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RESPONSE TO SELECTION FOR OPEN FACE
AND GREASY FLEECE WEIGHT IN ROMNEY SHEEP

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ABSTRACT

Selection responses and genetic parameters were estimated on wool, body and reproductive traits in a New Zealand Romney flock. In 1956 the flock was divided into 3 sub-flocks, each of which has been a closed breeding group (consisting approximately 80 ewes and 4 rams) since 1958. In one group the most open-faced yearlings were retained for breeding, in another, those with heaviest yearling fleece weights, while in the third replacements were chosen at random.

Traits examined included post-shearing live weight (LW), greasy fleece weight (GFW), clean fleece weight (W), quality number (QN), character grade (CHG), staple length (SL), total crimp number (TCN), crimp frequency (CF), clean scoured yield (Y) and mean fibre diameter (MFD) for the ewes and ram and ewe hoggets; number of lambs born (LB) and number of lambs reared (LR) per ewe joined; date-of-birth (DOB), birth weight (BW), weaning weight (WW), medullameter index (MI) and face-cover grade (FC) for the ram and ewe hoggets and the standard deviation of the fibre diameter (SFD) and percent medullated fibres (PMF) for the ewe hoggets.

The average inbreeding coefficient increased by approximately 0.10 in all 3 flocks over the 21 years evaluated. Within years, sheep with the highest inbreeding coefficients generally suffered a depression in the level of performance.

Heritabilities (h^2) and genetic correlations (r_g) were calculated using the paternal half-sib correlation approach. Most h^2 estimates were similar to already published values. Estimates of the h^2 of ram hogget GFW were substantially smaller than corresponding ewe hogget values (0.07 to 0.15 cf 0.28 to 0.34). Face-cover grade h^2 in the face-cover flock appeared to be much reduced, suggesting a possible decline in genetic variation for this trait.

Phenotypic and genetic correlations were calculated amongst all hogget traits and between ewe hogget and ewe average lifetime performance traits. Very high genetic and phenotypic correlations were found between hogget GFW and hogget W. Ewe hogget GFW tended to be positively associated with LB and LR, both genetically and phenotypically. Hogget FC was generally unrelated to other hogget and ewe traits. Ewe hogget performance in LW, GFW, W, QN, SL, TCN, Y and MFD were generally moderately to strongly related with the performance of the same ewe in corresponding traits at older ages. There was often wide variation in the three (one from each group) genetic correlation estimates for each pair of traits. This variation was attributed to either the small number of observations available (about 80 sires per flock with 5 to 7 progeny per sire) or changing genetic variance and covariance components in the selection flocks.

Realized heritability (h^2_r) estimates for FC and hogget GFW ranged between 0.39 to 0.54 and 0.06 to 0.19, respectively. The h^2_r estimates of hogget GFW were in good agreement with the paternal half-sib correlation estimates of h^2 derived from the ram hogget data but were markedly less than equivalent estimates obtained from the ewe hogget

data. The h^2_{FC} estimates of FC were generally higher than paternal half-sib estimates, but were in good agreement with estimates derived by other workers.

In the face-cover flock correlated responses were generally small. Positive correlated responses of about 10% were recorded in LB and LR over the 21 years evaluated. In the fleece weight group the components contributing toward increased GFW all showed positive correlated responses. Lamb production (LB and LR) of the fleece weight group showed an increase of about 30%, relative to the control flock, over the 21 years studied.

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CHAPTER ONE

INTRODUCTION

Increasing the frequency of desirable genes in a population has long been recognized as a means of changing performance. Artificial selection (hereafter referred to as selection), whereby the breeder selects parents of the next generation on the basis of their high level of performance in some trait or combination of traits, is a widely used method of changing gene frequencies. A problem facing animal breeders is to determine what proportion of the phenotypic advantage of the parents, over the group from which they came (i.e. the selection differential), is passed on to the next generation. The heritable proportion of the selection differential is called the heritability of a trait. Estimates of heritability enable the prediction of the rate of response to selection.

Direct selection on a trait may cause correlated changes in other genetically-related characteristics. The direction and magnitude of genetic correlations are an important consideration in any selection plan.

Generally, estimates of heritability (h^2) and genetic correlations (r_g) are obtained through the analysis of covariation amongst relatives. These methods are reviewed by Turner and Young (1969). However, selection of superior performing animals may change the additive genetic variances and covariances, thereby changing the heritability and genetic correlations effective in later, selected, generations (Bohren *et al.*,

1966). Because of the possible changes in the heritabilities and genetic correlations, long-term predictions of direct and correlated responses to selection may be inaccurate. To improve the accuracy with which responses to selection may be predicted, heritability and genetic correlation estimates may be reassessed after every few generations of selection. Further information on direct and correlated responses to selection may be obtained from long-term selection experiments.

The major objective of this study was to analyse responses to selection from 1956 to 1976 in two single-trait selection flocks of Romney sheep.

Hogget greasy fleece weight was one of the traits subjected to selection. This trait was chosen for investigation for two main reasons; firstly, in the early 1950s there was some suggestion that the heritability of fleece weight was lower in Romneys than in Merinos, however there was not sufficient information available to verify or refute this claim (Rae, 1956). Secondly, little was known as to how other economically important traits would respond to selection on greasy fleece weight. Of particular interest was how ewe fertility would be affected, as Rae and Ch'ang (1955) had found some evidence of a small negative genetic correlation between greasy fleece weight and the number of lambs born per ewe joined.

The other trait chosen for investigation was hogget face-cover grade. During the 1940s and 1950s some evidence accumulated suggesting that woolly-faced ewes produced fewer lambs per ewe joined than did open-faced ewes. At this time farmers believed that woolly-faced sheep

produced heavier fleece weights than did open-faced sheep. Thus, it was important to determine the relationships amongst face-cover grade, greasy fleece weight and lamb production.

Due to the nature of the information collected from these single-trait selection experiments it was also possible to calculate heritability and genetic correlation estimates, using the paternal half-sib approach, and to evaluate the effect of the level of inbreeding on performance.

C H A P T E R T W O

REVIEW OF LITERATURE

2.1 Introduction

Several single trait selection experiments have been initiated with sheep in New Zealand and Australia. No analyses of selection experiments involving either greasy fleece weight or face-cover grade have been reported. Preliminary results from two greasy fleece weight selection experiments suggest that positive direct responses have been obtained, however no detailed analyses were available (Hight and Bigham, 1980; Clarke, 1980). This review will cover several experiments involving clean fleece weight and the relationships between face cover, lamb production and greasy fleece weight. Methods of evaluation of genetic responses to selection in domestic animals will also be presented.

At this point it should be noted that if realized heritabilities (h_r^2), as defined by Falconer (1960), are to be compared with heritability estimates of individual traits obtained through the analysis of covariance between relatives, then the experiments from which they are derived should involve single trait selection. If several traits are under selection the response to selection will be dependent on the relationships amongst the characteristics.

2.2 Fleece Weight

2.2.1 Introduction

There are no reported selection experiments involving single character selection for greasy fleece weight (GFW). Since GFW and clean fleece weight (W) are highly correlated (Mullaney *et al.*, 1970)

a series of experiments involving selection for, and sometimes against, clean fleece weight will be reviewed. The important features of the experiments reported by Turner *et al.* (1968), Mayo *et al.* (1969), Turner *et al.* (1970), Pattie and Barlow (1974), Barlow (1974), Heydenrych *et al.* (1977) and Turner and Jackson (1978) are summarised in Table 2.1.

Before discussing the methods of analysis and results some mention will be made of the selection techniques used. These will influence the comparison and interpretation of results.

2.2.2 Selection criteria

As shown in Table 2.1 only three of the seven papers to be reviewed are true single character selection experiments (Turner *et al.*, 1970; Pattie and Barlow, 1974; Barlow, 1974). Barlow (1974) included satisfactory semen quality as a criterion in ram selection; this may have resulted in correlated responses in reproductive performance.

2.2.3 Analysis of direct response to selection for clean fleece weight

Mayo *et al.* (1969), Pattie and Barlow (1974) and Heydenrych *et al.* (1977) were the only authors to estimate realized heritability values. Turner *et al.* (1968) and Turner *et al.* (1970) carried out multiple regression analyses using the response in clean fleece weight as the dependent variable and linear and quadratic terms of time as independent variables. Turner and Jackson (1978) also included the control group mean as an independent variable in their multiple regression analysis in an attempt to overcome fluctuations in the response due to genotype x

TABLE 2.1: SELECTION CRITERIA FOR THE VARIOUS CLEAN FLEECE WEIGHT SELECTION EXPERIMENTS

Author(s)	Selection Group	Main Character Selected	Age at Selection (mths)		Other Conditions of Selection
			Rams	Ewes	
Turner <i>et al.</i> (1968)	S	High clean fleece weight	10-11 and 15-16	15-16	Half-sib information included 1950-1959. Ceilings on fibre diameter and degree of skin wrinkle 1950-1964.
	MS	High clean fleece weight	10-11 and 15-16	15-16	Ceilings on fibre diameter and degree of skin wrinkle 1950-1959. Ceiling on fibre diameter replaced by one on crimp frequency 1960-1964.
	Control	Random	15-16	15-16	
Mayo <i>et al.</i> (1969)	Visual	-	15	15	Ewes and rams selected by a competent stud classer.
	Index	-	15	15	Ewes selected as for visual flock. 70% of rams culled visually then required number selected on clean fleece weight.
Turner <i>et al.</i> (1970)	W ⁺	High clean fleece weight	10-11 and 15-16	15-16	
	W ⁻	Low clean fleece weight	10-11 and 15-16	15-16	
	Control	Random	15-16	15-16	
Pattie and Barlow (1974) and Barlow (1974)	W ⁺	High clean fleece weight	15-17	15-17	Any rams with poor quality semen from the W ⁺ , W ⁻ and control groups were discarded.
	W ⁻	Low clean fleece weight	15-17	15-17	
	Control	Random	15-17	15-17	
Heydenrych <i>et al.</i> (1977)	Group 1	High clean fleece weight	18	18	For 1 and 3 the rams were selected only if their fibre diameter was lower than the average of their contemporaries and if the crimp frequency was greater than 9/25 mm.
	Group 3	Rams on high clean fleece weight. Ewes on high 42-day body weight	18	42 days	
	Group 5	Random	18	18	
Turner and Jackson (1978)	S	High clean fleece weight	15-16*	15-16*	As for S group, Turner <i>et al.</i> (1968), from 1950-1964.
	MS	High clean fleece weight	15-16*	15-16*	As for MS group, Turner <i>et al.</i> (1968), from 1960-1964.
	Control	Random			

* Age at selection changed to 12-13 months from 1973.

environment interaction. However, it was generally found that the partial regression coefficients due to the quadratic time term and the control mean were non-significant.

Realized heritabilities were calculated as the regression of cumulated direct response to selection on the flock average cumulated selection differential (FACSD) (Falconer, 1960). Pattie and Barlow (1974) and Heydenrych *et al.* (1977) essentially followed the method presented by Pattie (1965) for calculating the FACSD and cumulated direct response.

Pattie (1965) used three steps in calculating the FACSD:

- (a) The individual selection differentials were calculated as differences between individual performances and the mean performance of all the animals born in the same year, in the same flock,
- (b) the individual cumulated selection differentials were obtained by adding the animal's own selection differential to the mean individual cumulated selection differential of its parents, and
- (c) the FACSD was calculated by averaging all the individual cumulated selection differentials of parents in the selection group for each year.

Pattie and Barlow (1974) made two alterations to this procedure. Firstly, as suggested by Robards and Pattie (1967), to eliminate seasonal effects the selection differential was divided by the phenotypic standard deviation of the random flock. The direct response to selection was also divided by the phenotypic standard deviation. Secondly, in an attempt to account for inadvertent selection pressure in the random flock, the cumulated selection differential of the random flock was subtracted from the cumulated selection differential of the selection flocks. This second adjustment seemed to serve little purpose in the analysis carried out by Pattie and Barlow (1974) because they showed that the cumulated selection differential for the random flock fluctuated around zero.

Heydenrych *et al.* (1977) essentially followed the technique devised by Pattie (1965). However, when obtaining average cumulated selection differentials, within groups, they weighted the individual cumulated selection differentials by the number of progeny produced by the individual.

Mayo *et al.* (1969) calculated their FACSD in three steps:

- (a) the selection differential was calculated for the selection flock as a whole by deviating the mean of those selected to be parents from the mean of the unselected group,
- (b) each selection differential was then corrected as suggested by Morley (1955) for the absence of a selection differential in the ewes and to correct for the age at which ewes were replaced, and

- (c) the corrected selection differentials were cumulated across years.

Pattie and Barlow (1974) and Heydenrych *et al.* (1977) calculated the cumulated direct response as the deviation between selected and control flocks within each year. Mayo *et al.* (1969) did not explain how they calculated their cumulated direct response without having a control flock.

2.2.4 Analysis of correlated responses to selection for clean fleece weight

Barlow (1974) was the only author to produce estimates of realized genetic correlations. Turner *et al.* (1968) and Turner *et al.* (1970) calculated linear regression coefficients using time as the independent variable and the difference between selected and control groups in the correlated traits as the dependent variable. Heydenrych *et al.* (1977) and Turner and Jackson (1978) tested the differences between selected and control flock means for the various correlated traits as an estimate of whether or not some correlated response had occurred.

Barlow (1974) derived two estimates of each correlated response and thus obtained two estimates of each realized genetic correlation.

The two approaches to obtaining the correlated responses were:

- (a) to regress the cumulated correlated response on the cumulated selection differential for clean fleece weight, and

- (b) to regress the cumulated correlated response on the cumulated direct response in clean fleece weight.

Barlow suggested that the second approach would account for the non-linear direct response in clean fleece weight. The cumulated correlated responses were adjusted for seasonal effects by transforming all data to standard deviation units, as suggested by Robards and Pattie (1967). To adjust for unintentional directional selection in the control flock, Barlow added $i_{jk}h_j^2$ (where i_{jk} is the selection differential for the j^{th} trait in the k^{th} year and h_j^2 is the heritability of the j^{th} trait) to the cumulated correlated response in the j^{th} trait.

It is important to note the very small flock size used by Turner *et al.* (1970) (see Table 2.2). In particular, only one sire was used in each year in the W^+ and W^- flocks. The small number of animals could significantly affect the response of these flocks to selection, especially through chance fixation of genes.

2.2.5 Direct response to selection for clean fleece weight

In general clean fleece weight (W) showed positive responses to selection, although the magnitude and continuity of responses varied between experiments (see Table 2.3).

Turner *et al.* (1968) showed that substantial increases in W could be made under both selection regimes practised between 1950 and 1959. When the selection criteria were changed in 1960 (see Table 2.1) the advantage of the selected groups, in W , over the control group declined,

TABLE 2.2: NUMBERS OF EWES AND RAMS USED IN THE VARIOUS CLEAN FLEECE WEIGHT SELECTION EXPERIMENTS

Author(s)	Selection Group	Period	Number of Rams	Number of Ewes
Turner <i>et al.</i> (1968)	S	1950-1953	12	415-483
		1954-1964	5	194-249
	MS	1950-1964	5	108-250
	Control	1950	15	180
1951-1955		5	138-249	
1956-1964		10	205-249	
Mayo <i>et al.</i> (1969)	Visual Index	1953-1965	7	191-240
		1953-1965	7	191-254
Turner <i>et al.</i> (1970)	W ⁺	1954-1964	1	32-50
	W ⁻	1954-1964	1	32-50
	Control	(as for Turner <i>et al.</i> 1968)		
Pattie and Barlow (1974) and Barlow (1974)	W ⁺	1951-1965	5	100
	W ⁻	1951-1965	5	100
	Control	1950-1965	10-25	100
Heydenrych <i>et al.</i> (1977)	Group 1	1969-1975	5	160
	Group 3	1969-1975	5	160
	Control	1969-1975	16	160
Turner and Jackson (1978)	S	1966-1974	5	200
	MS	1966-1968	5	200
		1969-1974	5	100
	Control(C)	1966-1970	10	200
	Control(A)	1968-1974	20	400

TABLE 2.3: DIRECT RESPONSES TO SELECTION FOR HIGH CLEAN FLEECE WEIGHT

Author(s)	Selection Group	Period	Realized Responses		
			Rams	Ewes	Pooled
Turner <i>et al.</i> (1968)	S	1950-1959	2.11±0.33	2.45±0.49	-
	MS	1950-1959	1.88±0.56	2.73±0.61	-
Turner <i>et al.</i> (1970)	W ⁺		-	-	-0.07
	W ⁻		-	-	-3.38
Turner and Jackson (1978)	S		0.15±0.22	0.12±0.02	0.12±0.02
	MS		0.09±0.03	0.06±0.02	0.05±0.02
Pattie and Barlow (1974)	W ⁺	Gen. 0-2	0.65±0.12	0.53±0.17	0.59±0.11
		Gen. 3-5	0.08±0.07	0.06±0.19	0.07±0.09
	W ⁻	Gen. 0-5	0.38±0.02	0.44±0.03	0.41±0.02
Heydenrych <i>et al.</i> (1977)	Group 1	1971	-	-	0.39
		1972	-	-	0.31
		1973	-	-	0.41
		1974	-	-	0.12
		1975	-	-	0.41
	Group 3	1971	-	-	-0.11
		1972	-	-	0.28
		1973	-	-	0.14
		1974	-	-	0.07
		1975	-	-	0.37
Mayo <i>et al.</i> (1969)	Visual Index		-	-	0.23±0.74
			-	-	0.43±0.39

(See section 2.2.3 for explanation of realized responses)

the reduction in advantage being greater in the rams. The apparent lack of response was thought to be caused by severe droughts during 1960-1964, rather than the change in selection criteria. To test this theory the flocks were shifted to a more favourable environment. Turner and Jackson (1978) showed that response in W recommenced under the more favourable conditions.

In the improved environment, Turner and Jackson (1978) showed the MS group (see Table 2.1) produced a smaller response in clean fleece weight than the S group (see Table 2.1). The difference in response was probably due to the different restrictions placed on the two groups (see Table 2.1). Turner (1977) calculated the genetic correlation of W with crimp frequency (CF) and with mean fibre diameter (MFD) as being in the ranges -0.5 to -0.9 and +0.2 to +0.4, respectively. Consequently, Turner and Jackson (1978) argued that a limit on CF in the MS group would restrict increases in W to a greater extent than would the ceiling on MFD in the S group, because of the difference in magnitude of the respective genetic correlations.

Turner *et al.* (1970) reported a non-significant, negative, regression of clean fleece weight on time in their W^+ group. However a highly significant initial response occurred, due to the selection of high producing base flock parents. The authors again suggested that poor environmental conditions during the early 1960s caused the lack of continued response. In contrast to the W^+ group, the W^- group showed a very highly significant, negative, regression of clean fleece weight on time throughout the whole period.

Mayo *et al.* (1969) produced two realized heritability (h_r^2) estimates. However, these estimates cannot strictly be regarded as realized heritability values because selection was not based solely on W, (see Table 2.1). Although the two regression coefficients, 0.43 ± 0.39 and 0.23 ± 0.74 , fall within the expected range of heritability estimates for W, the high standard errors preclude any meaningful discussion of what degree of response has occurred.

Pattie and Barlow (1974) observed a non-linear response in their W^+ group (see Table 2.1). During the first two generations of selection a response of about one standard deviation in W resulted. Very little response was shown in the next three generations. In contrast the W^- group (see Table 2.1) showed continued response throughout all five generations. Because of the non-linear response in the W^+ group the data were divided into two periods, the response within each of these periods being linear, and h_r^2 estimates were calculated within each period. Realized heritability estimates from the W^- group and from generations 0-2 in the W^+ group compared favourably with a heritability estimate of 0.47 ± 0.07 , derived using daughter-dam regression in the base flock (Morley, 1955). As expected the h_r^2 estimates for generations 3-5 in the W^+ group were not significantly different from zero. Realized heritability estimates were not calculated over all 5 generations in the W^+ group.

Pattie and Barlow suggested that the lack of response in later generations was due to an increase in the size of the negative genetic correlation between fibre density (D) and MFD. An increase of this genetic correlation was observed by Brown and Turner (1968). Before

selection they estimated this correlation to be -0.56 ± 0.06 , but following several years selection the estimate had increased to -0.78 ± 0.06 . Pattie and Barlow stated that if the genetic correlation between D and MFD increased from -0.5 to -0.9 during selection, then the h_r^2 estimate could decrease from 0.42 to 0.18 . The magnitude of h_r^2 could then be responsible for the lack of response in later generations. Other factors that may have slowed the response in W were also discussed. No definite conclusion was reached as to the effect of sampling variation and directional drift, but it was thought unlikely that they could cause such a large reduction in response to selection. Inbreeding was shown to have reached only low levels which should not have affected response. Genotype x environment interaction was considered unlikely to have contributed to the lack of response since most years of the experiment were favourable for wool production. In a subsequent report Barlow (1974) concluded that some doubt existed as to whether the genetic correlation between D and MFD, *per se*, was a major factor causing the decline in response. As an alternative, he suggested that the expression of the W^+ flock genotype was probably suppressed under pasture conditions prevailing at Trangie during the experimental period.

Heydenrych *et al.* (1977) produced several estimates of h_r^2 . However, the selection flocks from which these estimates were derived were not subject to single trait selection (see Table 2.1). Consequently, these estimates are not acceptable as h_r^2 , but they can be interpreted as the amount of response in W, given the selection criteria stated in Table 2.1. The estimates of response in W suggest that progress was being made in increasing the amount of clean wool weight per animal.

2.2.6 Components through which direct response occurs

Turner (1958) divided W into five contributing components:

$$W = D \times A \times L \times SA \times R,$$

where D = fibres per unit area of skin,

A = the cross-sectional area of fibre,

L = fibre length,

SA = smooth body surface area, and

R = wrinkling factor.

This apparently straightforward breakdown of clean fleece weight has two important limitations. Firstly, the apportioning of variation in clean fleece weight will depend on how accurately the component was measured; e.g. inaccurate measurement of fibre length would reduce the proportion of variance attributed to that component. Secondly, the existence of correlations between the components would cause difficulties when attempting to apportion the variance in W between related components. A further problem is the difficulty in analysing multiplicative models. Henderson and Hayman (1960) and Turner and Young (1969) discussed several methods of analysis and the deficiencies associated with these approaches.

Within the limitations mentioned, the above breakdown can aid the explanation of how the response in clean fleece weight might have occurred.

Certain combinations of these components produce useful quantities:

$$SA \times R = \text{total wool-bearing surface area,}$$

$$SA \times R \times D = \text{total number of fibres,}$$

$$A \times L = \text{fibre volume, and}$$

$$A \times L \times D = \text{wool per unit area of skin.}$$

Turner *et al.* (1968), Turner *et al.* (1970) and Barlow (1974), divided the response in W into the various components. By inference, the response obtained by Heydenrych *et al.* (1977) can also be divided into the components. All four reports involved Merino sheep.

During selection for high clean fleece weight the contribution of SA and R is generally very small, thus the total wool-bearing surface area (SA x R) appears to be relatively constant. Most of the response comes from an increase in wool grown per unit area of skin (A x L x D). Barlow (1974) and Turner *et al.* (1970) showed that the initial response to selection was contributed by A, L and D. Barlow (1974) then showed that A caused the continuing response in W, but Turner *et al.* (1970) concluded that L and D were the important components. According to Turner *et al.* (1970) the contribution from A decreased as selection progressed. Turner *et al.* (1968) and Heydenrych *et al.* (1977) found that D was the greatest contributor toward the response in W. Both of these latter reports had ceilings on MFD that probably precluded A from contributing to the response in clean fleece weight.

2.2.7 Correlated responses to selection for clean fleece weight

Correlated responses to selection recorded by Turner *et al.* (1968), Turner *et al.* (1970) and Barlow (1974) are presented in Table 2.4. In interpreting these results it should be remembered that only the results of Turner *et al.* (1970) and Barlow (1974) have come about through single trait selection for W, consequently results from the other workers must be interpreted with particular consideration of the selection criteria.

TABLE 2.4: CORRELATED RESPONSES TO SELECTION FOR CLEAN FLEECE WEIGHT

Group Sex Trait	Turner <i>et al.</i> (1968)				Turner <i>et al.</i> (1970)	Barlow (1974) *			
	S		MS		W ⁺	W ⁺			
	Rams	Ewes	Rams	Ewes	Pooled	Rams	Ewes	Rams	Ewes
GFW	1.37	1.45	1.26	2.06	-0.60	0.21	0.03	0.22	0.02
Y	0.66	0.89	0.65	0.63	0.48	0.30	0.05	0.30	0.22
SL	0.18	0.63	0.21	0.51	0.28	0.15	0.06	0.15	0.11
MFD	-0.44	-0.15	-0.38	-0.06	-1.18	-	-	0.11	0.02
D	2.04	1.99	2.16	1.85	1.98	-	-	0.08	0.10
FR	-	-	-	-	-	-	-	0.08	0.03
CF	-1.70	-1.59	-1.34	-1.30	1.18	-0.22	-0.04	-0.29	-0.12
CHG	-	-	-	-	-	0.13	0.10	0.13	0.12
SCG	-	-	-	-	-	0.04	-0.30	0.05	0.05
HG	-	-	-	-	-	0.09	-0.01	-0.03	-0.24
FC	-0.77	0.04	-1.82	-1.03	-	-	-	-0.01	-0.05
LW	0.63	0.22	0.38	0.69	0.13	0.00	-0.31	-0.03	-0.05
WW	-	-	-	-	-	-0.04	-0.16	-0.04	0.02

* First column for rams and ewes includes all generations, whilst the second for each involves only generations 1 to 5. Regression coefficients use cumulative selection differential as independent variable. Trait abbreviations are explained in Table 3.4, except for D = fibre density and FR = fibre ratio.

(See section 2.2.4 for explanation of correlated responses)

Generally the correlated responses are in good agreement with each other; however mention should be made of some unexpected results. Turner *et al.* (1970) found a non-significant, negative, correlated response in greasy fleece weight (GFW). This could be expected considering the non-significant, negative, direct response in W. This could also explain the significant decrease in MFD and the non-significant increase in crimp frequency, when, according to the other reports, responses should have been in the opposite directions.

Table 2.5 summarizes the available estimates of genetic correlations between W and other traits in the reports discussed. The relationships between W and GFW, clean scoured yield (Y), MFD, staple length (SL), CF and quality number (QN) appear to be well established. Although six estimates are available for each of the relationships between W and handle grade (HG), character grade (CHG) and colour grade (CG) the values are too unstable to enable any suggestion of what the true relationship might be. The remaining associations have too few estimates available for any accurate assumption to be made about the true genetic correlation.

Table 2.6 summarizes available genetic correlations between GFW and various other traits.

2.3 Face Cover

Face-cover grades are used to describe the extent to which wool fibres cover the head, as compared with short kemps. Grading may also be influenced by the length and density of wool on the face. An explanation of the scoring system used in this

TABLE 2.5: AN INDICATION OF THE SIZE OF GENETIC CORRELATION ESTIMATES BETWEEN CLEAN FLEECE WEIGHT AND OTHER TRAITS

Trait	High Negative	Moderate Negative	Low Negative	Negligible	Low Positive	Moderate Positive	High Positive
GFW				I			IIIIIIIIII
Y					II	III	IIII
SL					IIIIII	III	II
MFD				III	IIIIII		
D				I	I		
CF	IIIII	IIII	I				
CHG		I		II	I	II	
SCG				IIII	I		I
HG	II		I	II		I	
QN	IIIII	I					
FC			I				
LW				I	II		
WW			I				
LB	I						
LR	I			I			

Trait abbreviations are explained in Table 3.4, except for D = fibre density.

For bounds of groupings see section 5.3.

For actual estimates see Chopra (1978).

TABLE 2.6: AN INDICATION OF THE SIZE OF GENETIC CORRELATION ESTIMATES BETWEEN GREASY FLEECE WEIGHT AND OTHER TRAITS

Trait	High Negative	Moderate Negative	Low Negative	Negligible	Low Positive	Moderate Positive	High Positive
✓ W Clean fleece wt							IIIIIIIIII
Y " scoured yield			II	IIIII	I		I
✓ SL Staple length				IIIII	IIIIIIIIII	IIIII	IIIIIII
✓ MFD Mean fibre diameter				IIIII	IIIII	IIIIIIII	
D fibre density				I			
XX CF Crimp frequency	IIIIII	I	I	II			
CHG Character grade		I	I	IIIIII	IIIIIIII	IIII	
X SCG Soured on grease		II	II	I			I
X HG Hair grade	II	II		II			
XX QN Quality no.	III	IIIIIIIIII	III	III			
X FC Fat content			I	I			
LW Loss during test				III	III	IIII	
WW Weaning wt			II	I	I	II	
BW Birth wt			I	II			
LB no of large born		I		I			
LR Lambing record				I			

Trait abbreviations are explained in Table 3.4, except for D = fibre density.

For bounds of groups see section 5.3.

For actual estimates see Chopra (1978).

study is given in section 3.1.2. High face-cover grades refer to open face sheep whilst low scores refer to covered-face, close-faced, wool-blind, muffled or woolly-faced individuals. Several other workers have also derived scoring systems: Terrill (1941), Turner *et al.* (1953), Cockrem *et al.* (1956), Coop (1956), Fail and Dun (1956) and Cockrem (1966).

The interest in face cover was stimulated by Terrill (1941), who reported that woolly-faced Rambouillets weaned less weight of lamb per ewe joined when compared with open-face Rambouillets. This was an important finding because during the 1930s and 1940s many farmers had selected sheep with wool cover over the face and legs in the belief that such animals had greater fleece weights. The results of Terrill (1941) were confirmed by Terrill (1949), Barton (1954), Fail and Dun (1956), Coop (1956), Cockrem *et al.* (1956), Inkster (1956), Cockrem (1958), Jeffries (1962), Dun *et al.* (1964) and Cockrem and Rae (1966) in Romney, Peppin Merino and Corriedale sheep. Two reports, Jefferies (1962) and Young *et al.* (1963), found no association between the level of face cover and lamb production in Australian Merinos. In both of these reports few sheep were found with woolly-face grades. This observation led Dun *et al.* (1964) to suggest that the extremes of face-cover grades had to be present for a difference in lamb production to be found. Mullaney (1966) reported that Corriedales with a more open face produced more lambs born than did close-faced Corriedales. In one good year when twinning was more frequent the Merinos also showed a significant difference in numbers of lambs born in favour of the open face animals. The Polwarths showed no consistent effect of face cover on fertility.

Whilst investigating the relationship between lamb production and face cover most authors also examined the association between fleece weight and face cover. Terrill (1941) and (1949), Fail and Dun (1956), Coop (1956), Cockrem (1958) and Cockrem and Rae (1966) all showed no relationship between face cover and wool production. Barton (1954) and Cockrem *et al.* (1956) found that open-faced ewes produced less wool than woolly-faced ewes. However, when the greater lamb production of the open-faced ewes was accounted for there was no difference in fleece production. In part of their experiment, Carman and Williams (1957) showed that open-faced Shropshires produced more wool than their woolly-faced contemporaries, however this advantage was not consistent over all years. Morley (1955) calculated a negative genetic correlation (-0.58) between face-cover grade and GFW, suggesting that selection for open-faced sheep would lead to reduced GFW. The phenotypic correlations calculated by Morley (1955) between FC and GFW were close to zero. While all previously mentioned reports were made after the trend to woolly-faced sheep had occurred, the result published by Spencer *et al.* (1928) should have provided a warning that face cover and fleece weight were not necessarily related.

Cockrem (1966) presented an hypothesis of how the extent of face cover might affect the physiological functioning of an individual. He showed that open-faced sheep had better control over their body temperature than did woolly-faced sheep. Cockrem suggested that better temperature control could explain the differences in lamb production and fleece production exhibited between open-faced and woolly-faced sheep.

Cockrem and McDonald (1969) could not find any consistent difference in body temperature between the various face-cover grades. They suggested that lack of variation in face-cover scores precluded the chance of finding a difference. Cockrem and McDonald (1969) showed a lower rate of implantation of the blastocyst in ewes with a higher body temperature.

No experiments involving single trait selection for, or against, face cover have been reported. Available estimates of the heritability of face cover are listed in Table 2.7. The general consensus of these estimates is that face cover should show rapid response to selection.

2.4 The Estimation of Genetic Response to Selection in Farm Species

2.4.1 Introduction

There are three main reasons why estimates of genetic response to selection may be required:

- (a) to enable the comparison of different selection programmes,
- (b) to evaluate the economic efficiency of running a selection programme, and
- (c) to provide an alternative method of estimating genetic parameters.

The remainder of this chapter will refer only to the estimation of genetic parameters from single trait selection experiments.

TABLE 2.7: AVAILABLE ESTIMATES OF THE HERITABILITY OF FACE-COVER GRADE

Author(s)	$h^2 \pm SE$	Method	Breed
Terrill (1941)	0.44	Daughter-dam regression	Rambouillet
Terrill and Hazel (1943)	0.32	-	-
Terill and Hazel (1946)	0.51±0.07	Daughter-dam regression	Rambouillet
	0.60±0.07	Paternal half-sib	Rambouillet
	0.56±0.05	Average of above two	Rambouillet
Watkins (1954)	0.62±0.05	Paternal half-sib	Hampshire
	0.34±0.08	Daughter-dam regression	Hampshire
Shelton <i>et al.</i> (1954)	0.48	Paternal half-sib	Rambouillet
Morley (1955)	0.38	Daughter-dam regression	Merino
Roberts (1959)	0.50	-	Merino
Carman and Williams (1957)	0.16±0.32	Daughter-dam regression	Shropshire

Three experimental designs are commonly used to enable the estimation of genetic response:

- (a) selection in one direction without a control,
- (b) selection in one direction with a control, and
- (c) divergent selection.

In some cases a combination of (b) and (c) may be used.

2.4.2 Selection in one direction without a control

In large animal experiments it is normally impossible to maintain a constant environment for each successive generation of animals, unless they are housed under artificial conditions. Consequently, when comparing the performance of successive generations a portion of the difference in performance will be due to changing environmental effects. These environmental effects, which vary from generation to generation but influence all individuals in any one generation in a similar fashion, are called "common" environmental effects.

The problem of selection in one direction without a control is to adjust for the common environmental influence. Goodwin *et al.* (1955) proposed a repeat mating concept to enable the estimation of genetic gain in poultry, without maintaining a control group. Repeat mating was discussed in the context of large animal breeding experiments by Dickerson (1960) and Smith (1962). By using some sires for two or more years a genetic link from year to year was formed. The genetic link

was then used to remove at least part of the environmental effect. This technique allowed more resources to be put into the selection group(s). Also, because genotypes were more similar in the repeat mating method, than in the control/selected group approach, the size of any genotype x environment interaction was reduced. Smith (1962) noted two problems that could prevent the efficient use of this technique. Firstly, the number of sires required to provide the genetic link could reduce the rate of genetic response, making it more difficult to identify the true genetic gain. Secondly, any selection and progressive culling of sires would throw doubt on estimates of the genetic parameters. Smith concluded that the use of a randomly bred control would be more efficient in identifying the true genetic gain than the repeat mating approach.

Henderson (1949) discussed a technique which enabled the separation of genetic and environmental effects when predicting dairy bull breeding values from daughter lactation records taken in different years. The method of estimation has become known as BLUP (Henderson, 1972), whereby estimates of the fixed effects are best linear unbiased estimates (BLUE) and predictions of realized values of the random effects are best linear unbiased predictions (BLUP). The application of BLUP methodology generates a set of normal equations known as mixed-model-equations (MME). BLUP has been widely used in the dairy industry to estimate bull and cow breeding values, free of environmental effects (Henderson, 1972). The success of the MME in separating genetic and environmental effects is dependent on genetic connectedness across environmental effects. The genetic ties arise through genotypes being completely or partially represented throughout the different environments.

In selection experiments, sires are often used in one year only to maximize genetic gains. For the genetic and environmental effects, particularly year effects, to be separated under these circumstances it is necessary to include a relationship matrix in the MME to supply the genetic ties between years. It would be possible, in theory to separate the genetic and environmental effects by including dams in the analyses, if several records in the different environments were available for each dam. However, this approach may not be feasible due to physical limitations ^{of computer technology} imposed by computers. The efficacy of the MME technique in estimating genetic trend when sires are only used in one year has not yet been adequately tested.

2.4.3 Selection in one direction with a control

The maintenance of control groups to aid the prediction of genetic trends free of environmental effects is well documented (Hill, 1972c). Formulae presented by Hill (1972b) can be used to compare the efficiency of running a control versus not maintaining a control group. If the common environmental variance (σ_c^2) is expected to exceed:

$$\frac{\sigma^2 Z h^2}{L} + \frac{\sigma^2}{K} - \frac{\sigma^2 Z h^4}{M} ,$$

where σ^2 = the phenotypic standard deviation of the trait,

h^2 = the heritability of the trait,

L = the size of the control breeding group,

K = the number of individuals recorded in the control group,

M = the number of animals recorded in the selected group, and

$Z = (t^2 + 2t + 2)/10$, if the selected and control groups are from different base flocks,

or $Z = (2t^2 + 2t + 1)/5$, if the selected and control groups are from the same base flock,

then a control group should be maintained. However, σ_C^2 has not often been quantified, except under laboratory conditions. It is therefore difficult to make a definite statement about the relative size of σ_C^2 , and the figure derived from the above formula in an outdoor, large-animal, experiment.

Hill (1972c) reviewed the different approaches available for maintaining a group in which the genotypes are representative of the original population prior to selection commencing. In experiments involving large farm species the control group is the most common approach to replicating genotypes over time.

One of the problems associated with control populations is directional genetic drift. To ensure that genetic drift is minimized the effective number (N_e) in the control should be as large as possible. For a random mating, discrete generation population, Hill (1972c) presented the following formula for the calculation of N_e :

$$\frac{1}{N_e} = \frac{1}{16M} \left[1 + \sigma_{mm}^2 + \frac{M}{F} + \frac{2M}{F} \text{Cov}(mm, mf) + \frac{M^2}{F^2} \sigma_{mf}^2 \right] \\ + \frac{1}{16F} \left[1 + \sigma_{ff}^2 + \frac{F}{M} + \frac{2F}{M} \text{Cov}(fm, ff) + \frac{F^2}{M^2} \sigma_{fm}^2 \right]$$

where M = the number of males,

F = the number of females,

σ_{mm}^2 and σ_{mf}^2 = the variances in the number of male progeny
and female progeny, respectively, from males,

σ_{ff}^2 and σ_{fm}^2 = the variances in the number of female progeny
and male progeny, respectively, from females,

and

$\text{Cov}(mm, mf)$ and $\text{Cov}(fm, ff)$ = the covariances between the number of female and male progeny from males and females respectively.

This formula also holds for overlapping generations if the following criteria are met by the control group (Hill, 1972c):

- (a) the numbers of animals entering the group each year and the age distribution within the group are both constant, and
- (b) the age distribution of parents of individuals born in any one year is constant.

Note that for overlapping generations M and F become numbers per generation and the variances and covariances become dependent on lifetime family sizes. Given that M and F are fixed, the remaining variables must therefore be minimized if N_e is to be maximized.

In random bred controls where all replacement stock are chosen entirely at random, there are no vitality or fertility differences between families, and if family sizes follow a Poisson distribution, then the formula for estimating N_e simplifies to:

$$N_{e1} = \frac{4MF}{M+F} ,$$

because $\text{Cov}(mm, mf) = \text{Cov}(fm, ff) = 0$, $\sigma_{mm}^2 = \sigma_{ff}^2 = 1$, and $\sigma_{mf}^2 = 1/\sigma_{fm}^2 = F/M$ (Hill, 1972c). If restricted, randomized, selection of replacement

stock occurred such that: each male has one son and F/M daughters, and each female has one daughter and a probability of M/F of having one son then:

$$N_{e2} = \frac{16MF}{M + 3F} ,$$

because $\sigma_{fm}^2 = (M/F)(1 - (M/F))$ and the other variances and covariances of family number are zero (Hill, 1972c).

Restricted, random, selection of replacements, as stated above, is unlikely to be feasible in many large animal experiments because of the chance that not every female will produce at least one daughter. However, it does provide the opportunity to illustrate how N_e may be increased. For example, if $M = 10$ and $F = 100$, then $N_{e1} = 36.4$ and $N_{e2} = 51.6$. Thus, it may be a worthwhile exercise to devise a restricted, randomized, selection procedure for control populations in large animal experiments.

Apart from control groups, other methods of maintaining genotypes over time can be used:

- (a) embryo storage: the techniques for long-term storage of mammalian embryos were developed during the 1970s (Whittingham, 1977). Fertilized ova were collected from the female reproductive tract and stored in liquid nitrogen at -196° C. Land (1977) considered these recently developed techniques adequate for the conservation of genotypes in place of control groups. Thus, if an estimate of the genetic response was required, a proportion of the stored embryos

would be allowed to develop producing a group of animals against which the selected animals could be compared, and

- (b) gamete storage: with the recent advances in the freezing of semen, storage has become a realistic alternative to the control group in large farm animal selection programmes. By inseminating a proportion of females in the selected group with semen collected from the original base-flock rams, and comparing the progeny with the offspring of selected sires, then an estimate of one-half of the genetic gain can be obtained (assuming that all animals being compared were run under the same conditions). An increase in the level of inbreeding in the selected groups may be a problem. The progeny of females inseminated with semen collected at the start of the experiment could benefit by some degree of heterosis. Thus, the actual amount of genetic response could be underestimated.

From the preceding discussion on selection in one direction, with a control, several points should be noted. With present technology the use of semen storage would appear to be a useful alternative to using a control group. The use of this technique would enable more resources to be devoted to the selection group(s). In the future, long-term storage of embryos could become a viable technique for storing examples of the original genotypes over time. The advantages of storing embryos, compared with storing semen, would be:

- (a) complete absence of random genetic drift (individuals produced through the use of stored semen would receive half of the random genetic drift from their dam), and
- (b) the absence of heterotic effects.

2.4.4 Divergent selection

With divergent selection the common environmental effects are assumed to be removed during the subtraction of the low line mean from the high line mean. Hill (1972b) showed that if M animals were available for a selection experiment then divergent selection and selection in one direction without a control were of about equal efficiency in estimating genetic parameters if $\sigma_C^2 = 0$. When σ_C^2 became greater than zero, divergent selection was more efficient. If a control group was used to take account of the common environmental effects, and the animals for the control came from the original M animals, Hill (1972b) concluded that divergent selection remained more efficient. However, if the control group was already present for some other purpose, then equality of efficiency may be retained.

A problem specific to divergent selection was that, if response in the high and low lines was not symmetrical, new errors were introduced into the prediction of genetic response.

2.4.5 Errors associated with estimating genetic response to selection

Hill (1972c) provided a review on the efficiency of estimating genetic change. He identified two types of error:

- (a) bias, and
- (b) sampling error.

Errors resulting from bias are difficult to quantify, particularly in the case of genotype x environment interaction associated with some trend or permanent change in the environment. An estimate of the magnitude of the random sampling error can be derived.

Sampling errors may arise from several sources:

- (a) drift variance (σ_d^2) in the control and selected groups, which increases roughly in proportion to the generation number,
- (b) error of measurement of genetic means from observations on phenotypes (σ_e^2), and
- (c) genotype x environment interaction.

Genotype x environment interaction (GEI) can be a source of error in selection experiments because different genotypes are often being evaluated in the same environment. In particular, a control group may be used to account for environmental fluctuations in selection experiments. If a true estimate of any genetic response is to be obtained the control group must accurately measure the changes in the environment as they affect the selected group. However, if the control and selected groups respond differently to the same environment then the estimate of the genetic response will be biased by the size of the GEI.

Bray *et al.* (1962) compared a number of approaches for separating environmental and genetic effects in selection experiments using *Tribolium castaneum*. They concluded that if GEI existed then base control groups were ineffective in separating genetic and environmental effects in the later generations of selected lines. To overcome the degree of genetic difference between the control and selected groups, Bray *et al.* (1962) examined a relaxed selection technique in which control lines were taken from the selected group at frequent intervals throughout the selection experiment. They showed that this technique more closely indicated how environmental shifts affected the later generations of the selected lines than did a random bred control group.

Chopra (1978) reviewed available information on GEI for growth characteristics, carcass characteristics, fleece characteristics and reproductive traits in ewes. Results were often variable for similar traits with some authors reporting significant GEI and others reporting no interaction. Few significant GEI were reported for the reproductive traits. From his own analysis Chopra (1978) showed significant sire x stocking rate interactions in hogget live weight, mean fibre diameter, standard deviation of fibre diameter and total crimp number. Considering the available information on GEI, steps should be taken to reduce the risk of them occurring, although they may not always be a problem.

Generally GEI are disregarded in selection experiments because of the difficulty in quantifying them.

To enable a discussion on the variance of the estimate of genetic response it is necessary to define the techniques used to evaluate the genetic response. Hill (1972a) defines four approaches:

- (a) the regression of cumulative response on cumulative selection differential (b_C),
- (b) the regression of individual generation response on selection differential (b_I),
- (c) the ratio of total response to total selection differential (b_R), and
- (d) a maximum likelihood estimator (b_L).

A fifth approach which is commonly used is:

- (e) the regression of cumulative response on time (b_T).

Regression analysis using time as an independent variable has been employed by several workers to reflect the rate of genetic response to selection. The use of b_T involves the implicit assumption that the selection differentials are approximately equal from year to year. Also, when selection differentials are approximately equal from year to year $b_R = b_I$, and consequently the variance of b_R is equal to the variance of b_I , i.e. $V(b_R) = V(b_I)$. The maximum likelihood estimator will not be discussed here.

TABLE 2.8: APPROXIMATE VARIANCE EQUATIONS FOR THE ESTIMATORS OF GENETIC RESPONSE. (From Hill (1972a) and Hill (1972b)).

Type of Selection Experiment	Variance of the Estimator b_C
Selection in one direction without a control	$\frac{12}{s^2 t(t+1)(t+2)} \left[\frac{t^2 + 2t + 2}{10} \sigma_d^2 + \sigma_e^2 \right]$
Selection in one direction with a control	$\frac{12}{s^2 t(t+1)(t+2)} \left[\frac{t^2 + 2t + 2}{10} \sigma_d^2 + \sigma_e^2 \right]$
	* $\frac{6}{s^2 t(t+1)(2t+1)} \left[\frac{2t^2 + 2t + 1}{5} \sigma_d^2 + \sigma_e^2 \right]$
Divergent selection	$\frac{6}{s^2 t(t+1)(2t+1)} \left[\frac{2t^2 + 2t + 1}{5} \sigma_d^2 + \sigma_e^2 + \frac{3t(t+1)}{2(2t+1)} h^2 \sigma_e^2 \right]$

Type of Selection Experiment	Variance of the Estimators b_R and b_I
Selection in one direction with or without a control	$\frac{t\sigma_d^2 + 2\sigma_e^2}{t^2 s^2}$
Divergent selection	$\frac{t\sigma_d^2 + \sigma_e^2 + h^2 \sigma_e^2}{t^2 s^2}$

where s = selection differential,
 t = number of generations,
 σ_d^2 = drift variance (see Table 2.9), and
 σ_e^2 = measurement error variance (see Table 2.9).

* If regression is through the origin.

TABLE 2.9: FORMULAE FOR THE CALCULATION OF σ_d^2 and σ_e^2

Type of Selection Experiment	Drift Variance (σ_d^2)	Measurement Error Variance (σ_e^2)
Selection in one direction without a control	$\frac{\sigma^2 h^2 (1-h^2)}{N_{NC}} + \frac{\sigma^2 h^4}{M_{NC}}$	$\frac{\sigma^2 (1-h^2)}{M_{NC}} + \sigma_c^2$
Selection in one direction with a control	$\frac{\sigma^2 h^2 (1-h^2)}{N_C} + \frac{\sigma^2 h^2}{L}$	$\frac{\sigma^2 (1-h^2)}{M_C} + \frac{\sigma^2}{K}$
Divergent selection	$\frac{2\sigma^2 h^2 (1-h^2)}{N_D} + \frac{2\sigma^2 h^4}{M_D}$	$\frac{2\sigma^2 (1-h^2)}{M_D}$

where σ^2 = phenotypic variation,

h^2 = heritability,

M = number of animals recorded in selection flock,

N = number of animals selected as replacements in selection flock,

K = number of animals recorded in control flock, and

L = size of control breeding flock.

To simplify the variance equations it will be assumed that selection differentials are constant for each generation. With this constraint the variances of b_C and b_R derived by Hill (1972a) and Hill (1972b) are presented in Table 2.8. The formulae for σ_D^2 and σ_E^2 are given in Table 2.9. The drift variance and measurement error for divergent selection are both increased by a factor of 2 compared with the other approaches (see Table 2.9). However, N_D and M_D are normally one-half the size of N_{MC} , or N_C , and M_{NC} , or M_C , in comparable experiments.

The contribution to drift variance from the selected animals is the same across all three approaches ($h^2(1 - h^2)/N$). The contribution from the number of animals measured is the same for divergent selection and selection in one direction without a control (h^4/M) but becomes h^2/L for selection in one direction with a control. Table 2.10 contains several examples of the comparative size of these two ratios. For these two quantities to equate the size of the control breeding flock (L) must be much larger than the number measured in the selection flock (M).

TABLE 2.10: A COMPARISON OF h^4/M_{NC} , $h^4/2M_D$ AND h^2/L USING A HERITABILITY OF 0.3

M_{NC} , $2M_D$ or L	h^4/M_{NC} or $h^4/2M_D$	h^2/L
20	0.0045	0.0150
50	0.0018	0.0060
100	0.0009	0.0030
200	0.0005	0.0015
500	0.0002	0.0006

Compared with divergent selection, the measurement error is increased by σ_C^2 for selection in one direction without a control, or σ^2/K for selection in one direction with a control.

Hill (1972a, b) showed that there was little difference in the efficiency of the three estimators b_C , b_I and b_R in estimating genetic response. The estimator b_R is slightly more efficient than b_C , when using either divergent selection or selection in one direction with a control, if either the heritability or the number of generations is high.

C H A P T E R T H R E E

MATERIALS AND METHODS

3.1 Materials

3.1.1 The sheep and their environment

The data came from two selection flocks and a control flock, all three groups having been derived from the same base Romney flock. Between 1956 and 1966 all three flocks were run on the flats of the Massey University farm "Tuapaka". Since 1966 the three flocks have been grazed on another area of Massey University land called the "Pahiatua Block". Some physical features of these two environments are recorded in Table 3.1.

The original base flock of Romneys was described by Rae (1958a). Prior to 1956 the base flock was randomly bred using rams from Manawatu and Wairarapa Romney stud flocks. Consequently, the base flock was considered as being representative of the Romney breed, as present in the Southern North Island at that time.

Prior to the 1956 mating, part of the base flock was divided into three flocks of approximately 80 ewes each. Each flock contained ewes ranging from 1½ to 4½ years of age in proportions similar to that of commercial flocks. Allotment of ewes to the three flocks was done randomly within ewe age. In 1956 and 1957 rams from local studs were used. In 1957 replacement 1½ year old ewes were allocated to the three flocks, at random, from the 1955 drop of lambs in the base flock. In 1958 the three flocks were closed. Replacement 1½ year old ewes and rams were selected according to the following criteria:

TABLE 3.1: SOME PHYSICAL ASPECTS OF THE TWO AREAS UPON WHICH THE EXPERIMENTAL FLOCKS WERE CARRIED

	Tuapaka* 1956-1966	Pahiatua Block 1967-1976
Altitude (metres)	60-90	60-90
Annual rainfall (mm)	1200-1400	1000-1200
Topography	Flat*	Mainly flat, some gullies
Soil type	Tokomaru silt loam	Tokomaru silt loam on flats, Halcombe hill soil in gullies
Drought susceptibility	Low	Moderate
Pasture species	Predominantly perennial ryegrass and white clover	Predominantly perennial ryegrass and white clover
Stocking rate (stock units per ha)	12-15	12-15

*Whilst at Tuapaka the experimental flocks were only run on the flat country. (Tuapaka is about 80% hard hill country.)

- (a) for the control group selection was at random,
- (b) for the face-cover group those with the most open faces were chosen, and
- (c) for the fleece weight group those with the heaviest hogget greasy fleece weights were selected.

Each flock was maintained at about 70 to 80 ewes per annum, with ewes being culled for age after their fourth lambing, i.e. at 5 years of age. The age structures of the flocks are shown in Table 3.2. Since 1958 four 1½ year old rams have been used for mating in each flock, each year, except for the years 1958 to 1961 when only two rams were used in the control flock. In some years a fifth, reserve, ram was used when one of the originally selected rams died, was injured or became infertile.

Breeding ewes from all flocks were kept together, except at mating when the 3 groups were run separately although every effort was made to maintain similar conditions across the groups. The flocks were managed as nearly as possible to commercial conditions. Breeding ewes were shorn once a year in November/December, at which time the greasy fleece weight and live weight after shearing were recorded. A mid-side sample of wool was collected to enable the evaluation of several wool characteristics.

TABLE 3.2: SIZE OF EWE MATING FLOCKS AND THEIR AGE COMPOSITION

Sub-Flock	Controls					Face Cover					Fleece Weight				
	2	3	4	5	Total	2	3	4	5	Total	2	3	4	5	Total
Age															
Year															
1956	25	19	18	15	77	24	19	17	14	74	24	19	20	15	78
1957	16	21	17	17	71	19	25	19	18	81	18	22	18	20	78
1958	18	17	22	14	71	16	18	24	19	77	18	16	21	18	73
1959	22	18	16	21	77	20	15	16	18	69	19	18	12	20	69
1960	22	21	17	15	75	23	20	12	13	68	27	18	17	11	73
1961	18	22	21	14	75	25	20	16	11	72	18	26	15	16	75
1962	21	16	22	21	80	17	23	20	13	73	18	19	25	13	75
1963	21	20	16	21	78	18	16	22	19	75	14	18	17	24	73
1964	24	19	20	15	78	24	18	11	19	72	22	15	17	15	69
1965	15	24	19	18	76	19	24	15	11	69	24	21	13	16	74
1966	22	13	25	16	76	20	17	23	13	73	21	22	20	10	73
1967	21	20	10	23	74	15	18	17	20	70	18	20	19	20	77
1968	29	21	19	10	79	26	15	17	15	73	22	15	17	16	70
1969	12	29	21	15	77	20	27	14	16	77	24	22	15	15	76
1970	18	12	26	20	76	20	19	25	14	78	19	23	23	15	80
1971	19	17	12	23	71	19	20	18	20	77	19	18	24	22	83
1972	23	18	16	10	67	22	19	18	16	75	20	16	18	21	75
1973	19	23	18	13	73	17	19	16	15	67	24	20	16	17	77
1974	23	17	23	16	79	29	18	17	14	78	21	24	20	14	79
1975	16	23	17	22	78	16	28	17	16	77	15	21	22	16	74
1976	21	14	22	15	72	18	14	23	13	68	24	13	21	23	81
Mean	20	19	19	17	75	20	20	18	16	74	20	19	19	17	75

Every year ewes within each flock were randomized, within age group, into one of four sire groups. In recent years harnessed, vasectomized rams were run with the ewes during the mating season, mid-March to mid-April, to identify in-heat ewes. These ewes were then hand-mated to their designated rams twice over a 24 hour period. This procedure enabled the rams to be kept entirely separate from the ewe flock, thereby minimizing the chance of an incorrect mating. Prior to using vasectomized rams each group of ewes was paddock mated with their assigned ram.

Lambing took place during August and September. The ewes were observed every day and new lambs were weighed, tagged and sexed. The birth rank, date of birth and dam tag number were also recorded.

Lambs were weaned in late November or early December, all lambs being weighed at this time. A proportion of ram lambs were randomly culled at weaning as there was not sufficient grazing for all lambs to be kept. Soon after weaning all lambs were shorn. This practice ensured a constant period of wool growth for all animals between lamb and hogget shearing.

Ram and ewe hoggets were grazed separately, but within sex all hoggets were run together. Hoggets were shorn at the beginning of October. Individual greasy fleece weights, including bellies and pieces, were recorded. A mid-side sample of wool was also collected. Immediately prior to hogget shearing each ewe and ram was graded for face cover according to the scoring system described in Section 3.1.2. After shearing, hogget live weights were recorded. Replacement ewes

and rams for the following mating season were chosen as required for each flock soon after hogget shearing. Table 3.3 shows the number of ram and ewe hoggets available for selection each year.

3.1.2 The data

Apart from the two traits under investigation for direct response, several other body and wool traits were recorded. Several ewe traits were recorded across ages. To simplify the analysis, an average lifetime record was calculated for each ewe having a complete set of 4 records. Ewe average lifetime records were subscripted by an "a", ewe hogget records with an "e" and ram hoggets with an "r".

The various traits, their abbreviations, and the years in which they were recorded are shown in Table 3.4.

Between 1956 and 1971 measurements were recorded in imperial units and post-1971 in metric units. All measurements were converted to metric units prior to analysis. BW and GFW were recorded to the nearest 0.1 kg, whilst WW and LW were measured to the nearest 0.5 kg. SL was recorded to the nearest mm.

Greasy fleece weight was recorded immediately after shearing. Belly-wool and pieces were included in the GFW.

To enable the calculation of Y, greasy mid-side samples were weighed after being conditioned at 65⁰F and 65% relative humidity for 48 hours. After scouring, the samples were again conditioned for 48 hours before reweighing. Clean scoured yield was then calculated as:

TABLE 3.3: NUMBER OF RAM AND EWE HOGGETS RECORDED IN EACH SUB-FLOCK

Year	Ewe Hoggets			Ram Hoggets		
	Control	FC*	FW+	Control	FC*	FW+
1956	33	34	36	0	28	25
1957	31	43	33	6	23	24
1958	34	28	34	6	25	24
1959	32	38	30	5	24	22
1960	38	27	36	5	24	24
1961	26	31	39	7	23	23
1962	30	32	29	10	29	28
1963	21	29	39	9	24	24
1964	29	30	39	11	27	23
1965	29	26	27	10	25	29
1966	38	47	33	5	26	26
1967	40	42	39	19	16	24
1968	34	32	46	9	25	20
1969	38	36	50	19	37	30
1970	28	23	38	12	29	29
1971	22	21	40	10	34	37
1972	27	32	36	12	31	22
1973	26	19	23	14	24	29
1974	23	33	46	13	23	21
1975	27	30	36	17	17	20
1976	28	42	31	22	25	32

* FC = face cover group.

+ FW = fleece weight group.

TABLE 3.4: TRAIT ABBREVIATIONS AND YEARS OF COLLECTION

Trait	Abbreviation	Years in which Data were Collected		
		Ewe Hogget	Ram Hogget	Ewe
Date of birth	DOB	*	*	na
Birth weight	BW	1956-75	1956-76	na
Birth rank	BR	*	*	na
Rearing rank	RR	*	*	na
Weaning weight	WW	*	*	na
Post-shearing liveweight	LW	*	1957, 1959-76	1958-76
Greasy fleece weight	GFW	*	*	*
Clean fleece weight	W	*	*	*
Quality number	QN	*	*	*
Character grade	CHG	*	*	*
Lustre grade	LG	1970-76	1970-76	1970-76
Handle grade	HG	1970-76	1970-76	1970-76
Scoured colour grade	SCG	1970-76	1970-76	1970-76
Staple length	SL	*	*	*
Total crimp number	TCN	1958-76	1958-76	1958-76
Crimp frequency	CF	1958-76	1958-76	1958-76
Clean scoured yield	Y	*	*	*
Mean fibre diameter	MFD	*	1957-76	1957-76
Standard deviation of fibre diameter	SFD	*	na	na
Percent medullated fibres	PMF	1956-70, 1972-76	na	na
Medullameter index	MI	1956, 1958-66	1956-66	1956-66
Face cover grade	FC	*	*	na
Number of lambs born	LB	na	na	*
Number of lambs reared	LR	na	na	*

* = full data sets, i.e. 1956-1976.

na = not applicable or not collected.

$$Y = \frac{\text{weight of scoured sample} \times 100}{\text{weight of greasy sample}}$$

Clean fleece weight was calculated as:

$$W = \text{GFW} \times Y/100.$$

Staple length was measured on the greasy mid-side sample. The measurement was made between the base and the tip of the staple. Care was taken not to stretch the staple.

The total number of crimps along a staple of greasy wool from the mid-side sample were counted. The crimp frequency, in crimps per 25 mm, was derived from the SL and the TCN.

Quality number was a visual appraisal of the spinnability, and hence fineness, of the wool sample. It was based mainly on staple crimp frequency and lustre (Wickham, 1971) and could be affected by observer variation.

Character grade, lustre grade and handle grade were subjectively graded on the greasy mid-side sample, whilst scoured colour grade was subjectively assessed on the scoured sample. These were graded on a 1 to 9 scale; the score of 9 being allotted to the expression considered most desirable and 1 to the least desirable. These grading systems have been discussed by Sumner (1969).

Character grade reflects clarity and evenness of staple crimp and absence of tapering tip and medullation. A staple with well-defined crimps was given a high score.

Lustre grades were assigned without reference to fineness. Lincoln-type wool would generally receive high grades.

Handle grade was assessed without regard to quality number. Soft wool was given high grades.

Discoloured, scoured, wool samples were assigned low scoured colour grades.

Mean fibre diameter in ewe hogget fleeces (MFDe) was estimated by the projection microscope method. This involved the measurement of 150 fibre snippets. The projection microscope approach also enabled the calculation of the standard deviation of the mean fibre diameter (SFDe) and the percentage of medullated fibres (PMFe). Mean fibre diameter for the ram hoggets (MFDr) and ewes (MFDa) was estimated using the airflow method (Ross, 1958). The airflow method does not allow the estimation of SFD and PMF.

Medullameter tests were carried out on all mid-side samples collected between 1956 and 1966. The operation of the medullameter, and the comparison of measurements obtained from it with the true degree of medullation, were discussed by McMahon (1937).

Face-cover grades were dependent on the presence or absence of wool fibres over three areas on the head:

- (a) the dorsal aspect of the nose,
- (b) the side of the nose, and
- (c) the poll.

Table 3.5 summarizes the grades and how they relate to wool fibre production at the above positions.

TABLE 3.5: SYSTEM OF GRADING FOR FACE COVER

Dorsal aspect of nose	Side of nose	Poll	Face-cover grade(s)
Present*	Present	Present	1-2
Partial*	Present	Present	3
Absent*	Present	Present	4-6
Absent	Partial	Present	7-8
Absent	Absent	Present	9-10
Absent	Absent	Partial	11-13
Absent	Absent	Absent	14-15

* Present, partial or absent refers to wool growth, as opposed to kemp growth, of any length visible without detailed inspection.

3.2 Statistical Methods

3.2.1 Introduction

For all traits ordinary least squares analyses were carried out within each of the three sub-flocks in an attempt to identify any changes that may have occurred during the 21 years of selection. Separate analyses were applied to the ewe hogget, ram hogget and ewe average lifetime performances.

Preliminary analyses were aimed at identifying which fixed effects should be included in the linear models applied to the data. These analyses identified selection flock, sex (for hogget data), year of birth, dam age, birth rank and rearing rank as being the important effects. First-order interactions did not show any significant influence.

During the preliminary analyses it was found that the within year regression coefficients of hogget greasy fleece weight on date of birth in the fleece weight group showed a consistent trend towards zero. The average regression coefficients, derived from the fleece weight group ewe hoggets, for the periods 1956-1962, 1963-1969 and 1970-1976 were -0.019, -0.012 and -0.001 kg per day. It was suspected that the trend in the regression coefficients could be due to a correlated response in date of birth, i.e. the fleece weight group tended to have an earlier average lambing date as the experiment progressed. Consequently, it was decided to treat date of birth as a trait rather than as a concomitant variable for analyses involving other characteristics. Interpretation of results concerning weaning weight, in particular, should take account of this deficiency.

Dam age, birth rank and rearing rank were combined to give one fixed effect. The resulting classifications are shown in Table 3.6.

TABLE 3.6: THE COMBINATION OF DAM AGE, BIRTH RANK AND REARING RANK TO GIVE ONE FIXED EFFECT

Birth rank	Rearing rank	Dam age			
		2	3	4	5
1	1	2	1	1	1
2	1	3	3	3	3
2	2	4	4	4	4

No account was taken of dam age within the twin birth rank class as few 2-year-old ewes gave birth to twins. In the ram hogget analyses only rearing rank was considered because of the small number of observations per level of fixed effect.

To simplify computing programmes the dam age, birth/rearing rank fixed effect was retained in analyses involving ewe-average-lifetime-performance, even though its contribution was not expected to be significant.

3.2.2 The effect of inbreeding

Inbreeding coefficients were calculated using the procedure suggested by Emik and Terrill (1949) and Cruden (1949). They showed that any diagonal element of the numerator relationship matrix consisted of the inbreeding coefficient of the individual (as defined by Wright, 1922) plus one.

The effect of the level of inbreeding on performance was assessed by regressing the individual's performance on their own inbreeding coefficient (individual performance was corrected for year, dam age and birth/rearing rank effects and each sex was analysed separately).

3.2.3 Phenotypic standard deviations and correlations

Estimates of the phenotypic standard deviations of traits and correlations between traits were obtained within each sub-flock from the ram hogget, ewe hogget and ewe average-lifetime-performance data sets. Correlations between the ewe average-lifetime-performance traits were not calculated. Within each of the aforementioned analyses the

following model was applied:

$$y_{ijk} = \mu + d_i + t_j + e_{ijk} ,$$

where y_{ijk} = an observation on the k^{th} animal, being of the i^{th} dam age, birth/rearing rank and being born in the j^{th} year,

μ = general mean,

d_i = the fixed effect of the i^{th} dam age, birth/rearing rank,

t_j = the fixed effect of the j^{th} year, and

e_{ijk} = the random residual associated with the k^{th} observation in the i^{th} dam age, birth/rearing rank and the j^{th} birth year.

The inbreeding coefficient was not included as a covariate as results indicated that the levels of inbreeding reached did not seriously bias the observed performance (see Section 4.2).

3.2.4 Least squares estimates of the genetic response

Using the same model applied in the previous section, estimates of the birth-year effects were obtained within each sub-flock from the ram hogget, ewe hogget and ewe average lifetime performance data sets. By subtracting the control group year effects from the corresponding selection group year effects, estimates of the genetic response were obtained.

3.2.5 Estimation of genetic correlations and heritabilities

Estimates of heritabilities (h^2) and genetic correlations (r_g) were derived for the ewe hoggets, ram hoggets and ewe average lifetime performance, within each sub-flock.

Heritabilities were estimated as:

$$h_1^2 = \frac{4\sigma_{S_1}^2}{\sigma_{S_1}^2 + \sigma_{e_1}^2},$$

and the genetic correlations as:

$$r_{g12} = \frac{\sigma_{S_1S_2}}{\sqrt{\sigma_{S_1}^2 \cdot \sigma_{S_2}^2}},$$

where $\sigma_{S_1}^2$ = the sire variance component for trait 1,

$\sigma_{S_2}^2$ = the sire variance component for trait 2,

$\sigma_{e_1}^2$ = the error variance component for trait 1, and

$\sigma_{S_1S_2}$ = the sire covariance component between trait 1 and
trait 2.

The variance and covariance components were obtained by following Method 3 of Henderson (1953).

The full model applied in each analysis was:

$$y_{ijkl} = \mu + d_i + t_j + s_{jk} + e_{ijkl},$$

Where

y_{ijkl} = an observation on the l^{th} animal being in the i^{th} dam age, birth/rearing rank, the j^{th} birth year and being sired by the k^{th} sire in the j^{th} year,

μ = general mean,

d_i = the fixed effect of the i^{th} dam age, birth/rearing rank,

t_j = the fixed effect of the j^{th} birth year,

s_{jk} = the random effect of the k^{th} sire used in the j^{th}

year. Sire effects are assumed to have mean = 0

and variance = $\sigma_{S_1}^2$, and

e_{ijkl} = the random residual effect associated with the l^{th} observation from the i^{th} dam age, birth/rearing rank, the j^{th} birth year and the k^{th} sire being used in the j^{th} year. Residual effects are assumed to have mean = 0 and variance = σ_e^2 .

To simplify further discussion the above linear model can be represented in matrix terms:

$$\tilde{y} = \tilde{X} \tilde{b} + \tilde{Z} \tilde{\mu} + \tilde{e} ,$$

where \tilde{y} = a vector of observations,
 \tilde{X} and \tilde{Z} = known matrices consisting of 0's and 1's,
 \tilde{b} = an unknown vector of fixed effects,
 $\tilde{\mu}$ = an unknown vector of random effects, with mean zero and a variance-covariance matrix \tilde{G} , and
 \tilde{e} = an unknown vector of random residual effects, with mean zero and a variance-covariance matrix \tilde{R} (it is assumed that the $\text{cov}(\tilde{\mu}, \tilde{e})$ is zero).

Assuming that \tilde{G} and \tilde{R} are of the form $\tilde{I}\sigma^2$, for scalar σ^2 , a set of normal equations which, when solved, produce least-squares solutions of \tilde{b} and $\tilde{\mu}$ are:

$$\begin{bmatrix} \tilde{X}' \tilde{X} & \tilde{X}' \tilde{Z} \\ \tilde{Z}' \tilde{X} & \tilde{Z}' \tilde{Z} \end{bmatrix} \begin{bmatrix} \tilde{b} \\ \tilde{\mu} \end{bmatrix} = \begin{bmatrix} \tilde{X}' \tilde{y} \\ \tilde{Z}' \tilde{y} \end{bmatrix} .$$

To enable the calculation of the reduction in sums-of-squares and sums-of-cross-products due to the random (sire) effect, after adjusting for the fixed effects, the following reduced model was fitted:

$$y_{ijl} = \mu + d_i + t_j + e_{ijl} ,$$

where all symbols are as previously defined.

Error variance and covariance components were then estimated by equating the error sums-of-squares (SS_e) and error sums-of-cross-products (SCP_e) to their expectations:

$$E(SS_e) = r(fm) \sigma_e^2$$

where $r(fm)$ = rank of the full model,

thus:

$$\hat{\sigma}_e^2 = SS_e / r(fm) .$$

Similarly, sire variance and covariance components were estimated by equating the sire sums-of-squares (SS_s) and sire sums-of-cross-products (SCP_s) to their expectations:

$$E(SS_s) = [\text{trace}(\underline{Z}'\underline{Z}) - \text{trace}((\underline{X}'\underline{X})^{-1}\underline{X}'\underline{Z}\underline{Z}'\underline{X})] \sigma_s^2 + r(fm) \sigma_e^2 ,$$

thus $\hat{\sigma}_s^2 = (SS_s - r(fm) \hat{\sigma}_e^2) / (\text{trace}(\underline{Z}'\underline{Z}) - \text{trace}[(\underline{X}'\underline{X})^{-1}\underline{X}'\underline{Z}\underline{Z}'\underline{X}])$,

where $(\underline{X}'\underline{X})^{-1}$ is a generalised inverse of $(\underline{X}'\underline{X})$.

Estimates of the standard errors for the heritability estimates were calculated using two methods. Swiger *et al.* (1964) presented the following approximate formula:

$$v(h^2) = \frac{32(N - 1)(1 - t)^2(1 + (k - 1)t)^2}{k^2(N - s)(s - 1)},$$

where $v(h^2)$ = the variance of the heritability estimate,

s = the number of sires,

N = the total number of observations,

$t = \sigma_S^2 / (\sigma_S^2 + \sigma_E^2)$,

$$k = \frac{N - \frac{\sum n_i^2}{N}}{s - 1}, \text{ and}$$

n_i = the number of observations in the i^{th} sire group.

The restriction of this approach was that a simple one-way random model was assumed. Since expectations of the sums-of-squares were included in the above formula, the equation was only strictly true for one-way models. When calculating standard errors for the heritabilities in this study, $\text{trace}(\underline{Z}'\underline{Z}) - \text{trace}((\underline{X}'\underline{X})^{-1}\underline{X}'\underline{Z}\underline{Z}'\underline{X})$ was substituted for the k value of Swiger *et al.* (1964).

C.R. Henderson (unpubl.) presented a method for determining estimates of the variances of the variance and covariance components and estimates of the covariances between variance components. These estimates were limited only by the inclusion of estimates of the parameters σ_{S1}^2 , σ_{S2}^2 , σ_{S1S2} , σ_{E1}^2 , etc. To obtain an estimate of the variance of the heritability these values were then included in the equation:

$$v(h^2) = (h^2)^2 \left[\frac{v(\sigma_S^2)}{(\sigma_S^2)^2} + \frac{v(\sigma_S^2) + v(\sigma_E^2) + 2\text{cov}(\sigma_S^2, \sigma_E^2)}{(\sigma_S^2)^2 + (\sigma_E^2) + 2\sigma_S^2\sigma_E^2} - \frac{2v(\sigma_S^2) + \text{cov}(\sigma_S^2, \sigma_E^2)}{(\sigma_S^2)^2 + \sigma_S^2\sigma_E^2} \right]$$

where $v(\sigma_S^2)$ = the variance of the sire variance component,
 $v(\sigma_E^2)$ = the variance of the error variance component, and
 $\text{cov}(\sigma_S^2, \sigma_E^2)$ = the covariance between the sire and error variance components.

This equation can be derived using the approximate formula for the variance of a ratio.

Estimates of the variances of the variance and covariance components and covariances between variance components obtained via Henderson's technique can also be used in the calculation of the standard error of the genetic correlation. Using the approximate formula for the variance of a ratio:

$$v(r_g) = (r_g)^2 \left[\frac{v(\sigma_{S_1 S_2})}{(\sigma_{S_1 S_2})^2} + \frac{v(\sigma_{S_1}^2)}{4(\sigma_{S_1}^2)^2} + \frac{v(\sigma_{S_2}^2)}{4(\sigma_{S_2}^2)^2} - \frac{\text{cov}(\sigma_{S_1 S_2}, \sigma_{S_1}^2)}{\sigma_{S_1 S_2} \cdot \sigma_{S_1}^2} - \frac{\text{cov}(\sigma_{S_1 S_2}, \sigma_{S_2}^2)}{\sigma_{S_1 S_2} \cdot \sigma_{S_2}^2} + \frac{\text{cov}(\sigma_{S_1}^2, \sigma_{S_2}^2)}{2\sigma_{S_1}^2 \cdot \sigma_{S_2}^2} \right] .$$

Because of the difficulty in calculating the covariances involved in the last three terms this formula was simplified to:

$$v(r_g) = (r_g)^2 \left[\frac{v(\sigma_{S_1 S_2})}{(\sigma_{S_1 S_2})^2} + \frac{v(\sigma_{S_1}^2)}{4(\sigma_{S_1}^2)^2} + \frac{v(\sigma_{S_2}^2)}{4(\sigma_{S_2}^2)^2} \right] .$$

Rae (1950) found that dropping these 3 terms did not appear to seriously bias the estimate of the variance in his analysis.

Tallis (1959) presented the following formula for calculating the standard error of r_g ; simplified by assuming the number of progeny per sire to be constant:

$$\begin{aligned}
 v(r_g) = & [(1 + r_g^2)(1 + r_b^2)(1 + (k-1)t_1)(1 + (k-1)t_2) \\
 & - 2r_g r_b (t_1 t_2 (1 + (k-1)t_1)(1 + (k-1)t_2))^{\frac{1}{2}} ((1 + (k-1)t_1/t_1) + (1 + (k-1)t_2/t_2)) \\
 & + (r_g^2(t_1 - t_2)^2 / 2t_1 t_2)] / d_s k^2 t_1 t_2 \\
 & + [(1 + r_g^2)(1 + r_w^2)(1 - t_1)(1 - t_2) - 2r_g r_w (t_1 t_2 (1 - t_1)(1 - t_2))^{\frac{1}{2}} \\
 & ((1 - t_1)/t_1) + ((1 - t_2)/t_2)) + (r_g^2(t_1 - t_2)^2 / 2t_1 t_2)] / d_j k^2 t_1 t_2 ,
 \end{aligned}$$

where d_s = the sire degrees-of-freedom,

d_j = the error degrees-of-freedom,

$k = \text{trace}(\underline{Z}'\underline{Z}) - \text{trace}((\underline{X}'\underline{X})^{-1}\underline{X}'\underline{Z}\underline{Z}'\underline{X})$,

$t_1 = \sigma_{S1}^2 / (\sigma_{S1}^2 + \sigma_{E1}^2)$,

$t_2 = \sigma_{S2}^2 / (\sigma_{S2}^2 + \sigma_{E2}^2)$,

$r_b = v_{12} / \sqrt{v_{11} v_{22}}$,

$r_w = v_{12} / \sqrt{v_{11} v_{22}}$,

v_{12} = the between sire covariance for traits 1 and 2,

v_{11} = the between sire mean square for trait 1,

v_{22} = the between sire mean square for trait 2,

v_{12} = the error covariance between traits 1 and 2,

v_{11} = the error mean square for trait 1, and

v_{22} = the error mean square for trait 2.

The method derived from Henderson's formula and the Tallis method were both used for estimating standard errors of the genetic correlations.

3.2.6 The use of mixed model equations to estimate genetic response

In these analyses the following model was assumed:

$$y_{ijkl} = \mu + d_i + t_j + s_{jk} + e_{ijkl} ,$$

where all symbols are as previously defined. In the preceding section the following set of normal equations were presented:

$$\begin{bmatrix} \underline{\underline{X}}' \underline{\underline{X}} & \underline{\underline{X}}' \underline{\underline{Z}} \\ \underline{\underline{Z}}' \underline{\underline{X}} & \underline{\underline{Z}}' \underline{\underline{Z}} \end{bmatrix} \begin{bmatrix} \underline{\underline{b}} \\ \underline{\underline{\mu}} \end{bmatrix} = \begin{bmatrix} \underline{\underline{X}}' \underline{\underline{y}} \\ \underline{\underline{Z}}' \underline{\underline{y}} \end{bmatrix}$$

When solved, these equations produced least squares solutions of $\underline{\underline{b}}$ and $\underline{\underline{\mu}}$. The mixed-model-equations (MME) can be generated by adding $\underline{\underline{A}}^{-1} \cdot \sigma_e^2 / \sigma_s^2$ to the $\underline{\underline{Z}}' \underline{\underline{Z}}$ portion of the normal equations, where $\underline{\underline{A}}^{-1}$ is the inverse of the numerator relationship matrix and $\underline{\underline{A}} = \underline{\underline{G}} \cdot 1 / \sigma_s^2$. The MME are:

$$\begin{bmatrix} \underline{\underline{X}}' \underline{\underline{X}} & \underline{\underline{X}}' \underline{\underline{Z}} \\ \underline{\underline{Z}}' \underline{\underline{X}} & \underline{\underline{Z}}' \underline{\underline{Z}} + (\underline{\underline{A}}^{-1} \cdot \sigma_e^2 / \sigma_s^2) \end{bmatrix} \begin{bmatrix} \underline{\underline{b}} \\ \underline{\underline{\mu}} \end{bmatrix} = \begin{bmatrix} \underline{\underline{X}}' \underline{\underline{y}} \\ \underline{\underline{Z}}' \underline{\underline{y}} \end{bmatrix} ,$$

which when solved, produce best linear unbiased estimates of estimable functions of $\underline{\underline{b}}$ and best linear unbiased predictions of $\underline{\underline{\mu}}$. The relationship matrix ($\underline{\underline{A}}$) was often assumed to be an identity matrix, because of the difficulty in computing an inverse of a large matrix. Henderson (1976) presented an algorithm which enabled the calculation of elements of the inverse without first computing the relationship matrix. This step made the inclusion of the $\underline{\underline{A}}^{-1}$ matrix feasible.

As discussed in section 2.4.2, it is necessary to include the inverse of the relationship matrix in the MME to estimate the genetic response to selection, free of environmental effects, when sires have

only been used for one year; and the linear model does not include dams as a random effect. This approach should transfer any genetic trend from the fixed effects to the breeding values of the sires. Thus by averaging the breeding values of animals born in any one year an estimate of the genetic trend should be obtained.

The MME were also used to obtain best linear unbiased estimates (BLUEs) of the year effects from the control flock. These estimates were then subtracted from observations in the selection flocks to adjust for the environmental fluctuations. The selection flock deviations were then analyzed using MME and the year effects were taken as being indicative of the genetic trend. In these analyses the relationship matrices were assumed to be diagonal.

3.2.7 Calculation of realized responses

Having obtained estimates of the genetic responses it was necessary to express the response in terms of selection pressure applied. Selection pressure was measured in terms of the selection differential.

To account for overlapping generations, cumulated selection differentials were calculated for each individual and then averaged within each year to give a flock-average-cumulated-selection-differential (FACSD). The individual cumulated selection differentials were calculated by adding the average of the parents cumulated selection differentials to the individuals own selection differential.

Realized responses were then estimated using two approaches:

- (a) by regressing the predicted genetic responses on the FACSD. Within this technique two regression coefficients were derived, firstly by the method of best fit and, secondly by forcing the regression through the origin. Because the control and selection flocks were derived from the same initial population, the origin should be known without error, and
- (b) by the ratio of total response to total cumulated selection differential.

Within each of the selection flocks the realized response pertaining to the trait under direct selection was the realized heritability. All other realized responses were realized correlated responses.

Standard errors of the realized heritabilities were calculated according to the formula derived by Hill (1972b) (see section 2.4.5).

Standard errors of the realized correlated responses were calculated using the following formula derived by A.L. Rae (pers. comm.):

$$V(b_{cy}) = \frac{6}{s^2 t(t+1)(2t+1)} \left[\frac{2t^2 + 2t + 1}{5} \cdot \sigma_d^2 + \sigma_e^2 \right],$$

where $V(b_{cy})$ = the variance of the correlated response in trait y,

given single trait selection on trait x,

$$\sigma_d^2 = \frac{h_y^2(1 - h_x^2 r_{xy}^2)\sigma_y^2}{N} + \frac{h_x^2 h_y^2 r_{xy}^2 \sigma_y^2}{L},$$

$$\sigma_e^2 = \frac{(1 - h_x h_y r_{xy})\sigma_y^2}{M} + \frac{\sigma_y^2}{K},$$

h_x^2 and h_y^2 = the heritabilities of traits x and y,

r_{xy} = the genetic correlation between traits x and y,

σ_y^2 = the phenotypic variance of trait y, and all other

symbols are as previously defined.

(This variance formula is for the regression of the estimated correlated response on the FACSD through the origin only.)

C H A P T E R F O U R

NON-GENETIC EFFECTS AND THE EFFECT OF INBREEDING

4.1 Introduction

After preliminary analyses it was decided not to include lustre grade, handle grade and scoured colour grade in any further evaluation as there were insufficient observations to obtain accurate results.

4.2 The Effect of Dam Age and Birth/Rearing Rank

For the analysis of ewe hogget and ewe average lifetime performance traits, dam age and birth/rearing rank were combined to give four classes (see section 3.2.1). In the solution of the mixed-model equations (MME) the first class was set equal to zero, consequently the estimates for the remaining three classes are relative to individuals with 3, 4 or 5 year old dams and being born as singles and reared as singles.

The effects of these classes on ewe hogget traits are given in Table 4.1. As expected, dam age and birth/rearing rank have little effect on the ewe average lifetime performance traits (see Table 4.3).

For the ram hogget data dam age and birth rank were not considered because of the small numbers recorded. Consequently, only the effect of being reared as a twin relative to being reared as a single is shown in Table 4.2.

TABLE 4.1: THE EFFECT OF DAM AGE AND BIRTH/REARING RANK ON THE PERFORMANCE OF EWE HOGGETS

Trait	G ₁	G ₂	G ₃	G ₄
WWe	0	-2.41 kg	-1.88 kg	-4.57 kg
LWe	0	-1.94 kg	-1.98 kg	-2.28 kg
GFWe	0	-0.15 kg	-0.15 kg	-0.17 kg
We	0	-0.10 kg	-0.07 kg	-0.10 kg
QNe	0	-0.24	-0.80	-0.51
CHGe	0	0.00	-0.49	-0.37
SLe	0	-0.16 cm	+0.18 cm	+0.62 cm
Ye	0	+0.80%	+1.68%	+1.07%
MFDe	0	-0.40 μ	-1.06 μ	+0.35 μ
SFDe	0	+0.02 μ	-0.19 μ	+0.30 μ
FCe	0	-0.14	-0.23	+0.25

G₁ = single birth/rearing rank; dam age = 3, 4 or 5 years.

G₂ = single birth/rearing rank; dam age = 2 years.

G₃ = twin birth, single rearing rank; all dam ages.

G₄ = twin birth/rearing rank; all dam ages.

TABLE 4.2: THE EFFECT OF REARING RANK ON THE PERFORMANCE OF RAM HOGGETS

Trait	G ₁	G ₂
Wwr	0	-4.33 kg
LWr	0	-2.81 kg
GFWr	0	-0.21 kg
Wr	0	-0.19 kg
QNr	0	-0.11
CHGr	0	-0.24
SLr	0	+0.24 cm
TCNr	0	-0.80
CFr	0	-0.20
Yr	0	-0.55%
MFDr	0	+0.26 μ
FCr	0	+0.56

G₁ = single rearing rank.

G₂ = twin rearing rank.

TABLE 4.3: THE EFFECT OF DAM AGE AND BIRTH/REARING RANK ON EWE AVERAGE LIFETIME PERFORMANCE

Trait	G ₁	G ₂	G ₃	G ₄
LBa	0	-0.03	-0.23	-0.02
LRa	0	-0.09	-0.18	-0.07
LWa	0	-1.12 kg	-2.61 kg	-1.46 kg
GFWa	0	-0.15 kg	-0.15 kg	-0.11 kg
Wa	0	-0.09 kg	-0.01 kg	-0.04 kg
QNa	0	-0.17	-0.09	-0.35
CHGa	0	+0.09	+0.14	-0.11
SLa	0	+0.05 cm	+0.31 cm	+0.43 cm
Ya	0	+0.70%	+2.90%	+1.13%
MFDa	0	-0.16 μ	-0.55 μ	+0.43 μ

G₁ = single birth/rearing rank; dam age = 3, 4 or 5 years.

G₂ = single birth/rearing rank; dam age = 2 years.

G₃ = twin birth, single rearing rank; all dam ages.

G₄ = twin birth/rearing rank; all dam ages.

4.3 The Effect of Inbreeding on Performance

The average level of inbreeding in each of the three sub-flocks increased at a rate of approximately 0.5% per year (see Figure 4.1).

According to the approximate formula given by Wright (1931):

$$\Delta F = (1/8N_M) + (1/8N_F) ,$$

where ΔF = the increase in inbreeding per generation,

N_M = the number of males used per generation, and

N_F = the number of females used per generation,

the expected rate of increase is 0.4% per year. Wright's formula applies to populations where no selection is practised. Consequently, it could be expected that the two selection groups might have a faster rate of increase in inbreeding, particularly in the face cover group where previous studies have indicated a moderate to high heritability.

To reduce the rate of increase in inbreeding in the control group, random selection of rams within sire lines could be used. Alternatively a larger number of sires used per year, say 10, would reduce the rate of increase in inbreeding to about 0.2% per year. An associated advantage of decreasing the rate of inbreeding is the reduction in the opportunity for genetic drift to occur. Table 4.4 shows the number of sires represented by their sons in the following generation (e.g. in the control group only three of the sires used in 1969 were represented by their sons in the following generation). Thus, there was only one year (1974) when all sires in the control group were represented by sons in the next generation; in many years only two were represented.

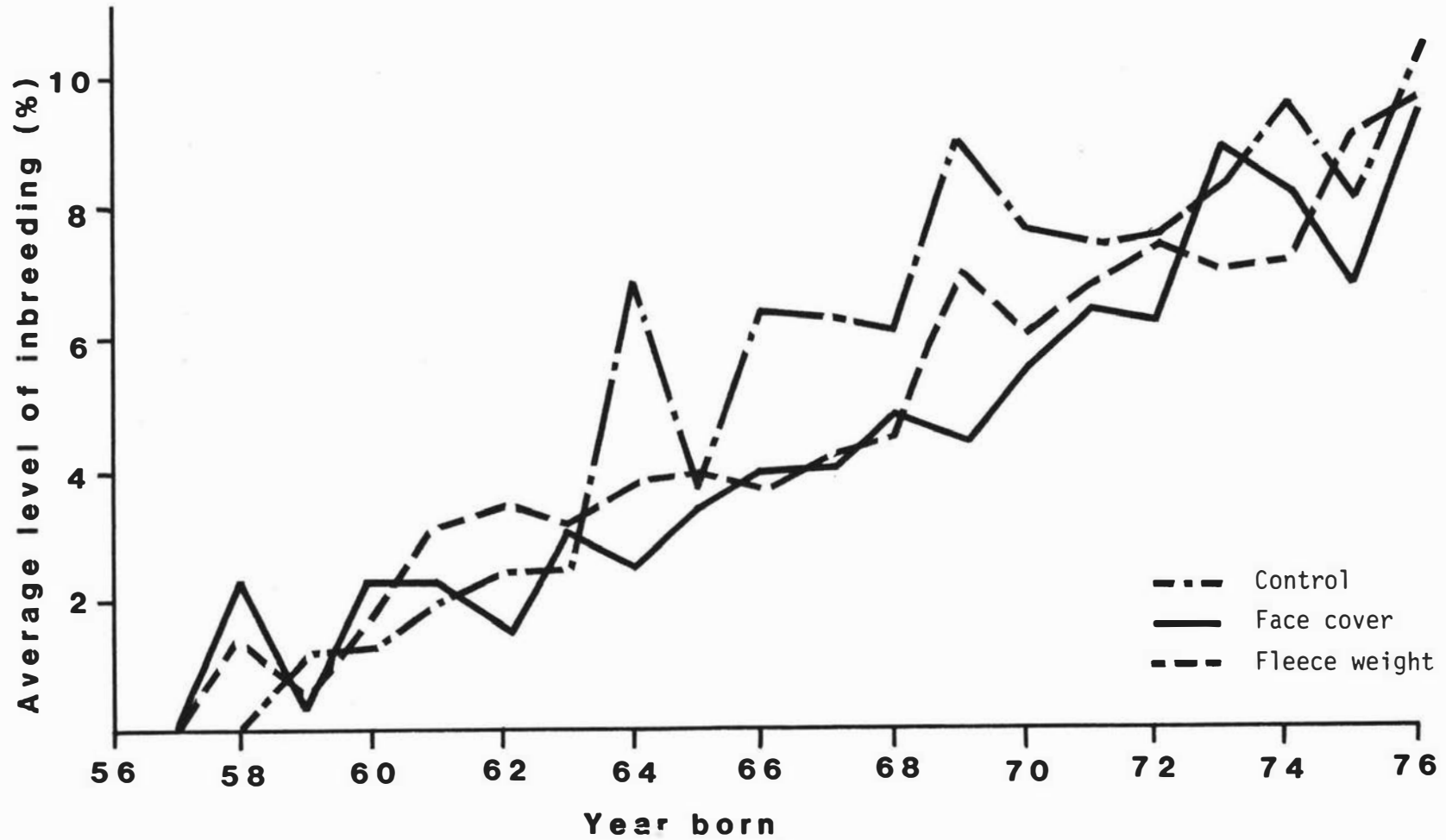


FIGURE 4.1: THE AVERAGE RATE OF INCREASE IN INBREEDING IN EACH OF THE THREE SUB-FLOCKS

TABLE 4.4: THE NUMBER OF SIRES REPRESENTED BY AT LEAST ONE SON
IN THE FOLLOWING GENERATION

Year	Control Group	Face-cover Group	Fleece-weight Group
1958	1	3	3
1959	2	3	2
1960	2	2	3
1961	2	4	2
1962	2	2	2
1963	2	3	3
1964	3	3	3
1965	2	2	2
1966	3	3	3
1967	2	3	3
1968	3	3	3
1969	3	2	3
1970	3	1	3
1971	2	3	3
1972	3	2	3
1973	3	3	2
1974	4	3	3

The effect of 10% increase in inbreeding on the traits recorded is shown in Table 4.5. Ten percent inbreeding was chosen as that was the average level of inbreeding reached in all 3 sub-flocks after 21 years of experimentation; thus, any trait markedly affected by a 10% increase in inbreeding could be easily identified. To simplify the interpretation of these values, the regression coefficients have been divided by the phenotypic standard deviation of the trait to which they refer. Thus, for example, the effect of an increase of 10% in inbreeding, in the ewe hogget fleece weight group, on greasy fleece weight was to reduce the performance by 0.113 of the phenotypic standard deviation (see Tables 5.1, 5.2 and 5.4 for the phenotypic standard deviations). Most traits suffered a depression in performance as inbreeding increased. The level of depression was variable throughout the three sub-flocks. In most cases ram hogget traits were affected to a greater degree than the ewe hogget traits.

In general, these results agree with those reviewed by Turner and Young (1969). The effect of 10% inbreeding does not greatly alter the performance in most traits. LW, GFW and W were the traits most affected. The loss in fleece mass was apparently due to decreases in body size, fibre diameter and, in some instances, staple length. No measurement of fibre density was available but it is generally accepted that inbreeding decreases the number of fibres per unit area. Inbreeding had a variable effect on lamb production. As expected, control and fleece weight group sheep with the highest inbreeding coefficients had lower lamb production. However, in the face cover group lamb production increased as inbreeding increased. This increase was unexpected since it is generally accepted that inbreeding causes an overall decrease in animal vitality.

TABLE 4.5: THE EFFECT OF 10% INBREEDING ON PERFORMANCE*

	Ewe Hoggets			Ram Hoggets			Ewe Average		
	Control	Face Cover	Fleece Weight	Control	Face Cover	Fleece Weight	Control	Face Cover	Fleece Weight
DOB	-0.004	0.121	-0.081	0.080	-0.037	-0.223	-	-	-
BW	-0.014	-0.216	-0.129	-0.066	-0.228	-0.162	-	-	-
WW	-0.101	-0.249	-0.111	-0.127	-0.146	-0.167	-	-	-
LW	-0.275	-0.251	-0.213	-0.325	-0.422	-0.381	-0.530	-0.304	-0.111
GFW	-0.104	-0.122	-0.113	-0.275	-0.458	-0.322	-0.389	-0.113	-0.235
W	-0.075	-0.100	-0.065	-0.302	-0.388	-0.360	-0.277	-0.156	-0.227
QN	-0.076	-0.028	-0.040	-0.149	0.099	0.110	-0.278	0.014	0.067
CHG	0.117	-0.062	-0.018	-0.178	0.070	0.009	-0.013	-0.548	-0.039
SL	0.034	-0.012	-0.047	-0.055	-0.327	-0.135	0.027	0.250	-0.338
TCN	-0.082	-0.045	-0.085	-0.172	-0.266	-0.007	-0.292	0.068	0.048
CF	-0.068	0	-0.070	-0.145	-0.058	0.032	-0.268	-0.095	0.211
Y	0.035	0.022	0.115	-0.149	0.096	-0.203	0.204	-0.159	-0.141
MFD	-0.166	-0.015	-0.039	-0.263	-0.305	-0.215	-0.150	-0.333	-0.100
SFD	-0.040	0.082	-0.107	-	-	-	-	-	-
PMF	-0.137	-0.060	-0.117	-	-	-	-	-	-
MI	-0.026	0.002	-0.052	-0.297	-0.102	0.229	-	-	-
FC	-0.099	0.075	0.019	0.082	-0.335	0.050	-	-	-
LB	-	-	-	-	-	-	-0.027	0.194	-0.281
LR	-	-	-	-	-	-	-0.027	0.026	-0.265

* Performance is in terms of standard deviations.
 (For example, the effect of 10% inbreeding on greasy fleece weight, in the ram hogget control group, was to decrease performance by 0.275 of a standard deviation. Standard deviations are in Tables 5.1, 5.2 and 5.4.)

CHAPTER FIVE

PHENOTYPIC AND GENETIC CORRELATIONS, HERITABILITIES AND
PHENOTYPIC STANDARD DEVIATIONS5.1 Phenotypic Standard Deviations

The phenotypic standard deviations presented in Tables 5.1, 5.2 and 5.4 were derived from the error mean squares obtained by applying the linear model given in section 3.2.3. For the hogget traits there was little difference between ewe and ram estimates, although the ram body weight and fleece weight traits appear to have slightly higher values. This is possibly due to the greater magnitude of the ram hogget performance in these traits.

The ewe average lifetime performance traits generally showed less variability than the equivalent ewe hogget traits (see Tables 5.1 and 5.4). Ewe average live weight was the only trait to show slightly greater variability than the corresponding ewe hogget trait. Ewe average GFW and W showed similar variability, whilst ewe average QN, CHG, SL, TCN, CF, Y and MFD all expressed less variability, than corresponding ewe hogget traits. The above results were not unexpected, since although the variability of any particular trait at each ewe age may be greater than the variability of the corresponding ewe hogget measurement, the variance of the average will be less than the variability shown at each ewe age, because the repeatabilities between the 4 ewe records will be less than one.

TABLE 5.1: PHENOTYPIC AND GENETIC CORRELATIONS AND PHENOTYPIC STANDARD DEVIATIONS FROM THE EWE HOGGET DATA

	DOB	BW(+)	WW	LW	GFW	W	QN	CHG	SL
DOB	9.30	0.24±0.39	-0.18±0.19	-0.08±0.10	-0.52±0.27	-0.59±0.31	0.35±0.19	0.40±0.17	-0.90±0.73
	8.78	0.46±0.36	*	-0.02±0.15	0.03±0.06	-0.09±0.09	0.35±0.15	-0.44±0.19	-0.74±0.31
	9.45	-0.37±0.34	-0.48±0.25	-0.16±0.07	-0.21±0.10	-0.23±0.13	0.23±0.09	0.49±0.15	-0.38±0.14
BW	-0.01	0.72	0.64±0.24	0.06±0.35	-0.21±0.42	-0.03±0.42	0.14±0.36	0.09±0.34	-0.22±0.55
	0.09	0.74	-0.14±0.98	-0.20±0.84	0.21±0.33	0.15±0.33	0.50±0.31	0.46±0.37	-0.30±0.34
	-0.01	0.70	0.49±0.34	0.67±0.26	0.56±0.32	0.56±0.37	0.50±0.35	0.74±0.28	-0.28±0.36
WW	-0.41	0.39	3.36	0.74±0.39	0.13±0.14	0.27±0.19	-0.37±0.16	-0.50±0.20	0.55±0.43
	-0.33	0.39	3.41	*	*	*	*	*	*
	-0.45	0.30	3.25	0.81±0.37	0.57±0.29	0.56±0.31	0.04±0.33	-0.13±0.05	0.00±0.03
LW	-0.22	0.25	0.52	4.54	0.64±0.37	0.74±0.40	0.02±0.02	-0.07±0.03	0.77±0.64
	-0.09	0.33	0.61	4.38	0.89±1.03	0.75±0.87	-0.18±0.19	0.42±0.45	0.49±0.56
	-0.20	0.20	0.58	4.18	0.64±0.27	0.47±0.25	0.47±0.14	0.00±0.01	-0.20±0.06
GFW	-0.18	0.20	0.35	0.47	0.48	1.00±0.68	-0.43±0.24	-0.03±0.05	0.58±0.62
	-0.18	0.18	0.39	0.55	0.49	0.96±0.82	-0.07±0.09	0.39±0.17	0.35±0.31
	-0.19	0.21	0.42	0.54	0.53	1.00±0.57	-0.09±0.08	-0.17±0.05	0.45±0.28
W	-0.19	0.17	0.32	0.41	0.94	0.40	-0.52±0.30	0.04±0.05	0.85±0.85
	-0.20	0.14	0.37	0.50	0.97	0.40	-0.29±0.16	0.28±0.12	0.58±0.31
	-0.20	0.17	0.39	0.49	0.95	0.46	-0.26±0.17	-0.25±0.09	0.45±0.28
QN	0.22	0.01	-0.07	-0.05	-0.23	-0.33	1.72	0.53±0.26	-0.80±0.80
	0.10	0.06	-0.08	-0.07	-0.26	-0.35	1.80	0.42±0.23	-0.93±0.41
	0.10	0.04	-0.07	-0.02	-0.22	-0.33	1.76	0.70±0.26	-0.37±0.22
CHG	0.06	0.06	-0.04	-0.02	0.06	0.05	0.26	1.11	-0.78±0.62
	-0.02	0.08	-0.02	0.06	0.07	0.06	0.37	1.13	-0.06±0.05
	0.08	0.07	0.04	0.07	0.06	0.01	0.39	1.11	-0.41±0.15
SL	-0.10	0.08	0.03	0.18	0.49	0.53	-0.58	-0.14	1.74
	-0.13	-0.04	0.16	0.26	0.50	0.55	-0.53	-0.09	1.69
	-0.12	-0.06	0.10	0.15	0.40	0.46	-0.54	-0.15	1.71
TCN	0.14	0.09	-0.01	0.04	0.08	-0.01	0.62	0.40	-0.12
	0.03	0.03	-0.01	0.08	-0.01	-0.07	0.63	0.44	-0.11
	0.07	0.09	0.01	0.04	0.02	-0.08	0.66	0.44	-0.17
CF	0.17	0.02	-0.03	-0.07	-0.23	-0.32	0.80	0.32	-0.64
	0.10	0.04	-0.09	-0.07	-0.26	-0.34	0.79	0.39	-0.58
	0.13	0.10	-0.05	-0.05	-0.19	-0.30	0.79	0.39	-0.61
Y	-0.08	-0.03	0.01	-0.03	0.13	0.45	-0.39	0.01	0.29
	-0.15	-0.10	0.03	-0.04	0.15	0.39	-0.43	-0.04	0.36
	-0.08	-0.05	0.06	0.04	0.16	0.46	-0.41	-0.11	0.33
MFD	-0.31	0.01	0.17	0.21	0.50	0.52	-0.33	-0.02	0.37
	-0.16	-0.03	0.21	0.27	0.56	0.59	-0.42	-0.03	0.51
	-0.14	-0.08	0.12	0.19	0.37	0.42	-0.35	-0.06	0.40
SFD	-0.23	-0.14	0.80	0.06	0.13	0.11	-0.20	-0.16	0.15
	-0.11	-0.14	0.09	0.07	0.15	0.16	-0.20	-0.06	0.10
	-0.10	-0.07	0.02	0.03	0.03	0.02	-0.07	-0.03	0.02
PMF	-0.03	-0.06	0.00	0.02	0.09	0.11	-0.16	-0.15	0.10
	-0.01	-0.11	0.02	0.03	0.14	0.13	-0.17	-0.11	0.11
	-0.06	0.03	0.07	0.12	0.14	0.16	-0.13	-0.12	0.10
MI	-0.03	-0.05	0.06	-0.02	-0.03	-0.03	-0.02	-0.16	0.10
	0.01	-0.14	0.03	-0.04	0.05	0.03	-0.10	-0.15	0.12
	0.00	-0.21	-0.13	-0.17	-0.06	-0.01	-0.07	-0.08	0.05
FC	0.00	0.09	0.09	0.23	0.09	0.07	-0.03	0.08	0.12
	-0.01	0.15	0.14	0.19	0.15	0.16	-0.11	0.00	0.18
	-0.08	0.03	0.15	0.20	0.14	0.11	-0.07	-0.02	0.15

Diagonal figures = phenotypic standard deviations; Genetic correlations above diagonal; Phenotypic correlations below diagonal.

Estimates are arranged in descending order of: control group, face-cover group, fleece weight group, respectively.

TABLE 5.1 (continued)

TCN(+)	CF(+)	Y	MFD	SFD	PMF(+)	MI(+)	FC	
0.06±0.38	0.32±0.36	-0.96±1.66	0.05±0.06	-0.36±0.19	*	#	0.23±0.11	DOB
0.08±0.35	0.52±0.32	-0.47±0.20	-0.78±0.38	0.54±0.70	-0.23±0.31	0.23±0.39	*	
0.03±0.28	0.21±0.29	-0.10±0.13	0.02±0.04	-0.22±0.08	0.37±0.24	0.23±0.40	-0.49±0.22	
0.13±0.42	0.21±0.37	#	-0.14±0.30	-0.08±0.33	*	#	-0.25±0.40	BW
0.22±0.37	0.41±0.38	-0.16±0.32	-0.16±0.44	-0.45±0.95	-0.18±0.36	0.14±0.45	*	
0.71±0.35	0.43±0.38	-0.12±0.66	-0.21±0.33	-0.28±0.29	0.39±0.34	-0.17±0.49	0.00±0.46	
-0.55±0.34	-0.59±0.33	#	-0.09±0.03	0.29±0.12	*	#	0.45±0.20	WW
*	*	*	*	*	*	0.16±0.51	*	
0.14±0.32	0.05±0.35	-0.54±0.55	0.17±0.09	0.30±0.11	0.48±0.27	0.51±0.71	-0.15±0.08	
-0.16±0.39	-0.47±0.36	#	0.21±0.11	0.37±0.15	*	#	0.03±0.07	LW
0.34±0.68	-0.07±0.71	-0.33±0.34	0.28±0.39	-0.05±0.19	0.73±0.68	-0.12±0.94	*	
0.48±0.24	0.49±0.27	#	-0.12±0.03	0.09±0.03	0.35±0.21	0.11±0.38	-0.38±0.15	
-0.42±0.44	-0.66±0.34	0.36±0.66	0.82±0.39	0.52±0.24	*	0.04±2.29	0.07±0.04	GFW
0.23±0.36	-0.02±0.37	0.19±0.09	0.34±0.29	0.12±0.21	0.27±0.28	0.09±0.36	*	
-0.13±0.35	-0.31±0.35	-0.40±0.40	0.42±0.20	0.39±0.13	0.71±0.20	0.33±0.38	-0.58±0.25	
-0.30±0.43	-0.66±0.32	0.42±0.93	0.82±0.40	0.57±0.26	*	0.11±2.50	0.12±0.06	W
0.10±0.37	-0.26±0.34	0.46±0.23	0.45±0.33	0.05±0.15	0.34±0.27	0.02±0.36	*	
-0.37±0.39	-0.59±0.35	-0.31±0.46	0.59±0.29	0.47±0.17	0.82±0.20	0.31±0.40	-0.75±0.35	
0.90±0.16	1.00±0.06	-0.95±1.71	-0.64±0.28	-0.55±0.25	*	#	0.19±0.08	QN
0.35±0.28	0.78±0.13	-0.79±0.32	-0.49±0.28	0.13±0.20	-0.15±0.28	0.30±0.39	*	
0.94±0.10	0.96±0.06	#	-0.58±0.22	-0.40±0.13	-0.21±0.22	-0.15±0.38	-0.12±0.07	
0.54±0.34	0.54±0.36	0.38±0.66	-0.29±0.10	-0.62±0.26	*	#	0.39±0.18	CHG
0.31±0.36	0.08±0.42	-0.22±0.09	0.20±0.09	0.83±1.07	-0.38±0.31	0.07±0.48	*	
0.54±0.20	0.63±0.20	-0.53±0.53	-0.22±0.06	-0.40±0.11	-0.17±0.22	-0.18±0.37	0.10±0.04	
-0.35±0.70	-0.68±0.22	#	0.79±0.66	0.75±0.60	*	#	-0.48±0.37	SL
-0.09±0.34	-0.64±0.21	0.95±0.38	0.82±0.46	0.64±0.84	0.18±0.28	-0.12±0.44	*	
-0.10±0.32	-0.54±0.24	0.53±0.62	0.43±0.19	0.28±0.09	-0.01±0.25	-0.39±0.51	-0.25±0.11	
2.81	0.93±0.10	0.50±1.10	-0.43±0.28	-0.41±0.32	*	na	0.29±0.42	TCN
3.12	0.81±0.11	-0.34±0.29	-0.37±0.37	0.12±0.62	-0.06±0.31	na	*	
3.07	0.89±0.07	#	-0.50±0.24	-0.34±0.25	-0.29±0.24	na	-0.27±0.39	
0.81	0.73	-0.46±0.64	-0.58±0.23	-0.50±0.31	*	na	0.16±0.43	CF
0.86	0.75	-0.76±0.21	-0.67±0.28	-0.07±0.60	-0.15±0.30	na	*	
0.87	0.71	#	-0.63±0.21	-0.41±0.27	-0.39±0.26	na	-0.12±0.42	
-0.24	-0.36	4.31	0.27±0.50	0.50±0.86	*	0.24±2.37	0.35±0.59	Y
-0.25	-0.40	3.72	0.50±0.27	-0.23±0.29	0.34±0.28	-0.28±0.41	*	
-0.29	-0.40	4.33	0.96±0.99	0.57±0.57	0.60±0.44	-0.19±0.63	-0.65±0.68	
-0.22	-0.38	0.21	2.71	0.66±0.27	*	#	-0.32±0.12	MFD
-0.21	-0.43	0.32	2.67	0.47±0.75	-0.03±0.31	-0.06±0.64	*	
-0.20	-0.35	0.28	2.81	0.41±0.15	0.38±0.20	0.32±0.36	-0.07±0.03	
-0.16	-0.20	-0.02	0.32	0.99	*	0.03±1.93	-0.05±0.03	SFD
-0.17	-0.19	0.08	0.39	0.98	0.02±0.80	0.64±0.42	*	
-0.08	-0.08	-0.02	0.28	1.03	0.23±0.20	0.03±0.34	-0.11±0.07	
-0.18	-0.18	0.11	0.22	0.24	6.43	#	*	PMF
-0.12	-0.16	0.04	0.23	0.16	8.05	0.31±0.33	*	
-0.16	-0.19	0.10	0.27	0.17	6.94	0.25±0.32	-0.44±0.27	
na	na	-0.03	0.04	0.14	0.32	6.10	#	MI
na	na	-0.08	0.11	0.22	0.29	10.28	*	
na	na	0.14	0.05	0.11	0.23	5.98	-0.73±0.57	
0.07	-0.02	-0.03	0.00	-0.04	-0.05	0.00	2.03	FC
-0.01	-0.10	0.09	0.12	-0.17	0.02	-0.05	1.86	
0.02	-0.07	-0.05	0.07	-0.09	-0.03	0.02	2.10	

* = negative sire variance component. # = estimate outside of theoretical bounds.

na = not available. + = standard error calculated using the method of Tallis (1959).

TABLE 5.2: PHENOTYPIC AND GENETIC CORRELATIONS AND PHENOTYPIC STANDARD DEVIATIONS FROM THE RAM HOGGET DATA

	DOB	BW(+)	WW	LW(+)	GFW	W	QN	CHG
DOB	8.52 9.51 8.94	na * 0.80±0.38	na -0.48±0.45 *	na 0.10±0.81 -0.24±0.34	na 0.66±0.76 0.34±0.21	na 0.39±0.32 0.35±0.18	na -0.15±0.07 0.26±0.11	na 0.22±0.12 -0.57±0.25
BW	0.03 0.01 0.18	0.76 0.79 0.74	na * *	na * 0.47±0.27	na * 0.53±0.48	na * 0.36±0.45	na * 0.06±0.34	na * -0.20±0.45
WW	-0.38 -0.32 -0.35	0.39 0.48 0.37	3.85 3.70 3.78	na 0.60±0.37 *	na # *	na # *	na -0.64±0.32 *	na -0.56±0.29 *
LW	-0.30 -0.06 -0.13	0.25 0.35 0.32	0.50 0.54 0.56	5.36 5.12 4.73	na 0.59±0.50 0.49±0.32	na 0.74±0.44 0.45±0.32	na -0.71±0.34 0.12±0.32	na -0.22±0.39 0.33±0.49
GFW	-0.22 -0.07 -0.14	0.20 0.07 0.25	0.21 0.20 0.37	0.52 0.44 0.53	0.51 0.59 0.59	na 0.84±1.88 1.00±1.09	na # -0.24±0.17	na -0.36±0.40 -0.16±0.10
W	-0.19 -0.08 -0.16	0.23 0.04 0.21	0.24 0.18 0.35	0.43 0.42 0.48	0.92 0.95 0.94	0.43 0.49 0.50	na # -0.36±0.21	na -0.30±0.22 -0.21±0.11
QN	-0.07 0.03 0.10	0.02 0.11 0.13	0.04 -0.01 0.10	0.05 -0.08 0.10	-0.05 -0.26 -0.11	-0.16 -0.38 -0.21	1.68 1.82 1.64	na 0.64±0.25 0.57±0.29
CHG	-0.04 -0.02 0.09	-0.01 -0.02 0.07	-0.04 -0.09 -0.05	0.06 0.08 -0.03	0.16 0.18 0.00	0.13 0.14 -0.02	0.13 0.26 0.36	0.90 1.15 1.07
SL	0.02 -0.03 -0.06	0.07 -0.12 -0.09	-0.10 0.02 -0.10	0.19 0.21 0.03	0.40 0.51 0.29	0.42 0.58 0.34	-0.31 -0.52 -0.55	0.12 0.06 -0.15
TCN	-0.03 0.02 0.10	0.12 0.10 0.08	0.02 -0.01 0.08	0.18 0.12 0.09	0.27 0.09 0.08	0.17 -0.03 0.00	0.66 0.66 0.65	0.29 0.51 0.40
CF	-0.03 0.03 0.11	0.07 0.14 0.12	0.09 0.00 0.11	0.03 -0.01 0.05	-0.02 -0.18 -0.08	-0.11 -0.31 -0.16	0.77 0.81 0.77	0.17 0.37 0.37
Y	0.02 -0.07 -0.11	0.14 -0.07 -0.02	0.12 0.01 0.04	-0.09 0.11 0.03	0.05 0.23 0.17	0.43 0.51 0.49	-0.35 -0.49 -0.32	-0.06 -0.05 -0.06
MFD	-0.18 -0.09 -0.17	-0.12 -0.08 0.00	-0.03 0.04 0.07	0.17 0.21 0.21	0.43 0.55 0.51	0.41 0.62 0.55	-0.10 -0.51 -0.35	0.14 0.02 -0.05
MI	0.24 0.01 0.08	0.14 -0.11 -0.04	-0.15 0.18 0.00	na na na	-0.23 0.09 -0.03	-0.17 0.11 0.03	-0.12 -0.16 -0.11	0.17 -0.18 -0.15
FC	0.03 0.01 -0.06	0.10 0.09 -0.08	0.19 0.14 0.06	0.17 0.26 0.11	0.12 0.05 0.06	0.06 0.05 0.05	-0.01 0.01 -0.05	0.06 0.14 0.00

See Table 5.1 for legend.

TABLE 5.2 (continued)

SL	TCN(+)	CF(+)	Y	MFD(+)	MI(+)	FC	
na 0.17±0.09 -0.11±0.06	na -0.04±0.58 0.15±0.35	na -0.18±0.49 0.16±0.33	na -0.18±0.11 0.28±0.14	na -0.06±0.43 -0.14±0.50	na 0.19±0.76 #	na 0.32±0.24 -0.21±0.09	DOB
na * -0.01±0.36	na * 0.06±0.33	na * 0.11±0.32	na * -0.32±0.50	na * -0.06±0.43	na * -0.13±0.43	na * -0.08±0.34	BW
na 0.21±0.10 *	na -0.64±0.62 *	na -0.50±0.51 *	na 0.81±0.50 *	na 0.45±0.42 *	na 0.32±0.55 0.61 3.20	na -0.70±0.50 *	WW
na 0.21±0.37 0.47±0.30	na 0.03±0.46 0.76±0.30	na -0.17±0.39 0.41±0.30	na 0.46±0.38 0.68±1.96	na 0.14±0.35 -0.22±0.50	na -0.71±1.04 -0.04±0.44	na 0.57±0.58 0.11±0.30	LW
na 0.56±0.78 0.44±0.35	na -0.37±0.85 0.26±0.54	na -0.66±0.55 0.21±0.54	na 0.47±0.57 0.95±0.68	na 0.86±0.00 0.21±0.66	na -0.18±0.89 0.31±0.42	na -0.58±0.70 -0.07±0.04	GFW
na 0.78±0.73 0.53±0.34	na -0.42±0.67 0.22±0.49	na -0.79±0.37 0.11±0.48	na 0.90±0.79 0.94±0.69	na 1.00±0.00 0.15±0.61	na 0.01±0.72 0.24±0.43	na -0.36±0.32 0.00±0.01	W
na # -0.65±0.30	na 0.60±0.22 0.94±0.09	na 0.96±0.06 0.91±0.07	na -0.63±0.33 -0.56±0.31	na -0.63±0.20 -0.57±0.32	na -0.66±0.56 -0.06±0.30	na 0.21±0.13 0.19±0.06	QN
na -0.37±0.12 -0.45±0.21	na 0.78±0.21 0.70±0.26	na 0.70±0.23 0.75±0.23	na -0.14±0.06 -0.37±0.20	na -0.46±0.30 -0.29±0.56	na -0.85±0.45 -0.48±0.40	na 0.73±0.48 -0.35±0.15	CHG
1.46 1.53 1.56	na -0.59±0.34 -0.54±0.27	na -0.92±0.13 -0.73±0.15	na 0.75±0.36 0.60±0.34	na 0.49±0.23 0.45±0.36	na -0.07±1.60 -0.43±0.38	na -0.46±0.29 0.37±0.13	SL
0.10 -0.10 -0.24	2.85 2.97 2.76	na 0.87±0.07 0.97±0.03	na -0.21±0.37 0.11±0.92	na -0.72±0.28 #	na # -0.37±0.32	na # -0.38±0.29	TCN
-0.49 -0.57 -0.65	0.80 0.85 0.87	0.62 0.69 0.63	na -0.47±0.26 -0.32±0.73	na -0.73±0.18 #	na # -0.22±0.34	na 0.88±0.57 -0.39±0.27	CF
0.16 0.40 0.26	-0.21 -0.33 -0.18	-0.27 -0.48 -0.24	4.71 4.37 4.14	na 0.58±0.23 0.65±1.23	na 0.34±0.73 -0.03±0.47	na 0.11±0.08 0.30±0.14	Y
0.18 0.54 0.36	0.06 -0.25 -0.27	-0.06 -0.48 -0.38	0.07 0.45 0.27	2.09 2.39 2.05	na 0.33±0.71 0.01±0.40	na -0.53±0.54 0.86±0.40	MFD
0.20 0.10 0.11	na na na	na na na	0.02 0.07 0.17	na na na	10.42 6.15 6.60	na 0.08±0.80 0.10±0.33	MI
-0.04 0.13 0.08	0.11 0.12 -0.01	0.11 0.05 -0.05	-0.13 0.02 0.00	0.02 0.06 0.16	0.07 0.08 -0.09	2.20 1.73 2.00	FC

TABLE 5.3: GENETIC CORRELATIONS BETWEEN EWE HOGGET AND EWE AVERAGE LIFETIME PERFORMANCE TRAITS

	LBa	LRa	LWa	GFWa	Wa	QNa
DOBe	-0.19±0.16	-0.01±0.07	0.10±0.07	#	0.70±0.74	-0.10±0.12
	*	*	0.57±0.42	0.43 0.23	0.29±0.16	0.15±0.10
BWe	0.53±0.50	0.43±0.37	0.02±0.07	-0.11±0.07	-0.06±0.04	0.06±0.06
	-0.53±0.37	-0.88±1.57	0.41±0.27	0.11±0.18	-0.20±0.19	0.81±0.60
WWe	*	*	-0.28±0.99	#	#	#
	*	*	*	*	*	*
LWe	0.29±0.21	0.41±0.74	0.88±0.49	0.07±0.17	0.24±0.26	0.12±0.08
	*	*	0.33±1.08	-0.46±0.94	-0.38±0.80	-0.65±1.31
GFWe	0.63±0.66	0.92±0.83	-0.68±0.45	0.42±0.29	0.44±0.31	-0.66±0.40
	0.84±0.75	0.78±1.50	0.41±0.48	0.05±0.29	0.22±0.34	-0.45±0.40
We	*	*	*	*	*	*
	1.00±1.19	0.91±0.96	0.66±0.83	0.71±0.64	0.69±0.63	-0.51±0.44
QNe	0.52±0.39	0.92±1.65	0.22±0.19	0.57±0.80	0.66±0.79	-0.90±0.71
	*	*	*	*	*	*
CHGe	0.90±1.33	-0.10±0.27	-0.33±0.46	1.00±1.39	1.00±1.52	-0.85±1.07
	0.30±0.23	0.70±1.27	0.41±0.27	0.51±0.80	0.65±0.86	-0.84±0.74
SLe	*	*	*	*	*	*
	#	#	#	#	#	#
TCNe	0.28±0.25	0.14±0.29	-0.13±0.09	0.64±0.73	-0.05±0.40	0.35±0.81
	*	*	-0.28±0.22	#	#	1.00±1.01
CFe	0.58±0.45	0.30±0.20	#	0.32±0.12	0.06±0.10	0.98±0.51
	0.04±0.08	0.14±0.28	0.10±0.07	-0.65±0.75	1.00±1.09	0.77±0.76
MFDe	*	*	-0.58±0.55	#	#	0.23±0.38
	-0.30±0.24	-0.43±0.29	0.99±0.47	0.40±0.16	0.31±0.14	0.71±0.33
SFDe	-0.42±0.51	-0.40±0.84	-0.05±0.11	-0.83±1.25	-0.22±0.72	-1.00±1.55
	*	*	#	0.72±0.96	0.77±1.06	0.03±0.55
PMFe	-0.73±0.60	-0.92±0.65	#	-0.94±0.45	-0.78±0.40	-0.39±0.29
	-0.34±0.57	-0.31±0.60	-0.20±0.58	0.19±0.74	-0.05±0.70	0.29±0.66
FCe	*	*	-0.07±0.63	-0.03±1.07	-0.17±1.83	#
	0.75±0.65	0.44±0.72	0.89±0.53	-0.37±0.34	-0.64±0.35	0.87±0.19
Ye	-0.54±0.59	-0.43±0.61	-0.14±0.60	0.22±0.84	-0.08±0.74	0.66±0.44
	*	*	-0.86±1.34	0.11±1.94	0.12±3.52	#
MFDDe	#	0.99±0.95	#	-0.05±0.40	-0.37±0.39	1.00±0.17
	*	*	*	*	*	*
PMFDe	*	*	0.75±0.51	0.96±0.50	#	#
	#	#	-0.54±0.41	-0.11±0.13	0.56±0.52	-0.44±0.42
FCDe	-0.25±0.17	-0.42±0.75	0.35±0.18	0.83±0.89	0.89±0.87	-0.80±0.63
	*	*	*	*	*	*
PMFDe	0.13±0.18	0.03±0.10	-0.57±0.31	0.48±0.26	0.80±0.46	-0.60±0.34
	-0.19±0.44	-0.53±1.47	0.27±0.58	#	#	#
FCDe	*	*	*	*	*	*
	#	-0.73±0.95	-0.08±0.11	0.48±0.59	0.07±0.11	-0.14±0.16
FCDe	0.13±0.93	0.53±1.06	-0.24±1.31	*	*	#
	*	*	*	*	*	*
FCDe	0.57±0.66	0.71±1.04	0.34±0.47	0.61±0.35	0.85±0.40	-0.96±0.29
	0.69±0.51	0.76±1.38	0.09±0.12	-0.23±0.22	-0.45±0.40	0.23±0.16
FCDe	*	*	#	#	-0.53±1.64	-0.54±1.68
	*	*	*	*	*	*

See Table 5.1 for legend.

TABLE 5.3 (continued)

CHGa	SLa	TCNa	CFa	Ya	MFDa	
-0.89±0.84	*	0.12±0.50	0.42±0.57	-0.33±0.22	0.43±0.29	DOBe
0.64±0.38	-0.42±0.29	#	#	*	-0.39±0.26	
0.58±0.40	-0.99±0.96	-0.73±0.59	-0.43±0.60	0.02±0.02	-0.33±0.23	
-0.33±0.27	*	0.68±0.40	0.73±0.50	-0.51±0.27	-0.10±0.07	BWe
#	#	*	*	*	0.91±3.02	
*	*	*	*	*	*	
-0.20±0.17	*	0.05±0.37	-0.21±0.42	0.20±0.09	-0.26±0.11	WWe
0.19±0.41	-0.28±0.59	*	*	*	0.86±1.76	
-0.74±0.47	0.63±0.59	-0.02±0.56	0.01±0.59	0.09±0.05	#	
-0.26±0.26	*	-0.02±0.55	-0.52±0.64	0.20±0.13	0.53±0.36	LWe
*	*	#	#	*	*	
-0.03±0.03	-0.55±0.65	-0.12±0.47	0.19±0.49	-0.21±0.21	0.37±0.33	
-0.09±0.07	*	-0.46±0.35	-0.70±0.33	0.37±0.22	0.80±0.41	GFWe
*	*	*	*	*	*	
#	1.02±1.49	*	*	0.11±0.16	#	
0.23±0.21	*	-0.48±0.38	-0.68±0.36	0.42±0.30	0.82±0.46	We
*	*	*	*	*	*	
#	#	*	*	*	*	
#	*	0.73±0.32	0.51±0.43	-0.80±0.69	-0.41±0.36	QNe
-0.32±0.24	-0.80±0.75	0.34±1.03	0.83±0.52	*	0.05±0.31	
0.31±0.16	-0.25±0.38	0.83±0.21	0.81±0.20	-0.64±0.31	-0.19±0.18	
0.09±0.34	*	0.11±0.69	0.24±0.79	-0.82±0.61	-0.18±0.13	CHGe
-0.48±0.43	-0.09±0.18	0.06±1.20	0.08±1.19	*	0.63±0.59	
0.78±0.37	-0.37±0.37	0.52±0.31	0.53±0.32	-0.23±0.09	0.22±0.08	
-0.26±0.34	*	-1.00±0.75	#	0.66±0.84	0.56±0.65	SLe
0.02±0.16	#	#	0.41±1.94	*	#	
0.36±0.18	1.00±1.04	0.29±0.55	-0.13±0.52	0.41±0.27	-0.36±0.18	
-0.56±0.76	*	0.50±0.38	0.24±0.56	-0.42±0.46	-0.74±0.35	TCNe
0.12±0.55	0.30±0.54	#	0.91±0.00	*	-0.41±0.50	
0.02±0.39	0.13±0.54	1.00±0.18	0.78±0.22	-0.84±0.32	-0.27±0.34	
-0.21±0.17	*	0.75±0.32	0.65±0.36	-0.48±0.41	-0.69±0.35	CFe
0.05±0.99	-0.24±0.77	0.95±0.91	#	*	0.51±1.38	
-0.19±0.44	-0.31±0.48	0.84±0.24	0.84±0.20	-0.91±0.31	-0.04±0.41	
*	*	*	*	*	*	Ye
-0.06±0.03	1.00±0.70	-0.34±0.75	#	*	0.85±0.62	
0.46±0.35	0.82±0.88	-0.59±0.70	#	#	0.78±0.61	
0.04±0.03	*	-0.39±0.33	-0.51±0.34	0.40±0.22	1.00±0.52	MFDe
*	*	*	*	*	*	
-0.18±0.12	0.69±0.61	-0.28±0.38	-0.42±0.37	0.70±0.38	#	
-1.00±2.36	*	0.43±0.74	-0.42±0.65	0.99±2.09	0.72±1.58	SFDe
*	*	*	*	*	*	
-0.90±1.13	#	0.12±0.58	0.50±0.61	-0.91±1.10	0.45±0.62	
#	*	-0.55±0.68	-1.00±0.78	#	#	PMFe
*	*	#	1.06±5.30	*	*	
-0.10±0.45	0.71±0.70	-1.00±0.33	-1.01±0.34	0.59±0.37	0.92±0.51	
-0.58±0.48	*	-0.17±0.47	-0.44±0.53	-0.45±0.21	-0.17±0.08	FCe
0.25±0.77	-0.35±1.13	#	#	*	#	
*	*	*	*	*	*	

TABLE 5.4: PHENOTYPIC CORRELATIONS BETWEEN EWE HOGGET AND EWE AVERAGE LIFETIME PERFORMANCE TRAITS AND PHENOTYPIC STANDARD DEVIATIONS FOR EWE AVERAGE LIFETIME PERFORMANCE TRAITS

	LBa	LRa	LWa	GFWa	Wa	QNa	CHGa	SLa	TCNa	CFa	Ya	MFDa
DOBe	-0.01	-0.02	0.08	0.07	0.07	0.15	0.24	0.08	0.28	0.19	0.06	-0.02
	-0.11	-0.08	0.05	-0.10	-0.09	-0.02	0.07	-0.05	0.03	0.05	0.01	0.01
	-0.03	-0.08	0.17	0.02	0.01	-0.08	0.03	0.03	-0.06	-0.04	-0.03	0.00
BWe	0.14	0.21	0.24	0.17	0.12	-0.02	0.03	0.09	0.05	0.00	-0.07	-0.08
	0.00	0.00	0.21	0.22	0.21	0.13	0.22	0.09	0.15	0.08	0.08	-0.03
	0.00	-0.03	0.22	0.14	0.12	-0.01	0.05	0.00	-0.01	-0.01	0.05	0.02
WWe	0.06	0.15	0.28	0.15	0.11	-0.04	-0.03	0.08	-0.05	-0.08	-0.02	-0.03
	0.24	0.20	0.35	0.32	0.26	0.08	0.11	0.16	0.20	0.10	-0.09	-0.01
	0.18	0.18	0.15	0.10	0.08	0.07	0.07	-0.02	0.04	0.04	0.00	-0.02
LWe	0.17	0.24	0.49	0.21	0.18	-0.03	-0.09	0.09	0.03	-0.03	0.00	0.07
	0.29	0.21	0.59	0.30	0.25	0.11	0.16	0.15	0.19	0.09	-0.03	0.02
	0.08	0.03	0.52	0.05	0.00	0.04	0.05	-0.09	-0.03	0.03	-0.11	0.03
GFWe	0.15	0.15	0.32	0.64	0.62	-0.31	0.10	0.39	-0.08	-0.28	0.28	0.37
	0.30	0.21	0.33	0.56	0.55	-0.17	0.17	0.34	-0.04	-0.18	0.21	0.30
	0.14	0.10	0.21	0.44	0.39	-0.15	-0.05	0.15	-0.09	-0.13	0.07	0.20
We	0.10	0.11	0.26	0.61	0.64	-0.40	0.13	0.43	-0.16	-0.36	0.40	0.40
	0.26	0.19	0.27	0.56	0.58	-0.24	0.15	0.38	-0.11	-0.25	0.30	0.36
	0.14	0.09	0.17	0.51	0.53	-0.32	0.01	0.26	-0.20	-0.27	0.29	0.32
QNe	-0.06	-0.07	0.02	-0.20	-0.33	0.69	0.01	-0.44	0.51	0.64	-0.49	-0.32
	0.02	0.02	0.05	-0.18	-0.23	0.64	0.24	-0.43	0.55	0.67	-0.22	-0.37
	-0.15	-0.16	0.04	-0.20	-0.27	0.66	0.18	-0.44	0.61	0.68	-0.29	-0.40
CHGe	-0.06	-0.04	0.00	0.10	0.07	0.12	0.26	-0.10	0.16	0.15	-0.02	0.02
	0.00	0.00	0.13	-0.01	-0.03	0.25	0.24	-0.12	0.27	0.28	-0.09	-0.06
	-0.05	-0.11	0.03	0.00	0.00	0.39	0.25	-0.25	0.32	0.37	0.00	-0.08
SLe	0.04	0.08	0.14	0.37	0.45	-0.49	0.02	0.61	-0.41	-0.44	0.41	0.23
	0.05	0.05	0.09	0.27	0.30	-0.39	-0.11	0.43	-0.22	-0.37	0.22	0.32
	0.04	0.03	-0.03	0.14	0.22	-0.38	0.02	0.48	-0.18	-0.36	0.30	0.23
TCNe	-0.02	0.01	0.04	0.01	-0.08	0.50	0.12	-0.11	0.59	0.53	-0.26	-0.34
	0.08	0.08	0.18	0.01	-0.06	0.50	0.27	-0.20	0.54	0.56	-0.25	-0.32
	-0.10	-0.14	-0.01	-0.14	-0.18	0.52	0.20	-0.29	0.57	0.58	-0.21	-0.34
CFe	-0.04	-0.05	-0.04	-0.21	-0.32	0.67	0.04	-0.43	0.53	0.67	-0.44	-0.40
	0.06	0.06	0.11	-0.11	-0.18	0.61	0.29	-0.38	0.56	0.66	-0.31	-0.42
	-0.10	-0.12	0.02	-0.17	-0.25	0.58	0.15	-0.47	0.54	0.64	-0.33	-0.36
Ye	-0.09	-0.08	-0.06	0.16	0.30	-0.43	0.14	0.31	-0.27	-0.39	0.52	0.25
	0.02	0.02	-0.14	0.18	0.28	-0.34	0.01	0.29	-0.25	-0.35	0.42	0.35
	0.04	-0.02	-0.04	0.30	0.43	-0.42	0.10	0.28	-0.29	-0.35	0.52	0.35
MFDe	0.12	0.14	0.13	0.37	0.41	-0.37	0.05	0.31	-0.23	-0.36	0.29	0.60
	0.12	0.12	0.08	0.31	0.34	-0.31	-0.02	0.36	-0.23	-0.35	0.24	0.58
	0.16	0.14	-0.04	0.25	0.32	-0.41	-0.23	0.26	-0.32	-0.36	0.30	0.64
SFDe	-0.03	-0.02	-0.05	0.12	0.10	-0.20	-0.18	0.08	-0.25	-0.25	0.00	0.27
	0.01	0.01	-0.09	0.03	0.03	-0.14	-0.17	0.16	-0.06	-0.13	0.01	0.13
	0.00	0.06	-0.08	0.08	0.05	0.07	-0.18	-0.05	0.05	0.07	-0.09	0.19
FCe	0.09	0.15	0.23	0.08	0.05	-0.04	-0.03	0.14	0.08	-0.01	-0.05	-0.04
	-0.03	-0.03	0.13	0.14	0.15	0.03	0.01	0.15	0.09	0.02	0.11	0.08
	0.00	0.00	0.06	-0.02	-0.03	-0.09	0.14	0.12	-0.03	-0.08	-0.02	-0.07
Pheno. Std Devn	0.37	0.37	4.96	0.54	0.47	1.45	0.75	1.47	2.02	0.41	3.38	2.20
	0.36	0.38	4.61	0.53	0.45	1.44	0.73	1.28	2.35	0.42	2.77	2.04
	0.32	0.34	5.04	0.51	0.44	1.49	0.76	1.42	1.89	0.38	3.06	2.20

Estimates are arranged in descending order of: control group, face-cover group, fleece weight group, respectively.

The two traits under direct selection, face-cover grade and hogget greasy fleece weight, do not appear to have undergone reduced variability in the corresponding selection flocks, compared with that exhibited by the control flock.

5.2 Phenotypic Correlations

Phenotypic correlations between ewe hogget traits, ram hogget traits and between ewe hogget and ewe average lifetime traits are presented in Tables 5.1, 5.2 and 5.4, respectively. In general there are few differences between the estimates derived from each sub-flock. Also there does not appear to be any effect of sex on the magnitude of correlations within the hogget traits.

Some of the hogget correlations warrant comment:

- (a) the moderately-sized phenotypic correlations between LW and GFW (0.44 to 0.55) are similar to two previous estimates derived from Romney ewe hogget data of 0.50 and 0.61 (Tripathy, 1966; Sumner, 1969). Hogget live weight and W are also moderately correlated (0.41 to 0.50). Hogget live weight and weaning weight show a moderate relationship (0.50 to 0.61); these estimates being slightly greater than the value of 0.49 derived from Romney data by Baker *et al.* (1979),
- (b) there is a very strong positive correlation between GFW and W (0.92 to 0.97). Mullaney *et al.* (1970) derived estimates between 0.85 and 0.93 for the same relationship in Merino, Corriedale and Polwarth sheep. Greasy fleece weight is

moderately associated with MFD and SL (0.37 to 0.56 and 0.29 to 0.51, respectively). These estimates are in good agreement with values presented by Tripathy (1966), 0.53 for GFW/MFD; Rae (1958b), 0.45 for GFW/SL and Sumner, 0.36 for GFW/SL from Romney ewe hoggets. Clean fleece weight shows a similar degree of relationship with MFD and SL,

- (c) quality number exhibits low/moderate negative correlations with SL, MFD and Y (-0.31 to -0.58, -0.10 to -0.51 and -0.32 to -0.49, respectively); strong positive correlations with TCN and CF (0.62 to 0.66 and 0.77 to 0.81, respectively) and a low/moderate positive association with CHG (0.13 to 0.39). These estimates are also similar to those derived by Rae (1958b), Tripathy (1966) and Sumner (1969). The strong association between QN and CF suggests that CF is the characteristic most emphasized when QN is assessed. Considering the negative associations between QN and SL and QN and MFD, it is not surprising to find a low negative correlation between QN and GFW (-0.05 to -0.26),
- (d) character grade is phenotypically unrelated to many of the measured traits; however, there are low/moderate, positive, correlations between CHG and TCN (0.29 to 0.51) and CHG and CF (0.17 to 0.39), and, as previously mentioned, CHG and QN,
- (e) staple length and MFD tend to be positively associated to a low/moderate degree (0.18 to 0.54), although only one of the six estimates falls below 0.36. Apart from the one low

value, the others are similar to an estimate of 0.48 derived from Romney ewe hogget data by Tripathy (1966),

- (f) generally, SFD appears to be poorly correlated with most traits. A low/moderate, positive, association is shown between SFD and MFD (0.28 to 0.39), i.e. as the MFD increases so does the variability of the diameter of the fibres,
- (g) there is a low phenotypic association between PMF and MI (0.23 to 0.32). However, the MI measurement tends to be affected more by large diameter medullated fibres, whereas PMF includes any medullated fibres observed through the projection microscope, and
- (h) face cover appears to be phenotypically unrelated to the other traits investigated. Shelton *et al.* (1954) presented significant correlations between FC and GFW and FC and W; woolly face-cover grades being associated with higher fleece mass. Although the equivalent correlations in this study are small (0.05 to 0.16), they all show an association of higher fleece mass with open face. Morley (1955) and Cockrem and Rae (1966) showed significant associations between open face and higher hogget live weight. This relationship is also found in this study but the correlation estimates are low (0.11 to 0.26).

The phenotypic correlations between ewe hogget and ewe average lifetime traits show some interesting associations:

- (a) LWe, GFWe, We, QNe, SLe, TCNe, CFe, Ye and MFDe are all relatively good indicators of how the ewe will perform in the corresponding traits later in life. However, CHGe is a poor indicator of CHGa. Thus, culling on the basis of hogget fleece character, as is often practiced by New Zealand farmers, will not guarantee a flock of mature ewes with fleeces of good character,

- (b) ewe hogget face-cover grade (FCe) is poorly related to mature ewe traits. This apparently poor association with lamb production is in contrast to most of the reported findings (see section 2.3). There are two possible reasons for the poor association. Firstly, the correlation involves two discrete traits, when in fact an assumption of the product-moment correlation approach is that the data must be continuous. Secondly, it seems likely from previous investigations (see section 2.3) that there is a non-linear relationship between FC and LB or LR, i.e. the very woolly-faced sheep (say grades 1 to 4) have poor lambing performance, but above grade 4 there may be little or no association with LB or LR. The only other available estimates of the phenotypic correlation between FCe and lamb production involve Merinos and were also very low (-0.09 to 0.05, Young *et al.* 1963),

- (c) GFWe is positively associated with LBa and LRa. Lewer (1978) in his review of literature listed the following phenotypic correlations between lambs weaned and GFW; -0.12, -0.01, -0.02, -0.08, -0.08, 0.03, 0.02, 0.03 and 0.04. From his own Perendale data Lewer (1978) estimated the following values; -0.11, -0.05, -0.17 and -0.09 at ewe ages of 2, 3 4 and 5 years, respectively. However it is a common observation that ewes rearing twins or triplets will produce less wool. Although some of the estimates reviewed by Lewer (1978) involve negative associations between ewe hogget GFW and lamb production, they were generally small and unlikely to be significantly different from zero,
- (d) WWe and LWe show small positive associations with LBa and LRa. These estimates are similar to those reviewed and derived by Ch'ang and Rae (1972).

5.3 Genetic Correlations

As stated in the statistical methods section, two techniques were used to derive standard errors (SE) for the genetic correlations. To enable a comparison of the two SE estimates a sample of the control ewe hogget genetic correlations is presented in Table 5.5.

The following pattern can be observed:

- (a) when the genetic correlation is near zero (e.g. LWe/QNe) the Tallis method provides a large estimate of the SE in comparison to the size of the correlation coefficient. The second method provides a much smaller estimate,

TABLE 5.5: A COMPARISON OF TWO METHODS OF DERIVING STANDARD ERRORS FOR GENETIC CORRELATIONS USING CONTROL EWE HOGGET INFORMATION

	LWe	GFWe	QNe	CHGe	Ye
LWe	-	0.64±0.24	0.02±0.35	-0.07±0.34	1.00±1.10
	-	±0.37	±0.02	±0.03	±1.73
GFWe	-	-	-0.43±0.33	-0.03±0.36	0.36±0.88
	-	-	±0.24	±0.05	±0.66
We	0.74±0.24	1.00±0.02	-0.52±0.31	0.04±0.37	0.42±0.64
	±0.40	±0.68	±0.30	±0.0	±0.93
QNe	-	-	-	0.53±0.29	-0.95±0.00
	-	-	-	±0.26	±1.71
CHGe	-	-	-	-	0.38±0.91
	-	-	-	-	±0.66
SLe	0.77±0.49	0.58±0.39	-0.80±0.17	-0.78±0.55	#
	±0.64	±0.62	±0.80	±0.62	
MFDe	0.21±0.27	0.82±0.14	-0.64±0.21	-0.29±0.27	0.27±0.65
	±0.11	±0.39	±0.28	±0.10	±0.50
SFDe	0.37±0.31	0.52±0.31	-0.55±0.29	-0.62±0.28	0.50±0.93
	±0.15	±0.24	±0.25	±0.26	±0.86
FCe	0.03±0.36	0.07±0.39	0.19±0.38	0.39±0.34	0.35±1.00
	±0.07	0.04	±0.08	±0.18	±0.59

Correlation estimate outside of theoretical bounds.

Upper standard error (SE) derived using the method of Tallis (1959).

Lower SE derived as stated in section 3.2.5.

- (b) when the genetic correlation is near +1 or -1 and the estimate involves traits with h^2 greater than about 0.2 (e.g. GFW/W), Tallis's approach gives a very small estimate of the SE whilst the other method provides a much larger estimate,
- (c) when the genetic correlation is near +1 or -1 with at least one of the traits having an h^2 of less than about 0.2 (e.g. LW/Y) then both SE estimates are large, and
- (d) when the genetic correlation falls into the range of -0.2 to -0.8 or +0.2 to +0.8 the two methods supply similar SE estimates.

It is not clear as to why these differences in SE estimates have occurred. Two possible reasons are, firstly, Tallis (1959) assumes an equal number of progeny recorded per sire, whereas in this study the number of progeny per sire varies between 2 and 15. Secondly, as shown in section 3.2.5, the second approach to estimating standard errors did not include three covariance terms, because of the difficulty in estimating them. The formula of Tallis (1959) included these covariances.

On the basis of the preceding discussion the second approach to calculating the SE estimates was favoured over Tallis's method.

Genetic correlation estimates, and their SEs, between ewe hogget traits, ram hogget traits and between ewe hogget and ewe average lifetime performance traits are given in Tables 5.1, 5.2 and 5.3, respectively.

The estimates are quite variable and at best they should only be grouped broadly as suggested by Brown and Turner (1968):

-0.6 and lower	high negative,
-0.4 to -0.6	moderage negative,
-0.2 to -0.4	low negative, and
-0.2 to 0	negligible,

this same pattern is then repeated for positive correlations.

Estimates of the genetic correlations amongst control ram hogget traits were not calculated due to the small number of observations per sire.

For the ewe and ram hogget correlations the estimates are essentially similar but some differences are not covered by the SEs. Within each hogget sex there are often differences between the three sub-flock genetic correlation estimates.

Some of the more important genetic correlations amongst the hogget traits are:

- (a) the high, positive, genetic relationship between greasy fleece weight and clean fleece weight indicates that selection for GFW should be adequate to improve W. Because wool buyers initially assess the value of a line of wool on the estimated amount of clean fibre, some people have advocated the selection of replacement stock based on W. Using the formulae of Falconer (1960) for predicting direct and indirect responses to selection, indirect selection for W, using GFW, is between

85% and 100% as efficient as direct selection for W (using genetic parameter estimates from this study). Any extra genetic gains achieved by selecting for W would be unlikely to offset the extra costs incurred in obtaining an estimate of the clean scoured yield,

- (b) greasy fleece weight is moderately/highly correlated with LW, SL and MFD. Consequently, selection based on hogget GFW should result in bigger sheep with coarser, longer fleeces,
- (c) the genetic correlation between QN and MFD is somewhat stronger than the phenotypic relationship. However, attempts to increase QN should be avoided due to consistently negative correlations with GFW and W,
- (d) genetic associations between hogget face-cover grade and other hogget traits are variable. There is some indication of negative correlations between FC and SL and FC and MFD; however these are not consistent. The possibility of these associations existing is supported by several negative estimates of the correlation between FC and GFW. Morley (1955) reported genetic correlations of -0.58 and -0.29 between FC and GFW and FW and W, respectively, in a flock of Australian Merino sheep,
- (e) the genetic relationships between GFW/W and PMF/MI are consistently positive. Selection for increased fleece mass could therefore lead to a small increase in the proportion of

medullated fibres. For Romney breeders this should not be of great concern since Romney wool is predominantly used for the manufacture of carpets. However, Ross *et al.* (1981) noted that increasing the proportion of medullated fibres in Romney wool could limit the flexibility of its end use as an apparel wool, and

- (f) Chopra (1978) reported a genetic correlation of 0.69 between TCN and GFW in a flock of Romney sheep. Estimates in this study vary between -0.42 and +0.26. Consequently, the suggestion of indirect selection for GFW through TCN is not supported.

Some interesting genetic relationships occur between the ewe hogget and ewe average lifetime traits (see Table 5.3):

- (a) both WWe and LWe are positively associated with LBa and LRa, thereby suggesting that selection for increased live weight should also increase lamb production. Young *et al.* (1963) and Ch'ang and Rae (1972) also found positive genetic correlations between ewe hogget live weight and lamb production,
- (b) GFWe and We also tend to be positively related with LBa and LRa. This is important from a selection viewpoint as several authors have produced negative estimates of relationships (Lewer, 1978). Most of these negative estimates were found in the Merino or Rambouillet breeds,

i.e. fine-woolled sheep. Also the GFW measurements were mainly on ewes older than 2 years, compared with the ewes in this study which were 15 months of age. Thus, it is possible that the true genetic correlation between coarse wool from 15 month ewes and lamb production is positive,

- (c) it is important to note the consistently negative relationship between SLe and LB and LR because if attempts were made to increase GFW by selecting for a long staple, lamb production could suffer,
- (d) GFWe is moderately to highly correlated with both GFWa and Wa, thereby suggesting that selection based on the hogget trait is sufficient to gain response in the mature fleece weight,
- (e) from the available estimates involving FCe, there appears to be a high positive genetic association with lamb production. This is in contrast to the phenotypic estimates which were very close to zero. Young *et al.* (1963) reported the following FC/lamb production genetic correlations: 0.54, 0.65, 0.10, 0.22, -0.12 and -0.28, estimated from a flock of Australian Merino sheep. The consensus of these estimates suggests that selection for an open face in the ewe hogget could be beneficial in terms of lamb production,

- (f) the F_{Ce}/GFW_a and F_{Ce}/W_a genetic correlations are consistently negative. These figures suggest that open faced ewe hoggets will tend to leave progeny with lower mature fleece weights, and
- (g) ewe hogget quality number is positively correlated with ewe average lifetime greasy fleece weight production. This relationship is unexpected as an increase in Q_{Ne} should, according to the other genetic correlations, result in smaller ewes, shorter staples and finer fibres. Consequently, the increase in GFW_a would have to be accounted for by an increase in the non-fibre component of GFW. This is possible because a strong negative correlation between Q_{Ne} and Y_a does exist. The relationship between Q_{Ne} and W_a is negligible.

It is difficult to undertake any meaningful discussion of many of the remaining genetic correlations because of the apparent instability of estimates obtained from the three sub-flocks. The variability of these estimates could be due to selection or the small number of observations available for estimation of the genetic correlations. Bohren *et al.* (1966) investigated the rate of change in genetic variances and covariances when selection was practised. They showed that genetic covariances would readily change in a selection situation, and consequently that genetic correlations were only valid for a few generations. Thus, in theory, genetic correlations should have been calculated every 2 or 3 generations, however the small number of observations in this study did not allow this to be undertaken.

5.4 Heritabilities

Two estimates of the standard error (SE) were obtained for each heritability estimate (see section 3.2.5). Table 5.6 presents these two estimates, along with the heritabilities, for the ewe hogget control group traits. The SE estimates obtained using the approach of Swiger *et al.* (1964) are never greater than those obtained by the other method, although the difference in magnitude never exceeds 0.05. The similarity of the SE estimates is probably due to the relatively constant family size (for most traits there were between 2 and 15 progeny measured per sire). Because the method of Swiger *et al.* (1964) assumes a one-way analysis-of-variance model the SE presented in Tables 5.7, 5.8 and 5.9 will be derived from the other approach unless otherwise stated.

Heritabilities derived using the paternal half-sib correlation method are given in Tables 5.7, 5.8 and 5.9 for ewe hogget, ram hogget and ewe average lifetime performance traits, respectively.

Generally, h^2 estimates for corresponding traits in each of the three sub-flocks are in agreement with each other and with estimates reviewed by Chopra (1978). However, some unexpectedly low h^2 estimates are not consistent with previously reported values; SLe, Ye and MIe in the control group, LWe, CHGe, MFDe and SFDe in the face cover group and WWe and FCe in the face cover group.

Because insufficient progeny were recorded per sire in the ram hogget control group, no heritability estimates were calculated for that group. Several discrepancies occur between h^2 estimates from the

TABLE 5.6: A COMPARISON OF TWO METHODS OF DERIVING STANDARD ERRORS FOR HERITABILITIES USING CONTROL EWE HOGGET INFORMATION

Trait	h^2	SE1	SE2
WWe	0.35	± 0.15	± 0.14
LWe	0.34	± 0.15	± 0.14
GFWe	0.28	± 0.14	± 0.13
We	0.26	± 0.14	± 0.13
QNe	0.31	± 0.15	± 0.13
CHGe	0.35	± 0.15	± 0.14
SLe	0.09	± 0.11	± 0.11
Ye	0.04	± 0.10	± 0.10
MFDe	0.64	± 0.20	± 0.16
SFDe	0.39	± 0.16	± 0.14
FCe	0.28	± 0.14	± 0.13

For calculation of SE1 see section 3.2.5.

SE2 = the approach of Swiger *et al.* (1964).

TABLE 5.7: ESTIMATES OF HERITABILITY AND THEIR STANDARD ERRORS FROM THE EWE HOGGET DATA

Trait	Control Group	Face Cover Group	Fleece Weight Group
DOBe	0.26±0.15	0.25±0.13	0.41±0.14
BWe	0.32±0.14*	0.28±0.13*	0.19±0.10*
WWe	0.35±0.15	#	0.24±0.11
LWe	0.34±0.15	0.06±0.10	0.52±0.16
GFWe	0.28±0.14	0.34±0.14	0.34±0.13
We	0.26±0.14	0.36±0.14	0.23±0.11
QNe	0.31±0.15	0.39±0.15	0.36±0.13
CHGe	0.35±0.15	0.25±0.12	0.50±0.15
SLe	0.09±0.11	0.33±0.14	0.33±0.13
TCNe	0.27±0.13*	0.33±0.14*	0.32±0.12*
CFe	0.27±0.14*	0.32±0.13*	0.26±0.12*
Ye	0.04±0.10	0.40±0.15	0.05±0.09
MFDe	0.64±0.20	0.21±0.12	0.49±0.15
SFDe	0.39±0.16	0.04±0.10	0.63±0.17
PMFe	#	0.36±0.13*	0.51±0.13*
MIe	0.01±0.14*	0.53±0.21*	0.39±0.19*
FCe	0.28±0.14	#	0.16±0.10

negative sire variance component

* standard error estimated by the method of Swiger *et al.* (1964)

TABLE 5.8: ESTIMATES OF HERITABILITY AND THEIR STANDARD ERRORS FROM THE RAM HOGGET DATA

Trait	Face Cover Group	Fleece Weight Group
DOBr	0.17±0.14	0.32±0.16
BWr	#	0.32±0.16*
WWr	0.19±0.14	#
LWr	0.26±0.15*	0.42±0.17*
GFWr	0.07±0.12	0.15±0.14
Wr	0.11±0.13	0.21±0.15
QNr	0.46±0.16	0.58±0.17
CHGr	0.50±0.16	0.27±0.15
SLr	0.39±0.15	0.47±0.17
TCNr	0.29±0.15*	0.50±0.18*
CFr	0.47±0.17*	0.59±0.18*
Yr	0.33±0.15	0.22±0.15
MFDr	0.50±0.17*	0.18±0.15*
MIr	0.19±0.20*	0.83±0.27*
FCr	0.13±0.13	0.52±0.17

negative sire variance component

* standard error estimated by the method of Swiger *et al.* (1964)

TABLE 5.9: ESTIMATES OF HERITABILITY AND THEIR STANDARD ERRORS FROM THE EWE AVERAGE LIFETIME PERFORMANCE DATA

Trait	Control Group	Face Cover Group	Fleece Weight Group
LBa	0.22±0.23	#	0.19±0.24
LRa	0.07±0.21	#	0.24±0.24
LWa	0.48±0.25	0.26±0.27	0.41±0.26
GFWa	0.14±0.22	0.50±0.28	0.68±0.27
Wa	0.16±0.22	0.42±0.28	0.47±0.26
QNa	0.22±0.23	0.34±0.27	0.73±0.27
CHGa	0.18±0.23	0.46±0.28	0.57±0.27
SLa	#	0.31±0.27	0.18±0.24
TCNa	0.60±0.28*	0.14±0.28*	0.56±0.28*
CFa	0.40±0.27*	0.14±0.28*	0.49±0.28*
Ya	0.56±0.26	#	0.63±0.27
MFDa	0.74±0.27	0.29±0.27	0.61±0.27

negative sire variance component

* standard error estimated by the method of Swiger *et al.* (1964)

two selection flocks; TCNr, M_{Ir} and FCr estimates are lower in the face cover group, whilst CHGr and MFDr estimates are lower in the fleece weight group. Negative sire variance components occur for B_{Wr} in the face cover sub-flock and for W_{Wr} in the fleece weight sub-flock. The remaining estimates are similar to those reviewed by Chopra (1978).

In an attempt to identify whether genetic variation was being affected by selection in the face cover and fleece weight groups, the data were divided into the periods 1956 to 1966 and 1967 to 1976 and h^2 estimates calculated within each period. However, due to the relatively small number of sires observed, the h^2 estimates were too unstable to suggest whether any changes in genetic variation had occurred.

From the available information, there does not appear to be any noticeable loss in genetic variation for GFW in the fleece weight flock. However, genetic variation for FC may be declining, because of the negative sire variance component in the ewe hoggets and the greatly reduced h^2 estimate, for the face cover group, in the ram hogget data. The previously mentioned discrepancies between h^2 estimates obtained from the different sub-flocks may suggest that changes in genetic variation have occurred in several other traits.

Although heritability estimates were obtained from the ewe average lifetime data, they are of limited value because it will be too late to apply selection once the required information is collected. These estimates are presented in Table 5.9.

CHAPTER SIX

THE USE OF THE INVERSE OF THE RELATIONSHIP MATRIX
IN MIXED-MODEL-EQUATIONS

As suggested in section 2.4.2 it was hoped to utilize genetic relationships between animals across generations within a flock to correct for the year to year environmental differences. This would then provide an alternative to the requirement of a control group without having to use sires in more than one year to provide the genetic link.

In preliminary analyses only sires were included as random effects in the mixed-model-equations (MME). Consequently, only the genetic relationships between sires, in different generations, provided the link across environments. The relationships between rams included the contributions through both the dam and the sire. This caused computational problems since Henderson's (1976) algorithm could not be used to produce the inverse of the relationship matrix. To enable the inclusion of contributions from both the dam and sire the relationship matrix itself had to be derived, whereas Henderson's (1976) algorithm avoids this step. After producing the relationship matrix the relationships amongst the sires included in the MME had to be extracted. The sire relationship matrix was then inverted using ordinary matrix inversion procedures.

By adding the inverse of the sire relationship matrix times the ratio of error variance to sire variance (σ_e^2/σ_s^2) to the $\tilde{Z}'\tilde{Z}$ portion of

the MME (see section 3.2.6) it was expected that the genetic trend would be reflected in the relative breeding values of the sires used across time. However, only a small portion of the genetic trend was reflected in the realized heritability estimates calculated by regressing the average sire breeding value estimates on the flock average cumulated selection differentials (FACSD). For example, the realized heritability estimate for ewe hogget GFW was 0.0086 (see Table 6.1 for average sire breeding value estimates and Table 7.4 for the FACSD). This estimate was not large enough to explain an apparent genetic response of about 0.6 kg in ewe hogget GFW during the 21 years of selection evaluated.

A possible reason for the failure of this approach was the sparseness of the inverse of the relationship matrix. Thus, the genetic relationships between sires alone may not have been sufficient to enable effective separation of genetic and environmental effects. If the analysis had been repeated with dams and sires included as random effects the inverse of the associated relationship matrix would have been less sparse. This may have resulted in a more effective separation of the genetic and environmental effects. Nevertheless, practical computing problems would arise by including dams as random effects; the number of simultaneous equations to be solved would have increased to about 500 in this study.

Considering the cost of maintaining a control group, both in money terms and in lost opportunity to have a larger selection group, it would appear desirable to further examine this approach to determine its potential in supplying estimates of the genetic trend free of environmental influences.

TABLE 6.1: AVERAGE YEARLY SIRE BREEDING VALUE ESTIMATES FOR EWE HOGGET GREASY FLEECE WEIGHT WITH THE INCLUSION OF THE INVERSE OF THE RELATIONSHIP MATRIX IN THE MIXED MODEL EQUATIONS*

Year	Average Predicted Breeding Value (kg)
1956	0.001
1957	-0.008
1958	-0.009
1959	-0.030
1960	-0.019
1961	0.055
1962	-0.002
1963	0.024
1964	-0.020
1965	-0.005
1966	-0.003
1967	0.034
1968	0.006
1969	0.087
1970	-0.009
1971	0.041
1972	0.007
1973	-0.002
1974	0.011
1975	0.027
1976	0.047

* Using data from the fleece weight flock.

(The regression of the average predicted breeding value on FACSD resulted in a coefficient of 0.0086 kg.)

C H A P T E R S E V E N

DIRECT RESPONSES TO SELECTION

7.1 Introduction

The ratios of error variance to sire variance components (σ_e^2/σ_s^2) for inclusion in the MME were mostly estimated from the control sub-flocks for ewe hogget and ewe average lifetime performance traits. The estimates from the control sub-flock were chosen because they were least likely to have been affected by selection. Because control group estimates of the sire variance components for ewe hogget PMF and ewe average SL were negative, and were very small for ewe hogget SL and MI compared with the two selection groups, the control group ratios for these traits were replaced by the average of the ratios from the two selection flocks. The ram hogget ratios were taken as being the average of the two selection sub-flock ratios, since no variance components were estimated for the control sub-flock.

Preliminary analyses showed that the predicted sire breeding values and the estimates of the fixed effects were relatively insensitive to changes in the magnitude of the ratio. Table 7.1 presents a sample of estimates of the year effects from 1971 to 1976 and predicted sire breeding values from the analysis of ewe hogget GFW in the fleece weight group. The σ_e^2/σ_s^2 ratios of 3, 8, 10 and 12 equate to heritabilities of 1.0, 0.44, 0.36 and 0.31, respectively.

Since the estimates of direct responses (and correlated responses) were derived from the year effects (see section 3.2.6) the σ_e^2/σ_s^2 ratios were grouped in the following fashion to reduce computing workload:

TABLE 7.1: THE EFFECT OF THE MAGNITUDE OF THE σ_E^2/σ_S^2 RATIO ON SOLUTIONS TO THE MIXED MODEL EQUATIONS

Effect	Level	Ratio			
		3	8	10	12
Year	1971	2.84	2.85	2.85	2.86
	1972	3.88	3.89	3.89	3.89
	1973	4.02	4.02	4.02	4.02
	1974	3.28	3.26	3.25	3.25
	1975	3.79	3.79	3.80	3.80
	1976	3.68	3.70	3.70	3.70
Sire*	11	0.32	0.25	0.23	0.22
	21	-0.25	-0.16	-0.14	-0.13
	31	-0.18	-0.15	-0.14	-0.13
	41	-0.19	-0.09	-0.08	-0.07
	51	-0.21	-0.14	-0.13	-0.11
	61	0.00	0.00	0.00	0.00
	71	-0.09	-0.05	-0.05	-0.04
	81	0.05	0.03	0.03	0.02
	91	0.29	0.22	0.20	0.19

* 11 refers to sire number 1 in year 1 (i.e. 1956),
21 refers to sire number 1 in year 2, etc.

The solutions in the table pertain to ewe hogget GFW
in the fleece weight group (solutions are in kg).

- (a) for traits with a heritability of 0.5 to 1.0 a ratio of 5 was assumed,
- (b) for heritabilities of less than 0.2 the actual ratio was used, as a relatively large change in the ratio resulted from a small change in the heritability, and
- (c) for heritabilities between 0.2 and 0.5 three groupings were used; 0.2 to 0.3, 0.31 to 0.4 and 0.41 to 0.5. The mid-points of these groupings equate to ratios of 15, 10 and 8, respectively.

7.2 Direct Response to Selection for Open Face

The rates of responses to selection, as estimated using mixed-model equations (MME), for open face in the ewe and ram hoggets are shown in Figures 7.1 and 7.2. The responses to selection were also estimated using ordinary least squares (OLS) techniques. The OLS and MME estimates of response are very similar, consequently OLS values are not shown in the figures. Any differences that do occur between the OLS and MME estimates will be due to the extra variance accounted for in the MME by including the random sire effect. The inclusion of sires is expected to take account of differing numbers of progeny per sire and also differences in sire breeding values.

The flock-average-cumulated-selection-differential (FACSD) increased in a linear fashion in both sexes (see Table 7.4). The rate of accumulation was just under one-half of a face-cover grade per year. In both sexes, the rate of accumulation appeared to lessen between 1971

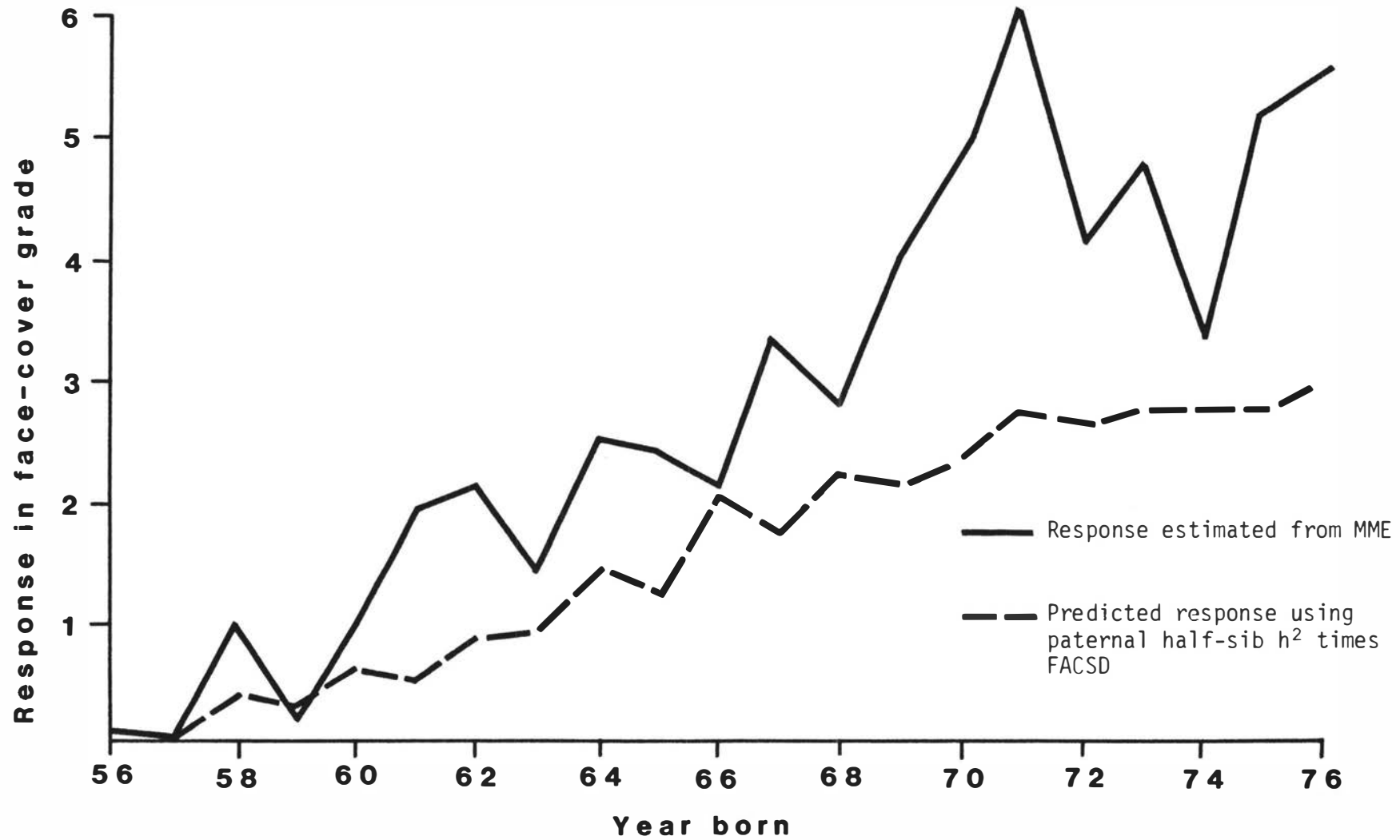


FIGURE 7.1: ESTIMATED AND PREDICTED RATES OF RESPONSE TO SELECTION FOR EWE HOGGET FACE-COVER GRADE

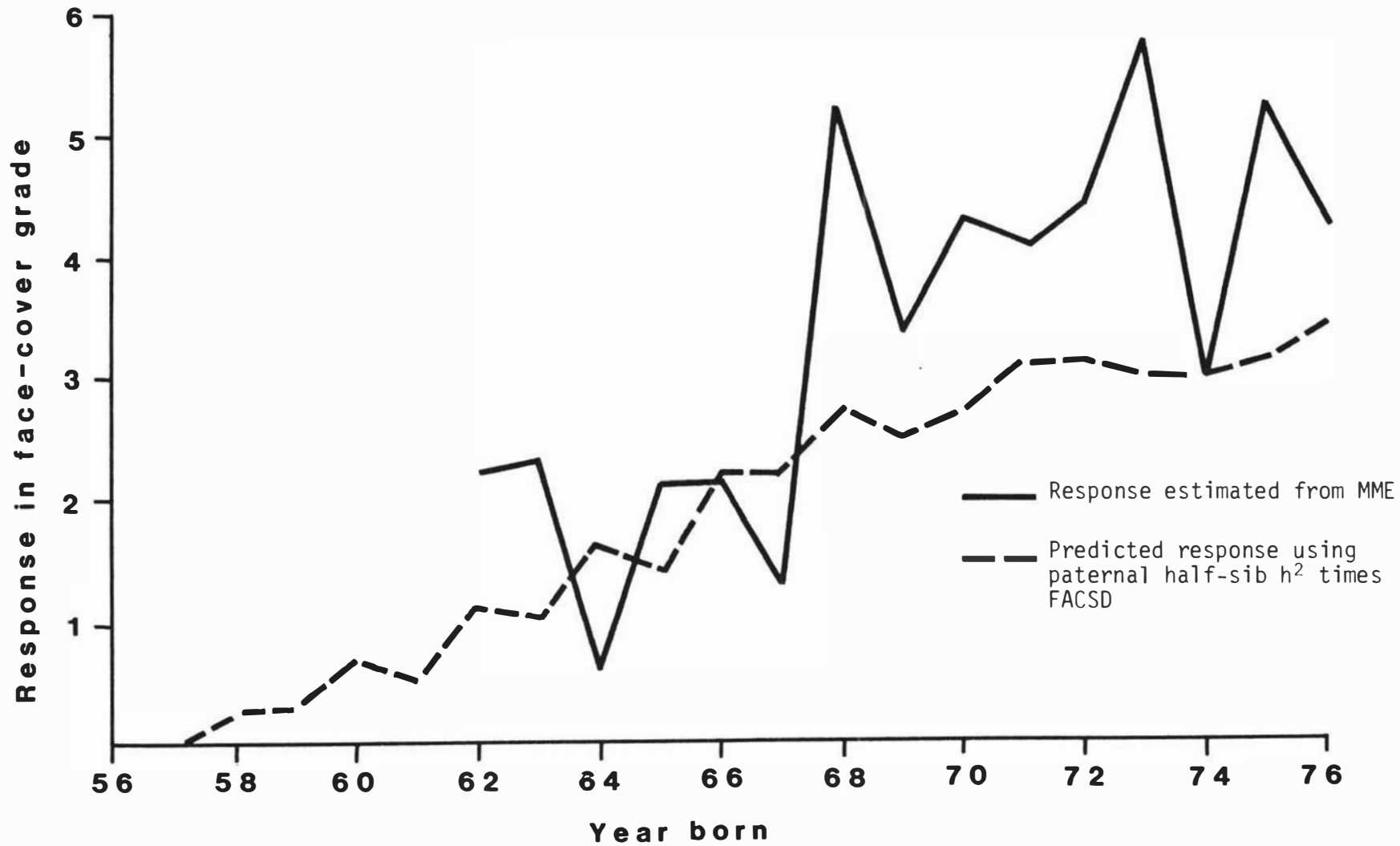


FIGURE 7.2: ESTIMATED AND PREDICTED RATES OF RESPONSE TO SELECTION FOR RAM HOGGET FACE-COVER GRADE

and 1975. This would agree with the suspected loss of sire variance in the face cover sub-flock, for FC (see section 5.4). Verification of this suggested plateauing of response would require the evaluation of information from several more years.

Realized heritabilities (h_f^2) were estimated using 3 techniques:

- (a) the best fit regression of estimated response to selection on FACSD,
- (b) the regression of estimated response to selection on FACSD, but with the regression forced through the origin, and
- (c) the ratio of total estimated response to the total FACSD.

Because the control and selected sub-flocks originally came from the same base flock, the regression of estimated genetic response on flock average cumulated selection differential should pass through the origin (Hill, 1972b). The various h_f^2 estimates and their standard errors are presented in Table 7.2.

There is good agreement between all estimates and they also compare favourably with the available estimates of heritability listed in Table 2.7. For every one face-cover grade of selection differential, between 0.4 and 0.5 of a face-cover grade was obtained in selection response.

TABLE 7.2: ESTIMATES OF REALIZED HERITABILITIES AND THEIR STANDARD ERRORS FOR FACE-COVER GRADE

	Ewe Hoggets			Ram Hoggets		
	\hat{h}_r	\pm SE1	\pm SE2	\hat{h}_r	\pm SE1	\pm SE2
Least squares estimate of response, best fit regression	0.46	0.19	0.04	0.46	0.15	0.14
MME estimate of response, best fit regression	0.47	0.19	0.04	0.46	0.15	0.11
Least squares estimate of response, regression through the origin	0.49	0.18	0.03	0.40	0.20	0.04
MME estimate of response, regression through the origin	0.49	0.18	0.02	0.44	0.20	0.03
Ratio of total response (MME estimate) to total FACSD	0.54	0.19	-	0.39	0.21	-

SE1 = standard error using the formula of Hill (1972b)

SE2 = standard error of the regression coefficient

The two h_F^2 estimates using the ratio approach are somewhat more variable compared with those obtained using regression techniques. This is not surprising considering the variation exhibited by the estimated responses to selection. If the experiment had been terminated in 1971 the h_F^2 estimate would have been 0.61, but if 1974 had been the end point, then the h_F^2 estimate would have been 0.34 (from the ewe hogget data). Consequently, if the estimates of response are variable it does not appear advisable to use the ratio approach.

There is little difference between realized heritability estimates derived from the ewe hogget compared with the ram hogget data. Realized heritability estimates based on MME and OLS estimates of response are similar. Forcing the regression through the origin did not greatly alter the h_F^2 estimates compared with the values obtained using best-fit regression.

Two estimates of the standard errors (SE) were calculated. It was thought that drift variance could markedly contribute to the SE, considering that 7.5 generations had elapsed since the beginning of the experiment (the average generation interval was estimated at 2.8 years using the method of Pattie (1965)). The SEs estimated using the standard error of the regression coefficient are generally much less than those estimated using the formulae of Hill (1972b) which take account of the variation contributed by random genetic drift (see Table 7.2). The standard errors of the regression coefficients are always smaller when the regression is forced through the origin (compared with best-fit regression) because the origin is assumed to be known without error.

As discussed in section 2.4.3, the degree of random genetic drift in the control group could have been reduced if restricted-randomized selection of replacement stock had been practised. However, the real effect on the SE of realized heritability estimates would probably have been small in this study.

Although the restricted selection procedure described in section 2.4.3 is probably not workable for large animal experiments, it may be used to illustrate the small change that occurs in the SE compared with the use of randomized selection of replacements. The effective size of the breeding group and the effective number measured would have increased from 43 to 59 and 90 to 146, respectively, if restricted selection of control replacements rather than random selection had been used in this experiment. However, these increases would have only reduced the SE of the ewe hogget realized heritability for face-cover grade from 0.18 to 0.17 (using the method of regressing through the origin). If 10 rams had been used in the control breeding group (compared with the 4 actually used) then the above SE would have decreased from 0.18 to 0.15. Thus, in practice, restricted random selection of replacements in the control flock would have had little effect on the accuracy with which the rate of genetic gain was predicted in this study.

Also included in Figures 7.1 and 7.2 are the predicted rates of response in face-cover grade, using the paternal half-sib estimates of heritability (0.28 and 0.32 for the ewe and ram hoggets, respectively) times the FACSD. As expected, the predicted responses are somewhat less than the responses estimated from the MME, since the realized heritability estimates are closer to 0.5 than 0.3.

Results from this study suggest that selection for high face-cover grades should result in a flock of open-face sheep in relatively few generations of selection, depending on the intensity of selection.

7.3 Direct Response to Selection for High Hogget Greasy Fleece Weight

The MME estimates of genetic response to selection in the ewe and ram hoggets are presented in Figures 7.3 and 7.4. By visual examination of the estimated responses no suggestion of a selection plateau was found. The flock average cumulated selection differential increased at the linear rate of approximately 0.2 kg per year in both the ewe and ram hoggets (see Table 7.4).

The realized heritability estimates and their standard errors were calculated following the same procedures mentioned in section 7.2. The various estimates are shown in Table 7.3. As with the realized heritability estimates for face-cover grade, there were no important differences between:

- (a) estimates obtained using OLS and MME estimates of genetic response,
- (b) ewe hogget and ram hogget estimates, and
- (c) best fit regression estimates, estimates from regression through the origin and estimates from the ratio method.

Standard errors estimated using the variance of the regression coefficient again did not appear to take account of the drift variance

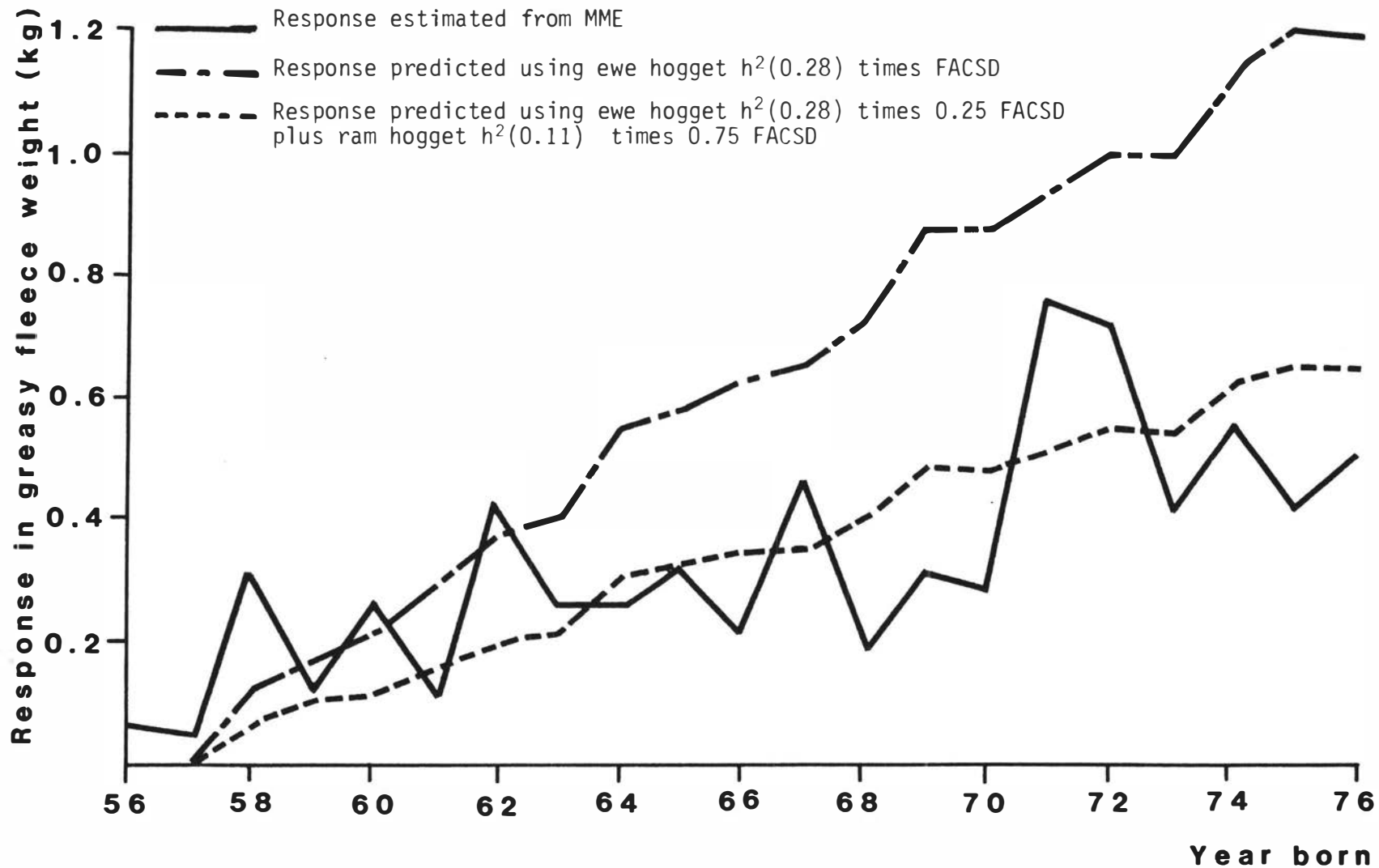


FIGURE 7.3: ESTIMATED AND PREDICTED RATES OF RESPONSE TO SELECTION FOR EWE HOGGET GREASY FLEECE WEIGHT

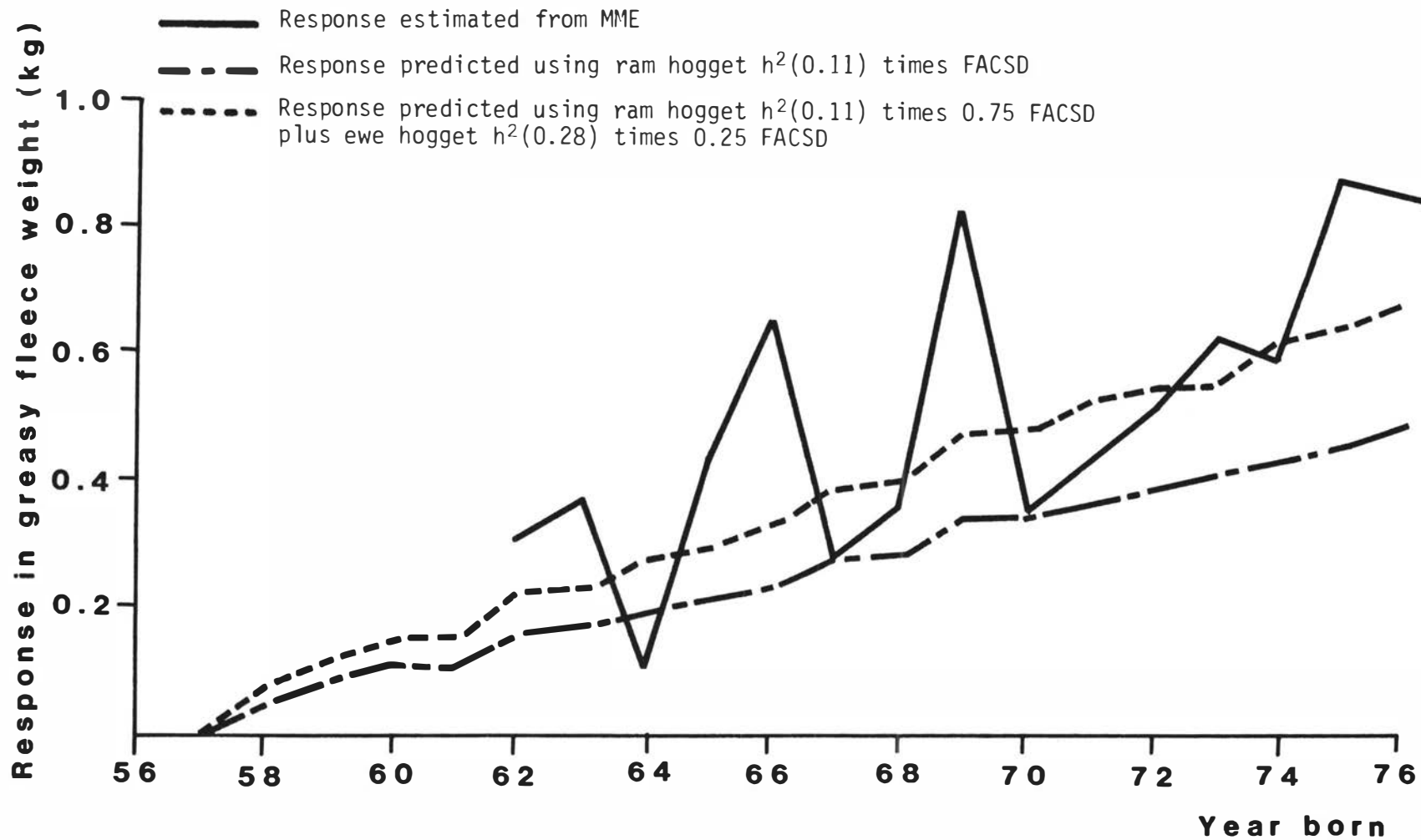


FIGURE 7.4: ESTIMATED AND PREDICTED RATES OF RESPONSE TO SELECTION FOR RAM HOGGET GREASY FLEECE WEIGHT

TABLE 7.3: ESTIMATES OF REALIZED HERITABILITIES AND THEIR STANDARD ERRORS FOR GREASY FLEECE WEIGHT

	Ewe Hoggets			Ram Hoggets		
	\hat{h}_r^2	\pm SE1	\pm SE2	\hat{h}_r^2	\pm SE1	\pm SE2
Least squares estimate of response, best fit regression	0.09	0.10	0.03	0.06	0.10	0.08
MME estimate of response, best fit regression	0.10	0.10	0.02	0.16	0.10	0.04
Least squares estimate of response, regression through origin	0.13	0.09	0.02	0.16	0.09	0.03
MME estimate of response, regression through origin	0.14	0.09	0.01	0.17	0.09	0.01
Ratio of total response (MME estimate) to total FACSD	0.12	0.10	-	0.19	0.10	-

SE1 = standard error using the formula of Hill (1972b).

SE2 = standard error of the regression coefficient.

and generally resulted in much smaller SE values compared with those estimates derived using the formula of Hill (1972b).

Pattie and Barlow (1974) cited McGuirk (1973) as having observed little difference between standard error estimates which included a contribution from drift variance compared with those which did not. However, McGuirk (1973) only used 14 points to predict the regression, thereby resulting in a large SE of the regression coefficient. Evidence from this study suggests that to avoid underestimating the SE of realized heritability estimates drift variance should be accounted for.

Compared with heritability estimates derived using the covariance of relatives techniques, the h^2_{F} values in Table 7.3 are smaller than expected. In his review, Lewer (1978) showed that most h^2 estimates of greasy fleece weight lay between 0.3 and 0.6, whilst only 3 out of the 34 quoted values fell below 0.3. However, the h^2_{F} estimates of 0.1 to 0.2 found in this study are consistent with the heritabilities derived via the paternal half-sib technique, using ram hogget data (0.07 and 0.15). Thus, it appears that there may be some effect of sex on the heritability of hogget GFW.

Kyle and Terrill (1953), Young *et al.* (1960) and Eikje (unpubl.) reported lower heritability estimates for fleece weight in ram hoggets compared with ewe hoggets, however the differences were non-significant. Baker *et al.* (1979) presented heritability estimates for GFW of 0.27 ± 0.09 and 0.41 ± 0.10 for ram and ewe hoggets, respectively. They considered the difference between the two estimates to be significant.

In this study, the additive genetic variance components for ewe and ram hogget GFW were about 0.08 and 0.04, respectively. Corresponding environmental variance components for ewe and ram hogget GFW were 0.23 and 0.34, respectively. These values are in good agreement with those of Baker *et al.* (1979) who also reported greater environmental variation but less additive genetic variation for GFW in ram hoggets compared with ewe hoggets.

Eikje (unpubl.) and Baker *et al.* (1979) also reported smaller ram heritability estimates for body weights, compared with ewe estimates. Thus, some evidence is accumulating to suggest that real differences in heritabilities between sexes might exist.

Figures 7.3 and 7.4 show the predicted rate of response to selection for high hogget GFW using paternal half-sib heritability estimates of 0.28 and 0.11 for the ewe hoggets and ram hoggets, respectively. As expected, the rate of response is overestimated in the ewe hoggets but slightly underestimated in the ram hoggets. This occurs because a greater proportion of the selection differential is due to ram selection rather than ewe selection. In this study the ram selection differential was approximately three times the size of the ewe selection differential. By accounting for the greater contribution of the ram selection differential the actual responses shown in Figures 7.3 and 7.4 are closely predicted.

The practical significance of this result is that since commercial farmers have only a limited opportunity to increase the selection intensity for GFW through ram selection (most commercial sheep-farmers

in New Zealand buy their rams from a specialized ram breeder), they may be able to obtain significant genetic gains through more intense selection for GFW in the ewes. For example, by subjectively assessing GFW a selection differential of 0.15 kg may be obtained in the replacement ewes (this equates to culling 15% of the poorest performing ewes; if a phenotypic standard deviation of 0.5 kg is assumed). A selection differential of this size enables a genetic response of 0.02 kg per generation (assuming a ewe heritability of 0.28 for GFW). Through objective measurement of ewe hogget GFW a selection differential of 0.35 kg may be possible, i.e. 40% of the poorest performing ewes are culled for GFW. A ewe selection differential of 0.35 kg would result in a genetic response of 0.05 kg per generation. To obtain a similar response per generation via ram selection a selection differential of about 0.5 kg would be required (assuming a ram heritability of 0.11 for GFW). It is likely that many commercial breeders would find it difficult to achieve such a selection differential unless they have access to rams with high predicted breeding values for GFW. Furthermore, the breeder would have to reduce the attention paid to other traits such as reproductive rate. However, in most situations the genetic average of the commercial flock will lag behind the genetic average of the stud flock and part of the required selection differential from the rams would be supplied through this difference. Thus, it appears that selection for GFW via the ewes may be important if the difference between ewe and ram heritability for GFW, as suggested by this study, is real.

TABLE 7.4: FLOCK AVERAGE CUMULATED SELECTION DIFFERENTIALS (FACSD) FOR EACH SEX IN THE TWO SELECTION FLOCKS

Year	Fleece Weight Flock		Face Cover Flock	
	Ewes ¹	Rams ¹	Ewes ²	Rams ²
1956	0	0	0	0
1957	0	0	0	0
1958	0.44	0.44	1.26	0.96
1959	0.61	0.69	0.89	1.02
1960	0.79	0.91	2.23	2.06
1961	1.03	0.92	1.89	1.61
1962	1.32	1.35	3.10	3.45
1963	1.42	1.43	3.06	3.10
1964	1.97	1.75	4.86	4.90
1965	2.07	1.93	4.42	4.43
1966	2.23	2.12	7.14	6.91
1967	2.33	2.50	6.16	6.86
1968	2.58	2.63	7.74	8.47
1969	3.12	3.07	7.59	7.73
1970	3.10	3.16	8.37	8.41
1971	3.34	3.38	9.78	9.68
1972	3.60	3.54	9.38	9.62
1973	3.57	3.70	9.75	9.51
1974	4.02	4.00	9.71	9.49
1975	4.27	4.17	9.66	9.65
1976	4.23	4.46	10.22	10.68

¹ FACSD for hogget greasy fleece weight (kg).

² FACSD for hogget face-cover grade.

CHAPTER EIGHT

CORRELATED RESPONSES TO SELECTION

8.1 Introduction

Because of the findings in Chapter seven only correlated responses using MME estimates of genetic response, which are then regressed through the origin, are presented, unless otherwise stated. Standard errors based on the work of Hill (1972b) are included.

8.2 Correlated Responses to Selection for Open Face

The correlated responses (CR) in other traits to selection for open face are presented in Table 8.1. The CR is initially expressed in terms of change in the trait (in original units of measurement) resulting from the application of a selection differential of one grade in face cover; e.g., the CR in ram hogget live weight is +0.29 kg for a selection differential of one face-cover grade. An indication of the relative importance of the CR is given by the standardized correlated response. This was derived by dividing the original CR by the phenotypic standard deviation of the trait (as given in Tables 5.1, 5.2 and 5.4). Thus, the standardized CR in ram hogget live weight is 0.05 of a phenotypic standard deviation per face-cover grade of selection differential.

In general there have been no major correlated changes in the traits measured. An important result is the small change in both the GFW and W traits. Thus, it appears that the selection of open-face hoggets will not reduce the amount of wool clipped, as was implied by the negative

TABLE 8.1: CORRELATED RESPONSES TO SELECTION FOR OPEN FACE AND THEIR STANDARD ERRORS

Trait	Ewe Hogget		Ram Hogget		Ewe Average	
	CR ¹ ±SE	STD ²	CR ¹ ±SE	STD ²	CR ¹ ±SE	STD ²
DOB (days)	-0.10±0.65	-0.01 ³	0.02±0.62	0 ³	-	-
BW (kg)	0 ±0.06	0 ³	-0.02±0.05	-0.03 ³	-	-
WW (kg)	0.02±0.27	0.01	0.08±0.22	0.02	-	-
LW (kg)	0.20±0.36	0.04	0.29±0.40	0.05	0.51±0.46	0.10
GFW (kg)	-0.02±0.03	-0.04	-0.03±0.02	-0.06	-0.02±0.03	-0.04
W (kg)	-0.01±0.03	-0.03	-0.02±0.02	-0.05	0 ±0.03	0
QN	-0.04±0.13	-0.02	0 ±0.15	0	-0.02±0.09	-0.01
CHG	0.01±0.09	0.01	0 ±0.07	0	0.01±0.04	0.01
SL (cm)	0.07±0.13	0.04	0.07±0.12	0.05	0.01±0.10	0.07
TCN	0.04±0.20	0.01 ³	0 ±0.23	0	0.10±0.21	0.05 ³
CF	0 ±0.05	0 ³	-0.01±0.06	-0.02	0.01±0.03	0.02 ³
Y (%)	0.25±0.14	0.06	-0.03±0.32	-0.01	0.34±0.34	0.10
MFD (μ)	-0.13±0.29	-0.05	-0.16±0.15	-0.08	-0.26±0.25	-0.12
SFD (μ)	-0.09±0.08	-0.09	-	-	-	-
PMF (%)	-0.10±0.56	-0.02 ³	-	-	-	-
MI	0.29±0.51	0.05 ³	-	-	-	-
LB	-	-	-	-	0.01±0.02	0.03
LR	-	-	-	-	0.01±0.01	0.03

¹ CR = correlated response in original units of measurement per face-cover grade of selection differential.

² STD = correlated response per face-cover grade of selection differential standardized by dividing by the phenotypic standard deviation for that trait.

³ Least squares estimate of response used as MME estimate unavailable.

genetic correlation estimated by Morley (1955) and also by the several negative estimates found in this study (see Tables 5.1, 5.2 and 5.3). A possible reason for the negligible change in GFW and W is that both the hogget and mature live weights of face-cover group animals have increased slightly. Because LW and GFW tend to be positively related, both phenotypically and genetically, the slight increase in body size may have offset the effect of any negative genetic correlation between FC and GFW.

A slight increase in the clean scoured yield in the ewe hogget and ewe average lifetime data is apparent. However, no change was shown in the ram hogget data.

There was a small reduction in the MFD and a slight increase in SL as the sheep became more open faced. Thus, selection for open face apparently led to finer, longer fleeces. However, both correlated responses were small in relation to their standard errors.

A positive correlated response occurred in both LB and LR. The genetic correlations between FC and LB/LR presented by Young *et al.* (1963) were generally positive, as were those derived in this study (see Table 5.3). Thus, these correlated responses are in the expected direction. During 21 years of selection the correlated responses amounted to about 10% in both LB and LR. Clarke (1978) reported a response of 31% in the number of lambs reared per ewe mated after 25 years of selection for twinning ability only, in a flock of Romney sheep. This equates to a response of about 26% in 21 years. Without accounting for flock size and selection intensity in particular, the correlated response in LR, to selection for open face, is a little under one-half of

that which might be expected through direct selection for twinning ability. The degree of response in the face-cover group is dependent on obtaining one face-cover grade of selection differential every 2 years. In an already open-face flock of sheep, it would be difficult to obtain a selection differential of this size.

Estimates of the standard errors of the correlated responses were relatively unaffected by the magnitude of the estimate of the genetic correlation used in the formula given in section 3.2.7. For example, by substituting -1, 0 and +1 for the genetic correlation between F_{Ce} and L_{We} the corresponding SEs of the CR in ewe hogget live weight were all +0.36. Similarly, SEs of the CR in ewe hogget greasy fleece weight were +0.03, +0.04 and +0.03, respectively.

8.3 Correlated Responses to Selection for High Hogget Greasy Fleece Weight

The various correlated responses (CR) to selection for high hogget greasy fleece weight, and their standard errors, are given in Table 8.2. Correlated responses are expressed in a similar fashion to that stated at the beginning of section 8.2, except that the correlated responses are expressed in changes per kg of GFW selection differential.

Hogget clean fleece weight (W) showed a strong positive response. This was expected considering the high positive genetic correlations between GFW and W derived in this study, and by other other workers (see Tables 2.6, 5.1, 5.2 and 5.3). It has been suggested that selection for W would result in greater net economic gains through greater response in the amount of clean fibre produced per animal, compared with selection for GFW. The strong CR in W, to selection for GFW, obtained in this

TABLE 8.2: CORRELATED RESPONSES TO SELECTION FOR HIGH HOGGET GREASY FLEECE WEIGHT AND THEIR STANDARD ERRORS

Trait	Ewe Hogget		Ram Hogget		Ewe Average	
	CR ¹ ±SE	STD ²	CR ¹ ±SE	STD ²	CR ¹ ±SE	STD ²
DOB (days)	-0.62±1.58	-0.07 ³	-0.21±1.64	-0.02 ³	-	-
BW (kg)	0 ±0.14	0 ³	-0.03±0.14	-0.04 ³	-	-
WW (kg)	0.23±0.67	0.07	0.38±0.56	0.10	-	-
LW (kg)	0.40±0.87	0.09	0.39±1.02	0.07	0.68±1.12	0.14
GFW (kg)	-	-	-	-	0.24±0.07	0.44
W (kg)	0.13±0.07	0.33	0.14±0.06	0.33	0.24±0.06	0.51
QN	-0.21±0.32	-0.12	-0.22±0.39	-0.13	-0.56±0.23	-0.39
CHG	-0.05±0.22	-0.05	-0.07±0.18	-0.08	-0.07±0.11	-0.09
SL (cm)	0.38±0.31	0.22	0.35±0.31	0.24	0.63±0.24	0.43
TCN	-0.02±0.49	-0.01 ³	-0.19±0.59	-0.07	-0.40±0.51	-0.20 ³
CF	-0.07±0.13	-0.10 ³	-0.10±0.15	-0.16	-0.13±0.09	-0.32 ³
Y (%)	0.59±0.35	0.14	0.08±0.82	0.02	1.18±0.82	0.35
MFD (μ)	0.32±0.70	0.12	0.29±0.40	0.14	0.16±0.61	0.07
SFD (μ)	-0.02±0.20	-0.02	-	-	-	-
PMF (%)	-0.19±1.33	-0.03 ³	-	-	-	-
MI	-0.18±1.27	-0.03 ³	-	-	-	-
FC	-0.09±0.36	-0.04	-0.02±0.41	-0.01	-	-
LB	-	-	-	-	0.07±0.06	0.19
LR	-	-	-	-	0.07±0.04	0.19

¹ CR = correlated response in original units of measurement per kg of GFW selection differential.

² STD = correlated response per kg of GFW selection differential standardized by dividing by the phenotypic standard deviation for that trait.

³ Least squares estimate of response used as MME estimate unavailable.

study imply that the extra cost incurred in estimating the clean scoured yield (to enable selection on W) would not be offset by greater genetic gains in clean fleece weight. This is consistent with the paternal half-sib estimates of the heritabilities and genetic correlations derived in this study, i.e. GFW and W have similar h^2 estimates and a high genetic correlation exists between them.

The increases in GFW and W have been accompanied by strong correlated responses in ewe hogget and ewe average Y. Ram hogget clean scoured yield showed only a small positive response. The genetic correlations calculated in this study (see Tables 5.1, 5.2 and 5.3) were too variable to enable any accurate prediction as to how Y would respond to selection on GFW. Previous estimates of the GFW/Y genetic correlation tended to be small (see Table 2.6). Thus, the correlated responses in ewe hogget and ewe average Y in this study were probably greater than expected. Turner (1977) suggested that if clean scoured yields became too high some fibre damage may result from weathering and dust and that an optimum Y may exist for a particular environment. If this suggestion is correct it may be necessary to impose a ceiling on Y when selecting for high GFW.

The response in ewe average GFW and W were also strongly positive. The response in both of these traits has been greater than in the corresponding ewe hogget traits. The larger response in ewe average GFW can be explained if this trait has a high h^2 and is strongly correlated (genetically) with GFWe. The two available estimates of the genetic correlation are 0.57 and 1.00 for the control and fleece weight groups, respectively. The face cover and fleece weight groups both

give high estimates of GFWa h^2 (0.50 and 0.68, respectively) but the control flock estimate is low (0.14). Assuming heritabilities of 0.15 and 0.5 for hogget GFW and ewe average GFW and a genetic correlation of 0.6 between these two traits, the predicted correlated response in GFWa to a 1 kg selection differential in hogget GFW is +0.29 kg. This compares favourably with the estimated correlated response of +0.24 kg; the response in ewe average W would follow as a consequence of a high GFWa/Wa genetic correlation.

There has been a general tendency for the average date-of-birth (DOB) of the ewes and rams to decrease. This has probably been caused by selection for high GFW without first adjusting for DOB. This suggests that there is genetic variation in DOB and that earlier birth is associated with higher GFW. The available estimates of this genetic correlation (see Tables 5.1 and 5.2) are too variable to decide whether or not the above suggestion is true.

Birth weight (BW) did not change appreciably in either sex. WW increased in both the ewes and rams, a response which was consistent with the estimates of GFW/WW genetic correlations in Tables 5.1 and 5.2. Hogget live weight and mature ewe live weight also increased and again these responses are as expected from the genetic correlations in Tables 5.2, 5.2 and 5.3.

As expected, all SL and MFD measurements showed positive correlated responses. The actual change in MFD is probably unimportant as an increase in hogget GFW of 1 kg will only increase the MFD by about 1.5 microns. Such an increase in MFD is unlikely to affect the value of

Romney wool in New Zealand, since, at present, there is little fineness premium on wools coarser than about 29 microns. Similarly, the change in SL is only very small. No estimates of follicle density are available so it is not possible to break down the response in GFW into its various components, as suggested in section 2.2.6.

Quality number showed a consistent decrease in magnitude as the experiment progressed. The assessment of QN is partially dependent on crimp frequency; the higher the CF the higher the QN. The consistent decline in CF would also contribute to the reduction in QN.

Face-cover grade decreased in both the ewe and ram hoggets, however the response is unlikely to be significant. The genetic correlations in Tables 5.1 and 5.2 suggest a negative FC/GFW genetic correlation. Morley (1955) calculated a negative genetic correlation of -0.29 between these two traits. A possible reason for the small correlated response in FC is that the fleece weight sub-flock had an average FC grade of about 5 when the experiment started; i.e., tending to a woolly-faced condition. For the hoggets to become selected as parents they obviously had to be in condition to produce a good fleece weight. Since hogget live weight and GFW tend to be positively correlated phenotypically this could preclude any very woolly-faced sheep from being selected, thereby avoiding any large correlated response in FC.

CHG, TCN, SFD, PMF and MI all show small non-significant correlated responses.

The two measures of lamb production LB and LR, both show positive correlated responses. These responses are as expected according to the genetic correlations estimated in this study and by Young *et al.* (1963). Lewer (1978) cited several workers who had found negative relationships between lamb production and GFW; Lewer (1978) also derived several negative estimates of the genetic correlation between GFW and LR. However, most of these estimates involve genetic correlations using GFW taken after the age of 18 months. Of the four estimates based on hogget GFW only one is strongly negative; it is in Merinos and involves only lambs weaned at 2 years-of-age. The estimates of correlated responses for LB and LR are both +0.07% (per kg of selection differential for hogget GFW). These figures suggest that a total CR of about 30% should have occurred in the fleece weight group, compared with the control group, between 1956 and 1976. However, the MME estimates of genetic response suggest that the total CR is closer to about 20%. However, the important result is that the correlated responses in both lamb production traits are positive. A possible explanation for the large CR in lamb production is that fixation of some gene (or genes) favourable for lamb production has occurred. Further information regarding the mode of inheritance of lamb production in the fleece weight group could be obtained by mating fleece weight and control group rams to a flock of unrelated Romney ewes. By comparing the lambing performance of the offspring, and perhaps later generations, any major genetic effects should be discernible. If similar CRs for lamb production can be identified in other greasy fleece weight selection experiments (Clarke, 1980; Hight and Bigham, 1980), then selection for high hogget GFW may serve as a useful means of indirect selection for lamb production.

Except for lamb production, the correlated responses to selection for high hogget greasy fleece weight agree with previously published information.

CHAPTER NINE

CONCLUSIONS

In the fleece weight selection flock greasy fleece weight increased at approximately 0.03 kg per year in both the ewe and ram hoggets, with no sign of any decline in the rate of response in later years. Realized heritability estimates of about 0.15 were in good agreement with paternal half-sib correlation estimates of GFW heritability in the ram hoggets. However, the response in hogget GFW was only about one-half of that which would have been predicted by equivalent ewe hogget heritability estimates. This apparent difference in heritabilities between the two sexes could be of practical significance to commercial breeders, in particular, who may obtain significant genetic gains through more intense selection for GFW in the ewes. Also, if the difference in heritabilities is real, predictions of direct responses to selection for GFW may be overestimated; because a greater proportion of the total selection differential normally comes from rams, but most heritability estimates are derived from ewe data. Furthermore, as stated by Baker *et al.* (1979) and Eikje (unpubl.) differences in heritabilities between sexes may lead to differential weightings being applied to ewe and ram records.

Several major correlated responses occurred in the fleece weight selection flock. Most importantly, there were strong correlated responses in hogget clean fleece weight and in ewe average lifetime greasy and clean fleece weight. After 21 years of selection for high hogget GFW each ewe produced, on average, between 4 kg and 5 kg more

greasy wool, during 5 years in the flock, than her contemporaries in the control group. Several of the other correlated responses were associated with the increase in fleece production, i.e. increased live weight, staple length and mean fibre diameter (on average, these traits increased by about 1.5 kg, 1.5 cm and 1.5 μ , respectively, during the 21 years evaluated). No measure of follicle density was available for this study. A large correlated response of 25% to 30% in lamb production was recorded after 21 years of selection for high hogget GFW. This large correlated response in lamb production was unexpected, and it is unlikely that it can be explained solely as a correlated response to selection for high hogget GFW. It is possible that the statistical techniques employed in this study may have overestimated the true correlated response, due to the discrete nature of the data; alternatively, chance fixation of some genes favourable to lamb production may have occurred.

The face-cover selection flock showed a considerable response in face-cover grade but may be approaching a selection plateau. Data from several more years will require evaluation before this possibility could be substantiated. No adverse correlated responses were observed in the face-cover selection flock. In particular, there was no loss of hogget or ewe fleece weight as the flock became more open faced. Positive correlated responses occurred in hogget and ewe live weight and in lamb production. During the 21 years of selection, lamb production (LB and LR) increased by about 10% compared with the control flock.

When calculating standard errors of the selection responses, it became apparent that it was necessary to account for random genetic

drift variance. Standard errors not including an estimate of the drift variance were substantially smaller than those that did.

Initial attempts to estimate genetic trends in the selection groups using best linear unbiased prediction (BLUP) methods produced low, unacceptable results. Presumably the use of the inverse of the sire relationship matrix did not supply sufficiently strong genetic ties across years to enable the separation of genetic and environmental effects. The utilization of relationship matrices in BLUP procedures warrants further research as it may obviate the need for control groups. In particular, the inclusion of ewe-ewe and ewe-ram relationships may strengthen genetic links between years sufficiently to enable to separation of genetic and environmental effects.

The ordinary least squares and mixed-model-equation (MME) techniques gave similar estimates of direct and correlated responses to selection. Consequently, for data sets like that used in this study there appears to be little benefit in using the more-complicated and time-consuming MME approach.

Heritabilities and genetic correlations were estimated within each of the 3 flocks, using the paternal half-sib approach. In general, heritability and genetic correlation estimates agreed with published values of these parameters. Some discrepancies did occur between estimates of the same parameter derived from the three sub-flocks. A possible explanation of the variable estimates is that the genetic variance and covariance components have changed in response to the selection operating in the two selection groups. Also, the small

number of observations available did not allow accurate estimation of the various genetic correlations, as is indicated by the generally large standard error estimates.

Standard error estimates of genetic correlations obtained by using the formula of Tallis (1959) did not appear to adequately reflect the variability of the parameter estimates under some circumstances. The SE estimates were often unnecessarily large when the genetic correlation was only very small, or unrealistically small when the genetic correlation neared -1 or $+1$. A second method of obtaining the standard errors was favoured. This approach involved estimating variances of variance and covariance components and covariances between variance components, as suggested by C.R. Henderson (unpubl.). These estimates were then included in an equation derived using the approximate formula for the variance of a ratio (see section 3.2.5).

Estimates of the heritability SE calculated using either the approach of Swiger *et al.* (1964) or the method described in section 3.2.5 were similar. This was probably due to the relatively stable family sizes. Thus, the comparatively simple method of Swiger *et al.* (1964) may be acceptable when relatively equal numbers of progeny are recorded per sire.

Maintenance of these experimental flocks utilizes land and labour resources which could be used for other projects. Completion of these analyses enables future policy to be considered. Questions still to be answered include:

- (a) are the sheep which produce heavy fleeces more, or less, efficient at utilizing feed than the lower producing control animals? Measurement of the amount of feed consumed by the fleece weight group compared with the control group should provide an answer to this question,

- (b) which of the components of GFW have contributed most to the increased fleece mass of the fleece weight group? Again a comparison of the control and fleece weight groups should provide the required information for this question,

- (c) is the face-cover selection flock approaching a selection plateau for face-cover grade? This question can only be answered by allowing the face-cover flock to undergo selection for several more years,

- (d) as a result of the genetic changes caused by selection, has the physiological functioning of the selected group animals been affected? This could be studied by examination of differences in blood metabolites between the selected and control groups,

- (e) what is the genetic basis of the high lamb production in the fleece weight group? By progeny testing fleece weight group rams over a flock of commercial ewes and observing the lamb production of the offspring, and perhaps later generations, the mode of inheritance of lamb production in this flock may be determined, and

- (f) how do rams from the fleece weight group compare with rams from other high producing strains of Romney sheep, for example rams from the Ruakura high fertility selection flock (Clarke, 1978) or from the Waihora ram breeding scheme (Hight *et al.*, 1975)? This question could be answered by progeny testing rams from the different strains using a flock of unrelated ewes.

To enable these questions to be solved all three experimental flocks should be retained for further evaluation.

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