last measurements in 1987 (birth year 1986).

MEASUREMENT.	SIGNIF. TRAIT	RAMS		EWES		SIGNIF. OF LINE
		HIGH	LOW	HIGH	LOW	
First[1]	Backfat(mm):	.				
	Unselected	3.65±0.16	1.96±0.09	4.93±0.23	2.90±0.15	**
	Selected	4.61±0.21	1.78±0.10	5.12±0.26	2.56±0.13	**
	LABF(%DEV):					
	Unselected	40.75±5.26	-19.94±2.85	27.49±4.79	-21.68±3.61	**
	Selected	46.51±7.44	-26.65±4.10	53.53±4.25	-33.54±2.10	**
Last	Backfat(mm)	7.46±0.48	3.94±0.16	___	___	**
	Body length(mm)	772.83±4.28	814.25±5.30	___	___	**
	Shoulder height(mm)	564.75±3.75	592.17±2.01	___	___	**
	LABF(%DEV)	43.38±8.42	-26.20±2.48	___	___	**
	LAL(%DEV)	-2.14±0.45	2.24±0.46	___	___	**
	LAH(%DEV)	-2.07±0.62	2.19±0.48	___	___	**

[1], First LABF on the unselected population of ram and ewe hoggets, the last measurement was assessed on the ram hoggets only. **$P \leq 0.01$;

[2], Abbreviations are defined in Table 3.3.

average of all LABF measurements (S4), Figure 3.1. The S3 was calculated as the difference between the mean of the best 50% (approximately) of ram or ewe hoggets and the unselected hoggets. These means are plotted in Figures 4.2 and 4.3 for rams and ewes, respectively. The S4 estimates were based on the average of all measurements assessed throughout the year, between the two selected sires and the selected population of rams. Yearly means for the selected two sires and the selected population of ram hoggets are plotted in Figure 4.4. Details of the calculation of the selection differentials are in Appendix 7.5.

Because the sires were not selected based on the first LABF measurement alone, the selection differential (S1) calculated will underestimate the total selection pressure applied to select the sires. The S1 which represents the selection pressure applied based on the first measurement only is plotted against S2 in Figure 4.5. This figure also shows the regression equation between the selection differentials. The regression coefficient of these equations shows the change in S2 per unit of change in S1.

Because the best animals were not always selected (due to the use of other visual criteria and body condition), selection differentials were also calculated for the top two rams per line, based on the first and all LABF measurements. The selection differentials were calculated in similar way as for S3 and S4 (Figure 4.1 and 4.4 for the first and all LABF measurements, respectively). Average performance was mostly
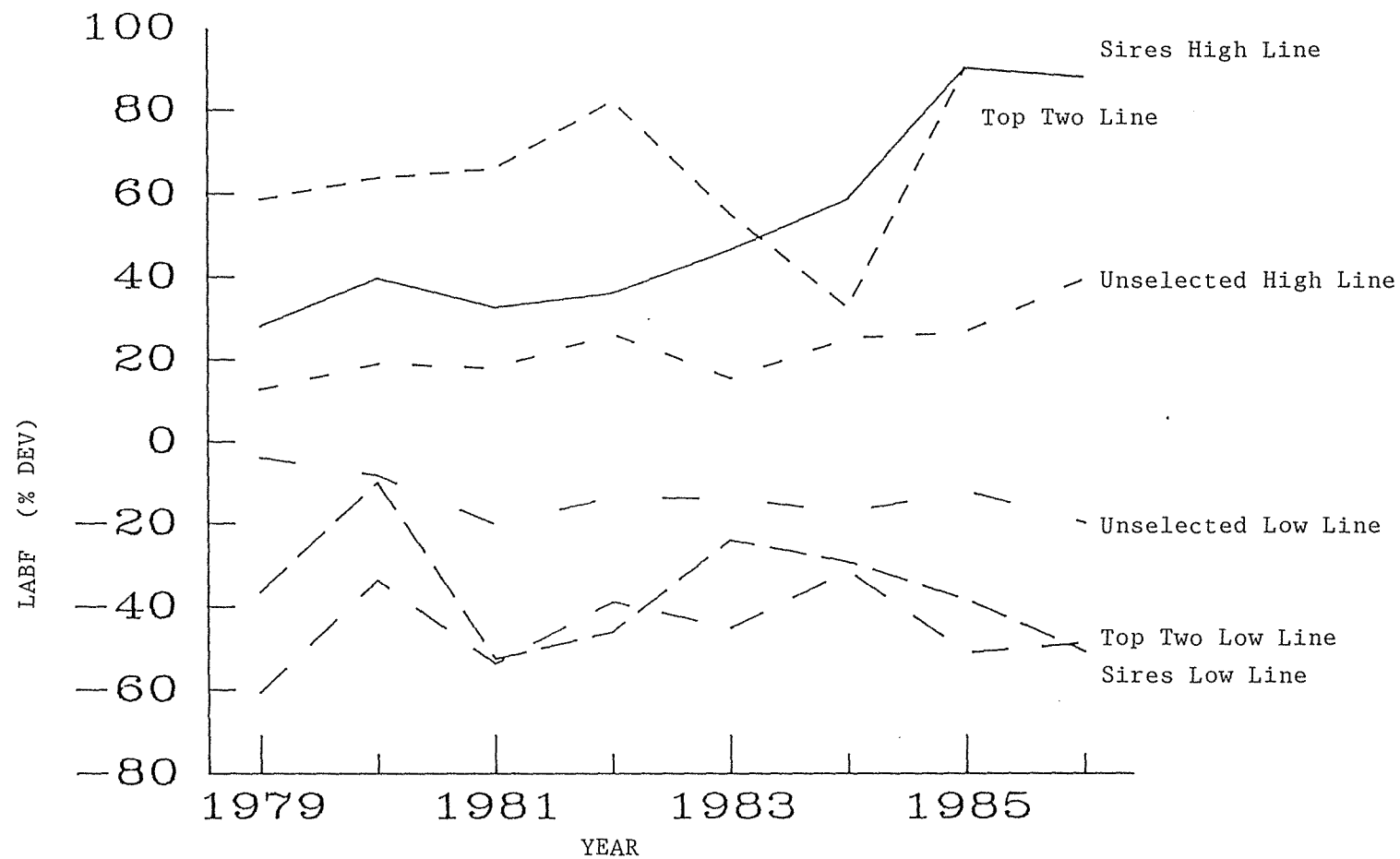
Figure 4.1 Line means for the two selected sires, top two rams and unselected population of ram hoggets based on the first LABF measurement only (used to obtain S1).
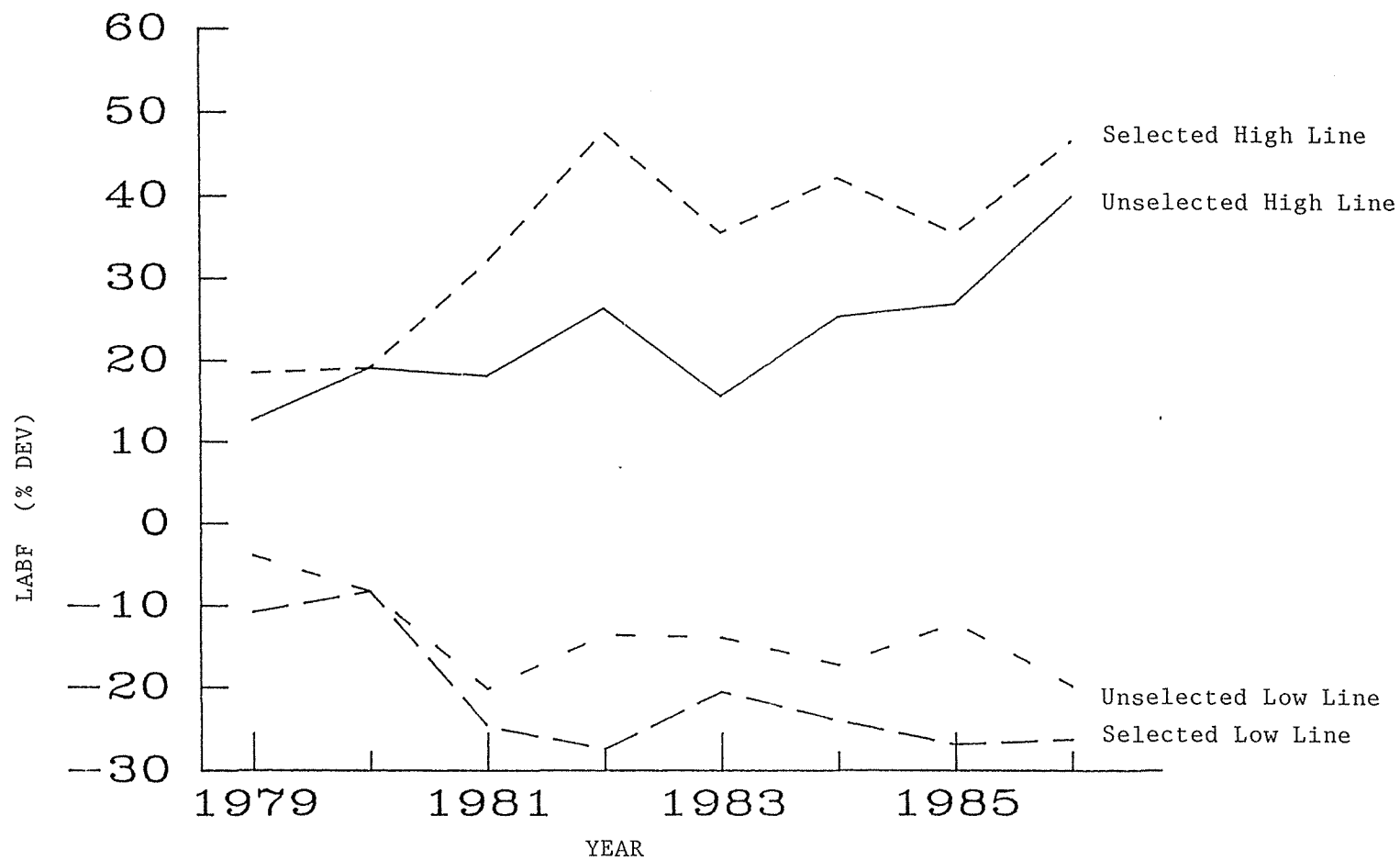
Figure 4.2   Line means for the top 50% (approximately) and unselected populations of rams based on the first LABF measurement only (used to obtain S3).
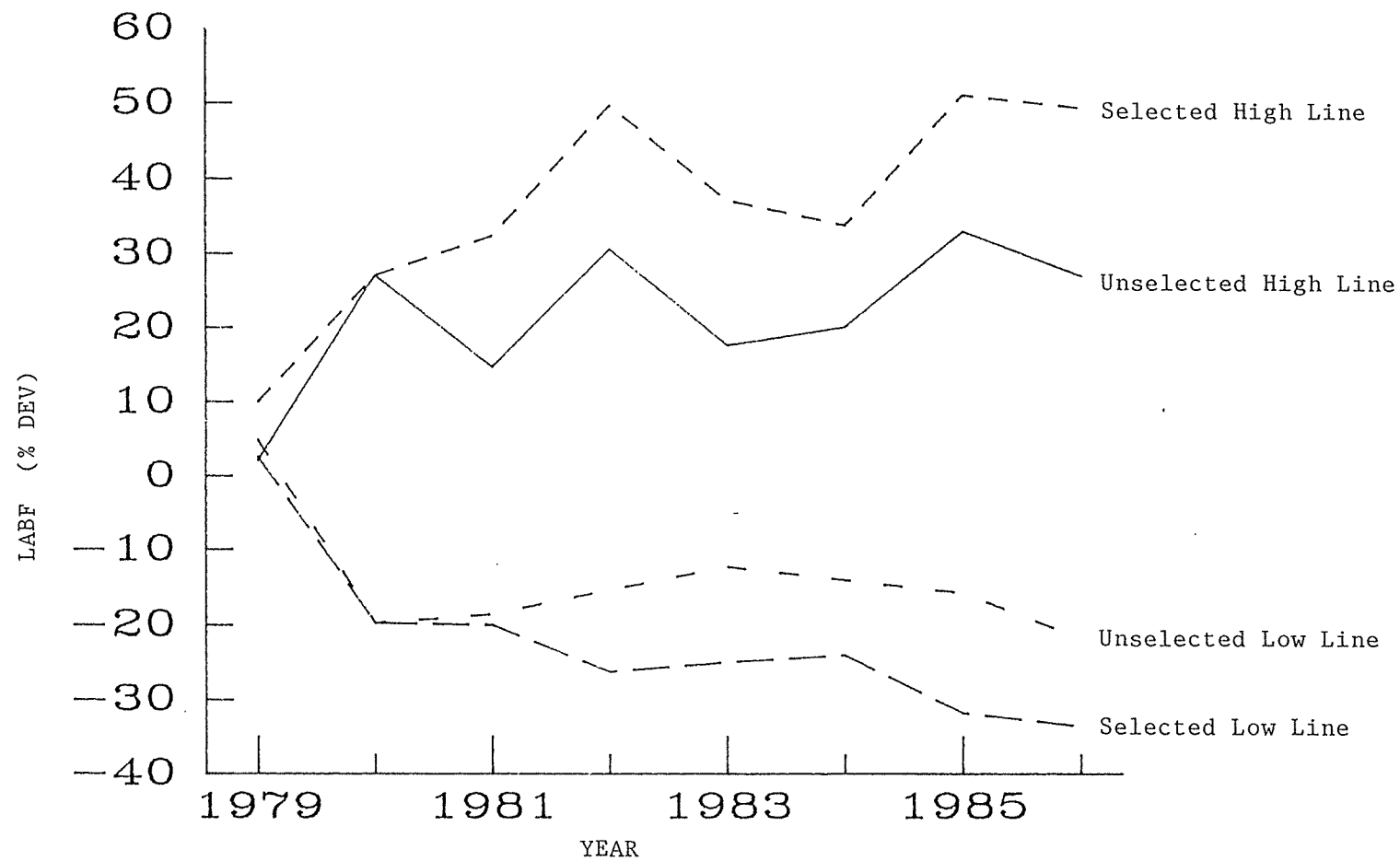
Figure 4.3 Line means for the top 50% (approximately) and unselected populations of ewes based on the first LABF measurement only (used to obtain S3).
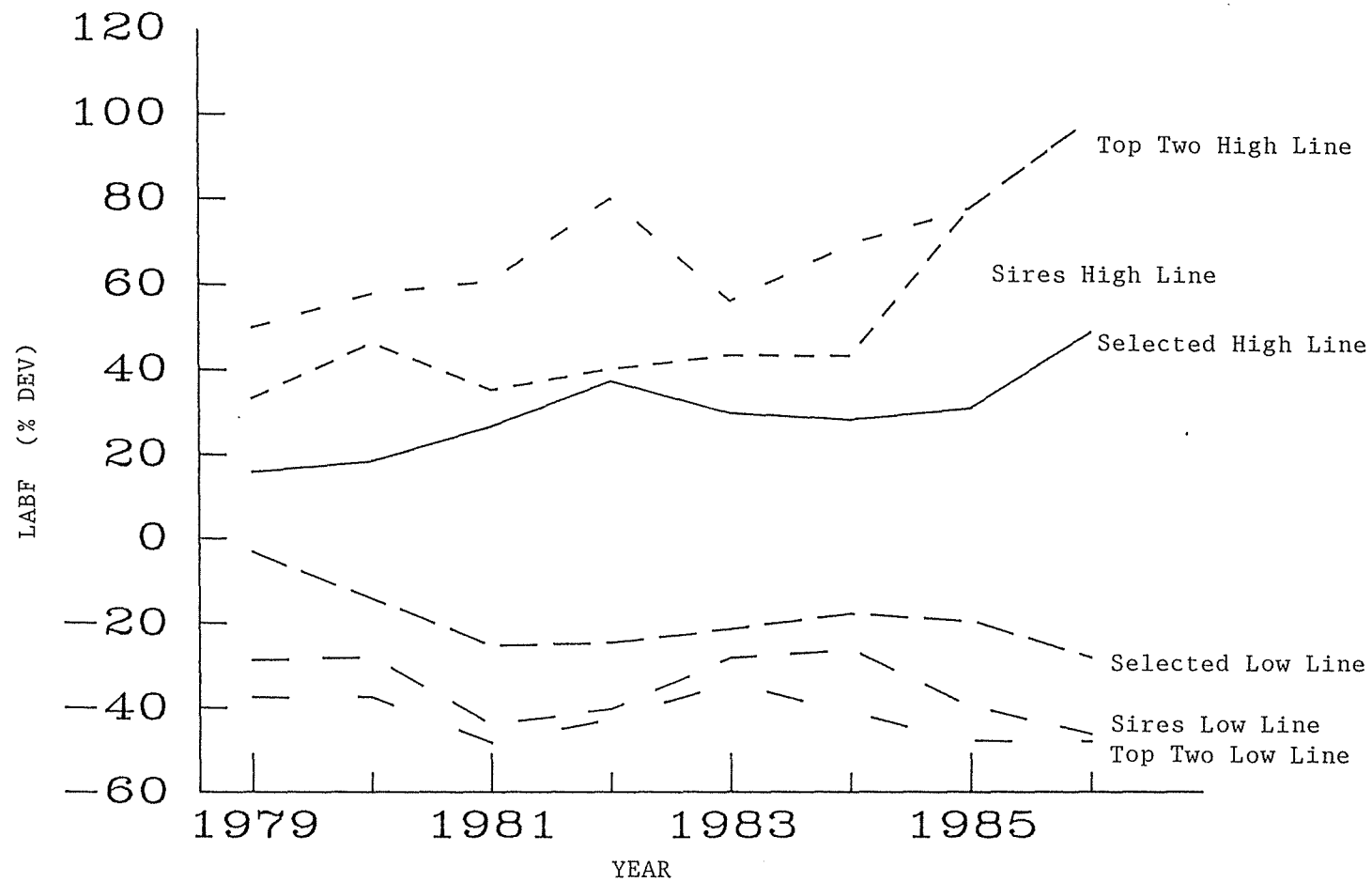
Figure 4.4   Line means for the two selected sires, the top two rams and the top 50%
(approximately) based on the average of all LABF measurements (used to obtain S4).

higher for the top two rams. The advantage of the top two rams was greater when all measurements were taken into account (Figure 4.4). A comparison of the two sets of animals enabled the loss in selection efficiency to be examined.

A group-average selection differential (GASD) was calculated as an intermediate step to obtaining the cumulated selection differential (CSD) (see section 3.3.5). The CSD was calculated in order to examine the total selection intensity applied based on the first LABF to select the sires. Figure 4.6 shows the cumulated selection differentials for both lines and sexes. Both rams and ewes followed the same trends of CSD accumulation within the lines. The CSD increased in an approximately linear fashion for both sexes in both lines. The rate of accumulation in ewes was 2.6%DEV / year and -1.3%DEV / year in the high and low lines, respectively and in rams 1.52%DEV / year and -1.3%DEV / year in the high and low lines, respectively. In high-line males, the rate of accumulation appeared to reach a plateau in the latter years of selection.

4.2.4 Yearly responses and divergences.

Yearly responses (YR) (the difference between means of successive years in the same line, section 3.3.3), for males were somewhat erratic in both lines (Figure 4.7). However, there was a positive response in five of the seven years for the high line
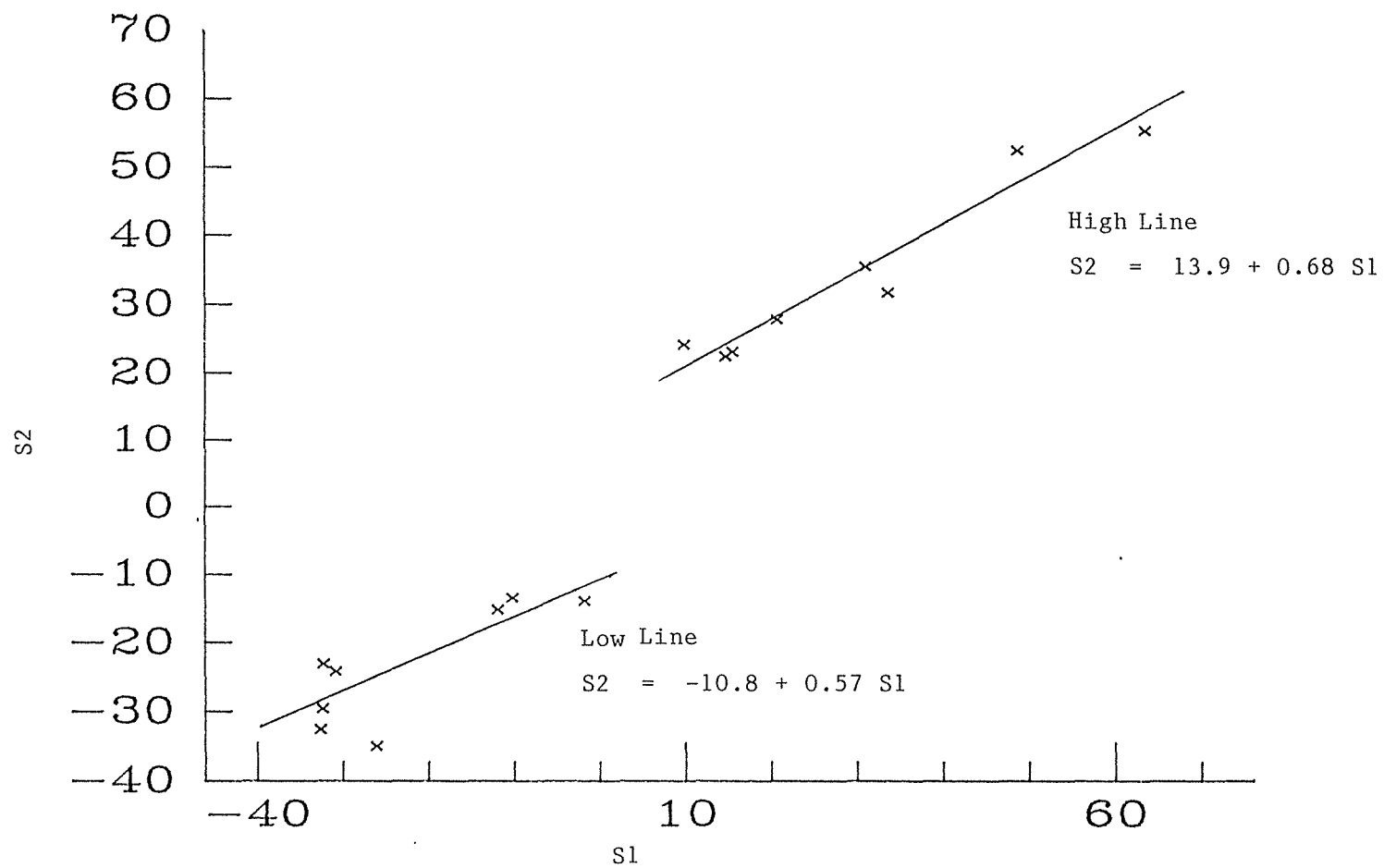
Figure 4.5 Plots and regression equations of selection differentials S1 and S2 for the ram hoggets.
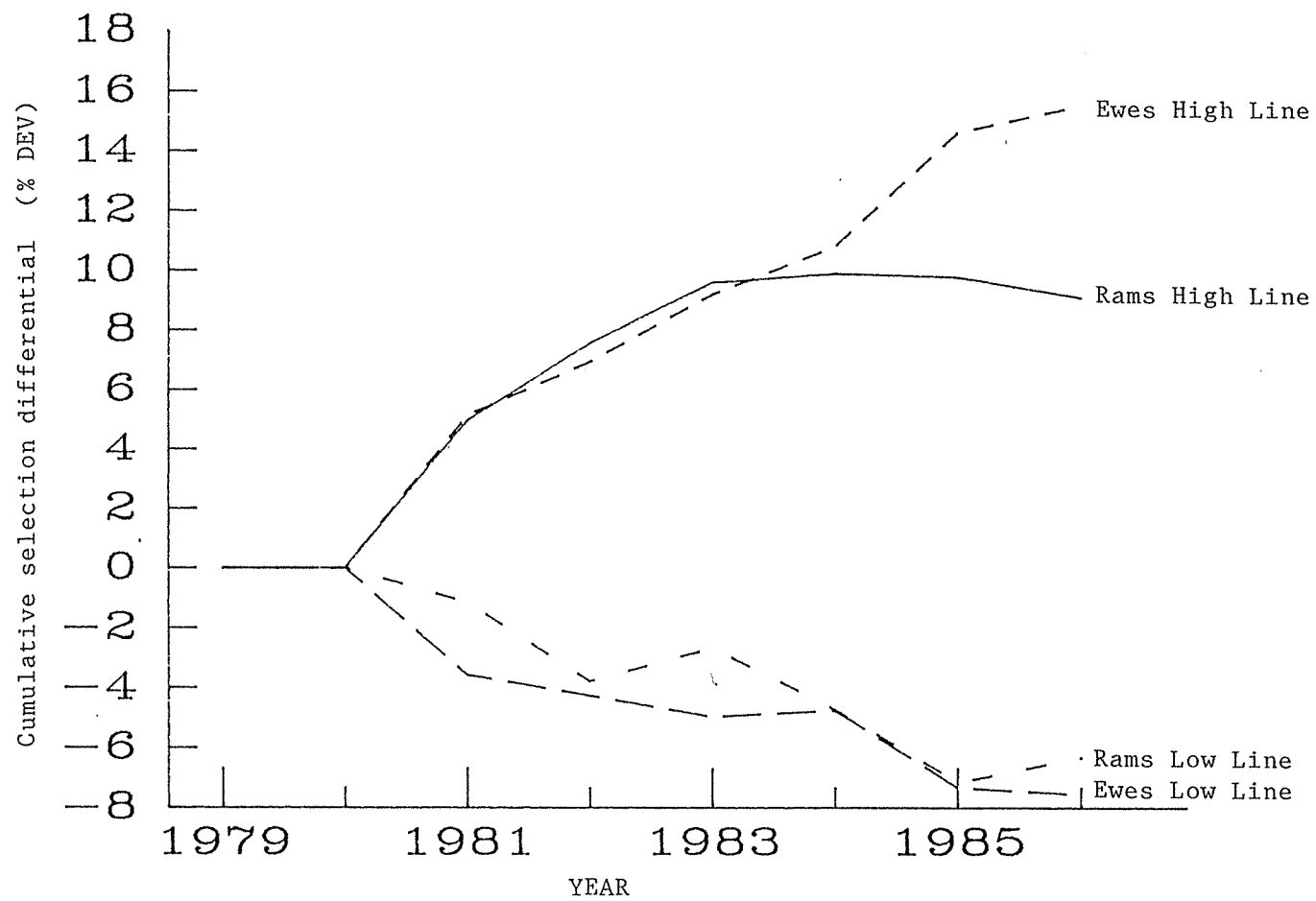
Figure 4.6   Cumulative selection differential (based on the first LABF measurement only) for the high and low LABF selection lines in ram and ewe hoggets.

and a negative response in five of the seven years for the low line. For the ewe hoggets, the high line showed a positive response in four of the seven years of selection, while the low line showed a negative responses in four of the seven years.

Figure 4.8 shows the divergences (difference between the high and low selection lines) in rams and ewes. A large response was exhibited by the females in 1980 with little change since. However, the response in males was more steady across time.

The cumulated yearly responses (CYR) to selection are shown in Figure 4.9. These were obtained by adding together consecutive yearly responses, within each line. The high line showed greater variation in the rate of accumulation than did the low line. The high line females showed greater response to selection than high line males. However, in the low line, males and females showed similar responses to selection. The divergent responses shown in Figure 4.8 already represent the cumulative response.

Subsequent to the initial culling based on the first LABF assessment, a second culling of rams was undertaken based an on average of all LABF measurements taken throughout the year. Yearly and cumulated responses to selection were calculated in a manner similar to that already described. Figure 4.10 shows the yearly responses based on all LABF measurements. The responses showed erratic trends. However, they were steadier than
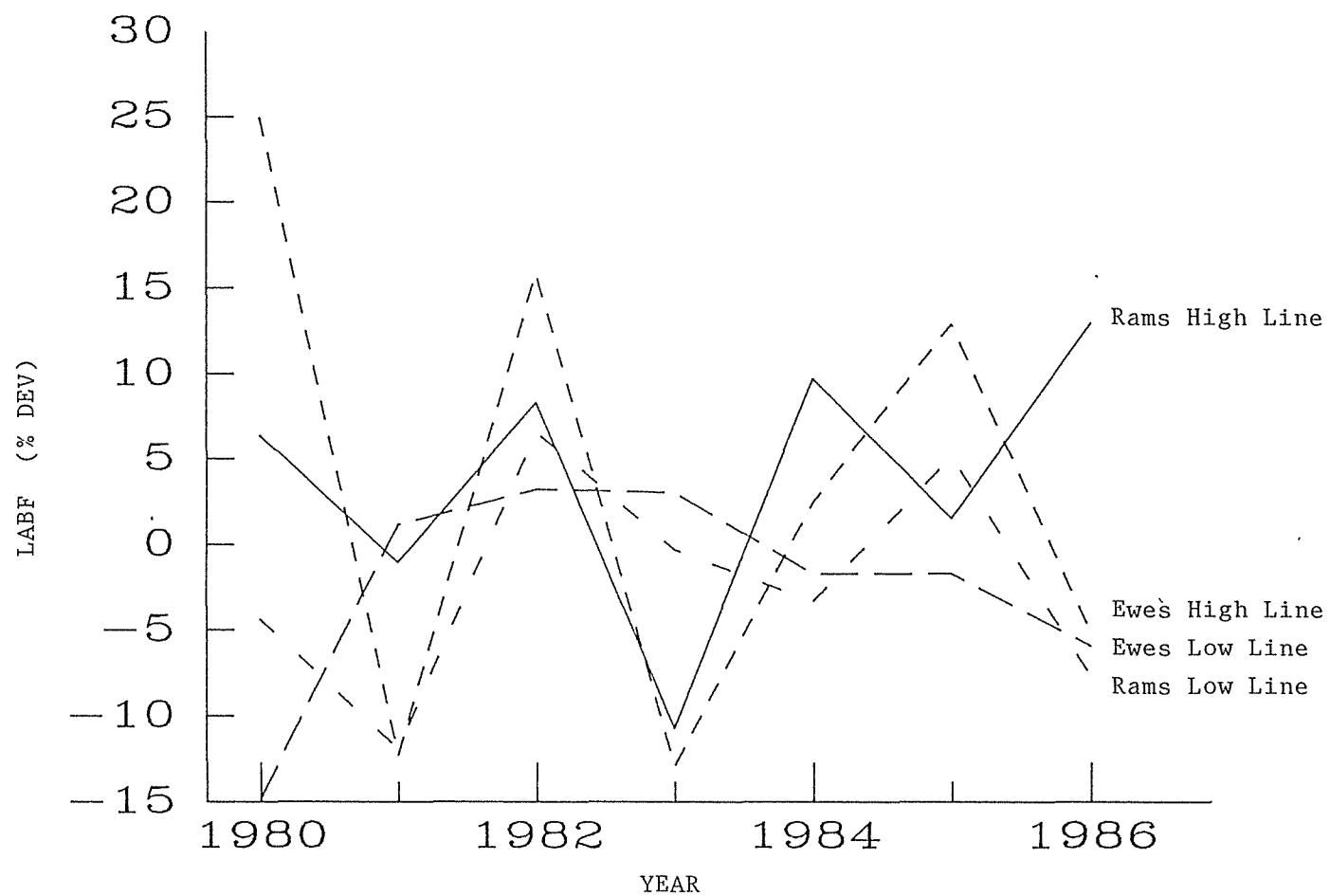
Figure 4.7 Yearly responses (YR) to selection for high or low LABF in the ram and ewe hoggets based on the first LABF measurement.
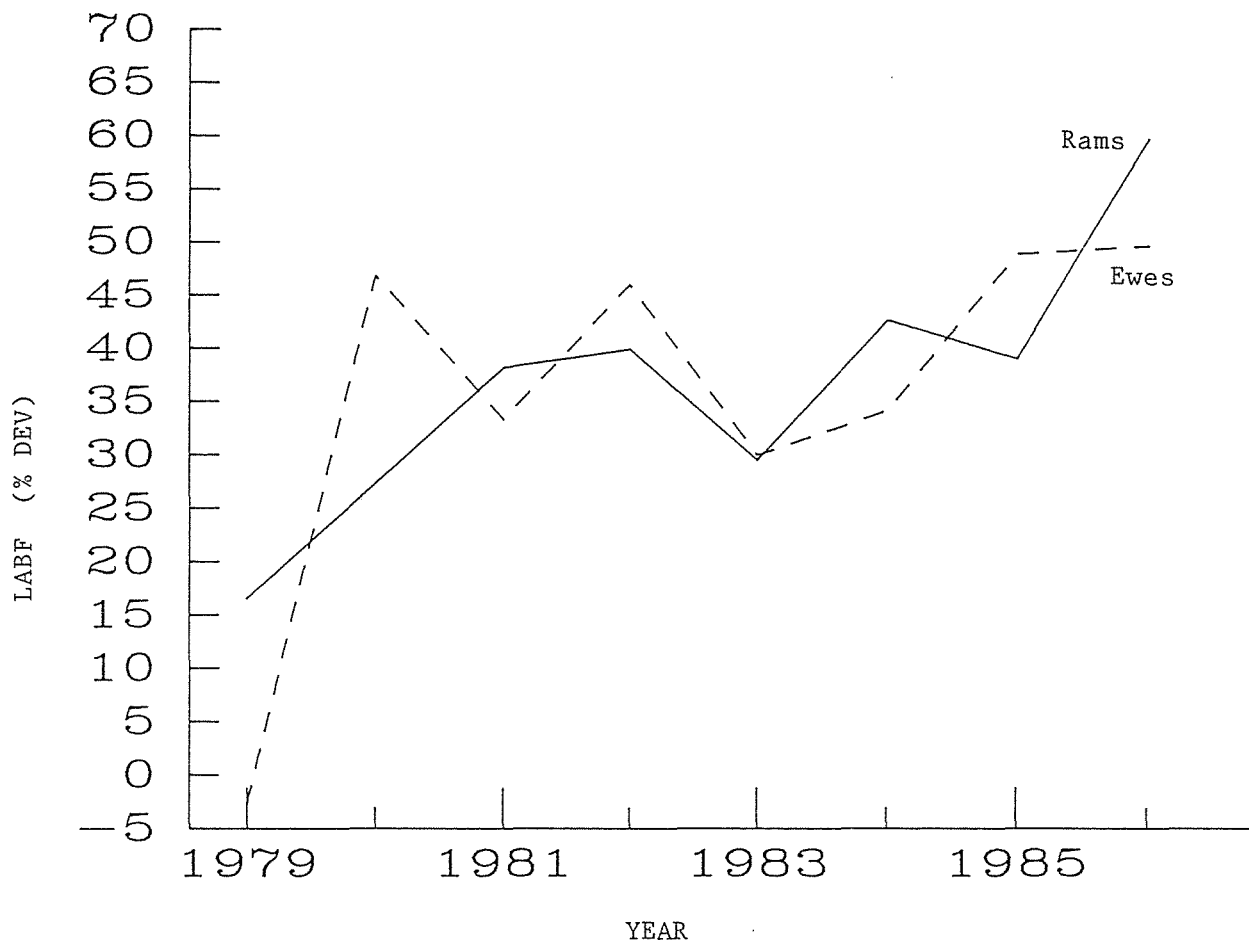
Figure 4.8   Divergence in LABF between selection lines for ram and ewe hoggets based on the first LABF measurement.

those found with the first measurement. The divergences are shown in Figure 4.11. The response accumulated steadily through the years with the exception of 1983, 1984 and 1985 where the divergence decreased compared with the response reached in 1982.

Cumulative yearly responses based on the average of all measurements showed similar trends to the yearly responses in both lines of selection (Figure 4.10).

4.2.5 Responses per unit of cumulated selection differential.

The cumulated selection differential was calculated based on the first LABF measurement, because all animals were present only at that measurement. However, it is recognised that this is not the actual selection pressure applied to select the sires. Figures 4.12 and 4.13 show the plots of the cumulated yearly response against the cumulated selection differential for ewes and rams in each selection line. Figures 4.14 and 4.15 show the plots of the divergence in the response to selection against the divergence in the cumulative selection differential. The regression coefficients represent the response to selection per unit of selection differential. These regression coefficients for the high and low lines or for divergence were higher in rams (0.87, 0.42 and 1.32, respectively) than in ewes (0.37, 0.13 and 1.10, respectively). Table 4.9 summarises these regression coefficients and their standard errors.
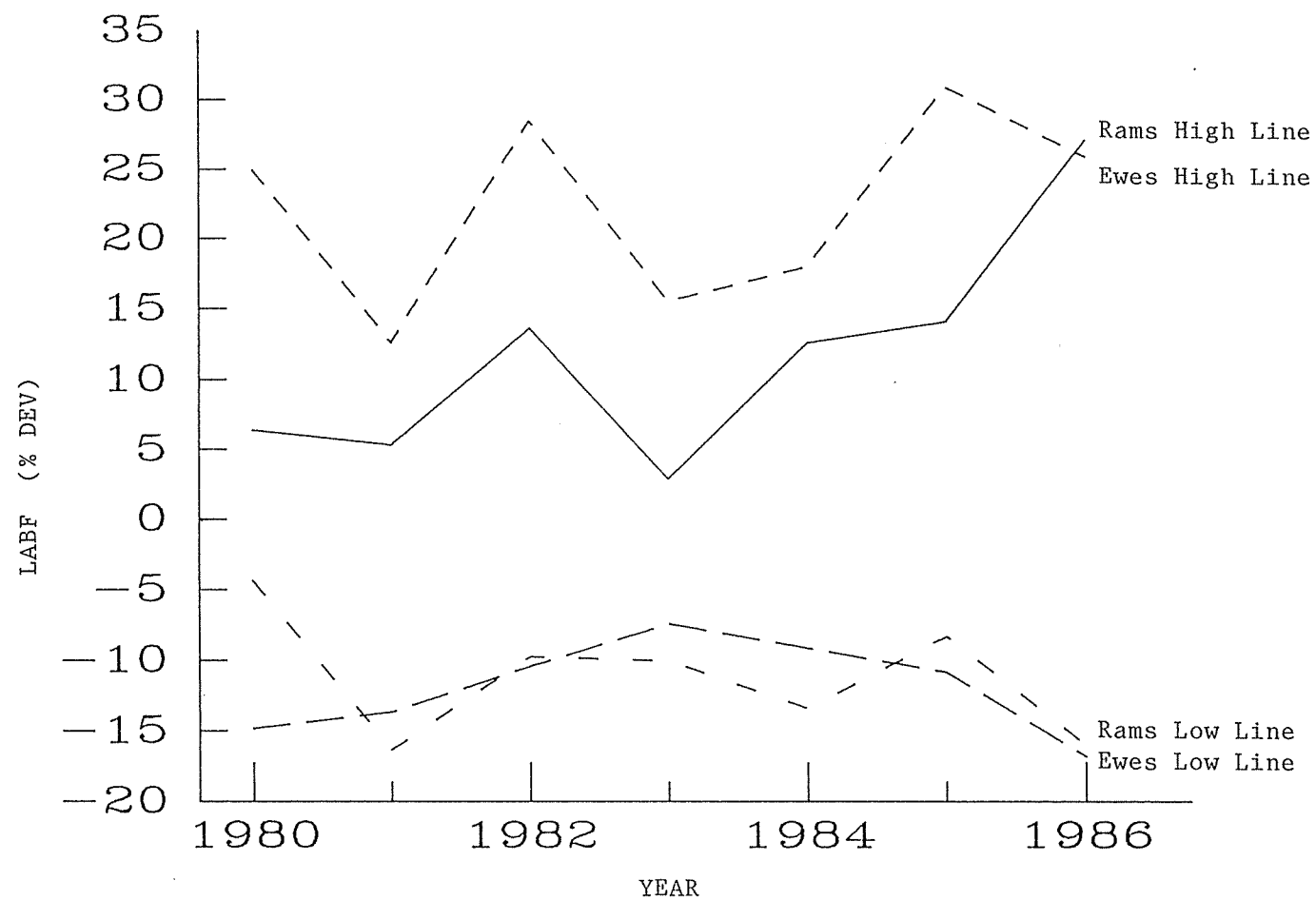
Figure 4.9   Cumulative yearly response to selection for high or low LABF in ram and ewe hoggets based on the first LABF measurement.
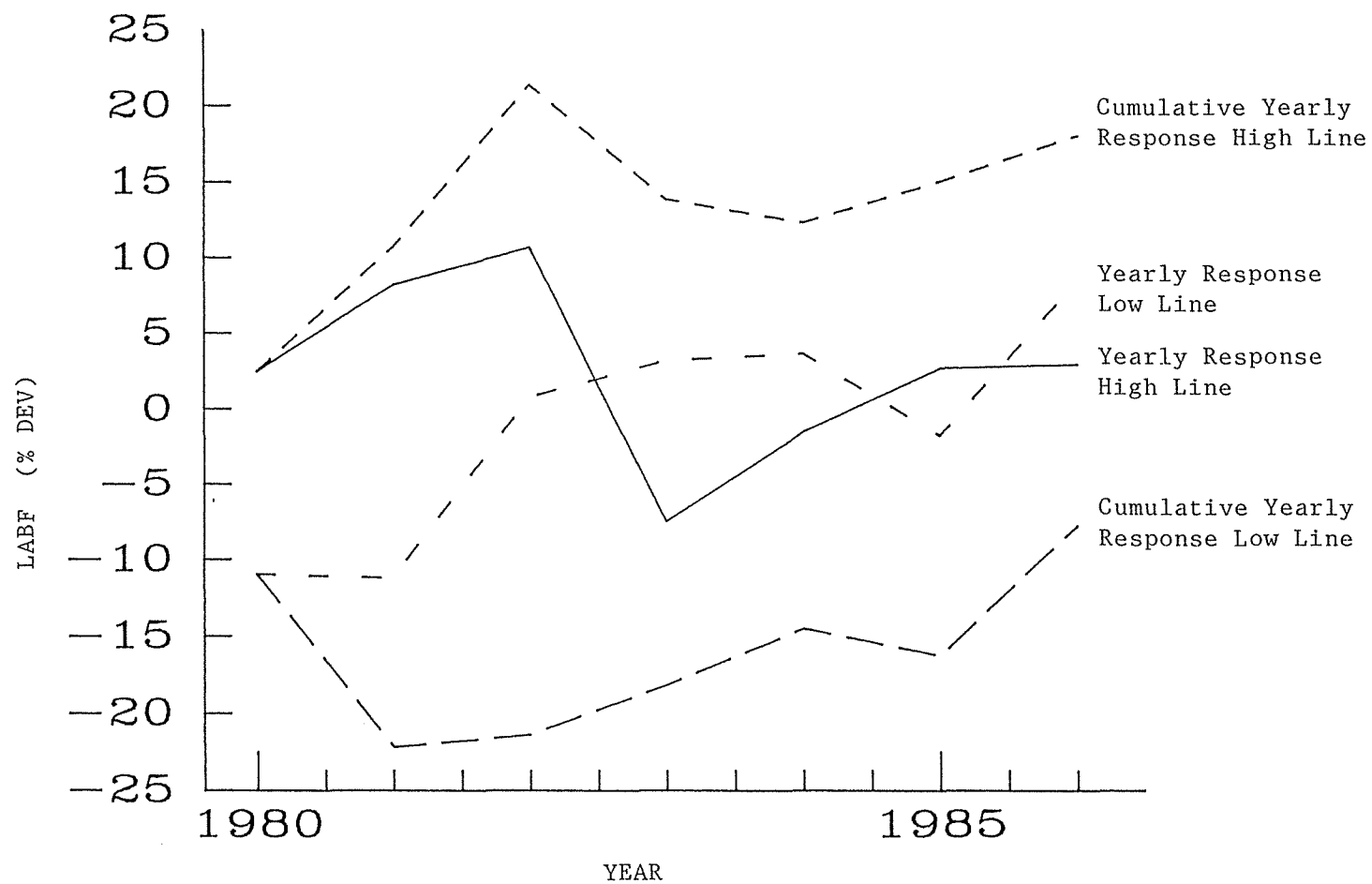
Figure 4.10   Yearly responses to selection for/against LABF based on the average of all LABF measurements on the top 50% (approximately) of rams hoggets.
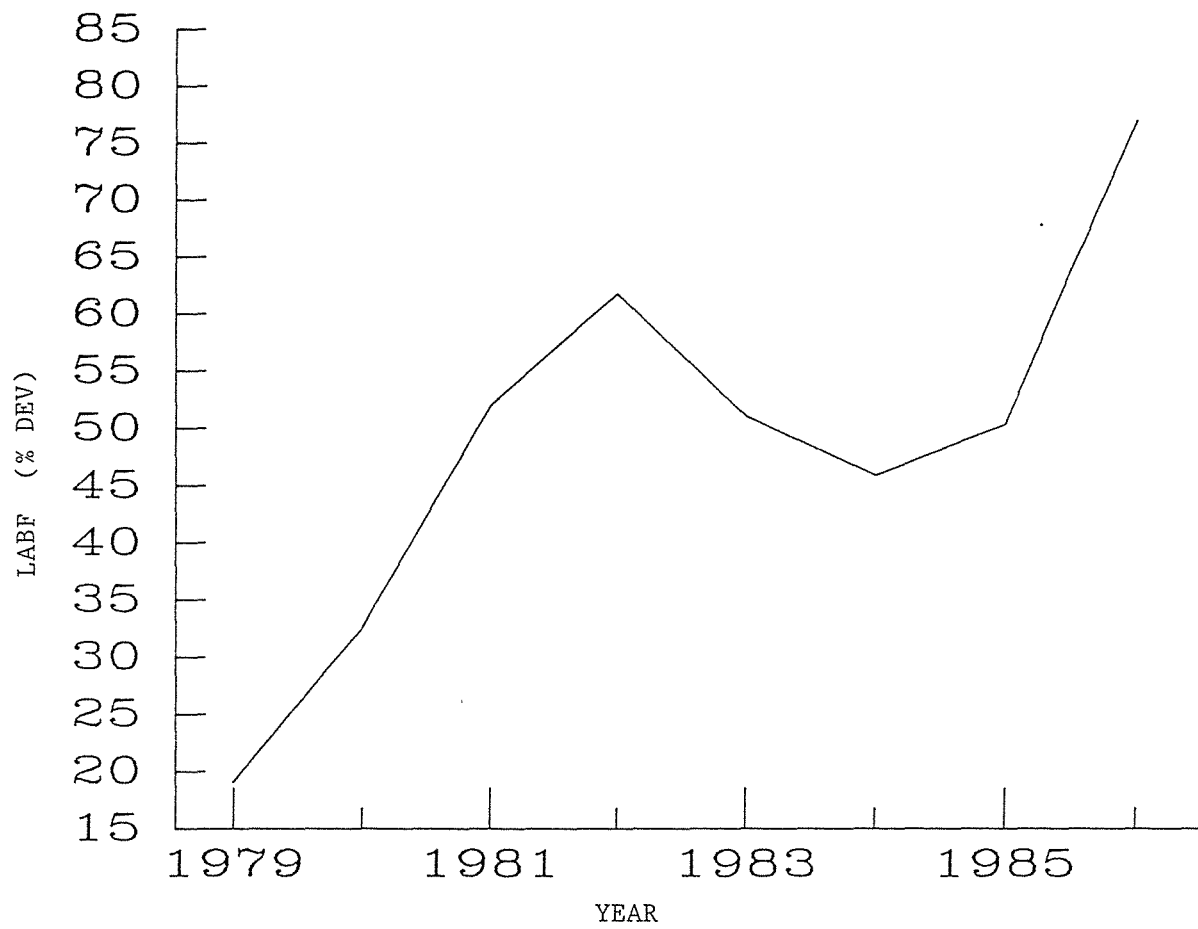
Figure 4.11 Divergence in LABF between the high and low lines based on the average of all LABF measurements in the top 50% (approximately) ram hoggets.
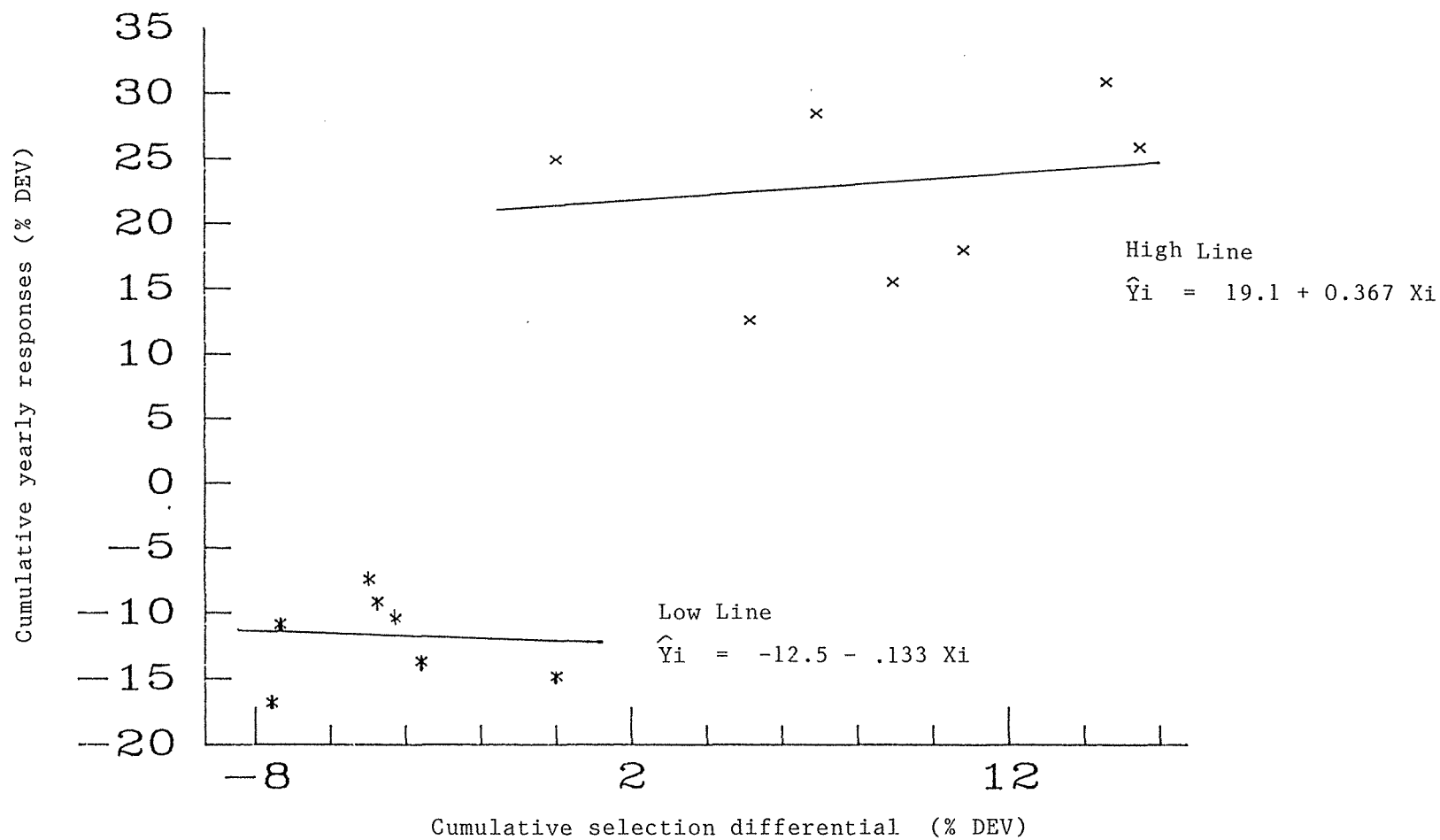
Figure 4.12   Plots of the cumulative yearly responses and cumulative selection differentials in the ewe hoggets based on the first LABF measurement.
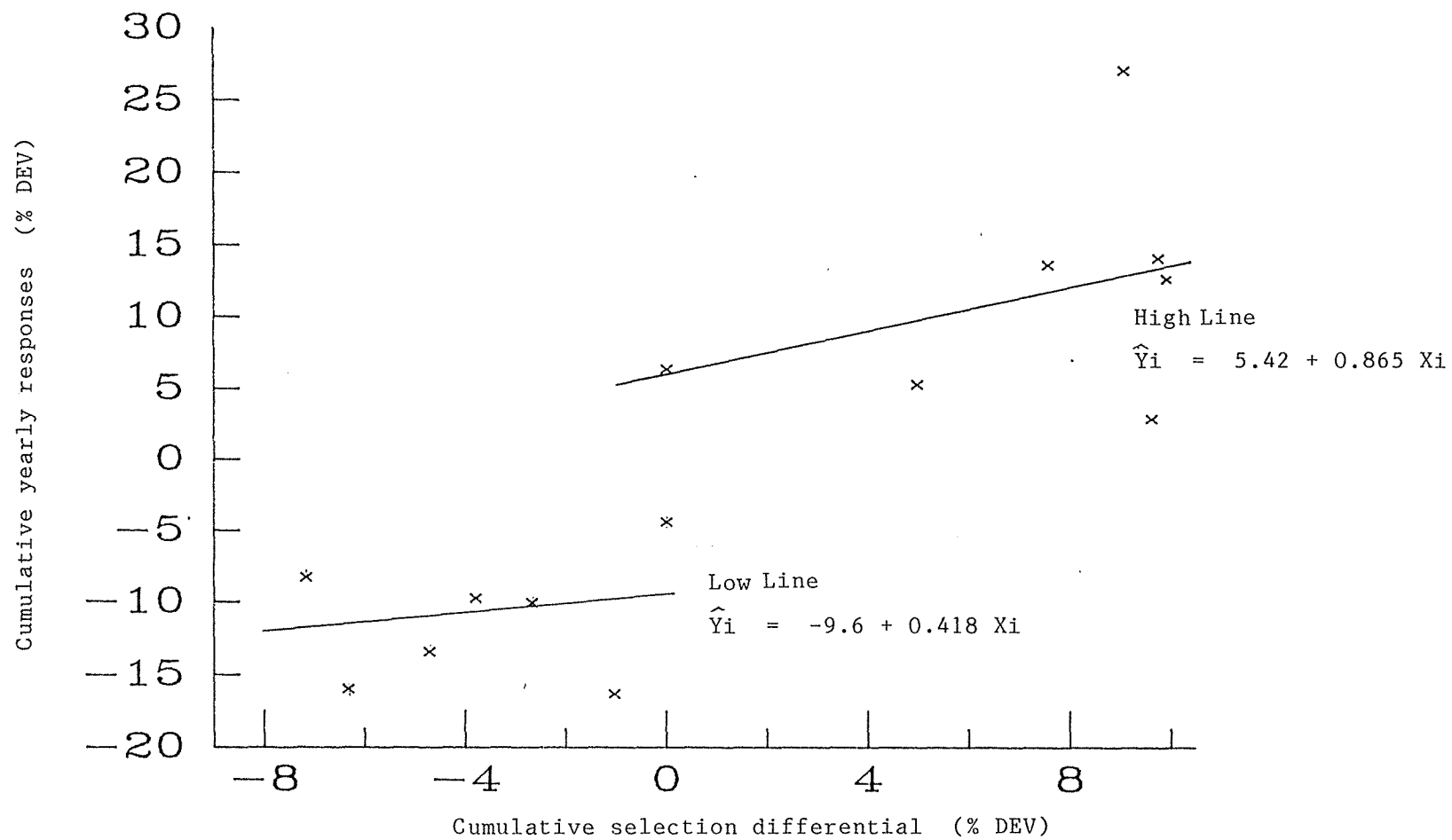
Figure 4.13 Plots of the cumulative yearly response and cumulative selection differentials in the ram hoggets based on the first LABF measurement.
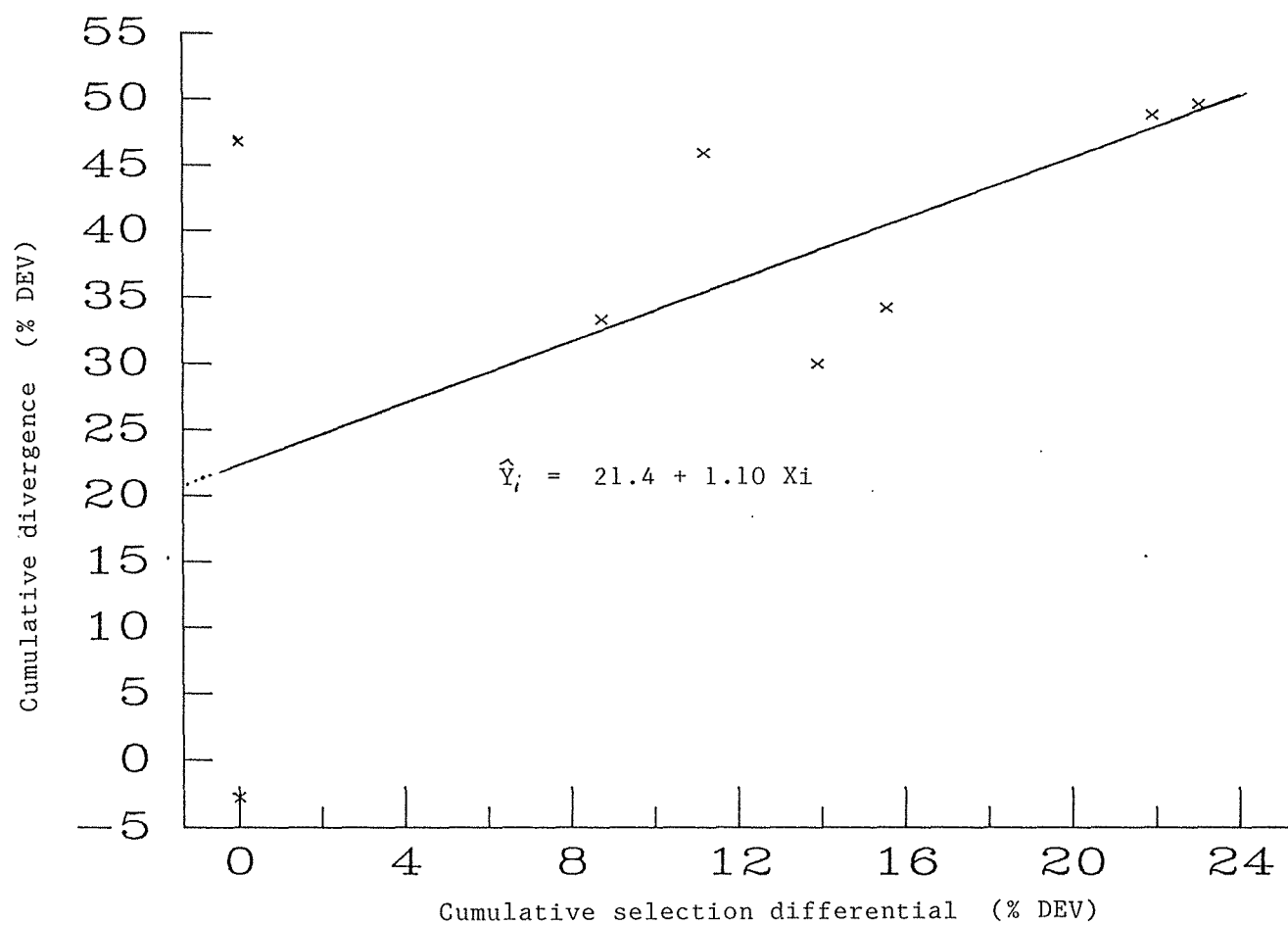
Figure 4.14   Plot of the divergence in the response to selection and the cumulative selection differential in ewe hoggets based on the first LABF measurement.

$$\hat{Y}_i = 23.4 + 1.32 \; Xi$$
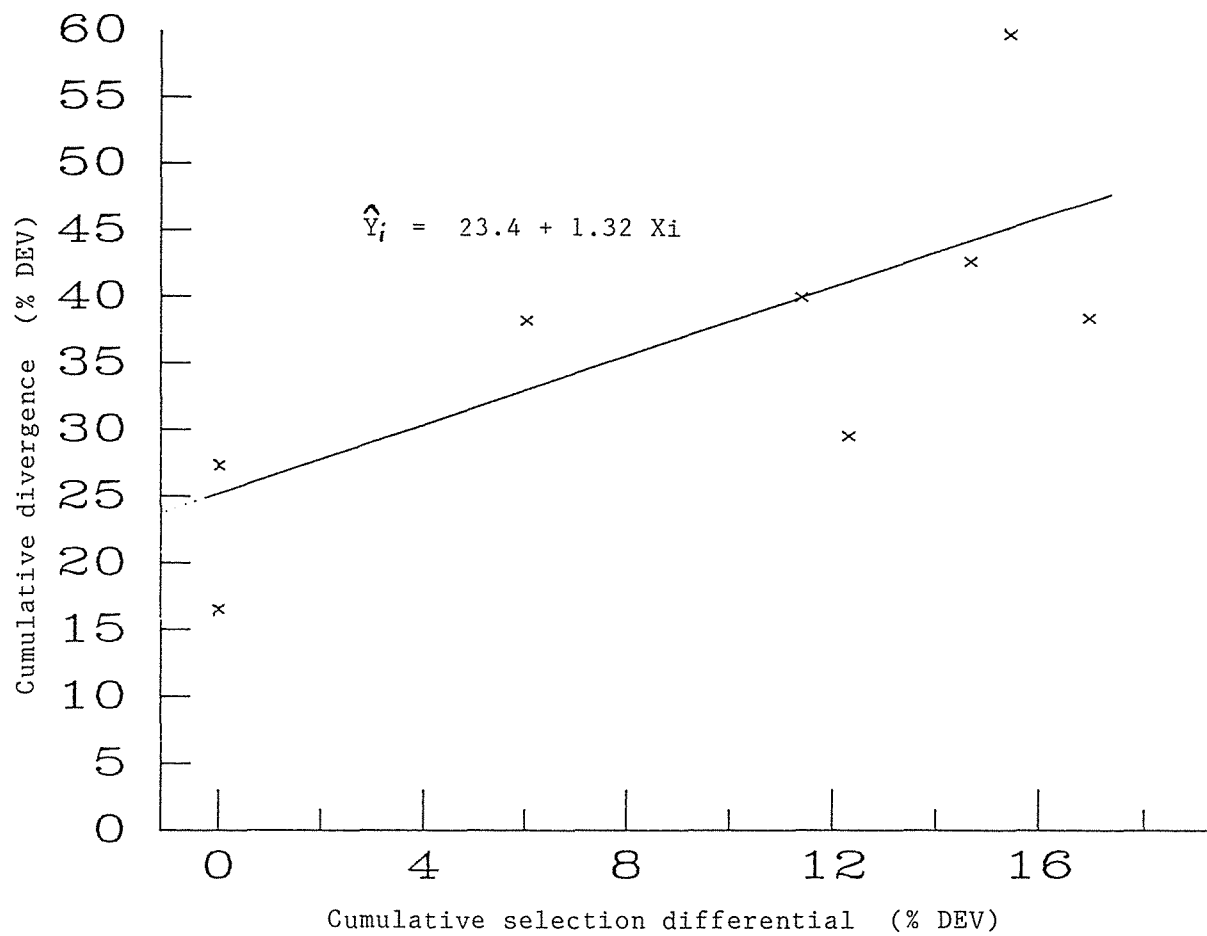
Figure 4.15   Plot of the divergence in the response to selection and the cumulative selection differential in ram hoggets based on the first LABF measurement.

4.3 Correlated responses

The correlated responses to selection for or against liveweight-adjusted backfat depth are shown in Tables 4.1, 4.2, 4.3, 4.4 and 4.7 for birth weight, pre-weaning growth rate (PrGR), post-weaning growth rate (PoGR) in rams and ewes, and for both body length and shoulder height, respectively. Table 4.10 summarises the correlated responses in all the traits for the last year of selection (1986). Table 4.11 presents the regression of year on the various correlated traits.

The analysis of birth weight, PrGR and PoGR indicated that selection for high or low LABF had not consistently affected these traits. Therefore, in spite of significant differences between the lines in some years, there was no significant trends in these correlated traits.

The selection for and against fatness has been accompanied by large correlated responses in LAH and LAL, with a divergence between the high and low backfat depth lines of about 4.0%DEVS occuring in both traits on the last year of selection only. Table 4.7 shows that the correlated responses in LAH and LAL were significantly positive throughout the all years of the study. However, the regressions of year on the responses in LAH and LAL were non-significant indicating that trends were relatively slow (Table 4.11).

Table 4.9. Regression coefficients ($\beta \pm SE$) of CSD on cumulated response within line of selection for LABF[1] in ram and ewe hoggets.

TECHNIQUE		RAMS	EWES
$\beta_{CYR-CSD}$[2]	HIGH LINE	0.87 ± 0.89	0.37 ± 0.72
	LOW LINE	0.42 ± 0.85	-0.13 ± 0.36
β_{D-CSD}[3]		1.32 ± 0.94	1.10 ± 0.26

[1], Abbreviations are defined in Table 3.3;

[2], Regression of CSD on CYR ;

[3], Regression of CSD divergence on lines divergence.

Table 4.10. Correlated responses to selection for high or low LABF in ram and ewe hoggets in 1986 calculated as the divergence between the high and low lines.

TRAIT	RAMS	EWES
Birth weight(kg)	0.00	0.03
Pre-weaning growth rate(g/day)	0.10	-1.18
Post-weaning growth rate in the pre-selection stage(g/day)	-5.12	-9.30
Post-weaning growth rate in the selected(g/day)	11.52	–
LAH(%DEVS)[1]	3.99	–
LAL(%DEVS)	3.64	–

[1], Abbreviations are defined in Table 3.3.

4.4 Genetic and phenotypic parameters.

4.4.1 Phenotypic correlations.

Product-moment correlations were calculated between consecutive adjacent measurements of LABF, LAH and LAL, and between all combinations of these traits using measurements taken on the same day.

After testing for homogeniety between values, they were pooled into a single value for each trait and each combination within selection line (Table 4.12). The correlation values within LABF, LAH or LAL were generally moderate to high. The correlations between the characteristics were generally low to moderate. The direction of the correlations were generally positive within traits, and for the LAH-LAL combination. However, the LABF-LAH and LABF-LAL combinations were generally negative.

Table 4.11.Regression coefficients($\beta\pm$SE)[1] of year on the correlated responses to selection for high and low LABF in ram and ewe hoggets.

Correlated trait	$\beta\pm$SE	
	Rams	Ewes
Birth weight(kg/year)	-0.08 ± 0.12	-0.05 ± 0.03
Pre-weaning growth rate(g/year)	-0.09 ± 0.49	-0.37 ± 0.31
Post-weaning growth rate in the pre-selection stage(g/year)	0.68 ± 1.14	0.86 ± 0.86
Post-weaning growth rate in the selected(g/year)	0.83 ± 1.21	–
LAH(%DEV)[2]	0.26 ± 0.15	–
LAL(%DEV)	-0.05 ± 0.19	–

[1], All the reported values were non-significant;

[2], Abbreviations are defined in Table 3.3.

4.4.2 Repeatability.

Repeatability (intra-class correlations, section 3.5.2) values were calculated across and within lines. However, because of the significant difference between lines found in preliminary analyses of LABF, LAH and LAL, only the within line estimates will be presented. Table 4.13 shows that each of the three characteristics were moderately to highly repeatable within and across years over the eight years examined. The major exception to this being LAL in the low line.

4.4.3 Heritability and genetic correlations.

Table 4.14 shows heritability estimates ($h^2 \pm SE$) for LABF using dam-offspring regression and correlations and paternal half-sib analyses. Estimates within line and poolled values were low to moderate. All the heritability estimates in Table 4.14 were calculated on the data expressed as percent deviations, without correction for other factors.

Heritability estimates ($h^2 \pm SE$) for LABF, LAL and LAH were obtained using Henderson's method 2 (see section 3.5.1) and are shown in Table 4.15. The year was divided into three periods (see Appendices 7.2, 7.3 and 7.4 for LABF, LAH and LAL period

Table 4.12. Pooled correlations between adjacent measurements of LABF[1], LAL and LAH, and between measurements of different traits recorded on the same day, for the two selection lines.

					YEAR				
TRAIT		1979	1980	1981	1982	1983	1984	1985	1986
Correlations within-trait, between-days:									
LABF:									
	HIGH	0.65	0.71	0.31	0.91	0.56	0.71	0.84	0.80
	LOW	0.74	0.32	0.61	0.84	0.36	0.59	0.86	0.45
LAH:									
	HIGH	0.43	–	0.71	0.77	0.77	–	0.79	0.42
	LOW	0.57	–	0.25	0.62	0.80	–	0.84	0.45
LAL:									
	HIGH	0.46	–	0.44	–	0.63	–	0.36	0.38
	LOW	0.55	–	-0.11	–	0.17	–	0.46	0.23
Correlations between-traits, within-days:									
LABF-LAH:									
	HIGH	-0.02	–	0.07	-0.34	-0.26	-0.10	-0.41	-0.23
	LOW	-0.09	–	-0.26	-0.25	-0.15	-0.41	-0.23	-0.06
LABF-LAL:									
	HIGH	-0.04	–	-0.09	–	-0.12	-0.07	-0.58	-0.04
	LOW	0.15	–	0.19	–	0.01	-0.09	-0.59	-0.39
LAH-LAL:									
	HIGH	0.05	–	0.11	–	0.24	0.49	0.22	0.28
	LOW	0.23	–	-0.02	–	0.05	0.30	0.04	0.06

[1], Abbreviations are defined in Table 3.3.

Table 4.13. Repeatabilities for LABF[1], LAL, and LAH in the ram hoggets

for each selection line and year.

CHARACTERISTIC	YEAR							
AND LINE	1979	1980	1981	1982	1983	1984	1985	1986
LABF :								
High line	0.28	0.67	0.31	0.53	0.47	0.48	0.71	0.74
Low line	0.64	0.34	0.56	0.46	0.37	0.54	0.61	0.34
LAL:								
High line	0.43	–	0.46	–	0.63	–	0.29	0.29
Low line	0.28	–	-0.09	–	0.19	–	0.13	0.27
LAH:								
High line	0.33	–	0.68	0.60	0.76	–	0.82	0.49
Low line	0.35	–	0.23	0.65	0.80	–	0.69	0.47

[1], Abbreviations are defined in Table 3.3.

Table 4.14. Heritability estimates($h^2 \pm SE$) for LABF[1] within selection line or after pooling across selection lines. (Number of observations and number of sires are shown in parentheses.)

Method	High line	Low line	Combined data sets
Dam/offspring correlation	0.32±0.12 (201,10)	0.43±0.12 (184,10)	0.37±0.09 (385,20)
Dam/offspring regression	0.29±0.13 (201,10)	0.41±0.14 (184,10)	0.33±0.07 (385,20)
Henderson's method 3	0.14±0.10 (483,14)	0.19±0.12 (424,15)	---

[1], Abbreviations are defined in Table 3.3.

Table 4.15. Heritability ($h^2 \pm SE$) estimates using Henderson's method 2 for LABF[1], LAH and LAL for three different periods through the year. (number of observations and number of sires in parenthesis.)

	Period[2]		
trait	I	II	III
LABF	0.18±0.26[3] (905,29)	-0.02±0.06 (408,24)	-0.05±0.10 (324,24)
LAL	-0.19±0.18 (168,12)	-0.08±0.10 (247,16)	--
LAH	0.34±0.16 (328,20)	0.27±0.14 (327,20)	--

[1], Abbreviations are defined in Table 3.3;

[2], Dates of the periods are in Appendices 7.2, 7.3 and 7.4;

[3], Calculated on the unselected population.

dates respectively), in a similar way to those for post-weaning growth rate, in order to estimate the heritability of the same trait at different times of the year. To appreciate the procedure used with Henderson's method 2, an example is given in Appendix 7.6

The only positive heritability estimate for LABF was obtained from the unselected population. Both heritability estimates for LAL were negative while the LAH values were moderate. Heritability estimates from the third period for LAL and LAH were not calculated because of the small number of observations.

Genetic correlations were not calculated due to the small number of observations.

CHAPTER FIVE   DISCUSSION

CHAPTER FIVE. DISCUSSION.

5.1 Introduction.

The major purpose of this study was to calculate direct and correlated responses to selection for high or low backfat depth in Southdown sheep. Despite the importance of fatness in sheep, Fennessy et al(1987) are the only workers to have provided a report of the results of a selection experiment to change carcass fatness in sheep. However, the results of several selection experiments for backfat have been published for poultry and pigs. These experiments have demonstrated that selection against subcutaneous backfat is likely to be successful in achieving leaner animals. In this chapter, results are discussed in relation to the published literature.

5.2 Non-genetic effects.

5.2.1 Birth weight, pre- and post-weaning growth rate.

Birth weight is closely related with newborn survival in sheep (Hunter, 1956; Bradford, 1972),in beef cattle (Koch, 1972), in swine (Robison, 1972) and in laboratory animals (Legates, 1972). Consequently, an understanding of factors which might affect its magnitude is important in designing selection programmes.

The effect of number of lambs in the litter on birth weight of lambs has been reported in many studies (e.g. Barnicoat et al, 1956; Sidwell and Miller, 1971; Falagan and Garcia de Siles, 1987). In this study, the advantage estimated for singles over twins (14%-28%) agreed closely to most of the published experiments.

The age of dam significantly affected the lamb birth weight. The lightest lambs were usually produced by 2yo ewes. There was not a consistent difference between 3-5yo and 6+yo ewes. The advantage of 3.5% to 14.5% and 9.4% to 16% of 3-5yo and 6+yo on 2yo, respectively, agreed with most of the results reported in the literature (e.g. Bichard and Cooper, 1966; Donald et al, 1968; Holtman and Bernard, 1969; Sidwell and

Miller, 1971).

The effect of sex on birth weight has been established in many studies. The estimated advantage for males in birth weight on females in this experiment (3%-8%) agrees with most of the estimated values in other experiments (e.g. Barnicoat et al, 1956; Bichard and Cooper, 1966; Carter et al, 1971; Juma et al, 1987).

The effects of number of lambs at birth, age of dam and sex on post-natal growth have been widely reported in the literature. The number of lambs per ewe at birth has the greatest effect on post-natal growth rate in the present experiment. Singles grew between 5.4% and 22.6% faster than twins in the pre-weaning stage. This is in agreement with most of the reports in the literature (e.g. Sidwell and Miller, 1971; Barnicoat et al, 1956; Carter et al, 1971; Falagan and Garcia de Siles, 1987).

In the present study, the post-weaning growth rate estimates from the unselected population of ram and ewe hoggets indicated that twins grew significantly faster than singles, regardless of sex. This effect of birth rank on post-weaning growth rate has been pointed out by several authors. Glimp (1971) indicated that pre-weaning growth rate of singles were 15.4% faster than twins, but that 60 days after weaning singles were growing only 7.7% faster. Vesely and Slen(1968) indicated that twins lambs tended to overcome, to a certain degree, the

original handicap in growth rate as they aged. Ch'ang and Rae (1970) reported a consistently higher growth rate for twins than for singles in Romney sheep. This decline in the singles superiority for post-weaning growth rate was accompanied by a sharp decline in the age of dam influence on lamb growth rate.

The birth rank and age of dam have been shown to affect birth weight and post-natal growth rate. Birth weight and post-natal growth rate are two characteristics directly affected by the maternal environment. Furthermore, the dam also influences both birth weight and growth rate traits through the genes she transmits to her offspring. (Ch'ang and Rae, 1961). The strong influence of age of dam is reflected by the difference in birth weight of lambs from ewe hoggets and mature ewes (Hight, 1982), whereas the influence of age of dam on growth rate prior to weaning is mainly due to milk production (Burris and Baugus, 1955; Slen et al, 1963)

The effects of birth rank and age of dam on post-weaning growth rate are thought to reflect the pre-weaning maternal handicap (Ch'ang and Rae, 1970). This could be partly a result from the lower milk production of younger ewes (Barnicoat et al,1949), or in the case of twins from competition from nutrients in utero and during suckling (Hunter, 1956). These induced levels of poorer nutrition in the pre-natal and pre-weaning stages are thought to result in higher postweaning growth rates in twins and lambs from the youngest or oldest dams. This is an example of the phenomenon known as compensatory growth

(Wilson and Osbourn, 1960; O'Donovan, 1984).

5.2.2 Liveweight-adjusted backfat (LABF), shoulder height (LAH) and body length (LAL).

In spite of some significant effects of birth rank and age of dam in some of the years, there were no consistent differences between twins and singles or between age of dam categories for LABF(Table 4.6). These results suggest that the the maternal environment has minimal effect on hogget LABF performance. These findings are in agreement with Hetzer and Miller(1972a). They found that the effect of age of dam was not significant for backfat at 79.4kg in both Duroc and Hampshire pigs. The regression coefficients of date of birth on LABF did not show any consistent significance between years.

Analysis of the data from rams remaining after the first stage of selection showed that birth rank was important in several years for period I, with twins consistently having less backfat than singles (Table 4.7). The effect of age of dam did not show any consistent trend. However, there was an indication in some years that 2yo and 6+yo ewes reared hoggets with less backfat than hoggets of 3-5yo ewes, which could be explained by the phenomenon of compensatory growth, as was discussed in the previous section. Despite the inconsistent significance of the age of dam, date of birth and birth rank effects, in periods II

and III, there was an indication that the 2yo ewes and 6+yo ewes, the youngest hoggets and the twins exhibited less LABF than 3-5yo ewes, older hoggets and singles, respectively.

The analysis for LAH showed few cases of significant non-genetic effects (Table 4.7). The significant effect of birth rank in some years, indicated that singles were sometimes taller than twins after correction for liveweight differences. The effect of age of dam did not show any consistent trends.

Similarly, the non-genetic effects were unimportant in controlling variation in LAL (Table 4.7).

The reduced impact of the non-genetic factors on LAH and LAL indicates that after adjustment to a common liveweight, these traits are little affected by the maternal environment at the hogget stage. However, other unmeasured environmental effects must be acting on these traits, since heritabilities are only in the low to moderate range (table 4.14).

5.3 Direct responses to selection.

The objective of this section is to discuss the effects of selection for high and low liveweight-adjusted backfat depth (LABF) over a period of 8 years (1979-1986). Implications of selection prior to the period evaluated here will also be discussed. Before discussing the direct responses to selection it is important to reiterate that the selection of the two sires per line was based on an average of all measurements throughout the year. However, because about 50% of the animals were culled after the first assessment, only this measurement was used in the calculation of the CSD. The yearly and cumulated responses to selection were calculated based on both the first and the average of all measurements in the ram hoggets. For ewe hoggets responses were calculated using only the first measurement.

The direct responses based on the first measurement are shown in Figures 4.7, 4.8 and 4.9. The first year of analysis for this study (1979) of divergent selection showed highly significant differences between the lines for LABF indicating that selection prior to 1979 had probably been effective. These differences became larger over the years of selection until in the eighth year the high line recorded 1.69mm (59.6%DEVS) and 2.00mm (49.55%DEVS) more backfat than the low line for rams and ewes, respectively (Figure 4.8). The effects of selection assessed by within line yearly responses (Figure 4.7) showed erratic trends. However, the cumulated yearly responses showed that the lines clearly diverged

over the years (Figure 4.9). The cumulative yearly responses assessed in this fashion showed that after 8 years of selection the lines diverged by 42.28%DEV and 42.75%DEV in rams and ewes, respectively. This indicates an agreement between the results obtained from the two different techniques of evaluating direct response to selection. However, the slight advantage for the divergence between lines could reflect the initial divergence between lines in the first year of selection.

In theory, the divergence between lines technique should provide a more accurate estimate of response. This is because the technique removes common environmental effect due to taking the difference between the yearly means from the 2 lines (Hill, 1972a). However, the yearly responses technique removes the effect of initial selection because of the substraction of the annual response between consecutive years. Thus, under the conditions of the current experiment it is difficult to identify which technique provides the most efficient selection response estimate.

The direct responses to selection, based on the average of all LABF measurements in rams only, are shown in Figures 4.10 and 4.11. In general, it can be observed that a steady response was obtained, which showed less variability in response throughout the years, because of the larger number of observations involved in their calculation (Rae, 1982). The divergence between lines based on the average of all measurements, showed a steady increase in response over the first three years and over the last two years, but between 1983 and 1985 there was a decrease compared with 1982

(Figure 4.11), which could be due to sampling fluctuations (Hill, 1972c).

As was stated in section 3.1, the selection lines were established in 1976. Selection was applied on a regular basis each year and was almost certainly responsible for at least part of the significant divergence in LABF noted in 1979.

A further deficiency in calculating the response to selection as presented here is that selection was actually based on the average of several LABF measurements, which will provide a more accurate measure of the genetic merit, compared with selection on the basis of the first measurement only. This can be explained by removal of the temporary environmental effects (Rae, 1982). However, it was not possible to assess the response based on the average of several measurements because about 50% of the animals were culled after the first LABF measurement.

5.3.1 Selection differentials.

The selection differential calculated using the first LABF measurement alone (S1) was regressed against the selection differential calculated after the second selection (S2), which combines the selection pressure applied in the first (S3) and second (S4) selections (Dickerson and Hazel, 1944), Figure 3.1. The S1 and S2 were compared using a simple linear regression in

order to examine their functional dependency. If the distribution of LABF trait in the selection lines is not modified after the first culling and the averaging of several LABF measurements does not change the variance, then this regression should be equal to 1.0.That is selection based in the first LABF assessment would be similar to the actual selection pressure applied using both the first and all LABF measurements. But, if β is different than 1.0, then it can be assumed that the selection pressure applied based on the first measurement is not representing the true selection intensity in the selection process.

The regression equations and plots in Figure 4.5 showed that for a unit of change in S1, there were corresponding changes of 0.68 and 0.57 units in S2 for the high and low LABF selection lines, respectively. The most likely explanation for these regressions being less than 1.0 is that by taking the average of several LABF measurements, the variation is reduced. Thus, the S4 component of S2 is smaller than the equivalent portion of S1. Therefore, in order to estimate the true selection intensity, all LABF measurements should be taken into account.

Similar amounts of selection pressure were applied, within each year of selection, to produce the high and low backfat lines (Figure 4.3). This resulted because approximately the same number of offspring were selected each year to maintain the lines (Table 3.1).

Selection differentials were also calculated for the top two rams within each selection line regardless of body condition and weight. The comparison between the selection differentials of the sires used and the top two rams enables an examination of the loss in selection efficiency. The selection differential calculated from either the first LABF measurement, or for all measurements at the end of each year, can be obtained from the difference between the line means plotted in Figures 4.1 and 4.4, respectively. From both figures, it can be seen that the top 2 rams were superior to the two rams chosen in all years except 1982 and 1984 in the low and high line, respectively. This inferiority for some years of the top two rams in the first LABF measurement indicates that in spite of the higher value after all measurements, the top two rams may be inferior when judged solely on the first measurement. The general superiority of the top two rams over the sires used indicates that there was a loss in selection pressure on LABF, primarily because selection was weighted by subjectively assessed body characteristics of the rams. The difference in average performance indicated that the top two rams were between 4.3%DEV and 39.9%DEV higher than the sires actually used.

5.3.2 Responses to selection per unit of cumulated selection differential.

The regression coefficients representing the cumulated yearly responses to selection and the cumulative divergence per unit of CSD are shown in Figures 4.12, 4.13, 4.14 and 4.15. These ranged from -0.13 ± 0.36 to 1.32 ± 0.94. There is a tendency for the regression coefficients to be higher in the high line and greater for the rams. However, the size of the standard errors of the regression coefficients does not allow any firm conclusion to be drawn.

Normally, the regression coefficients obtained by regression of CSD on selection response could be considered the realized heritability of the trait (Falconer, 1981). However, two factors invalidate the use of the realized heritability term in this study: a) it was assumed that at the first year (1979), that no prior selection pressure had been applied, when in fact there had been, and b) the selection intensity and the response to selection were estimated by calculating the CSD based on the first measurement rather than on all measurements assessed through the year. Furthermore, the small number number of observations per regression analysis during the selection period, and the small number of sires, will also influence the accuracy of the regression coefficients obtained. These factors suggest that this regression would not be a valid estimation of the realized heritability this population.

Hetzer and Harvey (1967) and Hetzer and Miller (1972a) reported a range of realized heritabilities for LABF between 0.29 and 0.60 in high backfat and between 0.30 and 0.73 in low backfat selection lines in pigs. These reflected moderate-high responses to selection for that trait.

Therefore, the findings of this and other studies suggest that moderate to rapid response to selection for/against LABF should be achievable in sheep.

5.4 Correlated responses.

5.4.1 Birth weight, pre- and post-weaning growth rate.

It appears that the divergence between the high and low LABF lines in birth weight for both rams and ewes has gradually decreased over the years (Table 4.1). Furthermore, the non-significant negative regression of year on the divergence between lines indicates that any change in birth weight as a consequence of direct selection for or against LABF will be very slow. Berruecos et al(1970) reported that selection for lower backfat depth in pigs, adjusted by liveweight, over 5 generations resulted in a non-significant negative correlated response in birth weight in pigs. Hetzer and Miller(1972a) reported a

negative genetic correlation between LABF and birth weight (calculated using both the offspring-midparent covariances and the realized correlated responses methods), after 11 and 13 generations of selection in Yorkshire and Duroc pigs, respectively. Recently, Fennessy et al(1987) pointed out that lambs from a lean line of Coopworth sheep were heavier at birth than lambs from the fat line. Therefore, it could be speculated that the non-significant correlated response in birth weight may eventually become significant after more generations of selection have been applied.

The correlated response in pre- and post-weaning growth rate (Tables 4.2, 4.3 and 4.4) did not show any significant differences between lines. These results are in agreement with a prior analysis of data from the same Southdown selection lines (Kadim, 1988) and with the findings of Merks(1987, 1988). Kadim(1987) reported that the high and low backfat depth lines had similar growth rates. Merks(1987, 1988) reported moderate negative and low positive genetic correlations (-0.31 ± 0.30 to 0.24 ± 0.08) in Dutch Landrace and Yorkshire pigs, between weight corrected for age (which is an estimate of growth rate) and backfat thickness corrected for weight. The results also partly agree with the findings of Hetzer and Miller(1972a). They reported that in Duroc pigs, post-weaning growth rate showed a significant improvement in both the high and low lines, whereas in the Yorkshire post-weaning growth rate decreased significatively in the low line without changing significantly in the high line. Olson et al(1976) reported a non-significant

negative genetic correlation between post-weaning growth rate to an age of 25 weeks and backfat thickness adjusted by skinning variation in lambs. Wolf et al,(1981) reported a negative genetic correlation across dam breeds between subcutaneous fat depth and ADG from birth to slaugther in lambs (-0.30±0.39). Whereas, Fennessy et al(1987) reported that lambs from the lean and fatty lines had similar post-natal growth rate in Coopworth sheep. These reports, and the findings of this study, suggest the existence of a low or slightly negative genetic correlation between growth rate and backfat thickness in sheep. The findings of this study suggest that no change in growth rate or body weights are expected in this experiment, because of the correction of backfat depth for weight using regression techniques. However, in experiments selecting against uncorrected backfat depth measurements, a decrease in growth rate or other weights could be expected.

5.4.2 Liveweight-adjusted shoulder height and body length.

The highly significant differences found between the selection lines indicate that selection for high and low LABF has resulted in taller, longer and leaner animals in the low LABF line, with the opposite in the high LABF line (Table 4.7).

Despite the slow progress through the years, indicated by the non-significant regression coefficients (Table 4.11), the

divergence between the selection lines for both traits is consistently positive. Although genetic correlations were not calculated in this study, the increases in length and height in the low backfat depth line and the decreases in height and length in the high backfat depth line are indicative of negative genetic correlations between LABF and LAL and LABF and LAH. An early (Barton, 1981) and a recent (Kadim, 1988) reports regarding these selection lines, pointed out that the low backfat depth selection line was longer, leaner and had a higher bone weight than the high backfat selection line, which could indicate a larger frame. Similar findings were reported by Hetzer and Miller(1972b) in pigs. They showed that in Duroc and Yorkshire pigs, body length and shoulder height had negative genetic correlations with backfat depth. Although Purser(1980a) did not report any objective assessments of fatness in his cannon bone length selection lines, he pointed out that from a subjective scoring of fatness the short cannon bone length lambs were fatter than the high cannon bone length lambs, but the differences were less evident in adult sheep. Therefore, the available information would suggest a low-moderate negative genetic correlation between LABF and LAL and LABF and LAH.

Physiological aspects of the genetic association between LABF, LAH and LAL traits are not still well understood in sheep. However, some attempts have been reported. Purser(1982) pointed out that selection for more prolific ewes has apparently resulted in a tendency to produce a longer-legged animal and that selection for/against cannon bone length has also resulted in

high prolific ewes, better body condition and an increase in the total productivity. He speculated that variation in pituitary function could be involved since pituitary gonadotrophins affect both bone and gonad development. More studies in this field are required to provide a better explanation of the physiological relationships between LABF, LAH and LAL.

The results of this study and earlier reports suggest that selection based on LAH or LAL or both body measurements should be effective in breeding for leaner sheep in on-farm programs where the taking of ultrasonic backfat depth assessments presents some difficulties. However, the simultaneous selection for LABF and the body measurements (LAH and LAL) should be more effective in breeding for leaner sheep than selection for either LABF or body measurements alone.

5.5 Phenotypic correlations and repeatabilities.

The pooled phenotypic correlations (see section 3.5.2) for consecutive measurements of LABF (Table 4.12) were moderate to high. Purchas et al(1981b) reported similar values for consecutive measurements in LABF in a study using date from Romney sheep and part of the Southdown data analysed in this study. They concluded that LABF, in terms of deviation values, was moderately repeatable. Therefore, sheep with high backfat depth at 7 to 8 months of age are likely to retain this characteristic up to at least 15 to 18 months

of age.

The pooled phenotypic correlations for consecutive measurements of LAL and LAH were low-moderate and moderate-high, respectively. These figures were slightly higher than those values reported by Purchas et al(1981b), which could be due to a larger number of animals used in this study. The low values reported for LAL trait are an indication of the difficulty of assessing this trait and the sensitivity to the way in which the animal stands.

The analysis of the combinations between LABF, LAH and LAL were in agreement with the values reported by Purchas et al(1981b), except the values calculated for LAH-LAL, were slightly smaller in this study. Although genetic correlations were not calculated in this study, the existing evidence suggested a negative genetic correlation between LABF and LAH and between LABF and LAL, but a positive one between LAL and LAH (see sections 4.2.5, 4.2.6, 4.4.6 and 5.2.2) This suggestion is supported by the trends of the values of the phenotypic correlations between the combinations of these variables (see Table 4.12).

The repeatability values for LABF, LAH and LAL in Table 4.13, suggest that LABF and LAH are moderate to highly repeatable. These values generally agree with the values reported by Purchas et al(1981b). The slightly smaller values calculated in this study could be due to the within line analysis. This is because the variance of a trait is greater when the units are randomly chosen from a population and allocated to a group than when the units are

chosen randomly and allocated in two divergent groups for the same trait (Steel and Torrie, 1981).

The comparison between the pooled phenotypic correlations (Table 4.12) and the repeatabilities (Table 4.13) indicated that the phenotypic correlations were higher than the repeatabilities. This observation agrees with the findings reported by Purchas et al(1981b). These higher values for the phenotypic correlations could be due to the lower variability between consecutive measurements. The results supports the view of McEwan et al(1987) and others that in vivo backfat depth measurements using ultrasonic instruments can be used to estimate fatness in sheep. To help minimise the generation interval, breeders would like to select replacement stock at the earliest possible age, providing that the animal is expressing its own genetic merit for leannness and that the UBF measurements are an accurate measurement of carcass leanness. Furthermore, the minimum number of assessments necessary before any selection can take place needs to be known. A detailed examination of this problem is beyond the scope of this study. However, if selection had been based on the first LABF measurement only in this study, the same rams would have been chosen in 7 of the 8 years of selection reported in this study (Figure 4.1). To provide accurate guidelines, more studies in this field are necessary.

5.6 Heritability.

Heritability estimates for LABF using four different methods in Southdown ram hoggets were given in Tables 4.14 and 4.15. The heritability values presented in Table 4.14 and the heritability in period I for LABF in Table 4.15 were calculated on the unselected population. These values differed depending on the method of calculation. The dam/offspring correlation and regression values were moderate while the paternal half-sibs estimates were low. However, they were within the range of heritability estimates previously recorded for backfat depth in live animals data (see Table 2.4).

Paternal half-sibs estimates using Henderson's method 2 and Henderson's method 3 were in agreement. In theory, the lack of adjustment for non-genetic effects (Henderson's method 3 in this study) should result in a lower heritability values. Whereas heritabilities calculated from corrected data (Henderson's method 2 in this study) should provide a larger ratio of additive genetic variance to phenotypic variance. However, the similarity of heritability estimates using both approaches indicated that the correction for the non-genetic factors did not have a major impact on the heritability value for LABF.

Heritability estimates for LABF were calculated in both the unselected and selected populations (Table 4.15). Enabling the examination of the effect of truncation selection on heritability

estimation. The heritability estimated in the unselected population was a low positive value, whereas the estimates in the selected population were nearly zero. This indicates that truncation selection based on LABF, removes the between sire variation. However, in the absence of selection, the high correlations between consecutive measurements and the high repeatabilities of LABF would imply the heritability of later assessments of LABF should be similar to those calculated for the first measurement.

The heritability estimates using regression and correlation were in good agreement, suggesting that variation of the trait in selected dams and unselected offspring is approximately the same. Therefore, the correlation method can be used to calculate heritability.

The comparison between the dam/offspring correlation and paternal half-sibs estimates (Tables 4.14 and 4.15) showed that dam/offspring correlation heritability estimates were noticeablely higher than the values provided by paternal half-sibs estimates. These lower values provided by paternal half-sib analysis are probably due to the small number of sires involved within and across lines, resulting in large sampling errors (Falconer, 1981).

Although, some low heritability values for LABF are reported in the literature (Table 2.4) and in this study, most evidence supports the existence of a moderate heritability in sheep. Furthermore, the selection responses obtained in the current selection experiment and in other experiments with sheep (Fennessy

et al, 1987) and pigs (Hetzer and Miller, 1967) would also support this argument. Therefore, selection for or against LABF should enable a moderate rate of progress in modifying backfat depth levels.

Heritability estimates for LAH (Table 4.15) were moderate. They were slightly smaller than the values reported by Hetzer and Miller(1972b) in pigs and with other traits indicative of height in sheep (Purser, 1980b), Table 2.3. Furthermore, the high correlated response in LAH in the current experiment, the high correlated response reported by Hetzer and Miller(1972b) and the large direct response obtained by Purser(1980b) would also support a moderate to high heritability for LAH. Because heritability estimates were calculated in the selected population in this study, it is expected that a reduction in the genetic variation and hence the heritability estimate would occur. The substantial correlated response in LAH in this experiment also suggests the existence of genetic covariation between LABF and LAH.

The heritability estimate for LAL in this study do not agree with those of Hetzer and Miller(1972b) who reported moderate to high values in pigs. The low values in this study for LAL could be due to the reduced number of observations for this character. In addition, the heritability estimates of LAL were also calculated from the selected population of hoggets. This most likely lead to a decrease in genetic variation in LAL, as noted above for LAH. Furthermore, The correlated response in LAL obtained in this experiment and the correlated response reported by Hetzer and

Miller(1972b) in pigs would support the existence of genetic variation in LAL, as well as there being genetic covariation between LABF and LAL.

CHAPTER SIX   CONCLUSIONS

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Despite the relatively brief duration of this divergent selection experiment (for high or low backfat depth), the results indicated clear trends in several traits.

Highly significant (P≤.01) differences between line means in rams were found from the first year of divergent selection, with the divergence between lines being 0.24mm (16%DEV). This significant difference was probably due in part to selection prior to 1979. The difference became steadily larger until in the last year of selection included in this study (1986), the divergence between line means was 1.69mm (59.6%DEV). The responses to selection in the ewe hoggets were larger than those showed by the ram hoggets. The ewe line means did not significantly differ in 1979, but by 1986 the lines differed significantly (P≤.01) by 2.00mm (49.57%DEV). Therefore, over the 8 years of individual selection included in this study increases in the differences between the lines for LABF assessed ultrasonically were found, which showed that selection for or against LABF was effective in Southdown sheep.

Because of the prior selection and the two stages of selection involved in the selection of the sires, there were difficulties in assessing the selection pressure, and hence the response to selection per unit of selection intensity. The selection intensity (CSD) was calculated based on the first LABF measurement, because all animals were present for this measurement only. However,

the true selection intensity applied for rams was dependent on the average of all LABF measurements. Therefore, the regression of CSD on response to selection resulted in coefficients which did not lend themselves to being interpreted as realized heritabilities.

For divergent selection experiments, with well established base populations prior to any selection, assessing response to selection as the divergence between lines should provide greater accuracy than using the difference between consecutive yearly means within line. However, the current selection experiment lacked a common base population, and the first three years of selection could not be included because of the inconsistent ultrasonic measurements. Therefore, the yearly response technique appeared to provide a better estimation of the selection response because it removed the effect of initial selection, prior to 1979. However, it does not remove the common environmental effect.

The comparison between the sires used and the top two rams based on LABF, only indicated that the loss in selection intensity was between 4.3%DEV and 39.9%DEV, when individual selection was based partly on a subjective assessment of body condition and physical soundnessof the potential future sire.

The average changes per annum in correlated traits were found to be non-significant. However, the correlated responses in LAH and LAL were positive, and the lines showed highly significant differences. The hoggets in the high LABF selection line were 41.4mm and 27.4mm shorter in length and height, respectively, than hoggets from the low

selection line in the last year of selection.

The small non-significant effect of selection for LABF on pre- and post-weaning growth rate was expected since selection was based on a liveweight adjusted trait.

Despite the decrease in the size of the divergence between lines for birth weight, it is difficult to draw a firm conclusion about this trait. However, according to the literature, a longer period of selection in the current experiment could eventually result in a significant negative correlated response in birth weight.

The repeatabilities indicated that LABF is moderate to highly repeatable, suggesting that one measurement at 6-7 months of age would provide adequate accuracy for the early selection of sires.This would permit a reduction in the generation interval and hence an increase in the genetic gain per unit of time. However, more studies are required in order to define an optimum selection policy regarding the earliest age at which selection could occur and the number of LABF measurements required to accurately assess backfat depth in the live animal.

The non-genetic effects showed to be unimportant for LABF, LAH and LAL.

A large impact of selection on heritability estimates was detected when truncation selection was practised on the unselected population of hoggets and further heritability estimates were calculated on the selected population. The heritability values for

LABF, LAH and LAL were low-moderate, moderate and low, respectively. It is concluded that truncation selection on LABF reduced the genetic variance of LAH and LAL, although not to the same extent as for LABF. However, heritability estimates in this study and the literature support a moderate value for these traits. Therefore, a moderate progress from selection involving these traits should be expected.

Although, genetic correlations were not calculated in this study between LABF, LAH and LAL, due to the small number of observations, the highly significant difference between lines for these traits and the phenotypic correlations would suggest that the combinations LABF-LAH and LABF-LAL are negatively genetically correlated while LAH and LAL are positively genetically correlated. These results would suggest that simultaneous selection for these three traits would produce leaner, taller and longer sheep.

This selection experiment for high and low LABF provides wide scope for further research. However, maintenance of the two selection lines utilizes land and other resources which could be used for alternative purposes. Thus, further studies in this area depends on the future policy about meat-sheep production in New Zealand, which should be addressed with consideration about the future national and international market conditions for sheep-meat. The short time this experiment has been running, and the enormous importance of the sheep-meat industry to New Zealand should make the retention of the two selection lines for further studies very important.

The study of the genetic, physiological, reproductive, health

and nutritional factors in these two lines should help in establishing optimum productive plans for sheep-meat producing systems. Since the causes and consequences of selection for or against fatness in sheep are poorly understood, the research in these selection lines should consider:

a) The minimum number of LABF assessments and the earliest age to select replacements. This point should consider the proper age when the animal is expressing its own genetic merit for the trait.

b) The study of physiological aspects explaining the interrelationships between LABF, LAH and LAL would help in determining the usefulness of LAH and LAL as alternative selection criteria. Other important physiological aspects include the study of physiological traits as possible genetic markers for leanness or fatness. Earlier attempts in this selection experiment have shown evidence for physiological indicators of leanness or fatness (Bremmers et al,1988; Carter, et al, 1986; Carter, 1987). However, additional evaluations are required to confirm these findings and to examine other possibilities.

c) Inbreeding effect. It is well recognized that inbreeding leads to a depression in productivity. The small numbers in the selection lines will result in relatively rapid accumulation in inbreeding, providing the opportunity to examine its effects on carcass traits.

d) <u>Food utilization efficiency</u>. The importance of food utilization efficiency in ruminants emphasizes the necessity of studies into the comparative efficiency of the two lines. Recently, Bremmers <u>et al</u>(1988) reported (from these selection lines) that the low backfat depth selection line broke down muscle protein more readily during underfeeding based on creatinine levels, whereas at high allowance they use dietary amino-acids more efficiently for production. However, the measurement of food utilization efficiency under direct grazing conditions should provide a better estimates of the sward utilization.

e) <u>Reproductive performance</u>. The correlated responses in reproductive traits, such as ovulation rate, embryonic mortality, birth weight and lamb survival, together with other traits should be analysed to evaluate the general reproductive performance of the selection lines. Early studies showed that there were no significant differences between the lines in lambing percentages over several years (Unpublished data).

f) <u>Wool production</u>. The study of wool production in the selection lines should provide an indication of the effect of selection for high and low LABF. Although the Southdown sheep is a well known meat breed, the relationship between meatiness and wool production is still of interest, given the substantial contribution of the wool-pull and the pelt to the returns per animal. Early, data on hogget fleece weights showed these to be very similar between the selection lines (Unpublished data).

g) <u>Evaluation of the genetic gain from crossing the lines with commercial flocks</u>. The Southdown breed had been used as a terminal breed for the production of export lamb carcasses. Therefore, the improvement of the lean meat production in the lean selection line should be examined by comparing their offspring with those of commercially available animals. Recently, Kadim(1988) reported that the progeny from low backfat depth selection line sires crossed with Romney ewes were leaner than the progeny of sires from the high backfat depth selection line. Similar findings were reported by Lord <u>et al</u>(1988) from the Invermay fat and lean selection lines with Coopworth sheep.

The first eight years of this selection experiment have been adequate to examine initial direct and correlated responses to selection. However, several more years of selection would be desirable to confirm the results obtained to date and to allow other slower responses to be detected.

APPENDICES

7.1. Dates of the three periods within year for the analysis of post-weaning

growth rate in ram hoggets from 1980 to 1986.

	PERIOD		
YEAR	pre-selection	winter	spring
1980	from weaning to April 23th.	——	from April 24th. to January 18th.
1981	from weaning to May 26th.	from May 27th. to September 14th.	from September 15th to December 1st.
1982	from weaning to March 26th.	from March 27th. to September 14th.	from September 15th. to December 5th.
1983	from weaning to March 9th.	from March 10th. to October 2nd.	——
1984	from weaning to May 6th.	from May 7th. to October 22th.	from October 23th. to December 4th.
1985	from weaning to May 6th.	from May 7th. to October 30th.	from October 31th. to December 12th.
1986	from weaning to April 16th.	from April 17th. to September 4th.	from September 5th. to December 4th.

7.2. Dates of the three periods within year for the analysis of LABF in ram hoggets from 1980 to 1986.

	PERIOD		
YEAR	I	II	III
1980	April 26th.	___	January 18th.
1981	May 26th.	September 14th.	December 5th.
1982	March 29th.	September 14th.	December 4th.
1983	March 9th.	October 2nd.	___
1984	May 6th.	October 22th.	December 4th.
1985	May 6th.	October 30th.	December 12th.
1986	April 16th.	September 4th.	December 4th.

7.3. Dates of the three periods within year for the analysis of LAH in ram hoggets from 1980 to 1986.

| YEAR | PERIOD | | |
	I	II	III
1980	——	——	——
1981	——	September 15th.	December 1st.
1982	May 16th.	October 28th.	——
1983	July 19th.	October 2nd.	——
1984	July 3th.	——	——
1985	June 11th.	October 30th.	——
1986	May 27th.	September 4th.	December 4th.

7.4. Dates of the three periods within year for the analysis of LAL

in ram hoggets from 1980 to 1986.

YEAR	PERIOD		
	I	II	III
1980	——	——	——
1981	——	September 14th.	December 1st.
1982	——	——	——
1983	——	October 2nd.	——
1984	July 3th.	——	——
1985	June 11th	October 30th.	——
1986	May 27th.	September 27th.	December 4th.

7.5. Calculation of selection differentials.

| | YEAR | | | | | | | | | | | | | | | |
| | 1979 | | 1980 | | 1981 | | 1982 | | 1983 | | 1984 | | 1985 | | 1986 | |
VARIABLE	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
μ	12.67	-3.87	19.05	-8.25	17.98	-20.19	26.30	-13.60	15.55	-13.92	25.28	-17.28	26.78	-12.15	39.76	-19.86
$\bar{X}1$	18.49	-10.79	19.05	-8.25	31.91	-24.73	47.59	-27.41	35.45	-20.54	42.03	-24.01	35.32	-26.85	46.39	-26.22
S3	5.82	-6.92	00.00	00.00	13.93	-4.54	21.29	-13.81	19.90	-6.62	16.75	-6.73	8.54	-14.70	6.63	-6.36
$\bar{X}2$	28.10	-36.50	39.76	-10.06	32.70	-52.45	36.17	-45.98	46.62	-24.11	58.93	-29.25	90.37	-38.21	88.46	-50.69
S1	15.44	-32.63	20.68	-1.81	14.72	-32.26	9.87	-32.38	31.07	-10.19	33.65	-11.97	63.59	-26.06	48.70	-30.83
$\bar{X}3$	15.94	-3.12	18.44	-14.09	26.65	-25.31	37.32	-24.49	27.78	-21.29	28.25	-17.63	30.95	-19.40	47.78	-28.10
S4	17.35	-25.60	27.85	-13.92	8.55	-18.54	2.89	-15.76	15.69	-6.82	15.08	-8.44	46.98	-20.20	45.97	-17.84
$\bar{X}4$	33.29	-28.72	46.30	-28.01	35.20	-43.86	40.21	-40.25	43.47	-28.11	43.32	-26.06	77.93	-39.60	93.75	-45.94
S2	23.17	-32.52	27.86	-13.92	22.48	-23.09	24.18	-29.57	35.59	-13.44	31.82	-15.17	55.52	-34.90	52.60	-24.20

where: μ, general mean in the unselected population for the first measurement;

$\bar{X}1$, general mean in the selected population for the first measurement;

$\bar{X}2$, general mean of the selected sires for the first measurement;

S3, simple selection differential, $(\bar{X}1 - \mu)$;

S1, total selection differential, $(\bar{X}2 - \mu)$;

$\bar{X}3$, general mean in the selected population for all measurements;

$\bar{X}4$, general mean of the selected sires for all measurements;

S4, simple selection differential, $(\bar{X}4 - \bar{X}3)$;

S2, total selection differential, $(S3 + S4)$.

7.6. An example of the calculation of heritability using

Henderson's method 2.

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a) <u>First model.</u> The LABF, LAH and LAL data was adjusted for all

fixed effects and the covariate date of birth on the unselected

population of hoggets (N=905 and 29 sires). The model was:

$$Y_{ijklmn} = \mu + A_i + D_j + BRK_k + SEX_l + G_{im} + \beta(x_{ijklmn}) + e_{ijklmn}$$

where the factors are defined as in section 3.3.7.1.

b) <u>Second model.</u> Once the data for LABF, LAH and LAL were adjusted

for the first model, and estimation of the sum of squares within

sire was calculated and then pooled across sires to obtain the

sum of squares due to sires. The model was:

$$Y_{ij} = \mu + S_i + e_{ij}$$

where: Y_{ij} = an observation (in the residuals) for

the jth individual in the ith sire,

μ = the general mean,

S_i = the effect of the ith sire (i = 1,..., 29), and

e_{ij} = the error associated with each observation in the residuals.

.

The analysis of variance for LABF on the unselected population is:

Source of variation	D.F	M.S	E.M.S
Sires	15	1968.92	$\sigma_e^2 + K_1 \sigma_s^2$
Error	871	786.45	σ_e^2
Total	904		

Coefficient of variance components:

$$K_1 = 1/S-1 \left[\sum_{i=1}^{29} n_i - \sum_{i=1}^{29} n_i^2 \bigg/ \sum_{i=1}^{29} n_i \right]$$

$$= 31.1$$

Variance components:

$$\sigma_e^2 = 786.45, \text{ and}$$

$$\sigma_s^2 = 38.02.$$

Heritability value:

$$h^2 = 4(\sigma_s^2)/\sigma_s^2 + \sigma_e^2$$

$$= 0.18.$$

Standard error of heritability, SE(h^2):

$$SE(h^2) = 4\left\{ 2(n_i-1)(1-t)^2 \left[1+(K_1-1)t\right]^2 /K_1^2(N-S)(S-1) \right\}^{\frac{1}{2}}$$

where: $t = \sigma_s^2 / \sigma_s^2 + \sigma_e^2$

$$= 0.046.$$

Therefore: SE(h^2) = 0.26.

REFERENCES

REFERENCES

Allen,P. and J.C.McCarthy (1980). The effects of selection for high
    and low body weight on the proportion and distribution of fat in
    mice. Animal Production. 31:1-11.

Alliston,J.C. (1983). Evaluation of carcass quality in the live
    animal. In: Sheep Production. Ed. W.Haresign. Butterworths.
    UK. pp.75-95.

Andersen,B.B. (1975). Recent experimental development in ultrasonic
    measurement of cattle. Livestock Production Science. 2:137-146.

Andersen,B.B.,H.Busk,J.P.Chadwickh,A.Cuthbertson,G.A.Fursey,D.W.Jones,
    P.Lewin, C.A.Miles and M.G.Owen. (1981). CEC Supported
    Ultrasonic Trial in UK and DK. In: In-vivo Estimation of Body
    Composition in Beef. CEC Workshop. Copenhagen. pp.13-38.

Atkins,K.D.(1986). A genetic analysis of the components of lifetime
    productivity in Scottish Blackface Sheep. Animal
    Production.43:405-419.

Atkins,K.D. and R.Thompson (1986). Predicted and realized responses
    to selection for an index of bone length and body weight in
    Scottish Blackface Sheep: II. Correlated responses in lifetime
    productivity. Animal Production.43:437-445.

Avery,P.J. and W.G.Hill (1977). Variability in genetic parameters
    among small populations. Genetical
    Research,Cambridge.29:193-213.

Barnicoat,C.R.,A.G.Logan and A.I.Grant (1949). Milk secretion studies
    with New Zealand Romney ewes. Journal of Agriculture Science.
    39:44-55.

Barnicoat,C.R.,P.F.Murray.,E.M.Roberts and G.S.Wilson (1956). Milk
    secretion studies with New Zealand Romney ewes. Parts V-XI.
    Journal of Agriculture Science. Cambridge. 48:9-35.

Barton,R.A. (1981). The new Southdown. Flock and Herd.5:18-21.

Barton,R.A.,R.M.Pratt and A.L.Rae (1986). Progeny testing for meat production in the Poll Dorset breed. Proceedings of the New Zealand Society of Animal Production.46:45-48.

Beatson,P.R. (1987). The inheritance of liveweight-corrected fat-depth in Coopworth ram hoggets. Proceedings of the Australian Association of Animal Breeding and Genetics.6:87-90.

Becker,W.A. (1984). Manual of Procedures in Quantiative Genetics. Academic Enterprises. Washington,D.C. 190 pp.

Becker,W.A.,J.W.Spencer,L.W.Mirosh,J.A.Verstrate (1978). Prediction of fat and fat free live weight in broiler chickens using backskin fat, abdominal fat, and live body weight. Poultry Science. 57:1117-1118.

Bennett,G.L.,J.N.Clarke,P.V.Rattray and K.S.McClean (1984). Relationship of subcutaneous fat depth and weight changes induced by stocking rate in four lines of lambs. Proceedings of the New Zealand Society of Animal Production.44:215-218.

Bennett,G.L.,D.L.Johnson and A.H.Kirton (1982). Genetic variation of Southdown lamb carcass traits. Ministry of Agriculture and Fisheries. Agricultural Research Division.Annual report. pp.33

Bennett,G.L.,H.H.Meyer and A.H.Kirton (1983a). Ultrasonic selection for divergence in loin fat depth in Southdowns and Suffolks. Proceedings of the New Zealand Society of Animal Production. 43:115-117.

Bennett,G.L.,A.L.Rae,J.N.Clarke and A.H.Kirton (1983b). Research studies for development of large lean sheep breed. Ministry of Agriculture and Fisheries, Agricultural Research Division.Annual report. pp.43

Benson,C.R.,J.S.Brinks,B.W.Knapp and O.F.Pahnish (1972). Response to selection in beef cattle. Journal of Animal Science. 34:886.

Berruecos,J.M.,E.U.Dillard and O.W.Robison. (1970). Selection for low backfat thickness in swine. Journal of Animal Science.30:840-848.

Bichard,M. and M.McG. Cooper. (1966). Analysis of production records from a lowland sheep flock. Animal Production.8:401-410.

Biswas,D.K.,P.V Hurt,A.B.Chapman,N.L.First and H.L.Self (1966). Feed efficiency and carcass desirability in swine. Journal of Animal Science.25:342-347.

Blair,H.T. (1981). Responses to selection for open face greasy fleece weight in Romney sheep. Ph.D. Thesis. Massey University. Palmerston North,New Zealand.

Blair,H.T. (1986). Responses to 27 years of selection for yearling fleece weight. Proceedings of the Third World Congress on Genetics Applied to Livestock Production. Vol.XII. Lincoln, Nebraska. U.S.A. pp.215-220.

Blair,H.T. and E.J.Pollak (1984). Estimation of genetic trend in a selected population with and without the use of a control population. Journal of Animal Science.58:878-886.

Botkin,M.P.,R.A.Field,M.L.Riley,J.C.Nolan and G.P.Roenhrkasse (1969). Heritability of carcass traits in lambs. Journal of Animal Science.29:251-255.

Bradford,G.E. (1972). The role of maternal effects in animal breeding. VII. Materenal effects in sheep. Journal of Animal Science. 35:1324-1334.

Bremmers,R.P.M.,P.F.Morgan,S.N.McCutcheon and R.W.Purchas (1988). Effect of plane of nutrition on energy and nitrogen retention and on plasma urea concentrations in Southdown ram hoggets from high and low backfat selection lines. New Zealand Journal of Agricultural Research. 31:1-7.

Brinks,J.S.,R.T.Clark,N.M.Kieffer,J.J.Urick (1965). Evaluation of response to selection and imbreeding in a closed line of Hereford cattle. Animal Breeding Abstracts. 34:173.

Brody,S. (1935). Nutrition. Annual Review of Biochemistry.4:383-412.

Burris,M.J. and C.A.Baugus (1955). Milk consumption and growth of suckling lambs. Journal of Animal Science. 14:186-199.

Cameron,N.D and C.Smith. (1985). Estimation of carcass leanness in young rams. Animal Production. 40:303-308.

Carter,R.C.,G.M.Carman,F.S.McClaugherty and P.S. Haydon (1971). Genotype-environment interaction in sheep II. Lamb performance traits. Journal of Animal Science.33:732-735.

Carter,M.L. (1987). A study of metabolic differences between fat and meaty Southdown sheep. M.Agr.Sc. Thesis. Massey University. Palmerston North, New Zealand.

Carter,M.L.,S.N.McCutcheon and R.W.Purchas (1985). Metabolic challenges as indicators of genotype. Proceedings of the Eleventh Workshop on overfatness and lean meat production from sheep. Massey Uiversity. Palmerston North, New Zealand. pp.17-19.

Cassuto,D.,A.E.Bell and A.L.Anderson (1970). Estimation of genetic gains in populations with overlapping generations. British Poultry Science. 11:217-230.

Ch'ang,T.S and A.L.Rae (1961). Sources of variation in the weaning weight of Romney Marsh lambs. New Zealand Journal of Agricultural Research. 4:578-582.

Ch'ang,T.S and A.L.Rae (1970). The genetic basis of growth, reproduction, and maternal environment in Romney ewes. I.Genetic variation in hogget characters and fertility of the ewe. Australian Journal of Agriculture Research. 21:115-129.

Clarke,J.N and H.H.Meyer (1982). Implications of experimental results in the crossbreeding of sheep in New Zealand. In: Proceedings of the world congress on sheep and beef cattle breeding. Vol.I. Eds. R.A.Barton and W.C.Smith. The Dumore Press LTD. Palmerston North, New Zealand. pp.133-146.

Cleveland,E.R.,R.K.Johnson and P.J.Cunningham (1988).   Correlated
       responses of carcass and reproductive traits to selection for
       rate of lean growth in swine.   Journal of Animal Science.
       66:1371-1377.

Cunningham,D.L.,G.F.Combs,Jr.,J.A.Saroka and   M.W.Lavorgna   (1987).
       Response to divergent selection for early growth of chickens fed
       a diet defficient in selenium. Poultry Science.66:209-214.

Cue,R.I. (1983). Correlated responses in lamb mortality due to long
       term selection for cannon bone length and fleece medullation in
       sheep. Animal Production.37:293-299.

Dalton,D.C. (1980). An Introduction to Practical Animal Breeding.
       Granada. U.K. 162 pp.

Dalton,D.C. and R.L.Baker (1980).   Selection experiments with beef
       cattle and sheep.In:Selection experiments in laboratory and
       domestic animals. Ed. A.Robertson.   Commonwealth Agricultural
       Bureaux,U.K. pp.131-143.

Davis,M.E. (1987).   Divergent   selection   for   postweaning   feed
       conversion in beef cattle: predicted response based on an index
       of feed intake and gain vs.feed:gain ratio. Journal of Animal
       Science. 65:886-895.

Dettmers,A.E.,W.E.Rempel and R.E.Comstock (1965). Selection for small
       size in swine. Journal of Animal Science.24:216-220.

Dickerson,G.E. and J.C.Grimes (1947). Effectiveness of selection for
       efficiency of gain in Duroc swine. Journal of Animal
       Science.6:265-287.

Dickerson,G.E. and L.N.Hazel (1944). Effectiveness of selection on
       progeny performance as a supplement to earlier culling in
       livestock. Journal of Agriculture Research. 69:459-476.

Donald,H.P.,J.L.Read and W.S.Russell (1968). A comparative trial of
       crossbred ewes by Finnish Landrace and other sires. Animal
       Production.10:413-421.

Dodd,C.J.,R.W.Purchas and G.L.Bennett (1986). Lean lamb selection. Ministry of Agriculture and Fisheries, Advisory Services Division. Wellington,N.Z.

Edwards,R. and I.T.Omtvedt (1971). Genetic analysis of a swine control population.II. Estimates of population parameters. Journal of Animal Science.32:185-190.

Eisen,E.J. and T.Bandy (1977). Correlated responses in growth and body composition of replicated single-trait and index selected lines of mice. Theoretical and Applied Genetics. 49:133-144.

England,D.C.,L.M.Winters and L.E.Carpenter (1954). The development of a boar of miniature swine-A preliminary report. Growth.18:207-214.

Falagan,A. and Garcia de Siles, J.L. (1987). Effect of sire breed on the performance of Aragon commercial crossbred lambs. 1. Growth traits. Animal Breeding Abstracts.55:769.

Falconer,D.S.(1953). Selection for large and small size in mice. Journal of Genetics. 51:470-501.

Falconer,D.S.(1954). Validity of the theory of genetic correlation. Journal of Heredity. 45:42-44.

Falconer,D.S. (1960). Selection of mice for growth on high and low planes of nutrition. Genetical Research,Cambridge.1:91-113.

Falconer,D.S. (1973). Replicated selection for body weight in mice. Genetical Research, Cambridge. 22:291-321.

Falconer,D.S. (1981). Introduction to Quantitative Genetics. Longman Group, Ltd. London,U.K. 340 pp.

Fennessy,P.F.,G.J.Greer and W.E.Bain (1987). Selection to change carcass fatness in sheep. Proceedings of the Fourth Congress of the Asian-Australasian Society of Animal Production. Hamilton, New Zealand. pp.382

Fortin,A. (1980). Fat Thickness measured with three ultrasonic instruments on live ram lambs as predictors of cutability. Canadian Journal of Animal Science.60:857-867.

Fortin,A. and J.N.B.Shrestha (1986). In vivo estimation of carcass meat by ultrasound in ram lambs slaughtered at an average live weight of 37 kg. Animal Production.43:469-475.

Fowler,S.H and M.E.Esminger (1960). Interactions between genotype and plane of nutrition in selection for rate of gain in swine. Journal of Animal Science. 19:434-449.

Freeden,H.T. and H.Mikani (1986). Mass selection in a pig population: realized heritabilities. Journal of Animal Science.62:1509-1522.

Garwood,V.A. (1987). Estimates of heritability for plasma very low density lipoprotein concentration and genetic correlations with lipid content,body volume, and density in Coturnix coturnix japonica. Poultry Science.66:1272-1275.

Gilmour,A.(1985). A generalized linear models programme(REG). New South Wales Department of Agriculture.Australia.

Glimp,A.G (1971). Effects of sex alteration, breed, type of rearing and creep feeding on lamb growth. Journal of Animal Science.32:859-862.

Gooden,J.M.,A.D.Beach and R.W.Purchas (1980). Measurement of subcutaneous backfat depth in live lambs with an ultrasound probe. New Zealand Journal of Agricultural Research. 23:161-165.

Goodwin,K.,G.E.Dickerson and W.F.Lamoreux (1955). A technique for measuring genetic progress in poultry breeding experiments. Poultry Science.34:1197.

Goodwin,K.,G.E.Dickerson and W.F.Lamoreux (1960). An experimental design for separating genetic and environmental changes in animal populations under selection. In: Biometrical Genetics. Ed. O.Kempthorne. Pergamon press. London, U.K. pp.117-138.

Gowe,R.S.,A.S.Johnson,J.H.Downs,R.Gibson,R.Mountain W.F.,J.H.Strain and B.F.Tinney (1959a). Environment and poultry breeding problems. 4.The value of a random-breed control strain in a selection study. Poultry Science. 38:443-462.

Gowe,R.S.,A.Robertson and B.D.H.Latter (1959b). Environment and poultry breeding problems.5.The design of poultry control strains. Poultry Science.38:462-471.

Gray,R.C.,L.F.Tribble,B.N.Day and J.F.Lasley (1968). Results of five generations of selection for low backfat thickness in swine. Journal of Animal Science.27:331-335.

Gregory,I.P.,E.M.Roberts and J.W.James (1978). Genetic improvement of meat sheep. 5.Heritability of postweaning weight and gain in Dorset and Border Leicester sheep. Australian Journal of Experimental Agriculture and Animal Husbandry.18:63-69.

Griffin,H.D. and C.C.Whitehead (1982). Plasma lipropotein concentration as an indicator of fatness in broilers: development and use of a simple assay for plasma very low density lipoproteins. British Poultry Science.23:307-313.

Hayes,J.F and J.C.McCarthy (1976). The effects of selection at differentes ages for high and low body weight on the pattern of fat deposition. Genetical Research,Cambridge.27:389-433.

Hazel,L.N. and E.A.Kline (1952). Mechanical measurement of fatness and carcass value on live hogs. Journal of Animal Science.11:313-318.

Henderson,C.R (1953). Estimation of variance and covariance components. Biometrics.9:226-252.

Henderson,C.R (1973). Sire evaluation and genetic trends. In: Proceedings Animal Breeding and Genetics Symposium in Honour of Dr.J.L.Lush. Champaign, Illinois. pp.10-41.

Henderson, C.R.,O.Kempthorne,S.R.Searle and C.M.Von Krosick (1959). The estimation of environmental and genetic trends from records subjected to culling. Biometrics. 15:192-218.

Hess,C.W.,H.M.Edwards,Jr. and E.F.Dembnicki (1962). Growth rate selection on a methionine deficient diet. Poultry Science.41:1042-1047.

Hetzer,H.O. and W.R.Harvey (1967). Selection for high and low fatness in swine. Journal of Animal Science.26:1244-1251.

Hetzer,H.O. and R.H.Miller (1970). Influence of selection for high and low fatness on reproductive performance on swine. Journal of Animal Science.30:481-495.

Hetzer,H.O. and R.H.Miller (1972a). Rate of growth as influenced by selection for high and low fatness in swine. Journal of Animal Science.35:730-742.

Hetzer,H.O. and R.H.Miller (1972b). Correlated responses of various body measurements in swine selected for high and low fatness. Journal of Animal Science.35:743-751.

Hight, G.K. (1982). Improving the efficiency of breeding schemes.In: Sheep Production: Breeding and Reproduction. Vol.I. Eds. G.A.Wickham and M.F.McDonald. NZIAS. New Zealand. pp.169-197.

Hill,W.G. (1971). Design and efficiency of selection experiments for estimating genetic parameters. Biometrics.27:293-311.

Hill,W.G. (1972a). Estimation of realized heritabilities from selection experiments. I.Divergent selection. Biometrics.28:747-765.

Hill,G.W. (1972b). Estimation of. realized heritabilities 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. 40:1-14.

Hill,W.G. (1972d). Estimation of genetic change. II.Experimental evaluation of control populations. Animal Breeding Abstracts. 40:193-208.

Hill,W.G. (1980). Design of quantitative genetic selection experiments. In:Selection Experiments with Laboratory and Domestic Animals. Ed. A.Robertson. Commonwealth Agricultural Bureaux,U.K. pp.1-13.

Hohenboken,W.D. (1985). Prediction and measurement of response to selection. In: General and Quantitative Genetics. Ed. A.B.Chapman. Elsevier. pp.167-186.

Holtmann,W.B and C.Bernard (1969). Effect of general ability and maternal ability of Oxford, Suffolk and Cheviot breeds of sheep on growth performance of lambs. Journal of Animal Science.28:155-161.

Hood,R.L. (1983). Changes in fatty acid synthesis associated with growth and fattening. Proceedings of the Nutrition Society.42:303-313.

Hood,R.L. and R.A.E.Pym (1982). Correlated responses to lipogenesis and adipose tissue cellularity in chickens selected for body weight gain, food consumption, and food conversion efficiency. Poultry Science. 61:122-127.

Hundley,W.S,Jr. and R.C.Carter (1956). Heritability of growth rate and market grade in mutton lambs. Journal of Animal Science..15:1226.

Hunter,G.L. (1956). The maternal influence on size in sheep. Journal of Agriculture Science. 48:36-60.

Irgang,R.,E.U.Dillard,M.W Tess and O.W.Robison (1985). Selection for weaning weight and post-weaning gain in Hereford cattle. II.Response to selection. Journal of Animal Science.60:1142-1155.

Jensen,N.E. (1977). Preliminary results from DANSCAN ultrasonic measurements of fat thickness and loin area of lamb. 28th. Annual meeting of the European Association for Animal Production. pp.1-7.

Jensen,P.H.B.,H.B.Craïg and O.W.Robison (1967). Phenotypic and genetic associations among carcass traits of swine. Journal of Animal Science. 26:1252-1260.

Johnson,D.L. (1981). Analysis of sheep selection experiments. Ministry of Agriculture and Fisheries, Agricultural Research Division. Annual report. pp.29

Juma,H.H.,J.E.Alkass and T.S.Aldoori (1987). Studies on some economic characteristics in Awassi and Arabi sheep. I. Birth and weaning weights. Animal Breeding abstracts.55:449.

Kadim,I.T (1988). A study of the carcass composition and meat quality of Southdown sheep selected for differences in backfat depth. Ph.D. Thesis. Massey University Palmerston North, New Zealand.

Kempster,A.J.,A.Cuthbertson,D.W.Jones and M.G.Owen (1977). A preliminary evaluation of the 'Scanogram' for predicting the carcass composition of live lambs. Animal Production.24:145-146.

Kempster,A.J.,A.Cuthbertson and G.Harrington (1982). Carcass evaluation in livestock breeding production and marketing. Granada. U.K. 306 pp.

Kirton,A.H. (1975). The relevance of carcass composition in the selection of live sheep. Sheepfarming Annual.Massey University. pp.117-125.

Kirton,A.H (1983). The effect of farm management practices on lamb carcase composition and quality. Wool Technology and Sheep Breeding. 31:27-33.

Koch, R.M. (1972). The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. Journal of Animal Science. 35:1316-1323.

Koch,R.M.,K.E.Gregory and L.V.Cundiff (1974). Selection in beef cattle. II. Selection response. Journal of Animal Science. 39:459-470.

Koch, R.M., L.A.Swiger, D.Chambers and K.E.Gregory (1963). Efficiency of feed use in beef cattle. Journal of Animal Science.22:486-494.

Krider, J.L., B.W.Fairbanks, W.E.Carroll and E.Roberts (1946). Effectiveness of selecting for rapid and slow growth rate in Hampshire Swine. Journal of Animal Science. 5:3-15.

Land,R.B. (1977). The genetics of breed improvement. In: Embryo Transfer in Farm Animals. Ed. K.J.Batteridge. Agriculture Canada.Monograph 16:57-59.

Lang,B.J. and J.E.Legates. (1969). Rate, composition and efficiency of growth in Mice selected for large and small body weight. Theoretical and Applied Genetics.39:306-314.

Lasslo, L.L., G.E.Bradford, D.T.Torell and B.W.Kennedy. (1985). Selection for weaning weight in Targhee sheep in two environments. I. Direct response. Journal of Animal Science. 61:376-386.

Leclerq,B.J.C.Blum and J.P.Boyer (1980). Selecting broilers for low or high abdominal fat: initial observations. British Poultry Science.21:107-113.

Legates,J.E. (1972). The role of maternal effects in animal breeding. IV. Maternal effects in laboratory species. Journal of Animal Science. 35:1294-1302.

Lord,E.A.,P.F.Fennessy and R.P.Littlejohn (1988). Comparison of geneotype and nutritional effects of body and carcass characteristics of lambs. New Zealand Journal of Agricultural Research. 31:13-19.

Marks,H.L. (1983). Selection for body weight at 8-weeks of age in dwarf and normal meat-type chickens originating from a common control population background. Poultry Science.62:227-234.

Marks,H.L. (1987). Selection for 8-week body weight in normal and dwarf chickens under different water/feed environments. Poultry Science.66:1252-1257.

McCarthy,J.C. and P.B.Siegel (1983). A review of genetical and physiological effects of selection in meat-type poultry. Animal Breeding Abstracts.51:87-94.

McEwan,J.C., P.F.Fennessy, J.N.Clarke, S.M.Hickey and M.A.Knowler (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., P.F.Fennessy and J.P.Hanrahan. (1987). Ultrasonic measurement of fatness in Sheep. Animal Breeding Abstracts. 55:366.

McPhee,C.P. and A.R.Neil (1976). Changes in the body composition of mice selected for high and low 8-week weight. Theoretical and Applied Genetics.47:21-26.

McGuirk,B.J., K.D.Atkins and R.Thompson (1986). Long-term selection experiments with sheep. Proceedings of the Third World Congress on Genetics Applied to Livestock Production.XII. Lincoln, Nebraska. U.S.A. pp.181-185.

McKay,R.M. and I.Garnett (1986). Prenatal and postnatal influences on growth and fat measurements in swine. Journal of Animal Science.63:1095-1100.

Merks,J.W.M (1987). Genotype X Environment interaction in pig breeding programmes. II.Environmental effects and genetic parameters in central test. Livestock Production Science. 16:215-228.

Merks,J.W.M (1988). Genotype X Environment interaction in pig breeding programmes. III.Environmental effects and genetic parameters in on-farm test. Livestock Production Science.18:129-140.

Meyer,H.H (1981). Breeding leaner lambs. Flock and Herd. 5:23.

Meyer,H.H., A.H.Kirton, J.F.Smith and K.T.Jagusch (1982). Breeding for leaner lamb carcasses. Ministry of Agriculture and Fisheries, Agricultural Research Division.Annual report. pp.32.

Meyer,W.E., W.G.Moody, G.D.Hunziger, T.P.Ringkob, M.A.Alexander, S.E.Zobrisby and H.B.Hedrick. (1966). Application of ultrasonic techniques in live animal and carcass evaluation. Research Bulletin No.905. University of Missouri-Columbia.

Moody,W.G.,S.E.Zobrisky,C.V.Ross and H.D.Naumann (1965). Ultrasonic estimates of fat thickness and longissimus dorsi area in lambs. Journal of Animal Science. 24:364.

Nestor,K.E (1984). Genetics of growth and reproduction in the turkey.9.Long-term selection for increased 16-week body weight. Poultry Science.63:2114-2122.

Nestor,K.E., W.L.Bacon and A.L.Lambio (1982). Divergent selection for body weight and yolk precursor in Coturnix coturnix japonica. 1.Selection response. Poultry Science.61:12-17.

Nestor,K.E.,W.L.Bacon,Y.M.Saif, and P.A.Renner (1985). The influence of genetic increases in shank width on body weight,walking ability and reproduction of Turkeys. Poutry Science. 64:2248-2255.

Nestor,K.E.,W.L.Bacon,N.B.Anthony and G.B.Havenstein (1987a). Divergence selection for body weight and yolk precursor in Coturnix coturnix japonica. 7.Influence of genetic changes in body weight and yolk precursor on egg production. Poultry Science.66:390-396.

Nestor,K.E.,W.L.Bacon,P.D.Moorhead,Y.M.Saif,G.B.Haveinstein and P.A.Renner (1987b). Comparison of bone and muscle growth in turkey lines selected for increased body weight and increased shank width. Poultry Science.66:1421-1428.

Newman,J.A.,G.W.Rahnefeld and H.T.Fredeen (1973). Selection intensity
     and response to selection for yearling weight in beef cattle.
     Canadian Journal of Animal Science. 53:1-12.

O'Donovan,P.B (1984). Compensatory gain in cattle and sheep.
     Nutrition Abstracts and Reviews.B.54:389-410.

Olson,L.W., G.E.Dickerson, J.D.Crouse and H.A.Glimp (1976). Selection
     criteria for intensive market lamb production:carcass and growth
     rate traits. Journal of Animal Science.43:90-101.

Osman,A.H and G.E.Bradford (1965). Effects of environment on
     phenotypic and genetic variation in sheep. Journal of Animal
     Science. 24:766-774.

Palsson,H. (1939). Meat qualities in the sheep with special reference
     to Scottish breeds and crosses.I. Journal of Agriculture
     Science.29:544-634.

Park,Y.I (1965). Age-constant feed efficiency of pigs. Journal of
     Animal Science. 24:819-822.

Parratt,A.C.,C.M.Burt,G.L.Bennett,J.N.Clarke,A.H.Kirton and   A.L.Rae
     (1987). Heritabilities,genetic and phenotypic correlations for
     carcass traits and ultrasonic fat depth of sheep. Proceedings
     of the Australian Association of Animal Breeding and Genetics
     6:76-78.

Pattie,W.A. (1964). Selection for and against weaning weight in
     Merino sheep. Proceedings of the Australian Society of Animal
     Production.5:152-155.

Pattie,W.A. (1965a). Selection for weaning weight in Merino sheep.
     I. Direct response to selection Australian Journal of
     experimental Agriculture and Animal Husbandry. 5:353-360.

Pattie,W.A. (1965b). Selection for weaning weight in Merino sheep.
     II. Correlated responses in other production characters.
     Australian Journal of Experimental Agriculture and Animal
     Husbandry. 5:361-368.

Pattie,W.A. and B.Trimmer (1964). The milk production of Merino ewes from flocks selected for high and low weaning weight. Proceedings of the Australian Society of Animal Production.5:156-159.

Proudman,J.A.,W.J.Mellen and D.L.Anderson (1970). Utilization of feed in fast and slow growing lines of chickens. Poultry Science.49:961-972.

Purchas,R.W. (1986). Principles of body growth. In: Sheep Production:Feeding, Growth and Health. Vol.II. · Eds. S.N.McCutcheon, G.A.Wickham and M.F.McDonald NZIAS. New Zealand. pp.27-56.

Purchas,R.W. and A.D.Beach (1981a). Between-operator repeatability of fat depth measurements made on live sheep and lambs with an ultrasonic probe. New Zealand Journal Experimental Agriculture.9:213-220.

Purchas,R.W.,A.L.Rae, R.A.Barton and A.D.Beach (1981b). The repeatability of ultrasonic fat depth measurements made on sheep up to 18-months of age. Proceedings of the New Zealand Society of Animal Production. 41:133-139.

Purchas,R.W.,A.L.Rae and R.A.Barton (1982). Repeatability of weight-corrected ultrasonic fat depth masurements made on ewes at intervals of one year. New Zealand Journal of Agricultural Research. 25:185-190.

Purser,A.F. (1980a). Cannon bone size and meat production in sheep. Animal Breeding Research Organization.,Annual report. pp.15-19.

Purser,A.F. (1980b). Comparison of expected and realized responses in three sheep selection experiments. In: Selection Experiments with Laboratory and Domestic Animals. Ed. A.Robertson. Commonwealth Agricultural Bureaux,U.K. pp.21-30.

Purser,A.B. (1982). Implications of sheep selection experiments. In: Proceedings of the World Congress on Sheep and Beef Cattle Breeding.Eds. R.A.Barton and W.C.Smith. Vol.I. The Dumore Press. Palmerston North, New Zealand. pp.239-248.

Pym,R.A.E. and P.J.Nicholls (1979). Selection for food conversion in broilers:Direct and correlated responses to selection for body-weight gain,food conversion and food conversion ratio. British Poultry Science.20:73-86.

Pym,R.A.E. and A.J.Solvyns (1979). Selection for food conversion in broilers: body composition of birds selected for increased body-weight gain,food consumption and food conversion ratio. British Poultry Science.20:87-97.

Rae,A.L. (1982). Selection and its effects. In: Sheep Production: Breeding and Reprodution. Vol.I. Eds. G.A.Wickham and M.F.McDonald. pp.60-110.

Rae,A.L. (1984). Development of selection programs for increasing lean meat production in sheep. Proceedings of the Australian Association of Animal Breeding and Genetics. 4:3-7.

Rahnefeld,G.W and I.Garnett (1976). Mass selection for post-weaning growth in swine. IV. Selection response and control population stability. Canadian Journal of Animal Science. 56:783-790.

Rehben, E. (1981). In-vivo estimation of body composition in beef (preliminary results). In: in-vivo estimation of body composition in beef. CEC Workshop. Copenhagen. pp.48-61.

Renden,J.A. (1987). Egg production efficiency of dwarf lines selected for high and low body weight as influeced by feed restriction. Poultry Science.66:1085-1089.

Richardson,R.H.,K.Kojima and H.L.Lucas (1968). An analysis of short-term selection experiments. Heredity. 23:493-506.

Roberts,R.C. (1979). Side effects of selection for growth in laboratory animals. Livestock Production Science.6:93-104.

Robertson,A. (1960). A theory of limits in artificial selection. Proceedings of the Royal Society.B. 153:234-249.

Robertson,A. (1982). Genetic aspects of growth. Proceedings of the World Congress on Sheep and Beef Cattle Breeding. Eds. R.A.Barton and W.C.Smith. Vol.I. The Dumore Press. Palmerston North, New Zealand. pp.427-437.

Robison,O.W. (1972). The role of maternal effects in animal breeding. V. Maternal effects in swine. 35:1303-1315.

Robison,O.W.,J.H.Cooksey,A.B.Chapman and H.L.Self (1960). Estimation of carcass merit of swine from live animal measurements. Journal of Animal Science. 19:1013.(Abstract).

Russel,A.J.F. and I.A.Wright (1982). The in vivo estimation of body composition in sheep and beef cattle.In: Proceedings of the world congress on Sheep and Beef Cattle Breeding. Eds. R.A.Barton and W.C.Smith. Vol.I. The Dumore Press LTD. Palmerston North, New Zealand. pp.407-414.

Sellier,P. (1980). Design and analysis of quantitative genetic experiments: A review with particular reference to pigs. Livestock Production Science. 7:539-554.

Shelton,M.,G.C.Smith and F.Orts (1977). Predicting carcass cutability of Rambouillet rams using live animal traits. Journal of Animal Science. 44:333-337.

Shrestha,J.N.B.,J.A.Vesely and J.P.Chesnais (1985). Genetic and phenotypic parameters for daily gain and body weights in Suffolk lambs. Canadian Journal of Animal Science. 65:575-582.

Shrestha,J.N.B.,J.A.Vesely,J.P.Chesnais and D.Cuthbertson (1986). Genetic and phenotypic parameters for daily gain and body weights in Dorset lambs. Canadian Journal of Animal Science. 66:289-292.

Sidwell,G.M. and L.R.Miller (1971). ·Production in some pure breeds of sheep and their crosses. II.Birth weights and weaning weights of lambs. Journal of Animal Science.32:1090-1094.

Siegel.P.B (1962). Selection for body weight at 8-weeks of age.1.Short-term response and heritabilities. Poultry Science.41:954-962.

Simm, G. (1983). The use of ultrasound to predict the carcass composition of live cattle: a review. Animal Breeding Abstracts. 51:853-875.

Slen,S.B.,R.D.Clark and R.Hironaka (1963). A comparison of milk production and its relation to lamb growth in five breeds of sheep. Canadian Journal of Animal Science. 43:16-21.

Smith,C. (1962). Estimation of genetic change in form livestock using field records. Animal Production. 4:239-251.

Smith,C. (1977). The use of stored frozen semen and embryos to measure genetic trends in farm livestock. Zeitschrift fiir Tierzuchtung und Zuchtungsbiologie. 94:119-130.

Snedecor,G.W. (1956). Statistical Methods. Iowa State College Press. Ames,Iowa. 534 pp.

Soller,M. and Y.Eitan (1984). Why does selection for liveweight gain increase fat deposition? A model. World's Poultry Science Journal. 40:5-9.

Soller,M. and A.Genizi (1967). Optimun experimental designs for realized heritability estimates. Biometrics. 23:361-365.

Steel,R.G. and J.H.Torrie (1981). Principles and Procedures of Statistics. McGraw-Hill. 633 pp.

Sutherland,T.M.,P.E.Biondini and G.M.Ward (1974). Selection for growth rate, feed efficiency and body composition in mice. Genetics. 78:525-540.

Swiger,L.A.,W.R.Harvey,D.O.Everson and K.E.Gregory (1964). The variance of interclass correlation involving groups with one observation. Biometrics.20:818-826.

Swiger,L.A.,R.M.Koch,K.E.Gregory and V.H.Arthaud (1962). Selecting beef cattle for economic gain. Journal of Animal Science. 21:588-592.

Thorsteinsson,S.S. and H.Bjornsson (1982). Genetic studies on carcass traits in Iceland twin ram lambs: I.Estimates of genetic parameters on carcass traits,liveweight at weaning and carcass weight. Livestock Production Science.8:489-505.

Thompson,J.M. (1982). Genetic manipulation of fatness in lamb carcasses. Proceedings of the Australian Society of Animal Production. 14:54-60.

Thompson,J.M. (1985). Reducing fatness in sheep and cattle. Proceedings of the Australian Association of Animal Breeding and Genetics.5:108-113.

Thompson,J.M.,R.M.Butterfield and D.Perry (1987). Food intake,growth and body composition in Australian Merino sheep selected for high and low weaning weight. 4.Partitioning of dissected and chemical fat in the body. Animal Production.45:49-60.

Turner,H.N. (1977). Australian sheep breeding research. Animal Breeding Abstracts. 41:9-31.

Turner, H.N. and S.S.Y.Young (1969). Quantitative genetics in sheep breeding. The McMillan Co. of Australia Pty Ltd. 332 pp.

Vesely,J.A. and O.W.Robison (1970). Genotype-sex interactions in sheep. Journal of Animal Science. 31:273-277.

Vesely,J.A and S.B.Slen (1968). Heritabilities of weaning weight, yearling weight, and clean fleece weight in range Romnelet sheep. Canadian Journal of Animal Science.41:109-114.

Vogt,D.W.,R.E.Comstock and W.E.Rempel (1963). Genetic correlations between some economically important traits in swine. Journal of Animal Science. 22:214-217.

Wethli,E. and J.P.H.Wessels (1973a). The relationships among thyroid gland activity, feed intake, mass gain, feed conversion, and final body mass in growing chickens. Agroanimalia. 5:71-82.

Wethli,E. and J.P.H.Wessels (1973b). The associations between body fat and thyroid activity, feed intake, mass gain, feed conversion, and final body mass in growing chickens. Agroanimalia. 5:83-88.

Whitehead,C.C. and H.D.Griffin (1984). Development of divergent lines of lean and fat broilers using plasma very low density lipoprotein concentration as selection criterion:The first three generations. British Poultry Science. 25:573-582.

Wilson,P.N. and D.F.Osbourn (1960). Compesatory growth after undernutrition in mammals and birds. Biological Reviews. 35:324-363.

Wolf,B.T.,C.Smith,J.W.B.King and D.Nicholson (1981). Genetic parameters of growth and carcass composition in crossbred lambs. Animal Production. 32:1-7.

Wood,J.D. and H.J.H.MacFie (1980). The significance of breed in the prediction of lamb carcass composition from fat thickness mesurements. Animal Production. 31:315-319.

Zoeller,K.O., J.F.Lasley, L.F.Tribble and B.N.Day (1964). Selection for thinner backfat in swine. Animal Breeding Abstracts. 32:516.