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A STUDY OF GENETIC AND ENVIRONMENTAL VARIATION
AND COVARIATION IN PRODUCTIVE TRAITS OF
A FLOCK OF PERENDALE SHEEP

A thesis presented in partial fulfilment
of the requirements for the degree
of Doctor of Philosophy in
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A B S T R A C T

Performance records on 1724 two-year, 1160 three-year, 726 four-year and 449 five-year Perendale sheep from the Massey University flock were analysed. These records were collected between birth-years 1961 and 1974 inclusive, and therefore different numbers of years were involved at each age. The data comprised 97, 82, 65 and 56 sire groups for the respective ages. There were 403 ewes in 56 sire groups which had four consecutive records between two- and five-years of age. There were 922 two-year, 584 three-year, 296 four-year and 125 five-year dam-daughter pairs, but the last age group of records was considered too few to justify analysis.

The dependent variables examined were quality number (QN), wool character (WC), staple length (SL), greasy fleece weight (GFW), fibre diameter (FD), and number of lambs weaned per ewe joined and present at lambing (NLW). Fibre diameter had been recorded in fewer years than the other traits and there were consequently less observations available.

The effects of the environmental factors of year, age of the dam of the ewe, rearing rank, NLW (wool traits only), and all interactions among them were assessed by computing the percentage of the total variance contributed by each factor for each variable. Quadratic components for these fixed effects were temporarily considered to be variance components for this purpose. Year effects were the most important source of environmental variation in wool characteristics, but were less important for NLW. None of the other main effects were consistently important (i.e. contributed greater than two percent of the total variation) in explaining the observed variability. Year x NLW was the only interaction

which contributed more than two percent of the total variance in any wool trait. The affected characteristics were two- and three-year QN, three-year FD and five-year SL. NLW (five-year-old ewes only) was affected by dam age x rearing rank and year x rearing rank interaction.

Heritability estimates calculated by paternal half-sib method (daughter-dam regression estimates in brackets) were in the range of 0.22 - 0.28 (0.39 - 0.66), 0.16 - 0.39 (0.12 - 0.25), 0.32 - 0.71 (0.25 - 0.36), 0.24 - 0.53 (0.43 - 0.62), 0.38 - 0.68 (0.45 - 0.50) and 0.02 - 0.24 (-0.02 - 0.03) for QN, WC, SL, GFW, FD and NLW respectively. Differences between ages were seldom significant and the relevance of such a comparison was discussed. Paternal half-sib heritability estimates for the average of four mature (two- to five-years) production records were 0.50, 0.61, 0.84, 0.44, 0.49 and -0.01 for the same respective characteristics. Binomial analysis methods resulted in heritability estimates for fertility (twinning in brackets) of 0.06 (0.12), 0.02 (0.15), -0.01 (0.13), and -0.15 (0.01) for two-, three-, four- and five-year-old ewes respectively.

Repeatability was estimated by averaging the regression of later on earlier record for all pairs of ages for wool traits and mature ages for reproductive characteristics and resulted in values of 0.46 (QN), 0.18 (WC), 0.50 (SL), 0.62 (GFW), 0.71 (FD), and 0.09 (NLW). Similar methods gave computed values for the repeatability of the difference between zero and one lamb weaned of 0.01, and between one and two lambs weaned of 0.13.

Genetic and phenotypic correlations between all variables were calculated separately at each age by paternal half-sib and daughter-dam methods. The correlations were positive for GFW - FD, GFW - SL, GFW -

WC, QN - WC and FD - SL, negative for GFW - QN, QN - FD and QN - SL, and mixed for FD - WC and SL - WC although the last of these were mostly positive. The phenotypic correlations between wool traits and reproduction were negative for NLW - GFW and NLW - SL and approximately zero for the remainder. Genetic correlations were negative for NLW - GFW, NLW - FD and NLW - SL, positive for NLW - QN and mainly positive for NLW - WC. Many of the genetic correlations involving NLW had large standard errors.

Application of the results was discussed in terms of the selection indices which were constructed.

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C H A P T E R O N E

INTRODUCTION

The interbred cross between Cheviot rams and Romney ewes, registered as the Perendale breed in 1960, has become widely used on the hill country of New Zealand since its inception. The New Zealand Perendale Sheep Society claims that 25 percent (Anon, 1977) of the national flock comprises Perendale sheep. This value is at best an estimate, as in the past, census figures have not been taken separately for the breed. There is no doubt however, that these sheep are important contributors to animal production in New Zealand. A brief history of the breed is included in a later section.

The objectives of this study were firstly to provide further estimates of the various genetic and phenotypic parameters for productive traits in the Perendale breed of sheep. Only in recent years have sufficient records become available from the Massey University flock to enable reliable estimates to be computed. Elliott (1975) examined records collected from observations on hoggets from the same flock as the data for this study, but the estimates which he derived may not be strictly applicable to the formulation of selection plans and indices involving older sheep. It seems a reasonable proposition that the physiological condition of the immature animal is such that a different environment mediates in the expression of the genotype. Another factor is that no information is available from hogget records pertaining to reproductive performance.

Selection of replacements for the flock can be made from amongst candidates born of parents of varying ages, which have been sequentially selected during their lifetimes. The average genetic merit of the

parental age groups (and their progeny) will therefore differ according to the number of cycles of culling they have survived. Comparisons between the expected breeding values of the progeny of parents of different ages requires a knowledge of parameters calculated at the various ages. No report has been published in terms of estimates calculated at a full range of usual mature performance ages. A second intention of this study was to provide this information for ewes up to five-years of age.

A third aim was to examine the average performance records of mature ewes, in particular the heritabilities, and genetic correlations with individual ages. This would enable the predictive value of each age record to be compared on a genetic basis. The phenotypic relationships between age records were also calculated, as a knowledge of repeatability is vital in determining current selection policy.

The fourth and final objective was to investigate the influence, and possible causes of some environmental factors on the expression of the productive traits studied. Assessment can then be made on the advisability of correcting for environmental effects.

Short and long term improvement is the concern of the sheep breeder, and data relevant to both current and future flocks will be presented in the form of genetic and phenotypic parameter estimates. The productive characters studied in this respect include both wool and reproductive traits.

C H A P T E R T W O

REVIEW OF LITERATUREI. Introduction

Few workers have investigated genetic and phenotypic parameters using data collected from sheep of normal reproduction age; the majority of estimates are derived from studies of 15- to 16-months or younger animals. Several comprehensive reviews have been published accumulating information on young sheep, but in some cases including estimates from two year and older animals. Morley (1951, 1955), Rae (1956), Turner (1956, 1964, 1977), Brown and Turner (1968), Turner and Young (1969), Lundie (1971), and Elliott (1975) are examples. The above comments do not apply to reproductive characteristics, since these are only observable in older sheep.

There are no estimates for two-year and older Perendale sheep since the breed is relatively new and only recently have sufficient records become available for analysis. Elliott (1975) analysed a subset of hogget records from the same files from which the data for the present study were drawn. Elliott's estimates from immature sheep form part of an age series with results from this thesis and will therefore be extensively cited. The only other estimates which will be quoted involving animals of less than two-years of age will be those from studies where data on both immature and mature sheep have been analysed.

For the purpose of this review, "mature" is defined as being of normal reproductive age (two years) or older.

II. Heritability

A. Introduction.

Hill (1974) argued that heritability of a trait is the most important single concept in applied animal breeding. No prediction of genetic gain is possible without recourse to heritability estimates (Turner and Young, 1969).

The concept of heritability is based upon the closer resemblance of related as compared with unrelated individuals. Lush (1940) defined heritability as the fraction of the observed variance in the trait which is caused by differences in heredity. He observed that in the narrow sense only additively genetic variance is considered, whereas in the broad sense, dominance deviations (non-additive effects of allelic genes) and epistatic deviations (non-additive effects of non-allelic genes) are included. Since it is genes and not genotypes which are transmitted from parent to offspring, an effect requiring the simultaneous presence of two or more genes is less likely to be passed on than an additive effect requiring only one gene. The additive variance, or the variance of breeding values is the most important component since it is the chief cause of resemblance between relatives (Falconer, 1960). Therefore heritability is most conveniently expressed as the proportion of the total phenotypic variance which is due to additive gene action; that is, in terms of Lush's "narrow" definition.

The true population value of heritability is never known, but can be estimated from samples from the population. The most commonly observed relatives for this type of study are daughter-dam pairs and paternal half-sib groups. The covariance between parent and offspring estimates half of the additive genetic variance plus a part of the

epistatic variation, but has the disadvantage that where the parent is the dam, maternal effects may also be included in the estimate. Regressions and correlations are calculated from the data, but the former is more meaningful for the computation of heritability where there has been selection of the independent variable, for example, dams in the case of daughter-dam pairs. Bias due to non-random mating or differential sire group treatment is removed by carrying out the analysis on an intra-sire basis.

The analysis of variance of paternal half-sib groups enables the additive genetic variance to be estimated free of any maternal component, but still including some epistatic effects. The intraclass correlation calculated from the between-sire component is multiplied by four to estimate heritability. The disadvantage in the method is that in multiplying by four, any errors are likewise multiplied. The standard error is computed as four times the error of the intraclass correlation and therefore can be large.

Heritability estimates show whether selection in the present generation is likely to result in improvement in the following generation. Mass (individual) selection will only be of value if the phenotypic differences between the candidates for selection are highly heritable; i.e. if phenotypic differences are largely genetic in origin. Where the heritability is low, selection on the basis of information on a number of relatives, repeated observations or correlated traits may be advisable.

Young and Turner (1969) suggested the following arbitrary classification on the basis of their experience.

Highly heritable	0.3
Intermediate	0.1 to 0.3
Weakly heritable	0.1

B. Wool Characteristics.

In a review of a large number of Australian experiments, Turner (1977) observed that "heritability levels are high for all wool characteristics". The tabulated data had been gathered from papers on young as well as mature sheep, but not on subjectively assessed traits. Examination of Tables 2.1 to 2.10 confirms Turner's opinion when applied to mature animals for those characteristics considered in this review.

Wickham (1973) stated that fleece weight is one of the few wool traits on which there is sufficient information to enable accurate estimates of responses. Corroborative evidence can be provided by this writer who found many references pertaining to greasy fleece weight, but few for some of the other characteristics, particularly when the criterion that they refer to two-year and older sheep was applied.

A particularly comprehensive study was that of Mullaney et al. (1970) which included heritability estimates for all of the wool traits relevant to this dissertation. Data were collected at 18- and 30-months from three breeds of sheep (Merino, Corriedale and Polwarth) over a period of three dam-years. The estimates were calculated by two methods, both involving the correlation between daughter and dam, applicable where there has been no selection applied, as mentioned earlier. The dam record for the first method was the individual observation, whereas for the second method the sum of the three dam records was used. Heritability estimates for greasy fleece weight over

the three breeds were within the range 0.39 to 0.51. Results derived from their second method were very similar in value between breeds, only 0.04 separating the highest and lowest heritability estimates. These estimates fall about the middle of the range of those published by other workers (Table 2.1) who analysed data from a diversity of breeds.

Three heritabilities for greasy fleece weight for mature sheep which are less than 0.30 are listed in Table 2.1 (Ghoneim et al., 1974; Eikje, 1971b; Eikje, 1975). The number of records analysed by Eikje (1971b) was not mentioned in the abstract but was assumed equal to the number stated in a previous paper (Eijke, 1971a) referred to by the author. If the assumption is correct, then very small standard errors could be expected. A later paper by Eikje (1975) included a comprehensive list of greasy fleece weight heritability estimates. Different analyses were carried out within breed, year, age and various pooled combinations by two methods, paternal half-sib and daughter on dam regressions. All except one set of estimates exceeded 0.30, the exception being the values quoted for two-year-old ewes (0.25 - 0.27). Estimates derived by regression methods are expected to yield higher values than those calculated by the analysis of variance of half-sib data since the former include maternal effects. Eikje (1975) recorded results opposite in comparative magnitude to expectation for his two-year-old ewes and explained that this may have resulted from inappropriate correction of some of the data. The same explanation may apply to the low values above.

The heritability estimate of Singh and Rempel (1967) was for greasy fleece weight per 45 kg bodyweight and hence is for a different character than the other estimates. It can be seen from the standard errors that

Table 2.1 Estimate of Heritability of Greasy Fleece Weight

Estimate	Breed	Age (Months)	Comment	Reference
0.51	Merino	30	DDC	Mullaney <i>et al.</i> (1970)
0.49	Merino	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.40	Corriedale	30	DDC	Mullaney <i>et al.</i> (1970)
0.46	Corriedale	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.39	Polwarth	30	DDC	Mullaney <i>et al.</i> (1970)
0.45	Polwarth	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.55	Rambouillet	Mean ²	PHS	Shelton and Menzies(1968a)
0.58	Rambouillet	Mean ²	PHS	Shelton and Menzies(1968b)
0.52	Rambouillet	Mean ²	DDR	Shelton and Menzies(1968b)
0.61	Welsh Mt.	24	DDR	Doney (1958)
0.47-0.49	Combined ³	24	PHS	Eikje (1975)
0.25-0.27	Combined ³	36	PHS	Eikje (1975)
0.41	Combined ³	12-36	DDR	Eikje (1975)
0.36	Combined ³	12-36	PHS	Eikje (1975)
0.38	Dala		DDR	Eikje (1975)
0.47	Rygja		DDR	Eikje (1975)
0.48	Cheviot		DDR	Eikje (1975)
0.40	Spaelsau		DDR	Eikje (1975)
0.51	Steigar		DDR	Eikje (1975)
0.31	Combined ⁴		PHS	Gjedrem (1966)
0.31	Minnesota		DDR ⁵	Singh and Rempel (1967)
			S.E.+0.7	
0.52	Galway	24	PHS	More O'Ferrall (1976)
0.41	Stavropol	24	DD?	Vachal (1962)
0.30	Crossbred ⁶	24	DD?	Vachal (1962)
0.37	Combined ⁷	24	DD?	Vachal (1962)
0.59	Texel	24	PHS	Kooistra (1966)
0.16	Awassi	60	DDR	Ghoneim <i>et al.</i> (1974)
0.47	Awassi	60	PHS	Ghoneim <i>et al.</i> (1974)
0.27-0.31	Dala	24-60		Eikje (1971b)
0.43-0.67	Shuman	30		Nakev (1973)
0.37	Polish Mt.	3rd st. ⁸	PHS	Nawara and Duniec (1972)

Table 2.1 Continued

0.33	Polish Mt.	4th sh. ⁹	PHS	Nawara and Duniec (1972)
0.32	Perendale	15-16	PHS	Elliott (1975)
0.30	Perendale	15-16	DDR	Elliott (1975)

1. Sum of three dam records between three- and seven-years of age.
2. Mean of weights between three- and seven-years of age.
3. Five Norwegian breeds.
4. Three Norwegian breeds.
5. Annual fleece weight per 45 kg bodyweight.
6. Stavropol - Mutton Merino cross.
7. Stavropol and Stavropol-Mutton Merino cross combined.
8. Third shear.
9. Fourth shear.

the estimate lacks precision and this may explain the low value. A similar criticism regarding standard errors could be levelled at the report of Gjedrem (1966). The primary purpose of his paper was to obtain estimates for inclusion in a selection index.

The figures noted by Shelton and Menzies (1968a, 1968b) were relatively high, but were based on composite records related to lifetime production. The observations analysed were the mean greasy fleece weights of at least three clips taken between the ages of three- and seven-years. This averaging would have influenced the estimate of heritability upwards.

Elliott (1975) calculated heritability estimates of 0.32 (paternal half-sib) and 0.30 (regression) from Perendale hogget records.

Heritabilities for the remaining wool characters have been recorded by Mullaney et al. (1970). None of their estimates for any of three breeds for fibre diameter mean, quality number, character or staple length fell below 0.31. Ranges are respectively 0.44 - 0.70, 0.33 - 0.60, 0.39 - 0.54, and 0.31 - 0.59 for 30 month-old ewes. Remaining estimates in Tables 2.2 and 2.4 for mature sheep are in general agreement with Mullaney et al. (1970).

Lower values were noticed by Elliott (1975) for heritability of quality number and character in Perendale hoggets, but the remaining wool traits compared well with other reports.

A wide range of estimates for the heritability of each of the wool characteristics is indicated by the tables presented. The variety of breeds and environments would contribute to the variability. However the results suggest that all wool traits reviewed will respond well to selection, as heredity is an important source of variation for each

Table 2.2 Estimates of Heritability of Quality Number

Estimate	Breed	Age (Months)	Comment	Reference
0.33	Merino	30	DDC	Mullaney <i>et al.</i> (1970)
0.43	Merino	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.39	Corriedale	30	DDC	Mullaney <i>et al.</i> (1970)
0.51	Corriedale	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.54	Polwarth	30	DDC	Mullaney <i>et al.</i> (1970)
0.60	Polwarth	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.59	Texel	24	PHS	Kooistra <i>et al.</i> (1966)
0.26	Perendale	15-16	PHS	Elliott (1975)
0.31	Perendale	15-16	DDR	Elliott (1975)

Table 2.3 Estimates of Heritability of Wool Character

Estimate	Breed	Age (Months)	Comment	Reference
0.42	Merino	30	DDC	Mullaney <i>et al.</i> (1970)
0.54	Merino	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.44	Corriedale	30	DDC	Mullaney <i>et al.</i> (1970)
0.45	Corriedale	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.39	Polwarth	30	DDC	Mullaney <i>et al.</i> (1970)
0.49	Polwarth	30	DDC ¹	Mullaney <i>et al.</i> (1970)
0.23	Perendale	15-16	PHS	Elliott (1975)
0.23	Perendale	15-16	DDR	Elliott (1975)

¹. Sum of three dam records.

Table 2.4 Estimates of Heritability of Staple Length

Estimate	Breed	Age (Months)	Comment	Reference
0.31	Merino	20	DDC	Mullaney <u>et al.</u> (1970)
0.43	Merino	30	DDC ¹	Mullaney <u>et al.</u> (1970)
0.42	Corriedale	30	DDC	Mullaney <u>et al.</u> (1970)
0.59	Corriedale	30	DDC ¹	Mullaney <u>et al.</u> (1970)
0.47	Polwarth	30	DDC	Mullaney <u>et al.</u> (1970)
0.53	Polwarth	30	DDC ¹	Mullaney <u>et al.</u> (1970)
0.57	Polish Mt.	3rd sh. ⁸	PHS	Nawara and Duniec (1972)
0.29	Polish Mt.	4th sh. ⁹	PHS	Nawara and Duniec (1972)
0.49	Perendale	15-16	PHS	Elliott (1975)
0.35	Perendale	15-16	DDR	Elliott (1975)

Table 2.5 Estimates of Heritability of Fibre Diameter

Estimate	Breed	Age (Months)	Comment	Reference
0.62	Merino	30	DDC	Mullaney <u>et al.</u> (1970)
0.64	Merino	30	DDC ¹	Mullaney <u>et al.</u> (1970)
0.56	Corriedale	30	DDC	Mullaney <u>et al.</u> (1970)
0.59	Corriedale	30	DDC ¹	Mullaney <u>et al.</u> (1970)
0.44	Polwarth	30	DDC	Mullaney <u>et al.</u> (1970)
0.70	Polwarth	30	DDC ¹	Mullaney <u>et al.</u> (1970)
0.54	Perendale	15-16	PHS	Elliott (1975)
0.47	Perendale	15-16	DDR	Elliott (1975)

1. Sum of three dam records.

8. Third shear

9. Fourth shear

fleece variable.

The assessment of age differences in heritability estimates is possible from only three of the papers reviewed (Mullaney et al., 1970; Nawara and Duniec, 1972; Eikje, 1975). These are listed in Tables 2.6 to 2.10 for comparison. A decrease with age from second shearing was reported by Nawara and Duniec (1972) for fleece weight heritability but the first shearing estimate did not follow the trend, being lower than for second shearing. Eikje (1975) analysed a very large data set and found that one-year-old ewes had a higher heritability for greasy fleece weight than two-year-old or three-year and older sheep. Two-year-olds were considerably lower than older and younger ewes, but this may have in part been due to adjustments made to the data of this group. Younger ewes (18-months) consistently had lower fleece weight heritabilities than older ewes (30-months-old) according to Mullaney et al. (1970). The discrepancy was 42, 45 and 64% for Merino, Corriedale and Polwarth breeds respectively.

Nawara and Duniec (1972) found an upward trend for the heritability of staple length from the first to third shearings, but this decreased for the fourth shearing. Mullaney et al. (1970) noted the same trend, 18-month ewes recording a lower heritability than 30-month ewes when the sum of three dam's records were correlated with individual daughters records. When single records on both relatives were analysed, 30-month never exceeded 18-month heritability and was generally lower by both methods.

No conclusion can be stated regarding any possible age trend in heritability estimate for wool characters from these few, often conflicting reports; however, age differences are apparent.

Table 2.6 Estimates of Heritability of Greasy Fleece Weight
at Different Ages

Estimate	Age (Month)	Reference
0.14-0.30	18	Mullaney <u>et al.</u> (1970)
0.39-0.51	30	Mullaney <u>et al.</u> (1970)
0.32-0.34	18 ¹	Mullaney <u>et al.</u> (1970)
0.45-0.49	30 ¹	Mullaney <u>et al.</u> (1970)
0.47-0.51	12	Eikje (1975)
0.25-0.27	24	Eikje (1975)
0.36-0.40	36	Eikje (1975)
0.47	1st shear	Nawara and Duniec (1972)
0.50	2nd shear	Nawara and Duniec (1972)
0.37	3rd shear	Nawara and Duniec (1972)
0.33	4th shear	Nawara and Duniec (1972)

Table 2.7 Estimates of Heritability of Staple Length at Different Ages

0.31-0.53	18	Mullaney <u>et al.</u> (1970)
0.31-0.47	30	Mullaney <u>et al.</u> (1970)
0.36-0.50	18 ¹	Mullaney <u>et al.</u> (1970)
0.43-0.59	30 ¹	Mullaney <u>et al.</u> (1972)
0.31	1st shear	Nawara and Duniec (1972)
0.45	2nd shear	Nawara and Duniec (1972)
0.57	3rd shear	Nawara and Duniec (1972)
0.29	4th shear	Nawara and Duniec (1972)

1. Sum of three dam records

Table 2.8 Estimates of Heritability of Fibre Diameter at Different Ages

Estimate	Age (Months)	Reference
0.30-0.49	18	Mullaney <u>et al.</u> (1970)
0.44-0.62	30	Mullaney <u>et al.</u> (1970)
0.46-0.49	18 ¹	Mullaney <u>et al.</u> (1970)
0.59-0.70	30 ¹	Mullaney <u>et al.</u> (1970)

Table 2.9 Estimates of Heritability of Quality Number at Different Ages

Estimate	Age (Months)	Reference
0.32-0.37	18	Mullaney <u>et al.</u> (1970)
0.33-0.54	30	Mullaney <u>et al.</u> (1970)
0.35-0.38	18 ¹	Mullaney <u>et al.</u> (1970)
0.43-0.51	30 ¹	Mullaney <u>et al.</u> (1970)

Table 2.10 Estimates of Heritability of Wool Character at Different Ages

Estimate	Age (Months)	Reference
0.32-0.39	18	Mullaney <u>et al.</u> (1970)
0.39-0.44	30	Mullaney <u>et al.</u> (1970)
0.41-0.78	18 ¹	Mullaney <u>et al.</u> (1970)
0.45-0.54	30 ¹	Mullaney <u>et al.</u> (1970)

1. Sum of three dam records.

C. Number of Lambs Weaned.

The reproductive level of a sheep flock is important to the profitability of the commercial enterprise for three reasons:

- (i) A high reproduction rate will allow a higher selection intensity to be applied to whatever trait the breeder considers important. Assuming that the selected traits are heritable, genetic gain will thereby be increased.
- (ii) The second point follows from the first. Having retained the necessary replacements, a larger number of surplus animals will be available for disposal by sale. Dickerson (1970) considers that sheep efficiency can best be achieved by increasing reproduction rate and hence meat production from surplus animals.
- (iii) Greater per-ewe production will reduce overheads on a live-stock unit basis.

Reproductive ability in terms of number of lambs weaned per ewe mated and present at lambing (NLW) includes components such as fertility (the ewe did or did not lamb) , prolificacy (single or multiple birth) and livability (live lamb or not), as defined by Shelton and Menzies (1970). These components are not independent, each later one being dependent upon the existence of the earlier parts. Subcomponents make further contributions, a notable example being mothering ability which affects livability. The final outcome of the effect of all these elements is measured as the trait number of lambs weaned.

Shelton and Menzies ' (1968b) estimates relate to various expression of lifetime production and therefore are expected to be higher than single record estimates. Values of 0.28 and 0.25 from these authors were for the heritability of lambs raised by a ewe during her

Table 2.11 Estimates of Heritability of Number of Lambs Weaned

Estimate	Breed	Age (Months)	Comment	Reference
0.00-0.15	Romney		DDR+PHS	Rae and Ch'ang (1955)
0.03	Merino	24	PHS	Young <u>et al.</u> (1963)
0.15	Merino	36	PHS	Young <u>et al.</u> (1963)
0.0	Merino	24	ML	Young <u>et al.</u> (1963)
0.29	Merino	36	ML	Young <u>et al.</u> (1963)
0.09	Merino	24+36	PHS	Young <u>et al.</u> (1963)
0.06	Merino	24	PHS	Kennedy (1967)
0.28	Rambouillet	Lifetime		Shelton and Menzies (1968a)
0.19	Rambouillet	Mean/yr		Shelton and Menzies (1968a)
0.28	Rambouillet	36-84	PHS Total	Shelton and Menzies (1968b)
0.25	Rambouillet	36-84	DDR Total	Shelton and Menzies (1968b)
0.22	Rambouillet	Mean	PHS	Shelton and Menzies (1968b)
0.27	Rambouillet	Mean	DDR	Shelton and Menzies (1968b)
0.00	Scottish BF		PHS	Purser (1965)
0.03	Welsh Mt.		PHS	Purser (1965)
0.08 ¹	Galway	24	PHS	More O'Ferrall (1976)
0.16	Galway	24	PHS	More O'Ferrall (1976)
0.24	Galway	Index	PHS	More O'Ferrall (1976)
0.08	Dala & Steigar	Mean	PHS	Gjedrem (1966)
0.01	Dala			Eikje (1975)
0.04	Rygja			Eikje (1975)
-0.01	Cheviot			Eikje (1975)
0.01	Spaelsau			Eikje (1975)
-0.01	Steigar			Eikje (1975)
0.03	Several	24		Eikje (1975)
0.04	Several	36		Eikje (1975)

1. Includes only ewes which weaned lambs

productive life, while heritabilities of 0.22 and 0.27 were recorded for the number raised expressed as an annual mean. These results confirmed an earlier set of estimates from the same authors (Shelton and Menzies, 1968a).

More O'Ferrall (1976) computed his results from two-year-old ewe records, and from an index combining various age records. As expected, the heritability estimate for NLW based on the index was highest at 0.24. When converted to a single record basis, this fell to 0.12, in agreement with other estimates in Table 2.11. Two-year-old ewe data yielded a heritability of 0.16, but when computed omitting barren ewe records, and ewes which did not rear a lamb, the figures became 0.08.

It seems clear from evidence provided in the literature that selection for fertility characteristics and in particular NLW, will at best result in slow progress. Additive genetic variance forms only a small part of the total variation, probably because reproduction is continuously subject to natural selection.

Age differences have been studied by few researchers. Eikje (1975) compared ewes of one-, two- and three-years and older, and found the middle group to have the lowest heritability for NLW, but (according to the author) this may have been an artefact of data adjustment procedures. A significant age trend was noticed by Purser (1965) for the Welsh Mountain breed which showed increased heritability with age. The same trend was apparent amongst the Scottish Blackface data analysed but was non-significant. Young et al. (1963) also found that the youngest age group had the lowest heritability value as indicated earlier. Data from two-year-old ewes indicated a negligible heritability

which rose to 0.15 and 0.29 at three-years by analysis of variance and maximum likelihood respectively. The second method pertains to binomial (0,1) data.

The possibility of an upward trend in heritability for NLW suggests that selection of replacements from older dams may be more accurate in increasing reproduction rate.

Turner and Young (1969) concluded their review of the genetic components of reproduction by stating that selection for number of lambs born (NLB) would be the most profitable method of increasing number of lambs weaned. Their argument was based on the higher heritability estimate for the former than for the latter obtained by Young et al. (1963). Purser (1965) agrees, stating that he found the genetic correlation between the two characteristics to be 0.5. However, easy-care breeds of sheep such as the Perendale owe much of their economic advantage in labour reduction to not being shepherded during the lambing period. Common practice is to ignore the flock until the bulk of the lambing activity has passed. Number of lambs present at the time of observation, which may be quite some time after birth, may not accurately reflect the number actually born. From the practical viewpoint, NLW may best be selected directly. Another consideration is that selection for NLW is equivalent to selecting the end product of all of the traits mentioned in the introduction to this section.

III. Genetic Correlations

A. Introduction.

Genetic correlations can arise from two sources: linkage between genes, and pleiotropy. Generally, linkage will be the least important as crossing-over will break up combinations of genes in the long term.

If pleiotropy was the only cause of genetic correlation, then the calculated coefficient would express the proportion of genes that the two associated traits have in common.

Turner (1977) listed three uses for genetic correlations.

- (i) To indicate the change which is likely to occur in characteristics, other than those under selection, in the next generation.
- (ii) To help decide what counter-selection may need to be applied to reduce the effect of such changes, or to prevent them.
- (iii) To decide whether an easily measured characteristic can be used to obtain genetic gains, instead of one more difficult (or more expensive) to measure.

As with heritability estimation, the methods commonly used in the computation of genetic correlation coefficients rely on the covariance between relatives, and again the most important relatives are offspring-parent and half-sib groups.

Following Brown and Turner (1968) the classification below will be used as guide for correlation coefficients:

High negative	-0.6 and lower
Medium negative	-0.4 to -0.6
Low negative	-0.2 to -0.4
Negligible	-0.2 to +0.2
Low positive	+0.2 to +0.4
Medium positive	+0.4 to +0.6
High positive	+0.6 and greater.

B. Between Wool Characteristics .

In dual purpose breeds, the selection potential for wool is diluted by the requirement that attention be concurrently given to other objectives. Young and Dunlop (1956) suggested that for the Merino breed, within any particular class, the greatest return would be achieved by selecting animals producing a heavy fleece with a high quality number, moderate length and of good colour and that attention to other characters would be economically unrewarding.

The genetic correlation between quality number and fleece weight, and between fibre diameter and fleece weight indicated a trend towards coarser wool as the weight of the greasy fleece increased in Merino, Polwarth and Corriedale breeds (Mullaney et al., 1970). Turner (1972) stated that wool weight and fibre diameter mean are always positively related, although the size of the correlation may not always be large.

The Corriedale breed was found by Mullaney et al. (1970) to have a negligible genetic correlation between these characters compared with the other two breeds which showed a medium correlation. The trend was not observed for the fleece weight-quality number relationships. Elliott (1975) found that fleece weight and quality number had a moderate negative genetic correlation derived from paternal half-sib data, which became a negligible positive value when calculated from the daughter-dam relationship. His results for fleece weight-fibre diameter were in agreement with others in Table 2.12.

Genetic correlations between greasy fleece weight and staple length are positive and generally of low to medium magnitude (Table 2.12).

Table 2.12 Estimates of Genetic Correlations. Wool Traits.

Value	Breed	Age (Months)	Comment	Reference
Greasy fleece weight				
- fibre diameter				
0.43	Merino	30	DD	Mullaney <u>et al.</u> (1970)
0.19	Corriedale	30	DD	Mullaney <u>et al.</u> (1970)
0.40	Polwarth	30	DD	Mullaney <u>et al.</u> (1970)
0.43	Perendale	15-16	PHS	Elliott (1975)
0.44	Perendale	15-16	DD	Elliott (1975)
- quality number				
-0.53	Merino	30	DD	Mullaney <u>et al.</u> (1970)
-0.48	Corriedale	30	DD	Mullaney <u>et al.</u> (1970)
-0.66	Polwarth	30	DD	Mullaney <u>et al.</u> (1970)
-0.48	Perendale	15-16	PHS	Elliott (1975)
0.09	Perendale	15-16	DD	Elliott (1975)
- staple length				
0.17	Merino	30	DD	Mullaney <u>et al.</u> (1970)
0.18	Corriedale	30	DD	Mullaney <u>et al.</u> (1970)
0.29	Polwarth	30	DD	Mullaney <u>et al.</u> (1970)
0.76	Perendale	15-16	PHS	Elliott (1975)
0.44	Perendale	15-16	DD	Elliott (1975)
- character				
-0.27	Merino	30	DD	Mullaney <u>et al.</u> (1970)
0.09	Corriedale	30	DD	Mullaney <u>et al.</u> (1970)
0.29	Polwarth	30	DD	Mullaney <u>et al.</u> (1970)
0.52	Perendale	15-16	PHS	Elliott (1975)
0.32	Perendale	15-16	DD	Elliott (1975)
Quality number				
- fibre diameter				
-0.50	Merino	30	DD	Mullaney <u>et al.</u> (1970)
-0.69	Corriedale	30	DD	Mullaney <u>et al.</u> (1970)
-0.47	Polwarth	30	DD	Mullaney <u>et al.</u> (1970)
-0.46	Perendale	15-16	PHS	Elliott (1975)
-0.27	Perendale	15-16	DD	Elliott (1975)
- staple length				
-0.57	Merino	30	DD	Mullaney <u>et al.</u> (1970)

Table 2.12 Continued

-0.61	Corriedale	30	DD	Mullaney <i>et al.</i> (1970)
-0.47	Polwarth	30	DD	Mullaney <i>et al.</i> (1970)
-0.63	Perendale	15-16	PHS	Elliott (1975)
-0.41	Perendale	15-16	DD	Elliott (1975)
- character				
0.55	Merino	30	DD	Mullaney <i>et al.</i> (1970)
-0.27	Corriedale	30	DD	Mullaney <i>et al.</i> (1970)
-0.21	Polwarth	30	DD	Mullaney <i>et al.</i> (1970)
-0.13	Perendale	15-16	PHS	Elliott (1975)
0.44	Perendale	15-16	DD	Elliott (1975)
Fibre diameter				
- staple length				
0.09	Merino	30	DD	Mullaney <i>et al.</i> (1970)
0.26	Corriedale	30	DD	Mullaney <i>et al.</i> (1970)
-0.63	Polwarth	30	DD	Mullaney <i>et al.</i> (1970)
0.53	Perendale	15-16	PHS	Elliott (1975)
0.31	Perendale	15-16	DD	Elliott (1975)
- character				
-0.63	Merino	30	DD	Mullaney <i>et al.</i> (1970)
-0.06	Corriedale	30	DD	Mullaney <i>et al.</i> (1970)
-0.13	Polwarth	30	DD	Mullaney <i>et al.</i> (1970)
0.09	Perendale	15-16	PHS	Elliott (1975)
0.10	Perendale	15-16	DD	Elliott (1975)
Staple length				
- character				
-0.16	Merino	30	DD	Mullaney <i>et al.</i> (1970)
0.23	Corriedale	30	DD	Mullaney <i>et al.</i> (1970)
0.40	Polwarth	30	DD	Mullaney <i>et al.</i> (1970)
0.47	Perendale	15-16	PHS	Elliott (1975)
0.03	Perendale	15-16	DD	Elliott (1975)

Since quality number and mean fibre diameter are both estimates of wool fineness, a large negative correlation is expected between them. The range of values for mature sheep (Mullaney et al. 1970) is from -0.47 to -0.69, the larger value showing agreement with theory. Both of the Perendale hogget estimates of Elliott (1975) are smaller than those above.

Mullaney et al. (1970) reported widely varying estimates of the genetic correlations between greasy fleece weight and character, between quality number and character, fibre diameter and staple length and between staple length and wool character which all showed a swing from positive to negative for different breed calculations. No other published data are available from animals of comparable age to theirs for confirmation.

Staple length and quality number are negatively genetically related with medium to high correlation coefficients. The values recorded by Mullaney et al. (1970) were in the range -0.47 to -0.61 for their three breeds of 30-month-old ewes, similar in magnitude to the estimate of Elliott (1975). The former authors reported a wide range of consistently negative genetic correlations between fibre diameter and character, whereas Elliott found positive but small associations.

From evidence presented here for mature sheep, the following conclusions could be drawn. Selecting for increased greasy fleece weight would result in a correlated response amongst the progeny of the selected group in the direction of increased staple length, coarser wool and possibly improved character. Selecting parents with the finest wool will cause the progeny to have lower fleece weight, but the effect on staple length is unclear.

A feature of some of the pairs of characteristics is the wide differences in the estimates of correlation between them. The paucity of data relevant to this review has meant that drawing firm conclusions from estimates available was not possible.

C. Wool Characters and Number of Lambs Weaned.

In considering the genetic correlation between reproductive and other traits, interest centres on attempting to select young animals on a character which has a strong genetic relationship with the number of lambs weaned at a later stage. If there is a consistently strong genetic correlation between some hogget trait and reproduction, then early culling on this characteristic should lead to the retention of ewes whose progeny will on average produce most lambs. Within-age genetic associations are also important as a selection tool, allowing prediction of correlated responses to selection at that age. A further variation is to correlate hogget records with combinations or means of later reproduction records.

The genetic correlation between greasy fleece weight and the number of lambs weaned per ewe joined has been investigated by several authors and has been reported to be variable in both sign and magnitude. Ch'ang (1955) noted that no previous attempt had been made to calculate genetic covariance between fleece weight and number of lambs weaned. He presented his results as regressions which indicated that the covariance between the characters was variable in sign at different ages in his sample of Romneys. However, there was a predominance of negative values, and Ch'ang concluded that selection for increased fleece weight would be accompanied by a reduction in fertility. This comment is supported by the conclusion of Shelton and Menzies (1968b)

Table 2.13. Estimates of Genetic CorrelationsN.L.W. with Wool Traits.

Value	Breed	Age* (Months)	Comment	Reference
N.L.W.				
- greasy fleece weight				
+ and -	Romney	24-60	Covariances(DD)	Ch'ang (1955)
-0.37	Rambouillet	(36-84) Av. x(24-84) Av.	PHS	Shelton and Menzies (1968b)
-0.25	Rambouillet	Lifetime Av. x(24-84) Av.		Shelton and Menzies (1968b)
-0.10	Rambouillet	Total x Mean		Shelton and Menzies (1968b)
-0.06	Merino	24x Hgt.	PHS	Young <u>et al.</u> (1963)
-0.11	Merino	36x Hgt.	PHS	Young <u>et al.</u> (1963)
0.34	Merino	(Σ first 3) x Hgt.	PHS	Young <u>et al.</u> (1963)
0.09	Combined ³	Mixed	PHS	Eikje (1975)
-0.06	Combined	Mixed	DDR	Eikje (1975)
-0.66	Combined ⁴	Mixed	PHS	Gjedrem (1966)
-0.85	Merino	24xHgt	PHS	Kennedy (1967)
- staple length				
0.32	Merino	24x Hgt.	PHS	Young <u>et al.</u> (1963)
0.09	Merino	36x Hgt.	PHS	Young <u>et al.</u> (1963)
0.21	Merino	(Σ first 3) x Hgt.	PHS	Young <u>et al.</u> (1963)
- fibre diameter				
-0.55	Merino	24x Hgt.	PHS	Young <u>et al.</u> (1963)
-0.13	Merino	36x Hgt.	PHS	Young <u>et al.</u> (1963)
-0.33	Merino	(Σ first 3) x Hgt.	PHS	Young <u>et al.</u> (1953)

3,4 Legend below Table 2.1

* Where the wool trait and fertility trait are measured at different ages, the first age is that for N.L.W. and the ages are separated by an x.

who analysed mean annual fleece weight and lambs raised. When the number of lambs raised was expressed as a total for ewes between three- and seven-years of age the genetic correlation coefficient was -0.10 , but this increased to -0.37 when the mean number of lambs raised per mating over the same age range was used and was reported as -0.25 when related to the number of lambs raised per mating during the ewe's lifetime. These figures are greater than recorded by some other investigators. This is probably in part an effect of the compound observations with which the authors worked.

Further confirmation of a negative genetic correlation between lambs weaned and greasy fleece weight is available in a paper by Kennedy (1967). He worked with wool production records from 15-16 month old ewes, and fertility observations taken at two years and found a correlation of -0.85 (Non-significant). Such a high estimate suggests that selection for greasy fleece weight would have a disastrous effect on reproduction rate. A large estimate of the genetic correlation can arise by chance from paternal half-sib methods when the genetic variance for one or both traits is very small. Kennedy (1967) used this method and calculated a heritability for NLW of 0.06. Large standard errors noted are a symptom of the same problem. Young et al. (1963) published a paper based on wool data collected at a similar age to Kennedy's but lamb production records were assembled at two-years, three-years and the sum of the first three lambings. Their estimates were -0.06 , -0.11 and 0.34 respectively. Eikje (1975) computed a positive estimate by analysis of variance (0.09) and negative by regression (-0.06) but both values are negligible. A high negative (-0.66) correlation was found by Gjedrem (1966) but was based

on a small sample of mixed age ewes.

Most of the genetic correlation estimates discussed so far in this section have failed to achieve significance, but are consistent enough in direction to suggest that selection for one may cause a decrease in the other. This is particularly unfortunate since these are the most important components of economic production from sheep. However, Turner (1972) stated that she believed they could be increased together providing attention is paid to both in the selection plan.

Because the above relationship is so important, the other wool-fertility associations have been largely ignored. One of the studies mentioned previously (Young et al. 1963) included genetic correlation estimates between fibre character measured at 15-16 months and lambs weaned at a later age. The values were -0.55, -0.13 and -0.33 for ewes lambing at two-years, three-years and for the sum of the first three lambings. The same authors found that staple length and NLW were positively correlated in the same groups of sheep (0.32, 0.09, 0.21).

IV. Repeatability

A. Introduction

Many of the productive characters of sheep can be measured at successive times during the life of the animal. It is therefore of interest to have an indication of the tendency of individuals to maintain their ranking relation to each other. This is the concept of repeatability. A high repeatability implies that there is a strong tendency for the ranking to be maintained.

Environmental variance can be divided into two categories. The first part is due to temporary circumstances associated with the within-individual variance. The second part is a variance component which contributes to permanent between animal differences (VE_p). The remaining segment of the permanent differences is the genetic variance (VG). Repeatability expresses the proportion of the variance of a single measurement (V_p) due to permanent differences between individuals (Falconer, 1960)

$$\text{Repeatability} = r = \frac{VG + VE_p}{V_p}$$

If VG is considered as only the additive genetic variance, then it can be seen that repeatability sets the upper limit to heritability since it will always exceed heritability so long as there are permanent environmental differences between individuals. One of the purposes of repeatability is, in fact, to allow the prediction of the upper limit of heritability. A second use is to allow computation of the gain in accuracy of selection due to repeated as compared to single measurements. Because a knowledge of phenotypic relationships allows the possibility of studying the effect of culling operations on subsequent performance of the retained portion of the flock, a third is to use the repeatability

estimates to predict increases in later production through selection.

Repeatability can be estimated as an intra-class correlation, the class in this case being the repeated observations on the individual ewe. It indicates how well the lifetime performance of an animal can be predicted on average from a single record. But it gives no clue as to which record gives the best estimate. For this reason, some researchers prefer to calculate the interclass correlation between each single record and lifetime performance in terms of average or total production. If the particular single record is included in the compound record, then a degree of spurious correlation can arise, as this would then be a correlation between a whole and one of its components. Turner (1958) has shown that the correlation between a whole and one of its components is $1/\sqrt{n}$ when the components are not correlated but have equal variance where n is the number of records making up the whole record. For example, when one record is correlated with the sum of five, a correlation of 0.4 can be expected even when there is no correlation between the five components. An alternative method is to correlate one record with the remaining life-time records. For practical purposes, valuable estimates are the correlation coefficient between early records and the sum or average of remaining records, and between pairs of records at (in particular) early and later ages.

B. Wool Characteristics.

The repeatability of greasy fleece weight has been estimated by many authors, while the other wool traits have received less attention. Various estimates for greasy fleece weight are listed in Table 2.14. Many of the papers cited have been reviewed by Turner (1956, 1977) who found estimates of repeatability between 0.6 and 0.7 for Merino and allied breeds, and 0.4 to 0.6 for British breeds. Most of the additional

papers listed are in good agreement with Turner's observations. The exceptions are Katada and Takeda (1959), Knothe (1964) and Guirgis and Galal (1972). The first of these presented a range of values the lowest of which (0.35) referred to the Corriedale. The estimate of 0.41 found by Knothe is low for the Merino breed, but falls within the suggested bounds for the British breeds. A remarkably low value for greasy fleece weight repeatability of 0.03 was not discussed or explained by Guirgis and Galal (1972), but they were working with a fairly small group of ewes, and the result could be due to sampling. They cited Kadry (1971) who also found a very low value of 0.1 from the same flock, which suggests that low repeatability may be a flock or breed characteristic.

Although Turner (1956) stated that Terrill (1939) recorded an estimate within the range of 0.6 to 0.7 for his Rambouillets, in fact it was not a true repeatability, but a correlation between yearling and lifetime (two- to five-years) records. Morley (1951) converted the figure of 0.59 to a repeatability of 0.45, outside Turner's Merino range.

In terms of correlation between pairs of records, repeatability is still maintained at a similar value for greasy fleece weight, although Young et al. (1960) found a decreasing correlation as records became further separated in time when the first observation was at 15-16 months of age. The same trend can be seen in the earlier estimates of Wright and Stevens (1953), but only two intervals were analysed in this case. The findings of Mullaney et al. (1970) are interesting in that for three breeds, pairs of records for older ewes were more highly correlated than for pairs of records from younger ewes. The authors studied pairs of records from ewes taken at 18- and 30-months, and pairs of successive records from mixed age mature ewes.

Table 2.14 Estimates of Repeatability of Greasy Fleece Weight

Estimate	Breed	Comment	Reference
0.61	Border L x Cheviot	2 records	Yalcin and Bichard (1964)
0.53	Border L x Cheviot		Yalcin and Bichard (1964)
0.64	Merino	2-5 records, unselected	Young <u>et al.</u> (1960)
0.60	Merino	2-6 records, selected	Young <u>et al.</u> (1960)
0.64	Merino	2-6 records, selected,adjusted	Young <u>et al.</u> (1960)
0.66	Merino	Rams	Young <u>et al.</u> (1960)
0.68	Merino		Beattie (1961)
0.74	Merino	2-5 records	Morley (1951)
0.72	Merino	2 records	Morley (1951)
0.51	Merino	3 records	Morley (1951)
0.77	Merino	4 records	Morley (1951)
0.67	Merino	5 records	Morley (1951)
0.41	Oxford		Fahmy and Bernard (1973)
0.57	Suffolk		Fahmy and Bernard (1973)
0.55	Crossbred		Fahmy and Bernard (1973)
0.52	Pooled		Fahmy and Bernard (1973)
0.03	Barki	168 records on 70 ewes	Guirgis and Galal (1972)
0.53	Merinc x Barki	141 records on 57 ewes	Guirgis and Galal (1972)
0.45	Rambouillet	5 records	Terrill (1939)
0.56	Rambouillet	1st records	Rasmussen (1942)
0.56	Can. Corriedale	1st records	Rasmussen (1942)
0.43	Romney x B.	1st 3 records	Rasmussen (1942)
0.61	4 Breeds	adjusted for breed	Blackwell & Henderson (1955)
0.57	3 Norwegian		Gjedrem (1969)
0.49	Norwegian		Eikje (1975)
0.46	Welsh Mt.	2 or more records	Dalton (1962)
0.58	Langhe	uncorrected for env.	Mason and Dassat (1954)
0.43	Langhe	corrected for env.	Mason and Dassat (1954)

Table 2.14 Continued

0.35-0.66	Corriedale	adjusted to 42mo. Katada and Takeda (1959)	
0.58	Merino	2-6 records/ewe. Nel (1964)	
0.66	Fr. Precoce	5 shearings	Peppel and Tapia (1962)
0.41	Ger. Precoce	5 shearings	Peppel and Tapia (1962)
0.41	Polish Merino		Knothe (1964)
0.32	Awassi		Ghoneim <u>et al.</u> (1974)
0.36	Awassi	correlation between pairs	Ghoneim <u>et al.</u> (1974)

Correlation between pairs of records

0.68	Merino	15-30 month	Young <u>et al.</u> (1960)
0.62	Merino	15-42 month	Young <u>et al.</u> (1960)
0.43	Merino	15-54 month	Young <u>et al.</u> (1960)
0.51	Corriedale	Hgt-2nd shear	Wright and Stevens (1953)
0.35	Corriedale	Hgt-5th shear	Wright and Stevens (1953)
0.63	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.79	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.62	Corriedale	18-30 month	Mullaney <u>et al.</u> (1970)
0.79	Corriedale	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.51	Polwarth	18-30 month	Mullaney <u>et al.</u> (1970)
0.84	Polwarth	mixed 18-54 month	Mullaney <u>et al.</u> (1970)

Correlation between single and compound records

0.62	Mutton Merino	Yrlg-lifetime	Gärtner and Ungern- Sternberg (1938)
0.57	Merino-Landschaf	Yrlg-average lifetime	Nothacker (1952)
0.63	Merino-Landschaf	Yrlg-lifetime	Wolf (1951)
0.44	Romney	Hgt-sum of 4 mature	Wright and Stevens (1953)
0.62	Romney	Hgt-sum of 5 (inc. Hgt)	Wright and Stevens (1953)
0.72	Corriedale	Pgt-mature average (3 records)	Wright and Stevens (1953)
0.84	Corriedale	Hgt-lifetime (inc. Hgt)	Wright and Stevens (1953)
0.61	Welsh Mt.	first-mean of sub- sequent	Doney (1958)

Table 2.14 Continued

0.72	Merino	Hgt-lifetime	Young <u>et al.</u> (1960)
0.86	Merino	30 month-lifetime	Young <u>et al.</u> (1960)
0.86	Merino	42-month-lifetime	Young <u>et al.</u> (1960)
0.86	Merino	54 month-lifetime	Young <u>et al.</u> (1960)
0.59	Rambouillet	Yrlg-lifetime average	Terrill (1939)
0.56	Perendale	Hgt- 2-5 year	Elliott (1975)

The correlation between a record taken at any early age and the sum or mean of records taken later has received attention from several authors as listed in Table 2.14. Some have included the single record in the lifetime performance (Wolf, 1951; Wright and Stevens, 1953; Young et al., 1960) producing a correspondingly higher estimate due to spurious correlation as described earlier.

All of the estimates of repeatability of staple length in Table 2.17 are above 0.3 except that of Guirgis and Galal (1972) which is noticeably lower (0.16). A higher value (0.32) was calculated by Kadry (1971) from data on the same flock. Discounting the one low value, the range is around 0.3 to 0.7.

Correlations between pairs of records for staple length are high (Table 2.17). Gjedrem (1969) correlated all pairs of records collected between six months and 66 months at 12 monthly intervals. The correlations ranged from 0.60 to 0.84. The lowest values involved earliest and latest ages, while the highest correlations were between consecutive records of oldest age groups. There was a noticeable increasing trend between ^{pairs of} adjacent or closely related observations as the animals became older. No other reports are comprehensive enough to suggest a similar trend.

Young et al. (1960) noted values greater than 0.83 for the correlation between single and lifetime staple length records (two- to four-years of age) for all three single ages studied. However, the single age was again a component of the lifetime data.

Beattie (1961), Young et al. (1960) and Gjedrem (1969) have all recorded repeatability estimates for fibre diameter between 0.50 and 0.70. Various estimates derived by Young et al. (1960) and Mullaney et al. (1970) between pairs of records fell within the same

Table 2.15 Estimates of Repeatability of Wool Character

Estimate	Breed	Comment	Reference
0.46	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.48	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.50	Corriedale	18-30 month	Mullaney <u>et al.</u> (1970)
0.46	Corriedale	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.50	Polwarth	18-30 month	Mullaney <u>et al.</u> (1970)
0.51	Polwarth	mixed 18-50 month	Mullaney <u>et al.</u> (1970)
<u>Correlation between single and compound records</u>			
0.28	Perendale	Hgt- 2-5 year	Elliott (1975)

Table 2.16 Estimates of Repeatability of Quality Number

Estimate	Breed	Comment	Reference
<u>Correlation between pairs of records</u>			
0.60	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.66	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.68	Corriedale	18-30 month	Mullaney <u>et al.</u> (1970)
0.70	Corriedale	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.71	Polwarth	18-30 month	Mullaney <u>et al.</u> (1970)
0.78	Polwarth	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
<u>Correlation between single and compound records</u>			
0.52	Perendale	Hgt- 2-5 year	Elliott (1975)

Table 2.17 Estimate of Repeatability of Staple Length

Estimate	Breed	Comment	Reference
0.58	Merino	unselected, 2-5 records/ewes	Young <u>et al.</u> (1960)
0.39	Merino	selected on CFW 2-6 records/ewes	Young <u>et al.</u> (1960)
0.57	Merino		Beattie (1961)
0.71	Merino		Morley (1951)
0.16	Barki	168 records on 70 ewes	Guirgis and Galal (1972)
0.32	Merino x Barki	141 records on 57 ewes	Guirgis and Galal (1972)
0.38	Barki		Kadry (1971)
0.57	Rambouillet	5 records	Terrill (1939)
0.56	Welsh Mt.	2 or more records	Dalton (1962)
0.64	Norwegian		Gjedrem (1969)
0.31-0.61	Corriedale		Katada and Takeda (1959)
0.32	Polish Merino		Knothe (1964)

Correlation between single and compound records

0.84	Merino	Hgt-lifetime	Young <u>et al.</u> (1960)
0.86	Merino	30 month-lifetime	Young <u>et al.</u> (1960)
0.84	Merino	42 month-lifetime	Young <u>et al.</u> (1960)
0.69	Rambouillet	Yrlg-lifetime	Terrill (1939)
0.49	Perendale	Hgt-lifetime	Elliott (1975)

Correlation between pairs of records

0.58	Merino	Hgt-30 month	Young <u>et al.</u> (1960)
0.55	Merino	Hgt-42 month	Young <u>et al.</u> (1960)
0.75	Welsh Mt.	20-32 month	Doney (1955)
0.75	Welsh Mt.	24-36 month	Doney (1958)
0.60-0.84	Norwegian	see text	Gjedrem (1969)
0.61	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.57	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.62	Corriedale	18-30 month	Mullaney <u>et al.</u> (1970)
0.63	Corriedale	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.67	Polwarth	18-30 month	Mullaney <u>et al.</u> (1970)
0.69	Polwarth	mixed 18-54 month	Mullaney <u>et al.</u> (1970)

Table 2.18 Estimates of Repeatability of Fibre Diameter

Estimate	Breed	Comment	Reference
0.60	Merino	selected on CFW 2-6 records/ewe	Young <u>et al.</u> (1960)
0.50	Merino	unselected 2-5 records/ewe	Young <u>et al.</u> (1960)
0.53	Merino	2-5 records	Beattie (1961)
0.69	Norwegian		Gjedrem (1969)
<u>Correlation between pairs of records</u>			
0.42	Merino	Hgt-30 month	Young <u>et al.</u> (1960)
0.55	Merino	Hgt-42 month	Young <u>et al.</u> (1960)
0.66	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.68	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.67	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.66	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.68	Merino	18-30 month	Mullaney <u>et al.</u> (1970)
0.66	Merino	mixed 18-54 month	Mullaney <u>et al.</u> (1970)
0.50-0.85	Norwegian	See text	Gjedrem (1969)
<u>Correlation between single and compound records</u>			
0.77	Merino	Hgt-lifetime	Young <u>et al.</u> (1960)
0.80	Merino	30-month-lifetime	Young <u>et al.</u> (1960)
0.88	Merino	42-month-lifetime	Young <u>et al.</u> (1960)
0.59	Perendale	Hgt-lifetime	Elliott (1975)

range. Gjedrem (1969) examined the phenotypic association between many pairs of records as described earlier. His range was 0.50 to 0.85 for fibre diameter with a tendency for the higher values to occur among consecutive records of older ewes. The correlations showed a decrease as records became further separated.

The concept of correlating an early record with lifetime records has been studied only by Young et al. (1960) and Elliott (1975) in regard to fibre diameter, and their high estimates are summarised in Table 2.18.

The correlations between pairs of records was given as 0.46 - 0.51 for character, 0.60 - 0.78 for quality number by Mullaney et al. (1970), while Elliott (1975) found that the correlations between hogget and mature total were 0.28 and 0.52 for the two traits respectively (Table 2.15).

Estimates of repeatability for the wool characters are generally high, which implies that selection on an early record should be the most efficient method of increasing production in the current flock. This idea is supported in particular by Young et al. (1960) who correlated single greasy fleece weight, fibre diameter and staple length records at various ages with lifetime production and found that hogget records gave just as good a prediction of lifetime performance as any other age.

C. Number of Lambs Weaned.

Considering the importance of reproduction rate, surprisingly few papers have been published referring to the repeatability of lambs weaned.

Young et al. (1963) used two methods on Merino data, the analysis of variance and a regression system adapted from Lush (1956). The methods gave similar estimates of 0.08 with ranges of 0.02 to 0.10 (Anova) and 0.04 to 0.11 (regression). They also found that the records

Table 2.19 Estimates of Repeatability of Number of Lambs Weaned.

Estimate	Breed	Comment	Reference
0.03-0.22 (Average 0.13)	Several	LW/EJ	Inskeep <u>et al.</u> (1967)
0.01	Merino	LW/EJ Anova	Kennedy (1967)
0.11	Merino	LW/EJ Regression	Kennedy (1967)
0.01	Scottish BF	LW/EJ	Purser (1965)
0.07	Scottish BF	LW/EL	Purser (1965)
0.07	Welsh Mt.	LW/EJ	Purser (1965)
0.10	Welsh Mt.	LW/EL	Purser (1965)
0.12-0.25	Romney	Successive record pairs	Rae and Ch'ang (1955)
0.00	BL x Cheviot	Shearling bred	Yalcin and Richard (1964)
0.10	BL x Cheviot	Shearling bred	Yalcin and Richard (1964)
0.08	BL x Cheviot	Lamb-bred	Yalcin and Richard (1964)
0.17	Romney	LW/EJ	Lundie (1971)
0.08	Merino	Regression	Young <u>et al.</u> (1963)
0.08	Merino	Anova	Young <u>et al.</u> (1963)
0.08	Merino	24 month	Young <u>et al.</u> (1963)
0.10	Merino	36 month	Young <u>et al.</u> (1963)
0.05	Merino	48 month	Young <u>et al.</u> (1963)

of three-year-olds were more repeatable than two- or four-year-old ewes. The same two methods were employed by Kennedy (1967) and results were obtained in agreement with the previous author. The regression methods have the highest estimate in both cases. Analysis of variance was preferred by Purser (1965). Lambs weaned per ewe mated was more repeatable amongst Welsh Mountain than Scottish Blackface, although the difference was less when the data were analysed on the basis of ewes lambing, which removes prenatal sources of variability. Yalcin and Bichard (1964) recorded intraclass correlation estimates of repeatability of lambs weaned based on ewes lambing and found none which exceeded 0.1. Two groups of data were collected from ewes first bred as shearlings, while a third was collected from ewes which were first mated as lambs.

Inskeep et al. (1967) used a novel method of pairing where the first and second records, and then the second and third, third and fourth were treated as pairs. Repeatability of NLW per ewe joined averaged over eight breed and crossbreed groups was 0.13 with a range of 0.03 to 0.22.

The two repeatability values available on the Romney suggest the possibility that the repeatability of lambs for this breed may be higher than for other breeds. Rae and Ch'ang (1955) calculated repeatability as a correlation between records at successive ages and noted values of 0.12 to 0.25. Lundie's (1971) estimate of 0.17 was computed by analysis of variance.

The repeatability of number of lambs weaned is low according to reports reviewed. This implies that temporary environmental factors have a large effect, while permanent environmental and genetic contributions to between sheep differences are small. A low genetic component has already been confirmed in the heritability section. The outcome is

that selection on the basis of performance at a single lambing is unlikely to result in a large increase in lifetime production of the flock. Efforts to increase average lamb production by early selection will be confounded by the inefficiency inherent in the low repeatability of reproductive traits.

V. Phenotypic Correlations

A. Introduction

The phenotypic correlation measures the association between observed characters within sheep. Causes of phenotypic correlation include the factors affecting the genetic covariance as outlined earlier, but in addition contributions can be expected from environmental sources.

Phenotypic correlations are calculated to enable an assessment to be made of the probable effects on other traits when selection is applied to a characteristic of interest within the current flock. If the correlated response is undesirable, then counter-selection may be necessary. A second usage for the correlation coefficient is to aid in establishing whether or not indirect selection for some difficult-to-observe trait can be more easily achieved by selecting for a correlated, easily measured character.

B. Wool Characteristics.

Phenotypic correlation between the various wool traits assembled from the literature are listed in Table 2.20. Some important conclusions to be shown from these estimates are that

- (i) Selection for fleece weight will cause correlated responses amongst the retained group towards increased fibre diameter, staple length and character, and decreased quality number.

Table 2.20 Estimates of Phenotypic Correlations. Wool Traits

Value	Breed	Age (months)	Comment	Reference
Greasy fleece weight				
- fibre diameter				
0.36	Merino	30		Mullaney <u>et al.</u> (1970)
0.32	Corriedale	30		Mullaney <u>et al.</u> (1970)
0.40	Polwarth	30		Mullaney <u>et al.</u> (1970)
0.50	Perendale	15-16		Elliott (1975)
- quality number				
-0.36	Merino	30		Mullaney <u>et al.</u> (1970)
-0.34	Corriedale	30		Mullaney <u>et al.</u> (1970)
-0.45	Polwarth	30		Mullaney <u>et al.</u> (1970)
-0.33 ¹	Romney & x breed		Qual.No.46-54	Henderson (1953a)
-0.37 ¹	3/4 breed		Qual.No.50-56	Henderson (1953a)
-0.47 ¹	½-breed x corriedale		Qual.No.54-64	Henderson (1953a)
-0.16	Perendale	15-16		Elliott (1975)
- staple length				
0.23	Merino	30		Mullaney <u>et al.</u> (1970)
0.33	Corriedale	30		Mullaney <u>et al.</u> (1970)
0.33	Polwarth	30		Mullaney <u>et al.</u> (1960)
0.27	Merino	Mixed		Beattie (1956)
-0.08	Merino	24		Beattie (1956)
0.44	Perendale	15-16		Elliott (1975)
- Character				
-0.09	Merino	30		Mullaney <u>et al.</u> (1970)
0.19	Corriedale	30		Mullaney <u>et al.</u> (1970)
0.06	Polwarth	30		Mullaney <u>et al.</u> (1970)
0.23	Perendale	15-16		Elliott (1975)
Quality number				
- fibre diameter				
-0.31	Merino	30		Mullaney <u>et al.</u> (1970)
-0.52	Corriedale	30		Mullaney <u>et al.</u> (1970)
-0.53	Polwarth	30		Mullaney <u>et al.</u> (1970)
-0.26	Perendale	15-16		Elliott (1975)

Table 2.20 Continued

- staple length				
-0.30	Merino	30		Mullaney <u>et al.</u> (1970)
-0.42	Corriedale	30		Mullaney <u>et al.</u> (1970)
-0.30	Polwarth	30		Mullaney <u>et al.</u> (1970)
-0.45	Perendale	15-16		Elliott (1975)
- character				
0.29	Merino	30		Mullaney <u>et al.</u> (1970)
-0.29	Corriedale	30		Mullaney <u>et al.</u> (1970)
0.04	Polwarth	30		Mullaney <u>et al.</u> (1970)
0.13	Perendale	15-16		Elliott (1975)
Fibre diameter				
- staple length				
-0.04	Merino	30		Mullaney <u>et al.</u> (1970)
0.27	Corriedale	30		Mullaney <u>et al.</u> (1970)
0.15	Polwarth	30		Mullaney <u>et al.</u> (1970)
-0.19	Rambouillet	12-108		Jones <u>et al.</u> (1944)
0.34	Perendale	15-16		Elliott (1975)
- character				
-0.34	Merino	30		Mullaney <u>et al.</u> (1970)
-0.01	Corriedale	30		Mullaney <u>et al.</u> (1970)
-0.18	Polwarth	30		Mullaney <u>et al.</u> (1970)
0.12	Perendale	15-16		Elliott (1975)
Staple length				
- character				
0.16	Merino	30		Mullaney <u>et al.</u> (1970)
0.19	Corriedale	30		Mullaney <u>et al.</u> (1970)
0.14	Polwarth	30		Mullaney <u>et al.</u> (1970)
0.10	Perendale	15-16		Elliott (1975)

1. Regression of fleece weight on quality number.

- (ii) Selection for staple length will increase fleece weight and character, but decrease quality number. The effect on fibre diameter is uncertain, but the quality number association with staple length, and the reasonably high correlations of 0.27 and 0.15 (Mullaney et al. 1970) and 0.34 (Elliott, 1975) suggest a positive association.
- (iii) The phenotypic correlations are generally smaller than the genetic equivalents, but of the same sign. The similarity in sign is of vital importance because it establishes that if the breeder's selection plans are defined in terms of the wool characters discussed here, then both his short and long term objectives will be satisfied without conflict.

C. Wool Characteristics and Number of Lambs Weaned.

The phenotypic correlation between wool characters and number of lambs weaned has been studied only for fleece weight, staple length and fibre diameter. In some cases various functions in relation to time or age have been used to transform single observations to compound observations. Shelton and Menzies' (1968b) figures associated fleece weight as a mean of at least three records collected between three- and seven-years of age, with number of lambs raised (compared with number born).

Many breeders would consider that it was desirable to be able to select hoggets on the basis of their greasy fleece weights, and would be interested in the later lamb production performance of the retained ewes. Kennedy (1967), Young et al. (1963) and Elliott (1975)

have produced the necessary correlations which are all negative, the largest being -0.12 . Cunningham and Gjedrem (1970) reviewed many papers and concluded that as they had found both positive and negative correlations, all small, between various measures of fertility, including NLW, and greasy fleece weight, the two characteristics are probably independent. If this is true, and there is no real evidence to the contrary, then selection for fleece weight will have no effect on lifetime fertility.

All of the correlations between staple length and number of lambs weaned, and between fibre diameter and NLW are similarly very small.

Table 2.21 Estimates of Phenotypic Correlations.
Number of Lambs Weaned With Wool Traits.

Value	Breed	Age (Months)	Comment	Reference
Lambs weaned				
- greasy fleece weight				
-0.12	Merino	24xHgt		Kennedy (1967)
-0.01	Merino	24xHgt		Young <u>et al.</u> (1963)
-0.02	Merino	36xHgt		Young <u>et al.</u> (1963)
0.03	Merino	(Σ first 3)xHgt		Young <u>et al.</u> (1963)
-0.08	Dala and Steiger	Mixed		Gjedrem (1966)
-0.08	Rambouillet		Mean FW Total lamb prod.	Shelton and Menzies (1963b)
0.02	Combined			Eikje (1975)
0.03	Galway		Index for NLW	More O'Ferrall (1976)
0.04		24		More O'Ferrall (1976)
- fibre diameter				
0	Merino	24xHgt		Young <u>et al.</u> (1963)
-0.02	Merino	36xHgt		Young <u>et al.</u> (1963)
0.09	Merino	(Σ first 3)xHgt		Young <u>et al.</u> (1963)
- staple length				
0.03	Merino	24xHgt		Kennedy (1967)
0.03	Merino	24xHgt		Young <u>et al.</u> (1963)
0.02	Merino	36xHgt		Young <u>et al.</u> (1963)
0.06	Merino	(Σ first 3)xHgt		Young <u>et al.</u> (1963)

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

MATERIALSI The Sheep and Environment

A. The Farm.

The data were collected from a Perendale flock run on the Massey University hill country farm about 4 km south of the western end of the Manawatu Gorge. The area of the farm is 425 hectares, consisting of about 325 hectares of hill and the remainder flats. The land to the back of the farm (south) is second to third class hill, much of which is easy contour, rising to an altitude of about 213 metres. The 110 hectares nearer the front of the property is of steeper contour.

B. The Perendale.

The Perendale was developed by interbreeding the Cheviot-Romney cross after early trial work beginning at Massey University in 1939. The Cheviot-Romney cross led to the establishment of the Perendale as a breed in 1960. The various papers published on the testing of the crossbred and its comparison with the Romney have been reviewed by Dalton (1971).

C. Management.

Only those aspects of management which affect the collection or analysis of records will be discussed.

The lambing season began about the 20th of August. One of the economic advantages of the Perendale is their "easy-care" potential at lambing and Peren (1970) stated that the breed is best left alone at this time. The older lambs may be three to five weeks of age when first handled at docking, although the youngest will only be a few days old. Welch and Kilgour (1970) found that in about ten percent of cases, ewe-lamb

relationships will be misidentified due to mis-mothering. Their results were based on a trial involving Romneys at a very high stocking rate (123 ewes per hectare) where the opportunities for mis-mothering would have been greater than in the commercial situation. Under extensive stocking conditions, incorrect identification from this cause would be reduced due to less contact between sheep, and the increased opportunity for the lambing ewe to isolate herself from the other sheep.

Lambs are weaned off the ewes during the first week in December.

The main ewe flock is shorn during the first or second week in November. The hoggets are shorn at the beginning of October when they are 12-13 months of age, and carrying eight to nine months' wool growth.

Hogget bodyweight is recorded in October after shearing. Selection of candidates for entry into the flock is based on maintaining the Perendale "type", and involves culling abnormally coarse woolled sheep (few fell below the 48s count benchmark), or those which fail to exhibit wool-free points. The selection of fine wool sheep was given particular emphasis in the early 1960s, but recently fertility has been given attention and the hoggets are now selected partly on an index based on their dams' performance. Poor conformation or physical unsoundness would also exclude a ewe from consideration as a replacement. About half of the hoggets available enter the flock as two-tooths. Towards the end of the period under consideration, this proportion represented about 230 sheep, but previously fewer replacements were available, or were required, when the flock was smaller.

Once a ewe is drafted into the stud flock she may be subject to continuing selection for fine wool and for reproductive performance and indirect selection for other traits as correlated responses. Ewes

culled in this way may remain in the commercial flock and therefore the overall selection is of minor intensity. Stud two-tooth ewes which fail to lamb or older ewes which do not maintain a 100 percent lambing average are deregistered. Deaths from disease or misadventure account for further losses and others are culled for ill-health and teeth wear.

Rams are selected for wool character, and for a quality number in the 50/52 range which is about average for the breed. The fertility rating of the dam and paternal grandam based on the lamb production index (Rae, 1958b) are also important factors. Particular attention is given to conformation and physical and sexual soundness. The majority of rams are used for only one year.

II The Data

Data were available on a mixture of stud and commercial sheep born from 1961 to 1972 inclusive. The distribution of ages within years is shown in Table 3.1. It can be seen that ages are partially confounded with years. It is also apparent that different numbers of years of data are available for each age, and this is a major factor in accounting for the reduction in total numbers of records from one age to the next.

Tables 3.1 and 3.2 do not include the progeny of any sire with less than three offspring.

diameter
Fibre_{mean} was not measured after record year 1972 and therefore the data available for this character are less than for the remaining traits. The initial analyses were performed on records which included a full set of observations including fibre diameter.

Table 3.1

Distribution of Ages Within Years

Age	Record Year												Total
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	
2	54 (54)	86 (86)	95 (95)	91 (91)	137 (137)	100 (100)	130 (130)	168 (133)	222 (216)	174 (163)	238	229	1724 (1205)
3		51 (51)	78 (78)	67 (67)	87 (87)	104 (103)	55 (55)	99 (90)	150 (148)	198 (198)	129	142	1160 (877)
4			48 (48)	68 (68)	60 (60)	51 (51)	67 (67)	50 (46)	63 (63)	113 (113)	113	93	726 (516)
5				36 (36)	63 (63)	45 (42)	39 (39)	54 (46)	28 (26)	50 (50)	54	80	449 (302)
5 Consec. Records (Final year)				25 (25)	57 (57)	40 (39)	40 (40)	52 (43)	29 (25)	42 (35)	49	69	403 (264)

Figures in parentheses refer to numbers of animals assessed for fibre diameter.

Table 3.2 Number of Sire Groups Analysed

<u>Age</u>	<u>Sires</u>	<u>Records/Sire</u> <u>Group</u>
2	97 (75)	17.8 (16.1)
3	82 (67)	14.1 (13.1)
4	65 (50)	11.2 (10.3)
5	56 (37)	8.0 (8.2)
5 Consec. Records	56 (36)	7.2 (7.3)

Table 3.3 Daughter-Dam Pairs

<u>Age</u>	<u>Pairs of Records</u>	<u>Dtrs./Dam</u>
2	922 (596)	1.6
3	584 (373)	1.4
4	296 (151)	1.3
5	125 (45)	1.3

Figures in parentheses refer to numbers of animals
assessed for fibre diameter.

Table 3.4 Numbers of Ewes With Records at Both Age 1 and Age 2

Age 1	Age 2			
	2	3	4	5
1	1650 (1186)	1112 (854)	710 (523)	455 (309)
2		1137 (832)	710 (490)	447 (298)
3			733 (515)	460 (303)
4				469 (311)

Figures in brackets refer to numbers of animals assessed for fibre diameter.

Table 3.5 Quality Number Codes

Quality Number	Code
44	44
44/46	45
46	46
46/48	47
48	48
48/50	49
50	50
50/52	51
52	52
52/54	53
54	54
54/56	55
56	56
56/58	57
58	58

Records were on file for ewes older than five years but the numbers declined greatly with each age increment. There were insufficient daughter-dam pairs at five years of age for the derivation of meaningful results, and these were not analysed.

The characters recorded and analysed were as follows:

(i) Greasy Fleece Weight.

Greasy fleece weight was measured as each fleece was removed and recorded to the nearest 0.01 kg. The weight includes belly wool.

(ii) Staple Length.

Staple length was measured to the nearest 0.5 cm by rule and represented the length from the cut end of the unstretched staple to a point midway between the beginning of the taper and the end of the longest fibre.

(iii) Quality Number.

Quality number was a subjective appraisal of wool fineness and is influenced by crimp frequency and lustre as well as technician variation. It is generally an inaccurate assessment of fibre fineness. Quality number grades were coded for ease of analysis, and the codes used are listed in table 3.5.

(iv) Fibre Diameter.

Fibre diameter was an assessment of mean diameter by the air flow technique (Ross, 1958). Estimates by this technique can be biased down-wards by the effect of medullation when this is present (Wickham, 1972).

(v) Character.

Character was graded on a one to nine scale and reflects clarity and evenness of crimp, and absence of tippiness and medullation.

Midside samples were the basis of the staple length, quality number, fibre diameter and character records.

(vi) Number of Lambs Weaned.

After mustering for docking, the dam-offspring relationship were established, the lambs were tagged and their dams recorded. Number of lambs weaned is a record of whether zero, one or two lambs, credited to a ewe at docking were still in the flock at weaning.

(vii) Hogget Body Weight.

Body weight is recorded to the nearest 0.1 kg when the hoggets are weighed within two weeks of October shearing. Only a minor part of the analysis involved this trait.

CHAPTER FOUR

METHODSI. Analysis of VarianceA. Least Squares and Computing Methods.

A preliminary analysis of variance was carried out as a first step in determining the importance of various factors in accounting for the observed variation in each measured variable. If the environmental effects in the data can be identified and removed, estimates of genetic parameters will then be free of these factors. To simplify computation, a subset of the data was selected in which each record had observations on all variables of interest. Fibre diameter had not been recorded in recent years and this limited the number of suitable records.

To account for disproportion in the various subclass numbers, the least squares method of fitting constants was used (Hazel, 1946; Kempthorne, 1952). The basis of the method is the minimization of the sums of squares of the deviations of the observations from their expected values under the model. Briefly the procedure is as follows:

A general mathematical model describing a datum can be written in matrix terms as:

$$Y = Xb + e$$

Y is a nxl vector of observations

x is a nxp incidence matrix of effects in the model

b is a pxl vector of unknown parameter values to be estimated

e is a nxl vector of random error effects

$$E(e) = 0, E(ee') = \sigma_e^2 I$$

It follows that

$$e = y - Xb$$

and since $E(y) = Xb$

$$\begin{aligned} e'e &= (y - E(y))' (y - E(y)) \\ &= (y - Xb)' (y - Xb) \\ &= y'y - 2b'X'y + b'X'Xb \end{aligned}$$

The calculation of the estimator of b which minimizes $e'e$ requires the differentiation of $e'e$ with respect to b and equating the partial derivative to zero. The normal equations which result are

$$\begin{aligned} X'X\hat{b} &= X'y \\ \text{or } \hat{b} &= (X'X)^{-1}X'y \end{aligned}$$

If $X'X$ is not of full rank, it has no inverse and therefore the equations have no unique solution, and b is not estimable. One of many solutions can be derived by use of a generalized inverse of $X'X$ which will allow linear functions of the elements of b to be estimated. The alternative is to apply restrictions to the $X'X$ matrix and $X'y$ vector and solve for $p-1$ of the b_i^0 's. The remaining b_i^0 is calculated as a function of the other b_i^0 's or set equal to zero, depending upon the restriction applied. A generalized inverse can be computed by restricting $X'X$, inverting, and calculating the missing rows and columns of the inverse as linear combinations of the other elements, analogous to finding the final b_i^0 above. The two methods give identical solutions corresponding to the constraint applied. In this analysis, the restriction used was that the sum of the constants calculated for each set of factors in the model should sum to zero

* $\hat{}$ is used to indicate an estimate. \hat{b} is an estimate of the parameter b .
 ** 0 is used to indicate a solution. b^0 is a solution to the normal equations, but does not estimate the parameter b .

($\sum b_i^0 = 0$), and the final b_i^0 within each factor was calculated as the negative sum of the other elements of the solution vector. Matrices of order less than 30 were inverted using the FORTRAN scientific subroutine package, otherwise the partitioning method was used as described by Searle (1966).

Wherever sires were included as a factor in a model, it was necessary to absorb the sire subclasses into the other effects to reduce the model to a manageable size. This was achieved by defining a compound parameter $s_{ij} = \mu + t_i + s_{ij}$ and absorbing all three terms. A programming method designed to partially avoid the storage restrictions of FORTRAN IV and which included absorption was developed, and will be briefly described in general terms.

Let a model be

$$Y_{ijk} = \mu + F_i + b_j + e_{ijk}$$

$$i = 1 \dots n$$

$$j = 1 \dots p$$

$$p \text{ is very much greater than } n$$

F_i represents all factors other than b_j in the model. The normal equations are partitioned as

$$\begin{bmatrix} A_{n \times n} & B_{n \times p} \\ B'_{p \times n} & C_{p \times p} \end{bmatrix} \begin{bmatrix} F_{n \times 1} \\ b_{p \times 1} \end{bmatrix} = \begin{bmatrix} X'y_1 \\ X'y_2 \end{bmatrix}$$

The method is simply to set up A , B , C , $X'y_1$ and $X'y_2$ as separate matrices as the data are read in. C is stored as a column vector, but is operated upon as though it were a diagonal matrix. It will therefore not have the usual effect of limiting the size of the matrix. The limitation in matrix size is now controlled by B . (B' is not created

at this stage but may be later by transposition). If the model included 50 F subclasses then B could be of order 50 x 1250 before the maximum storage limit of approximately 62500 elements was reached.

Absorption is completed as

$$S = A - B'C^{-1}B$$

$$Y = X'y_1 - B'C^{-1}X'y_2$$

C is a diagonal matrix and the inverse is calculated as the reciprocal of the individual elements. A solution (F^0) for the F parameters after (n-Rank (F)) restrictions have been applied is

$$F^0 = S^{-1}Y$$

The total reduction in sum of squares for the model is

$$*R(\mu, F, b) = F^0Y + y_2'XC^{-1}X'y_2$$

The absorption procedure is computationally more efficient where the absorbed factor contains a large proportion of the total subclasses in the model as it reduces the order of the matrix requiring inversion. The only inversion required is C^{-1} which may be large but generally is diagonal. It becomes inefficient for smaller classifications as the actual absorption process is intricate and would then result in an inversion of a matrix only slightly smaller than the original.

B. Fitting Models to the Data.

A model which could describe a datum on a wool trait is

$$Y_{ijklmn} = \mu + t_i + s:t_{ij} + d_k + r_l + w_m + td_{ik} + tr_{il} + tw_{im} + dr_{kl} + dw_{km} + rw_{lm} + e_{ijklmn}.$$

Where μ = the overall population mean when there are equal subclass frequencies.

* The terminology of Searle (1971a) will be used extensively throughout this text. R(.) implies reduction, and the letters within the parentheses refer to the model being fitted. R(.|..) means that one factor is fitted after another. The plural definition is also implied.

t_i = the effect of the i th year.

$i = 1$ to 10 (Two-year-old records)

$i = 1$ to 9 (Three-year-old records)

$i = 1$ to 8 (Four-year-old records)

$i = 1$ to 7 (Five-year-old records)

$s:t_{ij}$ = the effect of the j th sire nested within the i th year.

$j = 1$ to 75 (Two-year-old records)

$j = 1$ to 67 (Three-year-old records)

$j = 1$ to 50 (Four-year-old records)

$j = 1$ to 37 (Five-year-old records)

d_k = the effect of the k th age of the dam of the ewe observed.

$k = 1$ to 4 denoting two-, three-, four-, or five-year and older dams respectively.

r_l = the effect of the l th rearing rank.

$l = 1$ or 2 , specifying ewes reared as a single or ewes reared as a twin, respectively. The very few triplets available were included with the twins.

w_m = the effect of the number of lambs weaned.

$m = 1$ to 3 , determining zero, one or two or more lambs weaned respectively.

td_{ik} = the effect of interaction between year and dam age.

tr_{il} = the effect of interaction between year and rearing rank.

tw_{im} = the effect of interaction between year and number of lambs weaned.

dr_{kl} = the effect of interaction between dam age and rearing rank.

dw_{km} = the effect of interaction between dam age and number of lambs weaned.

Y_{ijklmn} = the observation on the n th individual, of the m th lambs weaned class, reared under the l th rearing rank regime, daughter of a ewe in the k th age group and the j th sire in the i th year.

e_{ijklmn} = a random error term peculiar to the observation specified by the i, j, k, l, m, n subscripts, describing the deviation of the observation from the expected value under the model.

All factors in the model were considered as fixed effects except the e_{ijklmn} and $s:t_{ij}$, which are defined as random factors with zero mean, and variance $\sigma^2_{s:t}$ respectively. The error is further assumed to be normally distributed for the purposes of the significance testing.

Year effects removed in the model are a conglomerate of factors which affect all animals in a particular classification group alike. Age, year of birth and year of observation are confounded as definition of any two automatically determines the level of the third. Separate analysis within each age combines years of birth and record. Therefore year effects in the context of this analysis include any factor which affects early development of the individual as well as environmental dissimilarities peculiar to the year in which the wool was grown or the lamb raised.

A model to describe an observation on the trait lambs weaned varied from that above by the exclusion of terms in w_m .

The model is:

$$Y_{ijkln} = \mu + t_i + s:t_{ij} + d_k + r_l + tf_{ik} + tr_{il} + dr_{kl} + e_{ijkln}$$

where the terms are as described previously.

In both situations, interactions involving sires were assumed to be unimportant.

The reductions in sums of squares and expectations for the main effects for the analysis of variance are shown in Table 4.1 ($q^2 =$ quadratic in a fixed effect).

Fitting more than two interactions simultaneously in a model becomes computationally cumbersome and therefore the FORTRAN program was designed to handle a large number of main effects, but only zero, one or two interaction classes. The interactions involving lambs weaned as a factor (which are only valid for the wool traits) were run first. The remaining three interaction classes then had to be run twice - once

Table 4.1 Main Effects and Nested Factor. Calculation of Reductions in Sums of Squares and Expectations of Mean Squares (EMS).

Factor	Reduction	EMS
Year	$R(t \mu, d, r, w)$ $\beta'Z^{-1}\beta$	$\sigma_e^2 + k_5q_t^2 + k_6\sigma_{s:t}^2$
Sire:Year	$R(s:t \mu, t, d, r, w)$	$\sigma_e^2 + k_4\sigma_{s:t}^2$
Dam Age	$R(d \mu, t, r, w)$ $\beta'Z^{-1}\beta$	$\sigma_e^2 + k_3q_d^2$
Rearing Rk	$R(r \mu, t, d, w)$ $\beta'Z^{-1}\beta$	$\sigma_e^2 + k_2q_r^2$
NLW*	$R(w \mu, t, r, d)$	$\sigma_e^2 + k_1q_w^2$
Error	$y'y - R(\mu, t, s:t, d, r, w)$	σ_e^2

The term $\beta'Z^{-1}\beta$ refers to direct method of sums of squares computation.

$q^2 =$ quadratic term (fixed effect).

* NLW omitted as an environmental effect from NLW models.

Table 4.2 Interactions Amongst Fixed Effects.
Calculation of Reductions in Sums of Squares and
Expectations of Mean Squares (EMS)

Interaction	Reduction	EMS
<u>Wool Traits</u>		
NLW x Year	$R (tw \mu, t, d, r, w, wd)$	$\sigma_e^2 + k_{15}q_{tw}^2$
NLW x Dam Age	$R (wd \mu, t, d, r, w, tw)$	$\sigma_e^2 + k_{14}q_{wd}^2$
Error	$y'y - R (\mu, t, s:t, d, r, w, tw, wd)$	σ_e^2
NLW x Rearing Rk	$R (rw \mu, t, d, r, w)$	$\sigma_e^2 + k_{13}q_{rw}^2$
Error	$y'y - R (\mu, t, s:t, d, r, w)$	σ_e^2
Dam Age x Rearing Rk	$R (dr \mu, t, d, r, w, td)$	$\sigma_e^2 + k_{12}q_{dr}^2$
Dam Age x Year	$R (td \mu, t, d, r, w, dr)$	$\sigma_e^2 + k_{11}q_{td}^2$
Error	$y'y - R (\mu, t, s:t, d, r, w, dr, td)$	σ_e^2
Year x Rearing Rk	$R (tr \mu, t, d, r, w)$	$\sigma_e^2 + k_{10}q_{tr}^2$
Error	$y'y - R (\mu, t, s:t, d, r, w, tr)$	σ_e^2
<u>Number of Lambs Weaned</u>		
Dam Age x Rearing Rk	$R (dr \mu, t, d, r, td)$	$\sigma_e^2 + k_9q_{dr}^2$
Dam Age x Year	$R (td \mu, t, d, r, dr)$	$\sigma_e^2 + k_8q_{td}^2$
Error	$y'y - R (\mu, t, s:t, d, r, dr, td)$	σ_e^2
Year x Rearing Rk	$R (tr \mu, t, d, r)$	$\sigma_e^2 + k_7q_{tr}^2$
Error	$y'y - R (\mu, t, s:t, d, r, tr)$	σ_e^2

All calculated by $\beta' Z^{-1} \beta$

for the wool characters, and once for lambs weaned.. The order of analysing interaction models and the expectation of the reductions in sums of squares are listed in Table 4.2.

C. Significance Testing.

Formal F-tests of significance were carried out on the factors affecting the wool variables. For reasons to be described, the tests were largely ignored in forming models for later analyses. The term used as the denominator in the test was the error below the factor in Tables 4.1 and 4.2 except in the case of the year effect which contains a sire: year component. Sire:year provides only an approximate test of year effects since k_4 and k_6 of Table 4.1 will be slightly different in value.

NLW raises a problem in significance testing since the observations are not normally distributed, thus breaching an assumption of the analysis of variance which requires that the experimental errors should be normally distributed. The NLW observation on a ewe will be zero, one or two (the occasional 'three' observation was included with the twins), and may be in a class of distributions in which the variance of an observation and its mean are correlated (Snedecor and Cochran, 1967; Cochran, 1947). Cochran (1947) reviewed previous work on the problem of failure of the assumptions of the analysis of variance and concluded that no serious error would result from using the F-test on non-normal data, but added that the tabulated probability would err towards understatement; that is too many tests would be declared significant. Lindman (1974) also suggested that the F-test is robust with respect to non-normality. It is not known whether in either case such gross deviations as are present here were investigated, but lesser aberrations such as kurtosis and skewness were discussed. Therefore no test of significance was applied to NLW. No real information was lost since the other methods

were available to assess the importance of the factors affecting the variable.

II. Accounting for Observed Variance.

A. Variance Component Estimation.

Variance components are required to allow the computation of the phenotypic and genetic parameter estimates. During the preliminary analyses of variance phase of the investigation, variance components were required to enable an assessment to be made of the importance of the factors in the model in accounting for the observed variance. The variance ratio, or F test will show where the means of the subclasses differ significantly in a statistical sense, but give no information as to the degree of this difference where large numbers of observations result in many error degrees of freedom. In these circumstances very small differences in subclass means may be statistically significant. The variance components were calculated and expressed as a percentage of the total observed variance. To enable the computations to be undertaken on all factors in the models, the fixed quadratic components were temporarily regarded as variance components.

Scheffé (1959) and Lindman (1974) both stated that non-normality does not bias point estimates of variance components and therefore the percentage variance accounted for by the various factors in the model was calculated from the expectations of the mean squares in the analysis of variance for NLW as well as the wool characters.

Henderson (1953b) described three methods which are suitable for estimating variance components with unbalanced data, known as Henderson's Method 1, Method 2, and Method 3. Searle (1968) discussed the methods in matrix terminology, and the attributes and limitations have been

further considered by Searle (1971a, 1971b) and Henderson et al. (1974).

Method 1 (the analysis of variance method) involves calculating uncorrected sums of squares and equating them to their expected values in an analogous fashion to the balanced data situation. Although easy to operate, the method has the major deficiency that where both fixed and random effects (other than μ) are defined in the model, variance components cannot be estimated free from bias by fixed effects.

Method 2 overcomes the shortcoming of Method 1 by first estimating the fixed effects by fitting constants and then correcting the data using these estimates. Method 1 is then used on the adjusted data to derive variance component estimates unbiased by fixed effects. Henderson et al. (1974) demonstrated that Method 2 is uniquely specified regardless of the particular solution for the fixed effects. This method has the limitation that it cannot be used whenever there are interactions between fixed and random effects, nor where random and fixed effects are nested within each other (Henderson et al. 1974).

Method 3 involves calculating the difference in sums of squares reductions due to fitting submodels by the fitting constants method. The variance components are estimated by equating the reductions to their expectations under the full models. The importance of this method is that the expected value of reduction due to fitting a single random effect contains only a variance component for that effect and the error variance. In particular, in the mixed model situation, the expectation of the reduction due to fitting a random effect is a function only of that random effect and σ_e^2 , but not of any fixed effect. A disadvantage is that in models containing a large number of effects it may be difficult to obtain the coefficients in the expectations, as the inverse of the full model matrix less the effect of interest,

is required. Method 3 was the preferred method for this analysis because variance components were required from a mixed model, and sires (a random factor) were nested within year.

A simplified procedure equivalent to fitting submodels (Harvey, 1960; Searle, 1966; Cunningham, 1970) was frequently used to calculate sums of squares for the fixed effects. This direct method, described in detail by Harvey (1960) requires the computation of the sums of squares as

$$SS_A = \beta_A' Z_A^{-1} \beta_A$$

where β_A' is the transpose of the column of constant estimates, β_A relating to factor A, and

Z_A^{-1} is the inverse of that part of the full model $(X'X)^{-1}$ matrix relating to factor A.

Where reductions in sums of squares were obtained by the direct method, the k coefficients of Table 4.1 and 4.2 were calculated by the equivalent procedure, and similarly for indirect reductions and coefficients. As an approximation, k_6 and k_4 of Table 4.1 were assumed equal.

B. Proportion-of-variance Calculations.

The proportion of variance accounted for by each factor was calculated from the positive variance components (including fixed effect quadratic components) and then converted to a percentage. For example variance due to year ($\%V_t$) for a wool character might be

$$\%V_t = \frac{q_t^2}{q_t^2 + \sigma_{s:t}^2 + q_d^2 + q_r^2 + q_{int(1)}^2 + \dots + q_{int(6)}^2 + \sigma_e^2} \times 100$$

where $int(i)$ = ith interaction

III. Environmental Effects.

Environmental effects were obtained as least squares estimates from fixed effects models and were required:

- (i) as correction factors for later analyses
- (ii) to allow investigation of the source of the differences which lead to large between group variances, by examination of the magnitude of the effects.

The analysis of fixed effects from a fixed-effects-only model will be biased unless it can be assumed that the effects omitted or unidentified are randomly distributed over the remaining factors. There was no evidence to the contrary and therefore the procedure was adopted.

Standard errors of a least squares effect were calculated according to the formulae given by Harvey (1960) as $(c^{ii} \sigma_e^2)^{\frac{1}{2}}$ where c^{ii} is the inverse diagonal element corresponding to that effect, and σ_e^2 is the estimate of the error variance.

A two-way interaction expresses the extent to which the difference between the levels of one effect are inconsistent at different levels of a second effect. The magnitude of a significant interaction shows the extent of the failure of the additive model. The consequence is that the interacting main effects in an interaction model only have meaning when the level of both is detailed. The interaction least squares effects should therefore be used as correction factors when the interaction has been shown to be an important source of variation. Environmental effects were only calculated for interactions which contributed at least two percent of the total observed variation. Standard errors were not computed as the effects are unlikely to be used as correction factors by other workers, who would require an estimate of their accuracy.

IV. Genetic and Phenotypic Parameters.

A. Paternal Half-sib Analysis.

1. Wool Traits and Number of Lambs Weaned.

The paternal half-sib method was used to estimate separately parameters for each age and for between-age and lifetime performance from variance and covariance components using Henderson's Method 3. Harvey (1970) showed that variance and covariance components can be calculated by similar procedures.

The preliminary estimation of the proportion of the observed variance accounted for by the various factors in the model formed the basis for choosing an appropriate model for each variable. Variance and covariance components for sire:year and error were estimated by including in the model, or correcting for, all main effects which had been previously shown to contribute greater than two percent of the total variance of any character. The variance due to NLW was removed by correcting the wool data using the environmental effects calculated earlier, thus enabling the variance components and covariance components between wool characters and NLW to be estimated together.

The correlation between the environmental effect of NLW as a ewe characteristic and wool traits requires that fertility status be included as a factor in wool characteristic analysis to ensure that the between sire component is only genetic in origin.

Part of the difference in the rearing rank of ewes is due to genetic differences between their dams. Insofar as these differences are heritable, including rearing rank in a model for NLW will remove a part of the genetic variance. Rearing rank was therefore ignored and considered as part of the random variation whenever the analysis involved NLW. Where necessary, wool characteristics were corrected for rearing rank in the covariance analysis.

The only interaction of importance and not excluded by other considerations was year x NLW, according to the preliminary analysis. Three age groups of wool characteristics were re-analysed with this interaction fitted and the variance and covariance components and the estimates of parameters derived from them were accepted.

A difficulty arose from the attempt made to generalise the FORTRAN IV program to handle data sets in which there was a large number of subclasses in one classification. It was earlier explained how $\mu + t_i + s:t_{ij}$ was absorbed as a compound parameter. The only main effects that should have been included in some models were those to be absorbed, and it was therefore necessary to include some other factor to make absorption possible. Dam-age was chosen as it could be included in a model for any of the traits.

Fibre diameter was analysed separately on a smaller data set and therefore variances and covariances involving this trait are estimated with lower accuracy than for the other characteristics.

The between-age analysis and lifetime performance study were run together, and the data were corrected for main effects as above. The hogget data were corrected for rearing rank using factors derived by Elliott (1975). Interactions were ignored.

Although the trait NLW falls into the category of coarsely grouped data, Turner and Young (1969) suggested that the analysis of variance is valid and genetic and phenotypic parameters can be approximated by this method. Scheffé (1959) and Lindman (1974) stated that the validity of the variance of the point estimates of the variance components which rely on normal-theory formulae is in doubt. The estimates, more appropriate for normally distributed data are used here as an approximation.

Heritability was estimated as

$$h^2_{\text{PHS}} = \frac{\sigma_a^2}{\sigma_p^2} = \frac{4\sigma_{s:t}^2}{\sigma_{s:t}^2 + \sigma_e^2}$$

Approximate standard errors were calculated following Swiger et al. (1964).

The genetic correlation between traits x and y were estimated from the sire variance and covariance components as:

$$r_{g_{xy}} = \frac{\text{Cov } a_x a_y}{\left[\begin{matrix} \sigma_{a_x}^2 & \sigma_{a_{xy}}^2 \\ \sigma_{a_{xy}}^2 & \sigma_{a_y}^2 \end{matrix} \right]^{1/2}} = \frac{4 \text{Cov } s_x s_y}{\left[\begin{matrix} 4\sigma_{s_x}^2 & 4\sigma_{s_{xy}}^2 \\ 4\sigma_{s_{xy}}^2 & 4\sigma_{s_y}^2 \end{matrix} \right]^{1/2}}$$

where a is an abbreviation for additive genetic, and s refers to the sire component.

Robertson (1959) derived sampling variances for genetic correlation coefficients, but his development is applicable to the special case where the heritabilities of the two characters are equal. A general formulation was published by Tallis (1959) which does not suffer from the above restriction, and this was the method used.

The phenotypic correlation between characters x and y is defined as:

$$r_{p_{xy}} = \frac{\text{Cov } p_x p_y}{\left[\begin{matrix} \sigma_{p_x}^2 & \sigma_{p_{xy}}^2 \\ \sigma_{p_{xy}}^2 & \sigma_{p_y}^2 \end{matrix} \right]^{1/2}} = \frac{\text{Cov } (s_x + e_x) + \text{Cov } (s_y + e_y)}{\left[(\sigma_{s_x}^2 + \sigma_{e_x}^2) \times (\sigma_{s_y}^2 + \sigma_{e_y}^2) \right]^{1/2}}$$

where p = phenotypic

e = error

This follows from

$$\sigma_{p_x}^2 = \sigma_{a_x}^2 + \sigma_{v_x}^2 \quad (v = \text{environmental})$$

$$E(\sigma_{s_x}^2) = 0.25 \sigma_{a_x}^2$$

and

$$E(\sigma_{e_x}^2) = 0.75 \sigma_{a_x}^2 + \sigma_{v_x}^2 \quad (\text{Kempthorne, 1969})$$

2. Fertility and Twinning

The data for these analyses form binomial distributions in which the alternative observations are that the ewe raised a lamb or did not (fertility), or the ewe weaned twins or did not (twinning). Although the phenotypic expression of fertility or twinning follows an all-or-none distribution, it is reasonable to postulate an underlying continuous distribution. Dempster and Lerner (1950) listed the assumptions involved.

- (i) The underlying variate is the sum of independent normally distributed environmental and genetic components.
- (ii) The character is exhibited only in those individuals in which the value of the underlying variate exceeds a certain threshold value.
- (iii) Gene substitutions have individually small and strictly additive effects on the underlying variate.

Binomially distributed data present difficulties in analysis by methods developed for continuous data as the mean and variance are correlated. The variance of a binomial distribution is $p(1-p)$, where p is the proportion of the population possessing some attribute and therefore varies more widely at the extremes of the 0,1 range for a given change in p than near the middle. Therefore methods of analysis appropriate for continuous data may only be an approximation for binomial data.

Equally serious is the effect on standard errors, which will also only be an approximation.

As the heritability of fertility and twinning were of interest, various methods of analysis for threshold traits were investigated.

Rae (1950) derived a system of finding scales to replace the observational scales, which maximize the regression of offspring on parent, or the correlation between half-sibs. Ch'ang (1955) illustrated the computational procedures involved and showed that the method gave higher heritability estimates than were obtained where a scale of equal intervals was used. However, the estimates obtained can only be applied relative to the scales derived and extrapolation and interpretation are difficult. Additionally, no method is available for calculating standard errors of the estimate.

The method of Lush, Lamoreux and Hazel (1948) is an analysis of variance procedure applicable to binomial data. To avoid the distortion which occurs in proportions at low incidences, the authors suggested the use of the probit transformation. Falconer (1965) used the same transformation in developing formulae in which the mean incidence (of disease) among the relatives of affected individuals was related to the mean incidence in the general population. The difference between the normal deviates of the population and affected relatives was transformed to the probit scale to give a direct estimate of the regression of relatives on affected individuals and hence heritability. Smith (1970) pointed out that although normality of the distribution for relatives is assumed, in fact they are related to a truncated part of the normal curve. Inasmuch as the character is heritable, the assumption will result in a bias which could be up to 10 percent (Smith, 1970; Edwards, 1969).

Unbiased versions of Falconer's model were published by Edwards (1969) and Smith (1970). However, as with Falconer's (1965) method, to remove the environmental effect of year it was necessary to subdivide

the data according to both dam and daughter birth years within each age separately, reducing the sub-class numbers in many cases to levels considered too small for reliability.

A maximum likelihood method applicable to binomial data was presented by Tallis (1962) and further developed by Brown et al. (1963). The sampling errors for the estimates derived by this procedure can be computed with the heritability estimates. The calculations involve the evaluation of many partial derivatives, and the method is an iterative procedure. The size of the data set involved in the analysis was expected to ensure standard errors of a reasonable size with the possible exception of the five-year set using other methods. It was considered that under the circumstances, the complexity of this method would not outweigh the benefits of the expected increase in accuracy.

The method of Robertson and Lerner (1949) was used to calculate the heritability of fertility and twinning because it was appropriate for the data and because it is simple to apply. However, as pointed out by Dempster and Lerner (1950) it may include a certain amount of non-additive variance.

The authors described their method in terms of realized genetic change and quantified heritability as

$$h^2 = \frac{\text{genetic improvement}}{\text{phenotypic selection differential}}$$

$$= \frac{\sigma^2 p}{\bar{p} (1-\bar{p})}, \text{ where } \bar{p} \text{ is the mean incidence of the trait}$$

Adapting the method to the fertility analysis, if s sires have n_i progeny of which a_i are fertile in a particular year then heritability is expressed as:

$$h^2 = \frac{\sum \frac{a_i^2}{n_i} - \frac{(\sum a_i)^2}{N}}{\bar{p}(1-\bar{p})} - (s-1)$$

rk
(all summations over $i = 1 \dots s$)

$$= \frac{\left[\sum \frac{a_i^2}{n_i} - \frac{(\sum a_i)^2}{N} \right]}{\left[\frac{\sum a_i}{N} - \left(1 - \frac{\sum a_i}{N}\right) \right]} - (s-1)$$

rk

where $N = \sum n_i$

\bar{p} = mean fertility rate

r = coefficient of relationship

$k = N - \frac{\sum n_i^2}{N} - (s-1)$

The square bracketed term in the numerator is the heterogeneity χ^2 in the $2 \times s$ contingency table formed by the a_i and $(n_i - a_i)$ elements .

Therefore

$$h^2 = \frac{\chi^2 - (s-1)}{rk}$$

and $E(\chi_{s-1}^2) = s-1$

Computation of the elements of this formula proceeded year by year and were pooled as follows:

Assume that there are y years data ($j = 1 \dots y$). The heritability calculated from the j th years data is then

$$h_j^2 = \frac{\chi_j^2 - s_j - 1}{rk_j}$$

$$h_{\text{pooled}}^2 = \frac{\sum \chi_j^2 - \sum (s_j - 1)}{r \sum k_j}$$

where the summations are over $j = 1 \dots y$.

Approximate standard errors were calculated according to the method of Swiger et al. (1964).

B. Daughter-dam Regression Analysis

The covariance between parent and offspring phenotypes estimates half of the additive genetic variance (Falconer, 1960). This covariance is commonly used to estimate heritability (Lush, 1940) and is the denominator required for genetic correlations (Hazel, 1943). Heritability can be estimated as either twice the regression of daughter on dam, or twice the daughter-dam correlation. The former was the preferred method for this study as it was known that some selection had been applied.

Three methods are available for the estimation of the regression of offspring on parent.

- (i) The regression of the phenotypic mean of all progeny on the parents record.
- (ii) The regression of each offspring on the parent, with the parents record repeated for each additional progeny.
- (iii) The weighted regression technique.

The first method gives minimum variance estimates when the correlation between offspring of one parent is equal to one, while the second is optimal when the correlation is zero. The true situation lies somewhere in between these extremes, and therefore Kempthorne and Tandon (1953) proposed the third method. However, this relies for its success upon an accurate guess of the value of the correlation (ρ) between deviations from the regression associated with progeny of the same parent. The parameter ρ is required as an element of the factor which weights the progeny mean. The weighting factor is also a function of the number of progeny. The precise effect of an inaccurate guess appears to be unknown, but it would result in an increase in the

sampling variance of the regression estimate. Bohren et al. (1961) studied the relative efficiencies of the various regression computation methods, and although they pointed out that ρ will only equal zero if the heritability is one or zero, they also showed that there is little difference between the efficiencies of methods (2) and (3) in terms of variance of the estimates when ρ is small. Method (1) was consistently less efficient. Kempthorne and Tandon (1953) also observed that the regression of progeny means on dams record was less efficient although the difference was not great. The other two methods resulted in identically equal standard errors. The authors stated that the inconsequential difference between the efficiencies of the three regressions was due to the small average number of progeny per dam (1.39). The average progeny group size in the data for this study slightly exceeded the average of Kempthorne and Tandon (1953) for the two- and three-year-old groups but was smaller for the remainder. The decision to use the repeated dams record method was taken on the basis of the above information plus the unknown magnitude of the effect of a guessed value of ρ .

Consideration was given to whether or not the regression should be calculated on an intra-sire basis, or whether sires should be ignored.

A summary of the data appears in the following table:

Age group	Number of sires		Pairs of records involved in (2)
	(1)	(2)	
	Total ≤ 3 progeny		
2-year-old	88	34	70
3-year-old	71	27	49
4-year-old	54	22	42

Since the accuracy of an estimate is dependent upon the number of observations (pairs) and the small progeny groups would have to be eliminated, it was decided that sires would be ignored. The rationale for this action comes from Turner and Young (1969) who indicated that when all sire groups are run together and mating is at random the between sire covariances have zero expectation. It was thought that some assortative mating may have been practised involving quality number. A study of selection differentials for mating groups within year suggested that only two sires may have been selectively mated. A similar result could be expected purely by chance.

The true estimate of heritability is computed when both dam and daughter are of the same age at the time of recording. Each animal of the pair will then have been observed in different years, for which account must be taken.

Dam-daughter pairs of the same age were assembled into a file and sorted first by daughter birth-year, and then sub-sorted on dam birth-year. After correction of the data for important environmental main effects and interactions, the analysis proceeded by dam birth-years, with corrected sums of squares and degrees of freedom being accumulated at the end of each dam year and further combined at the end of each daughter year until the file was completed, when the parameter estimates were calculated.

Heritability was estimated from

$$h^2 = 2 \frac{\text{Cov}(P, O)}{\sigma_P^2}$$

where P refers to parent and

O refers to offspring

The standard error method was supplied by Falconer (1960).

Combining the covariances between traits x and y measured on both parent and offspring, forms the basis of genetic correlation computation (Hazel, 1943).

The formula is:

$$r_{g_{xy}} = \frac{\text{Cov } P_{x y} + \text{Cov } P_{y x}}{2 \left[\text{Cov } P_{x x} \text{ Cov } P_{y y} \right]^{1/2}}$$

with standard errors given by Reeve (1955).

If the arithmetic mean is used in the numerator as above rather than (1943) the geometric mean as originally suggested by Hazel, a result is more probable. In the latter case, if the two numerator covariances are of opposite sign through sampling, the correlation is defined as indeterminate. Using the arithmetic mean does not guarantee a result however, as through sampling, one of the covariances in the denominator may be negative, and the square root of the product is then undefined.

C. Repeatability

1. Wool Characteristics

Repeatability calculated as an intraclass correlation refers to the average consistency of performance of the same ewe at different ages. It gives no information on differences between individual records as predictors of later performance. To obtain information on this aspect of production, interclass correlations can be calculated between pairs of ages. If required, the average relationship between pairs of records can be derived by pooling these correlations using Fisher's z transformation, as described by Snedecor and Cochran (1967) and this can be interpreted in the same way as the intraclass correlation.

Cunningham and Henderson (1965) described the use of the regression of later on earlier records as an estimator of the correlation between records. They showed that on the assumption that the phenotypic variance of the two records is the same, the regression estimator of repeatability is unbiased by selection based on the earlier record. Even if the variances are different, the regression of later on earlier record is of interest in quantifying the change in later production which may arise from selection on an earlier record. In the situation where the variances are heterogeneous, the regression will only approximate the correlation. As Ercanbrack (1968) pointed out, the failure of the estimation will depend upon the extent to which the true standard deviation of the dependent variable is larger or smaller than that of the independent variable.

The ewes on which the records were based have been shown to have been subjected to little selection, but the regression approach was used for the other reasons mentioned.

The wool records were corrected for year and NLW environmental effects before the regressions were calculated, and standard errors were calculated according to Falconer (1960).

The number of records involved in the calculation of each regression is detailed in table 3.4.

2. Number of Lambs Weaned

The regression of later performance on an earlier record is also appropriate for NLW (Lush, 1956). A separate regression coefficient was calculated for each pair of ages within birth year and pooled over years to obtain the tabulated values. The procedure is as follows: assume there are N_j ewes born in year j ($j = 1 \dots y$), with a fertility

record at the earlier of the two ages, with n_{ij} ($i = 0, 1, \text{ or } 2$) ewes in each class.

where $i = 0$ (ewe barren at the earlier lambing)

$i = 1$ (reared a single)

$i = 2$ (multiple lambs reared).

$$\sum_i n_{ij} = N_j$$

The mean number of lambs reared at the second lambing by ewes in each status class form a vector of three means \bar{m}_i . Then, the estimated repeatability of a difference between zero and one lamb

$$= \hat{t}_{0j} = \bar{m}_1 - \bar{m}_0$$

$$\text{Pooled over years } \hat{t}_0 = \frac{\sum w_{0j} \hat{t}_{0j}}{\sum w_{0j}}$$

where the summations are over $j = 1 \dots y$.

Similarly the repeatability of a difference between one and two lambs weaned

$$= \hat{t}_1 = \frac{\sum w_{1j} \hat{t}_{1j}}{\sum w_{1j}}$$

$$\text{where } w_{0j} = \frac{\sum^{k-1} (n_{0j} n_{1j})}{n_{0j} + n_{1j}}$$

$$w_{1j} = \frac{\sum^{k-1} (n_{1j} n_{2j})}{n_{1j} + n_{2j}}$$

k = number of records on each animal

(two in this case).

The w_{ij} 's are the usual weights for weighting a difference according to the inverse of its variance as shown by Turner and Young (1969), who also provided the method of calculating standard errors.

The regression method was considered appropriate as it allows a comparison between the repeatabilities of an initial difference of one lamb at different levels of production which may give an indication of the advisability of various flock improvement methods.

V. Selection

It was necessary to have a method of assessing the amount of selection which had been applied to each variable during the ewe's lifetime in the flock. The decision to retain an animal in the flock for a further year is based on many criteria. As well as direct selection for the well defined productive characteristics of interest in this study, there are other factors involved in indirect selection. Many of these factors may be correlated with productive traits. For example, if selection was being applied directly for fleece weight, a ewe may be culled for a disease which reduced fleece weight. If the disease was selected against directly, then an increase would be expected in fleece weight.

To estimate the total amount of selection applied to each trait, it was assumed that all animals above a certain truncation point were retained while the remainder were culled.

It was further assumed that all selection was based on each dependent variate in turn. Selection differentials were computed for each age after correcting for environmental factors where necessary. The selection differentials calculated in this manner represents the difference between the mean of the entire age group, and the mean of the selected group, and were expressed in standardized form after dividing by the standard deviation of the observations on the whole age sample. The process was repeated separately for the full data set which was used for paternal half-sib estimates, and for the dam data.

C H A P T E R F I V E

RESULTS AND DISCUSSIONI. Analyses of Variance and Environmental Effects

Computational procedures and models used in the analyses of variance and environmental effects have been described previously.

The main environmental effects with their standard errors are presented in tables 5.1 to 5.4 while selected interaction effects are tabulated later. The percentage variances accounted for by all factors in a model describing a dependent variable are listed in tables 5.5 to 5.8 and the statistical significance of the main, nested and interaction mean squares are included in the same tables.

The analytical results will now be presented by traits. The proportion of variance accounted for by various fixed factors will be discussed, and in this context, total variance refers to the sum of the quadratic and variance components.

A. Quality Number

Quality number is a subjectively-assessed characteristic based mainly on crimp frequency which crudely reflects fibre diameter (Ross, 1965). Other factors affect the grading such as length, handle and lustre, but variation in these characteristics does not necessarily reflect changes in fibre fineness (Wickham and Bigham, 1973).

Estimates of differences between subclasses will be slightly biased by selection which has been applied, but selection on quality number seems not to have been very intense (see table 5.12, next section). The differences will, however, accurately describe the situation as it exists in this flock.

Table 5.1 Two-year-old Ewes. Least Squares Estimates and Standard Errors of Environmental Effects

Factor	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
	(unit)	(grade)	(cm)	(kg)	(microns)	
Year						
1963	1.46+0.23	0.20+0.12	-0.12+0.20	0.02+0.06	-0.55+0.26	-0.08+0.07
1964	0.69 0.18	0.47 0.10	0.99 0.16	0.60 0.05	0.44 0.21	0.13 0.05
1965	-1.36 0.18	1.22 0.09	2.11 0.15	0.45 0.05	1.42 0.20	0.04 0.05
1966	-0.66 0.18	0.94 0.09	0.38 0.16	-0.29 0.05	-0.05 0.21	0.08 0.05
1967	-1.11 0.15	-0.39 0.08	1.72 0.13	0.43 0.04	0.41 0.17	0.03 0.04
1968	0.83 0.17	-1.80 0.09	1.51 0.15	0.11 0.05	0.03 0.20	-0.15 0.05
1969	1.26 0.15	-1.00 0.08	-0.40 0.13	0.25 0.04	-0.02 0.18	0.08 0.04
1970	0.41 0.14	-0.63 0.07	-0.41 0.12	-0.29 0.04	-1.80 0.17	0.06 0.04
1971	-0.50 0.12	0.44 0.06	-1.79 0.11	-0.19 0.03	-0.21 0.14	-0.07 0.04
1972	-2.97 0.13	-0.05 0.07	-0.83 0.12	-0.22 0.04	0.33 0.16	-0.03 0.04
1973	0.31 0.12	0.68 0.06	-0.58 0.10	-0.40 0.03	- -	-0.09 0.04
1974	1.65 0.12	-0.07 0.06	-2.57 0.11	-0.46 0.03	- -	0.02 0.04
Dam age						
2-year-old	-0.15 0.08	0.00 0.04	-0.11 0.07	-0.08 0.02	0.04 0.11	0.01 0.02
3-year-old	0.07 0.08	-0.03 0.04	-0.05 0.07	-0.01 0.02	-0.18 0.11	-0.02 0.02
4-year-old	0.01 0.09	-0.02 0.05	0.23 0.08	0.05 0.02	0.07 0.11	-0.01 0.03
5+-year-old	0.07 0.07	0.05 0.04	-0.07 0.06	0.03 0.02	0.07 0.09	0.02 0.02
Rearing Rank						
Single	0.01 0.05	0.00 0.02	0.02 0.04	0.05 0.01	-0.15 0.06	-0.01 0.01
Twin	-0.01 0.05	-0.00 0.02	-0.02 0.04	-0.05 0.01	0.15 0.06	0.01 0.01
N.L.W.						
0	-0.03 0.08	0.00 0.04	0.24 0.07	0.10 0.02	0.02 0.11	
1	0.03 0.07	0.03 0.04	0.05 0.06	0.00 0.02	0.06 0.09	N.A.
2	0.00 0.10	-0.03 0.05	-0.29 0.09	-0.10 0.03	-0.08 0.14	
General Mean	50.73 0.05	5.15 0.02	14.48 0.04	3.60 0.01	34.38 0.06	0.89 0.01
Standard Deviation (from error)	1.84	0.97	1.67	0.50	2.23	0.55

Table 5.2 Three-year-old Ewes. Least Squares Estimates and Errors of Environmental Effects.

Factor	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
Year	(unit)	(grade)	(cm)	(kg)	(microns)	
1964	0.73+0.30	0.15+0.13	0.96+0.20	0.32+0.06	0.46+0.28	-0.26+0.07
1965	-0.81 0.24	1.57 0.10	1.53 0.16	0.41 0.05	0.76 0.23	0.12 0.06
1966	-0.80 0.26	0.35 0.11	-0.03 0.17	-0.29 0.06	0.19 0.25	0.10 0.06
1967	-1.35 0.23	-0.47 0.10	0.76 0.15	0.06 0.05	0.81 0.22	-0.00 0.06
1968	1.20 0.21	-1.76 0.09	-0.06 0.14	-0.29 0.05	-0.33 0.21	-0.07 0.05
1969	1.19 0.28	-1.30 0.12	-0.10 0.19	0.28 0.06	0.03 0.27	0.04 0.07
1970	0.78 0.22	-0.44 0.09	-0.05 0.15	-0.11 0.05	-1.86 0.22	-0.10 0.05
1971	-0.90 0.18	0.81 0.08	-0.69 0.12	0.18 0.04	-0.25 0.18	0.09 0.04
1972	-1.81 0.16	0.19 0.07	-0.35 0.11	-0.05 0.04	0.17 0.16	0.10 0.04
1973	0.72 0.19	1.09 0.08	-0.21 0.13	-0.27 0.04	- -	0.01 0.05
1974	1.04 0.19	-0.19 0.08	-1.75 0.13	-0.24 0.04	- -	-0.03 0.05
Dam age						
2-year-old	-0.20 0.12	-0.06 0.05	-0.02 0.08	-0.09 0.03	-0.14 0.14	-0.03 0.03
3-year-old	0.08 0.12	0.05 0.05	-0.03 0.08	0.02 0.03	-0.12 0.14	0.01 0.03
4-year-old	0.04 0.13	0.04 0.06	0.08 0.09	0.03 0.03	0.13 0.14	0.01 0.03
5+-year-old	0.08 0.11	-0.03 0.04	-0.03 0.07	0.04 0.02	0.13 0.12	0.01 0.03
Rearing rank						
Single	-0.03 0.07	-0.02 0.03	-0.02 0.05	0.04 0.02	-0.27 0.08	-0.01 0.02
Twin	0.03 0.07	0.02 0.03	0.02 0.05	-0.04 0.02	0.27 0.08	0.01 0.02
N.L.W.						
0	-0.15 0.14	-0.04 0.06	0.24 0.09	0.08 0.03	0.14 0.15	
1	-0.03 0.10	0.02 0.04	0.01 0.07	-0.03 0.02	-0.11 0.11	N.A.
2	0.18 0.12	0.02 0.05	-0.25 0.08	-0.05 0.03	-0.03 0.13	
General Mean	50.75 0.06	4.93 0.03	13.73 0.05	3.44 0.01	34.91 0.08	1.05 0.01
Standard deviation (from error)	1.81	0.98	1.61	0.53	2.33	0.56

Table 5.3 Four-year-old Ewes. Least Squares Estimates and Standard Errors of Environmental Effects.

Factor	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
	(unit)	(grade)	(cm)	(kg)	(microns)	
Year						
1965	-0.93+0.23	0.46+0.13	1.40+0.20	0.21+0.06	0.39+0.29	0.08+0.08
1966	-0.98 0.20	0.25 0.11	0.65 0.17	-0.10 0.05	-0.12 0.26	0.14 0.07
1967	-1.13 0.21	-0.49 0.12	0.34 0.18	0.20 0.06	1.28 0.27	-0.03 0.07
1968	1.32 0.23	-1.48 0.12	0.09 0.19	-0.24 0.06	-0.02 0.29	-0.12 0.08
1969	0.96 0.20	-1.20 0.11	0.38 0.17	0.44 0.05	0.13 0.26	0.08 0.07
1970	0.70 0.20	-0.30 0.13	0.20 0.19	-0.14 0.06	-1.44 0.30	-0.28 0.08
1971	-0.78 0.21	1.14 0.11	-0.80 0.17	0.16 0.06	-0.57 0.26	0.03 0.07
1972	0.06 0.16	0.40 0.09	0.02 0.14	0.09 0.04	0.29 0.21	0.20 0.05
1973	0.25 0.16	1.10 0.09	0.04 0.14	-0.11 0.04	- -	-0.05 0.05
1974	0.54 0.17	0.12 0.10	-2.31 0.15	-0.52 0.05	- -	-0.06 0.06
Dam age						
2-year-old	0.01 0.13	-0.04 0.08	0.05 0.12	-0.05 0.04	-0.04 0.18	-0.04 0.04
3-year-old	0.06 0.13	-0.02 0.07	0.05 0.13	-0.02 0.04	-0.19 0.17	0.06 0.04
4-year-old	0.01 0.14	-0.04 0.08	-0.10 0.12	0.01 0.04	0.07 0.19	-0.02 0.04
5+-year-old	-0.08 0.12	0.10 0.07	-0.00 0.11	0.06 0.03	0.16 0.16	0.00 0.03
Rearing rank						
Single	-0.04 0.08	-0.02 0.05	-0.11 0.07	0.04 0.02	-0.14 0.11	-0.02 0.02
Twin	0.04 0.08	0.02 0.05	0.11 0.07	-0.04 0.02	0.14 0.11	0.02 0.02
N.L.W.						
0	0.17 0.16	-0.01 0.09	0.31 0.15	0.09 0.08	-0.09 0.22	
1	-0.18 0.11	-0.09 0.06	0.07 0.10	0.06 0.03	0.08 0.15	N.A.
2	0.01 0.12	0.10 0.07	-0.39 0.11	-0.15 0.03	0.01 0.16	
General Mean	50.66 0.07	4.67 0.04	13.09 0.06	3.31 0.02	35.22 0.10	1.18 0.02
Standard Deviation (from error)	1.78	0.96	1.51	0.48	2.28	0.59

Table 5.4 Five-year-old Ewes. Least Squares Estimates and Standard Errors of Environmental Effects

Factor	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
Year	(unit)	(grade)	(cm)	(kg)	(microns)	
1966	-0.77+0.25	-0.09+0.15	0.18+0.22	-0.20+0.08	-0.27+0.32	0.05+0.09
1967	-1.23 0.19	-0.44 0.11	1.25 0.17	0.50 0.06	1.01 0.25	-0.08 0.07
1968	1.31 0.22	-1.76 0.13	0.36 0.20	-0.29 0.07	0.00 0.29	-0.05 0.08
1969	1.34 0.24	-0.98 0.14	0.06 0.21	0.29 0.07	-0.32 0.31	0.02 0.09
1970	0.19 0.21	-0.18 0.12	0.55 0.18	-0.04 0.07	-1.04 0.29	-0.19 0.08
1971	-0.82 0.28	1.25 0.16	-0.77 0.24	0.07 0.09	0.64 0.36	0.15 0.10
1972	-0.26 0.23	0.55 0.13	-0.10 0.19	-0.05 0.07	-0.03 0.28	0.26 0.08
1973	0.18 0.21	1.10 0.12	0.24 0.18	0.04 0.06	- -	0.03 0.07
1974	0.05 0.18	0.56 0.11	-1.77 0.16	-0.32 0.06	- -	-0.20 0.07
Dam age						
2-year-old	0.09 0.14	-0.23 0.09	-0.13 0.15	-0.03 0.05	0.00 0.21	-0.06 0.05
3-year-old	0.21 0.14	0.12 0.09	0.08 0.15	0.03 0.05	-0.17 0.21	-0.01 0.05
4-year-old	-0.21 0.16	0.10 0.10	0.02 0.17	-0.05 0.06	-0.02 0.24	0.10 0.06
5+-year-old	-0.09 0.13	0.01 0.08	0.03 0.14	0.05 0.05	0.19 0.19	-0.03 0.04
Rearing rank						
Single	-0.20 0.09	0.06 0.05	-0.01 0.09	0.07 0.03	0.16 0.13	-0.03 0.03
Twin	0.20 0.09	-0.06 0.05	0.01 0.09	-0.07 0.03	-0.16 0.13	0.03 0.03
N.L.W.						
0	0.01 0.21	-0.08 0.13	0.03 0.22	0.04 0.08	-0.11 0.31	
1	0.08 0.13	0.07 0.08	0.09 0.14	0.05 0.05	0.00 0.19	N.A.
2	-0.09 0.14	0.01 0.09	-0.12 0.05	-0.09 0.05	0.11 0.21	
General Mean	50.69 0.09	4.41 0.05	12.41 0.08	3.13 0.02	35.16 0.12	1.27 0.03
Standard deviation (from error)	1.76	0.97	1.53	0.51	2.23	0.58

Table 5.5 Two-year-old Ewes. Percentage of Total Variance Attributable to Each Factor for Each Variable

Variable	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
Factor						
Year	36.2**	43.0**	41.0**	27.6**	9.8*	1.0
Dam-age	-	-	0.3	1.0**	-	-
Rearing-rank	0.0	-	-	1.8**	0.7*	-
Lambs-weaned	-	0.2	1.5**	1.8**	-	N.A.
Sire:year	1.9**	5.4**	7.2**	7.3**	11.9**	4.4
N.L.W. x Year	3.6**	-	0.0	0.8	-	N.A.
N.L.W. x Dam-age	-	-	-	-	0.1	N.A.
N.L.W. x Rearing-rank	0.7	0.8	-	0.0	0.1	N.A.
Dam Age x Rearing rank	0.3	-	-	1.5**	-	-
Dam Age x Year	-	1.9**	-	1.0	0.7	-
Year x Rearing rank	-	0.7	-	0.5	-	1.4
Error	57.3	48.0	50.0	56.7	76.7	93.2

N.A. Not Applicable

Statistical Significance of Mean Squares

* 0.01 < p < 0.05

** 0.01 > p

Table 5.6 Three-year-old Ewes. Percentage of Total Variance Attributable to Each Factor for Each Variable

Variable	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
Factor						
Year	19.5**	50.4**	13.6**	14.0**	7.6**	3.3
Dam-age	-	0.0	-	1.2**	-	-
Rearing-rank	-	-	-	1.2**	2.2**	-
Lambs-weaned	-	-	1.9**	1.5**	-	N.A.
Sire:year	2.4*	3.1**	10.2**	11.1**	11.1**	0.3
N.L.W. x Year	3.7*	0.0	0.6	-	2.5	N.A.
N.L.W. x Dam age	-	-	0.2	-	0.6	N.A.
N.L.W. x Rearing rank	-	-	-	0.6	-	N.A.
Dam Age x Rearing rank	0.1	-	-	-	0.1	-
Dam Age x Year	-	-	0.7	-	-	1.8
Year x Rearing rank	-	-	-	-	1.4	0.2
Error	74.3	46.5	72.8	70.4	74.5	94.4

N.A. Not Applicable

Statistical Significance of Man Squares

* 0.01 < p < 0.05

** 0.01 > p

Table 5.7

Four-year-old Ewes. Percentage of Total Variance Attributable to Each Factor for
Each Variable

Variable	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
Factor						
Year	21.9**	44.0**	9.7**	12.7**	6.5**	3.7
Dam-age	-	-	-	0.3	-	0.1
Rearing-rank	-	-	0.5	1.0**	0.3	-
Lambs-weaned	0.2	0.4	3.1**	6.0**	-	N.A.
Sire:year	6.7**	1.9	8.4**	8.0**	8.8**	5.3
N.L.W. x Year	-	-	-	-	-	N.A.
N.L.W. x Dam Age	-	-	-	-	0.5	N.A.
N.L.W. x Rearing rank	-	-	-	1.7*	-	N.A.
Dam Age x Rearing rank	-	0.3	-	0.6	-	-
Dam Age x Year	1.8	1.5	-	-	-	1.1
Year x Rearing rank	-	0.4	0.5	-	1.9	-
Error	69.4	51.5	77.8	69.7	82.0	89.8

N.A. Not Applicable

Statistical Significance of Mean Squares

* $0.01 < p < 0.05$

** $0.01 > p$

Table 5.8 Five-year-old Ewes. Percentage of Total Variance Attributable to Each Factor for Each Variable

Variable	Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	N.L.W.
Factor						
Year	32.1**	48.2**	9.1**	25.1**	4.9*	3.2
Dam-age	0.2	0.9	-	-	-	-
Rearing rank	2.0*	0.1	-	2.0*	0.4	-
Lambs-weaned	-	-	-	1.7	-	N.A.
Sire:year	8.6**	4.9**	15.9**	-	16.2**	-
N.L.W. x Year	0.4	-	6.0*	-	0.3	N.A.
N.L.W. x Dam-age	0.3	0.5	-	-	1.4	N.A.
N.L.W. x Rearing rank	-	0.5	-	-	-	N.A.
Dam-age x Rearing rank	-	-	1.0	0.3	-	5.1
Dam-age x Year	-	-	0.5	0.9	1.2	0.0
Year x Rearing rank	0.3	-	-	-	0.3	4.5
Error	56.1	44.9	67.5	70.0	75.3	87.2

N.A. Not Applicable

Statistical Significance of Mean Squares

* 0.01 < p < 0.05

** 0.01 > p

The general mean for each age shows that there is very little change in quality number with age, although the two younger ages have marginally higher grading (50.73 and 50.75) than the two older groups (50.66 and 50.69). The difference between adjacent ages never exceeds the standard error of the mean of either age. All of the means are considerably lower than the 52.24 recorded by Elliott (1975) for Perendale hoggets from the same flock.

Year was identified as the environmental factor controlling the greatest proportion of the variance in quality number. This source accounted for 19.5 to 36.2 percent of the total variation in quality number within age, with the extreme ages (two- and five-year-old) being affected to a considerably greater degree than the intermediate ages. Comparison of the estimates within each year shows that the deviation of the effects from the respective means is greatest for the two- and five-year-old ewes, and this suggests that the younger and older sheep are more sensitive to changing environmental conditions, such as nutritional stress, than the remaining ages. Generally, the deviation of the ages from their respective means within each year are in the same direction.

The 1972 record year is notable for the very large deviation of the two- and three-year-old groups. Quality number was initially based on Romney grades (which are lower) in that year, and by the time the error was discovered, the two- and part of the three-year samples had been scoured and therefore could not be re-assessed, although the remainder were re-examined and recorded. A wide variation in the deviation of ages was also calculated for the 1974 data when the technician sorted the samples according to tag year before commencing

grading. It is interesting to note that in that year the deviation of quality number from the respective means decreased by half a grade for each age increase.

Year effects on quality number are probably in the main an expression of differential nutrition levels in the year in which the fleece was grown (the effect on fibre fineness as opposed to the other contributors to quality number will be discussed in a subsequent section). Good feeding tends to lower quality number, presumably due to increased length growth (Ryder and Stephenson, 1968).

Sumner and Wickham (1969) discussed the effect of increased stocking rate on quality number. They suggested that coarser quality numbers were given to fleeces from ewes run at higher stocking rates as a result of the wool being more lustrous. There has been an increasing stocking rate in this flock over the years which may have added to the variability of quality number.

The age of the dam of the ewe had no important effect on quality number at any age. Two- and three-year-old daughters of two-year-old dams tended to have coarser wool than the daughters of older dams, but the standard errors were in most cases large in comparison with the estimates. Elliott (1975) observed the same dam-age relationship tendency for hoggets.

Rearing rank accounted for two percent of the variation in quality number of five-year-old ewes, but had no noticeable effect on the other groups. Among the five-year-olds, ewes reared as twins were 0.40 of a quality number finer than singles.

Hight et al. (1976) found that ewes rearing twins had fleeces with lower quality number than those rearing singles, which in turn were lower

than barren ewes. No similar trend with NLW was found here.

The only interaction of importance was year x NLW which affected the two- and three-year-old ewes, accounting for 3.6 and 3.7 percent of the total variance respectively (tables 5.5 and 5.6). In the case of two-year-old sheep, in seven of the twelve years, ewes which reared twins grew the coarsest wool, and in five of these years barren ewes grew wool with the finest count (table 5.9). On a within-year basis, these results are in reasonable agreement with those of Hight et al. (1976). If high fleece weight is used as a measure of a 'good' year it seems that a better environment tends to cause a decreased quality number among twin-rearing ewes relative to single-rearing or barren ewes. There was no logical pattern among the remaining years, nor among the interaction effects for the three-year-old ewes.

B. Wool Character

Wool character is a subjectively graded characteristic based on crimp clarity and evenness, staple formation, blockiness of the staple tip and freedom from medullation (Wickham and Bigham, 1973).

Character grade decreased steadily with age, the means being 5.15, 4.93, 4.67 and 4.41 for the two-, three-, four- and five-year-olds respectively. Elliott (1975) recorded the hogget wool character as 5.03. Henderson (1968) stated that dogginess, which is associated with poor character wool, is more frequent amongst older age groups, and that the fibres that are responsible grow from follicles which have a grossly enlarged lower outer root sheath just above the follicle bulb. The same author suggested the differential response to the stress of advancing age by large and small fibres is another explanation.

Year effects accounted for between 43.0 and 50.4 percent of the

Table 5.9 Two-year-old Ewes. Least Squares Estimates of Environmental Effects. Year x NLW Interaction on Quality Number

Year	Number of Lambs Weaned		
	0	1	2
1963	1.29	1.57	1.25
1964	1.37	0.63	0.63
1965	-1.31	-1.24	-1.77
1966	-0.52	-0.84	0.07
1967	-0.73	-1.13	-1.26
1968	1.03	0.86	-0.67
1969	1.15	1.37	1.02
1970	0.84	0.38	0.34
1971	-0.65	-0.55	1.29
1972	-4.05	-2.37	-3.75
1973	0.60	0.23	0.40
1974	1.35	1.70	1.51

total variation in character. The deviations from the age means for each group were fairly consistent in direction. Various environmental factors affect different components of character. Chapman (1964) found that high rainfall and high feeding levels increased dogginess but Short et al. (1958) thought that high feeding decreased dogginess due to the differential response of large primary fibres. However, Ryder and Stephenson (1968) concluded that nutrition effects would reduce character only if the stress was severe and prolonged. Infestation of the fleece by parasites which result in the sheep rubbing against obstructions can induce tippiness and lack of crimp (Wickham and Bigham, 1973). Year and year x sheep interactions can affect medullation (Goot, 1945). Year effects, which include environmental and management sources, as well as the problem of between- and within-observer repeatability can take many forms insofar as character is concerned.

None of the other environmental factors analysed had an important influence on character, and neither did any of the fixed interactions. The fairly large difference in favour of single-reared hoggets noted by Elliott (1975) had disappeared by the two-tooth stage.

C. Staple length

The greatest staple length was grown by two-tooth ewes and declined steadily thereafter with increasing age. The means were 14.48, 13.73, 13.09 and 12.41 cm. The two-year-old staple length is not strictly comparable with the other age groups as more than 12 months wool growth may have at times been measured. Ross (1965) also recorded a constant decrease with age, but Hight et al. (1976) reported that staple length peaked at three-years of age.

Differences between years explained 41 percent of the variation in two-year-old staple length, but this fell to 13.6 percent for three-year-olds and was below 10 percent for the other ages. Nutritional effects during the year of birth and the year in which the fleece was grown are instrumental in changing staple length. Short (1955) reported that Merino lambs from ewes which had had adverse nutritional treatment during pregnancy, produced fewer and longer fibres at 200 days than their counterparts from dams which were fed well. Schinckel and Short (1961) considered that the effect was permanent in respect to number of follicles, and concluded that the ability of follicles to produce fibre at maturity was unimpaired by pre-natal nutrition. Short (1955) also noted that high levels of nutrition during the last few weeks of pregnancy and during the early post-partum period can increase the number of follicles and increase the secondary: primary ratio (S/P) through an influence on the maturation of secondary follicles. Early post-natal feeding levels reduced the ability of the follicles to grow fibre. Longer fibres may be produced by sheep with low follicle population (Fraser, 1952; Schinckel and Short, 1961; Henderson, 1953a). Nutritional effects during the year of birth carried through to the year of fleece-growth, can cause differences between years at maturity. Differences between record-year nutritional levels can also cause variation (Ryder and Stephenson, 1968) by causing competition between the various tissues for nutrients.

Staple length showed a decreasing trend with time over the duration of the recording period, but particularly from 1970 onwards. These later years have been notable for summer droughts, severe at times, which could depress wool growth through nutritional deprivation.

In addition, stocking rates have increased steadily over the years, possibly leading to decreased wool production per sheep (Ryder and Stephenson, 1968).

A major source of variation in staple length is time between shearing (Wickham and Bigham, 1973). A short climatically-induced delay or management decision to alter shearing dates would be influential, particularly as wool growth rate is approaching its maximum in November (Henderson, 1968) when shearing is scheduled for completion.

The environmental effect of number of lambs weaned accounted for 1.5 to 3.1 percent of the variance in staple length within the three younger age groups but had no important influence on the five-year-olds. In the affected groups, barren ewes tended to have the longest staples and ewes which reared twins the shortest. The difference between raising zero and twins was in each case more than the disparity between rearing singles and twins implying that the stress of rearing multiple lambs is much greater than the stress of rearing a single lamb.

The age of the dam of the ewe and rearing rank were unimportant in explaining the variation in staple length.

The interaction of years with number of lambs weaned accounted for six percent of the variation in five-year-old ewes staple length. There was no consistency of ranking of NLW within year, and there was wide variation between subclass estimates within year.

D. Fleece Weight

The weight of greasy fleece produced by this flock of Perendales declined with increasing age but, as with staple length, there may be bias in the mean of the two-year-olds which in some years may have

been carrying more than twelve months wool growth. A decreasing wool weight has been observed by other researchers (Fahmy and Bernard, 1973; Wright et al., 1975; Thrift and Whiteman, 1970), but Hight et al. (1976) found from the average of six flocks that two-year-olds grew the lightest fleece, with three- and four-year-old ewes clipping the heaviest fleece. A similar trend was noted by Brown et al. (1966) who recorded peak wool production at 3½ years.

A decrease in greasy fleece weight with time was not unlike the trend observed in staple length. Turner (1958) showed that staple length is an important component of fleece weight and therefore a similarity of response to environmental pressures was not unexpected.

The main effects were all significant sources of variation in two- and three-year greasy fleece weight, but only year was important. In the remaining age analyses year, NLW (four-year-only) and rearing rank (five-year-old only) affected the total variation significantly, but the latter never reached the arbitrary two percent threshold. The extreme ages were more sensitive (27.6 and 25.1 percent of the observed variation) to differences between years than intermediate ages (14.0 and 12.7 percent).

Between-year effects are partly mediated through nutrition as well as other environmental and management factors. Adverse feeding levels during late pregnancy, and up to weaning can depress both initiation and development of secondary fibres, (Schinckel, 1953) and the effect can be permanent. Schinckel and Short (1961) studied the effect of different levels of feeding during pregnancy in Merino ewes, and also imposed high and low intake levels on their lambs up to 16-weeks of age. Lambs from low intake ewes were nine percent

lighter at maturity than lambs from well fed ewes, had about 15 percent fewer follicles, and produced about 8.5 percent less wool at maturity. A reduction of 10.5 percent in fibre weight resulted in about 12 percent less wool from adult ewes which had been poorly fed after lambing. Maximum fleece weights can be expected from ewes whose dams were well fed during late pregnancy, and who were themselves subject to high levels of nutrition during early life. Not only the level of nutrition, but also pasture species may affect wool production (Joyce and Newth, 1967; Bublath, 1969).

Although two-, three- and four-year-old daughters of two-year-old dams clipped less wool than daughters of older dams, the percentage variance controlled was never greater than 1.2 percent and therefore this source was relatively unimportant. The greatest difference was always between the fleece weights of daughters of two-year-old dams and the daughters of older ewes. The estimates for four-year-old daughters were small relative to the standard errors.

Being born and raised as a twin reduced the greasy fleece weight kilograms by 0.10[^] for two-year-olds, 0.08 for three- and four-year-olds, and 0.14 for five-year-olds. The five-year-old group analysis was the only one for which the variance caused by rearing rank reached two percent of the total but the consistency of the trend suggests that it is meaningful. Ewes nursing twin lambs have a higher intake, and provide more milk for their progeny (Coop and Drew, 1963) but the increase is insufficient to meet requirements, and the body weight and wool-producing ability of the multiple-born lamb is retarded relative to the single-born lamb. Twins therefore tend to be lighter than singles at all ages, although the percentage difference decreases as

the sheep get older (Dun and Grewal, 1963). It was reported by Turner (1961) that unhandicapped (singles from mature dam) 16-month-old Merinos produced 0.15kg more wool than their handicapped (twins from two-year-old dam) contemporaries. Follicle density and fibre diameter reductions accounted for more than half of the difference. Secondary follicle numbers were considerably lower within the handicapped group. Brown et al. (1966) confirmed that retardation of early development through maternal handicap is permanent.

The evidence provided in the literature and the results of this study suggest that early restriction on development, caused by competition of various sorts for nutrients, is influential in reducing mature fleece weight.

NLW had a significant effect on greasy fleece weight production of all but the five-year-olds, but in the two- and three-year groups differences accounted for less than two percent of the variation. For the three ages the order of the effect was the same - barren ewes produced more wool than ewes rearing single offspring, who in turn produced more than ewes weaning twins. Ross (1965) found the opposite age response to NLW, stating that although average wool production was least for ewes bearing twins, the effect was only noticed at five- and six-years of age. Thrift and Whiteman (1970) found that Dorset ewes produced about the same weight of wool regardless of their lambing status, whereas Western ewes which failed to lamb and those which gave birth to one lamb had heavier fleeces than those which gave birth to two, regardless of the number reared. This result suggests that pregnancy affect on greasy fleece weight production may be more important than lactation stress, and Brown et al. (1966) concurred. However, Ray and Sidwell (1964) and Mullaney et al. (1969)

disagreed, finding that the effect of lactation was more important. Hight et al. (1976) tabulated the fleece weight for six flocks according to NLW classification. The average over all flocks showed that dry ewes clipped 3.66kg, ewes weaning single lambs 3.46kg and ewes weaning multiple lambs 3.39kg. It is not surprising that disagreement should occur as to the relative importance of the lactation and pregnancy effects on wool production, as these effects are generally confounded with season of year.

Competition between the dam and lamb for nutrition could explain the decreased fleece weights of fertile as opposed to barren ewes. Pre-natal effects arise from a portion of the products of digestion being 'siphoned off' for the conceptus. Post-natal competition arises from the provision of milk by the ewe for the nourishment of the lamb. The high intake of a ewe rearing twins is insufficient to allow her to gain noticeably in bodyweight, whereas the same ewe will gain in bodyweight on less feed when rearing a single lamb (Coop and Drew, 1963).

E. Fibre Diameter

There is an upward trend in fibre diameter from the first to the third mature record (tables 5.1 to 5.4). The means were 34.38, 34.91, 35.22 and 35.16 for the four age groups respectively. Elliott's (1975) analysis of hogget records showed that fibre diameter for immature Perendales was much lower at 30.98. Ross (1965) also reported an increasing fibre diameter from two-year-old to four-year-old among Romneys with a decrease thereafter. Brown et al. (1966) reported that fibre diameter increased with age until it reached a peak at 6½ years in Merino sheep.

Differences between years had consistently less effect on this trait than on other wool characteristics, never explaining more than 10 percent of the observed variation, and decreased with age.

An influence of year of birth on mature fibre diameter measurement was recorded by Schinckel and Short (1961), who found that restricted intake by the dam during the pre-natal phase was associated with the production of slightly coarser fibres by the lamb. Low nutritional levels during early post-natal life caused finer fibres to be produced at maturity. Other workers have supplied evidence to show that pre-natal nutritional deprivation results in coarser, longer fibres in lambs (e.g. Henderson, 1953a; Schinckel and Short, 1961).

Rearing rank was a significant source of variation in fibre diameter of two- and three-year-old ewes, but only for the latter was more than two percent of the total variance accounted for by this factor. In the three-year analysis it was found that single lambs were 0.54 microns finer than twins. The two- and four-year-olds recorded the same rearing rank trend.

More than 2.5 percent of the total variance in fibre diameter could be attributed to the NLW x year interaction in the three-year-old analysis (Table 5.6) but no consistent trend was apparent.

F. Number of Lambs Weaned

There was a strong upward trend in NLW with age. This is a common observation recorded by many other writers (e.g. Fahmy and Bernard, 1973; Dickerson and Glimp, 1975; Turner and Dolling, 1965). However, insufficient age groups were analysed to investigate the age at which lamb production peaks. Turner and Young (1969) thought

that the general pattern is for a peak to be attained at between four- and seven-years of age.

Lax and Turner (1965) suggested that survival is also affected by dam age, a peak being recorded at the same age as for maximum lambing rate in their sheep. Hight and Jury (1970) also found an effect of age on survival, but suggested that there are differences between singles and twins, with the latter having the highest probability of surviving.

Year effects were of minor importance as a cause of variation in NLW and accounted for only 1 to 3.7 percent. Pre-tupping nutrition, both static (liveweight) and dynamic (liveweight change) is vitally important in influencing NLB and ultimately NLW (Wallace, 1961; Tribe and Seebeck, 1962; Coop, 1962, 1964; Hight and Jury, 1973). It was suggested by Coop (1962) that reproductive performance increased with age solely as a function of liveweight. Hight and Jury (1973) found that age differences could not be attributed to weight alone, and that heavier ewes reared more lambs at each age.

Between-year differences could arise from differences in pasture levels during the tupping season and for a short period preceding mating. Nutritional differences would then be a direct reflection of summer rainfall. Management attempts to flush ewes pre-tupping would be included in between-year differences.

None of the other main effects was important in affecting NLW, but it is interesting to note that, albeit small, there is a consistent disparity in favour of ewes reared as twins. In economic terms, this would be at least partially offset by the opposite observation for greasy fleece weight. Part of the rearing rank differences are

genetic in origin as rearing rank differences are an observation on the performance of the dam while NLW is an observation of the same trait on the daughter, and can form the basis of a heritability calculation.

Two interactions contributed more than two percent to the variance of NLW for the five-year-old analysis: year x rearing rank and dam-age x rearing rank. In studying year x rearing rank interaction it can be seen (table 5.10) that the order of performance of rearing rank within years changes with time. In the early years the tendency was for ewes born as twins to wean most lambs, but later this changed so that single born ewes weaned more lambs. It seems that, if twin lambs had an advantage in genotype for NLW during the early years, this advantage could not be expressed during the drought years from 1970 onwards.

In considering the interaction of dam-age with rearing rank, (table 5.11) it can be seen that the daughters born as twins from two-, three-, or four-year-old dams produced more lambs at weaning than single born daughters. For the daughters of five-year-old dams, the opposite occurred. The difference between the latter dam-age subclass means is very small and may be due to chance. A further point to note is that the difference between rearing rank classes decreases as the age of the dam increases, by far the largest difference being associated with two-year-old dams.

Table 5.10 Five-year-old Ewes. Least Squares Estimates of Environmental Effects. Year x Rearing Rank Interaction for NLW

Year	Rearing Rank	
	1	2
1966	0.04	0.05
1967	-0.16	0.07
1968	-0.16	0.30
1969	0.03	-0.05
1970	-0.20	-0.16
1971	0.19	-0.11
1972	0.30	0.19
1973	0.03	0.02
1974	-0.24	-0.15

Table 5.11 Five-year-old Ewes. Least Squares Estimates of Environmental Effects. Dam age x Rearing Rank Interaction for NLW

Dam Age	Rearing Rank	
	1	2
2	-0.04	0.25
3	0.17	0.21
4	-0.33	-0.36
5 - 5+	0.04	0.01

II Selection applied

The amount of selection applied to the ewes in the flock during the data collection period was computed by studying the selection differentials at each age. It is apparent from table 5.12 that most selection pressure on wool traits has been imposed at the hogget stage. The maximum selection intensity was applied to fibre diameter, which was lower by 0.15 standard deviations for those hoggets retained as breeding ewes than for all hoggets. Later selection was minor but in the same direction.

It is assumed that direct selection was not applied to reduce wool character, as an increase would be more desirable. The phenotypic correlations between character and other wool traits or hogget body-weight (Elliot, 1975) are not great enough to suggest that a correlated response has occurred. The decrease may have been correlated with some unrecorded culling variate. Selection for character at later ages is negligible and variable.

Staple length selection is of low intensity but continuous throughout the age range studied. This is undoubtedly a correlated response to other selection as increased staple length is a breeding objective. The same comments apply to fleece weight which decreases slowly but continuously after an initial large drop.

Quality number is the only wool trait to which conscious selection was applied. Apart from selection at the hogget stage, the effect of selection has been relatively unimportant.

Virtually no selection has occurred on the basis of two-year-old NLW performance, but the effect of culling some of the barren ewes at three- and four-years of age is more apparent as the mean of retained

Table 5.12 Difference in standard deviation units between the performance of all animals of age i,
and the age i performance of animals which succeed to age j

Age i	Age j	Hogget body weight	Quality number	Wool character	Staple length	Fleece weight	Fibre Diameter	N.L.W.
Hgt	2	0.27	0.13	-0.10	-0.04	-0.11	-0.15	-
Hgt	3	0.33						
Hgt	4	0.32						
Hgt	5	0.26						
2	3		0.00	0.01	-0.06	-0.04	-0.05	0.03
3	4		0.04	0.00	-0.02	-0.02	-0.02	0.20
4	5		0.02	-0.01	-0.04	-0.06	-0.02	0.11

ewes exceeds the mean of all ewes at those ages. The effect of selection of hoggets on their dams' performance was not calculated.

The hoggets retained in the flock for a further year were heavier than those which were culled, and represent 85 percent of all candidates for selection. Although ewes which remained in the flock as three- and four-year-olds were heavier on average as hoggets than were the two-year-old ewes, the difference is small. The trend does not continue into the final age group.

The only culling of mature ewes carried out as a matter of policy involved quality number and NLW. The size of the change in some of the other wool characteristics is surprising. However, for any particular trait analysed culling on the basis of that characteristic is relatively unimportant as an explanation of the total culling process.

III. Within-age Study

A. Heritability Estimates

The heritability estimates derived by both paternal half-sib (PHS), and the regression of daughter on dam (DDR) methods appear with their standard errors in table 5.13. The approximate amount of selection bias in each estimate is also included in the same table. This was calculated for the PHS estimates from results reported by Rönningen (1972a) who estimated the degree of bias when selection has been applied to progeny groups. A second paper by the same author (Rönningen, 1972b) considered the bias in various offspring-parent methods and prediction equations were developed. In both cases the biases were always negative.

The significance of differences between heritability estimates was assessed by calculating the standard error of the difference, and examining the discrepancy in terms of this standard error.

1. Quality Number

The heritability of fleece quality number was computed as 0.22 ± 0.06 , 0.27 ± 0.08 , 0.28 ± 0.11 and 0.25 ± 0.14 by PHS for the two-, three-, four- and five-year-old groups respectively. The equivalent estimates by DDR were 0.39 ± 0.08 , 0.48 ± 0.09 and 0.66 ± 0.14 for the first three ages. Probable selection biases indicate that the values presented could be 0.04 to 0.06 (PHS) or 0.07 to 0.11 (DDR) too low. As the calculated biases are in all cases not greater than the standard error, the implication is that they are unimportant.

The two- and three-years-old paternal half-sib heritability estimates are lower than any of those of Mullaney et al. (1970) for 30-month ewes of three breeds (Table 2.2). However, the comparable DDR estimates are in reasonable agreement with their Corriedale and Polwarth values.

No trend is apparent with age among the PHS estimates, all being about the same magnitude, but there is an upward trend with age according to the DDR heritability values. Elliott's (1975) hogget results were 0.26 ± 0.01 (PHS) and 0.31 ± 0.04 (DDR) which fall into the pattern of mature estimates. The only significant difference ($p < 0.05$) is between the DDR hogget and four-year-old estimates, and the reality of an age trend is doubtful. Mullaney et al. (1974) is the only source of between-age information on quality number heritability, and they report that 18-month were less than 30-month

Table 5.13 Heritability Estimates, Standard Errors and Approximate Biasses

Trait	Age	PHS		DDR			
		Estimate	Bias	Estimate	Bias		
Quality Number	2	0.22 \pm 0.06	-0.04	0.39 \pm 0.08	-0.07		
	3	0.27 \pm 0.08	-0.04	0.48 \pm 0.09	-0.08		
	4	0.28	0.11	-0.06	0.66	0.14	-0.11
	5	0.25	0.14	-0.06			
Wool Character	2	0.33	0.08	-0.03	0.21	0.06	-0.04
	3	0.26	0.08	-0.03	0.12	0.09	-0.03
	4	0.16	0.09	-0.02	0.25	0.11	-0.04
	5	0.39	0.16	-0.04			
Staple Length	2	0.44	0.08	-0.02	0.36	0.07	-0.05
	3	0.52	0.11	-0.07	0.33	0.09	-0.06
	4	0.32	0.11	-0.05	0.25	0.12	-0.05
	5	0.71	0.18	-0.12			
Fleece Weight	2	0.53	0.09	-0.07	0.45	0.07	-0.07
	3	0.52	0.11	-0.08	0.62	0.08	-0.09
	4	0.40	0.12	-0.07	0.43	0.11	-0.07
	5	0.24	0.14	-0.08			
Fibre Diameter	2	0.54	0.11	-0.10	0.50	0.08	-0.08
	3	0.54	0.13	-0.13	0.45	0.10	-0.08
	4	0.38	0.14	-0.11	0.45	0.17	-0.06
	5	0.68	0.23	-0.18			
NLW	2	0.14	0.05		-0.02	0.06	
	3	0.02	0.05	-0.00	0.01	0.09	-0.02
	4	0.24	0.10	-0.08	0.03	0.13	-0.02
	5	0.04	0.11	-0.02			
Fertility	2	0.06 \pm 0.04					
	3	0.02 \pm 0.02					
	4	-0.01	0.07				
	5	-0.15	0.16				
Twinning	2	0.12	0.05				
	3	0.15	0.07				
	4	0.13	0.09				
	5	0.01	0.05				

values, but the differences were not significant.

The sets of figures presented above are widely different between methods, DDR estimates always exceeding PHS estimates, although the difference was only significant at four-years. Points to consider are:

- (i) Bias could have arisen in the DDR estimates from maternal environment. This possibility is remote as the effect is unlikely to carry over to four-years, when the greatest differences occur, particularly as the recorded maternal effects (rearing rank and dam age) were found to be unimportant.
- (ii) As the DDR computations were carried out on considerably smaller samples, sampling errors may have been responsible for the discrepancy.
- (iii) The variance between sires could have been reduced by assortative mating. No evidence was found for non-randomization of ewes within mating groups but may nevertheless have occurred. If for example, many coarse woolled rams were assortatively mated to ewes with fine wool but each group mean deviated little from the flock mean the progeny groups would be more alike than where true random mating was practised. The between-sire variance, and PHS heritability estimate would then be reduced, without affecting the DDR estimate. Evidence against this explanation comes from the fact that the estimates for fibre diameter show no analogous differences.

2. Wool Character

Values calculated for the heritability of wool character were 0.33 ± 0.08 , 0.26 ± 0.08 , 0.16 ± 0.09 and 0.39 ± 0.16 using PHS procedures, and 0.21 ± 0.06 , 0.12 ± 0.09 and 0.25 ± 0.11 by the DDR method. These estimates relate to the age groups in increasing order. Selection has reduced heritability by 0.04 or less, which is considerably below any of the standard errors. Mullaney et al. (1970) have published the only wool character heritability estimates for mature sheep (Table 2.3), and their results can be compared with the two- and three-year values from the present study. For the three breeds that they studied, the estimates were consistently higher than for the Perendale sample. No published estimates are available with which to compare the older age results.

No regular age trend is perceptible in the heritability estimates even when Elliott's (1975) tabulated values of 0.23 ± 0.01 and 0.23 ± 0.03 are considered.

The differences between methods at each age and between ages within each method separately were not statistically significant.

3. Staple Length

The Perendale estimates for the heritability of staple length for two-, three-, four- and five-year-old ewes by PHS were 0.44 ± 0.08 , 0.52 ± 0.11 , 0.32 ± 0.11 and 0.71 ± 0.18 . Equivalent estimates for the first three ages by DDR were 0.36 ± 0.07 , 0.33 ± 0.09 and 0.25 ± 0.12 . Bias due to selection was of minor importance relative to the standard errors (Table 5.13). PHS estimates were more variable and consistently higher than those from the DDR analysis. The two- and

three-year-old heritabilities were within the range of those presented by Mullaney et al. (1970). Age was not explicitly quantified by Nawara and Duniec (1972) other than by shearing number, but their evaluation of heritability was 0.57 for two ages, within the range of PHS values presented here.

When they examined heritability of staple length based on the correlation between single records on the daughter and dam, Mullaney et al. (1970) found that although 18-month estimates were greater than or equal to 30-month values, the differences were smaller than the standard errors. There is an apparent peak in staple length heritability at third shearing according to Nawara and Duniec (1972) but it is not known how real this observation is as no standard errors were included in the abstract. Elliott's (1975) heritabilities of 0.49 ± 0.01 (DDR) and 0.35 ± 0.04 (PHS) form part of an age series with the present estimates, but no real trend is noticeable and the between-age differences are not significant in a statistical sense.

4. Fleece Weight

The individual age group heritability estimates from two- to five-year-old were 0.53 ± 0.09 , 0.52 ± 0.11 , 0.40 ± 0.12 and 0.24 ± 0.14 by PHS. For the two-, three- and four-year-old ewes the estimates were 0.45 ± 0.07 , 0.62 ± 0.08 and 0.43 ± 0.11 by the DDR method. The effect of selection was to bias the heritabilities downwards by an amount less than one standard error except in the case of the three-year-old (DDR) where the bias marginally exceeded the standard error of the estimate.

There are a wide range of heritability estimates recorded in table 2.1 and the Perendale values derived here are within the range of

those listed. There are no reports comparable with the four- and five-year-old estimates for the Perendales, but the two- and three-year-old heritabilities by either method compare well with many of those in the literature (Doney, 1958; Kooistra et al. 1966; Mullaney et al. 1970; Nakev, 1973; More O'Ferrall, 1976), but are higher than others (Váchal, 1962; Nawara and Duniec, 1972). Eikje's (1975) estimate for ewes over 36-months is near the five-year Perendale result, but less than the four-year value.

The hogget heritability estimates for fleece weight were 0.32 ± 0.01 (PHS) and 0.30 ± 0.03 (DDR) according to Elliott (1975). There is a decreasing tendency in PHS estimates after the hogget stage, but only the difference between hogget and two-year-old records are significantly different ($p < 0.05$), and the trend may not be real. There is no trend among the DDR heritability values, but the one- and three-year-old estimates were significantly different. Mullaney et al. (1970) found that 18-month estimates were always less than 30-month estimates but the difference was only significant in one out of three comparisons. The situation with Eikje's (1975) values is confused by the adjustment of the records of one age group, but the one-year estimate was higher than those recorded later for fleece weight. Nawara and Duniec (1972) found that the estimates of greasy fleece weight heritability decreased from second shearing onwards, but the actual age at second shearing was unspecified.

5. Fibre diameter

Estimates for fibre diameter heritability are presented in table 5.13 with the other characteristics, but are less precise at each age due to fewer records being available. Results from the PHS calculations were 0.54 ± 0.11 , 0.54 ± 0.13 , 0.38 ± 0.14 and 0.68 ± 0.23

for two- three-, four- and five-year-old ewes. Heritability estimates for the first three ages by DDR were 0.50 ± 0.08 , 0.45 ± 0.10 and 0.45 ± 0.17 . Although the extent of selection was greater for fibre diameter than for other wool traits, the bias failed to exceed one standard error for any estimate. The values derived from the analysis of the two younger groups, which compare in age with the sheep of Mullaney et al. (1970), are in good agreement with estimates listed in table 2.5.

Elliott's (1975) PHS (0.54 ± 0.01) and DDR (0.47 ± 0.02) estimates are similar to the mature values for fibre diameter heritability. There are no significant differences between any pairs of estimates. Consistent directional differences were recorded by Mullaney et al. (1970) (table 2.8) who found that 18-month estimates were always lower than those for 30-month ewes of three breeds, but the discrepancy was never significant.

6. Number of Lambs Weaned

Widely differing heritability estimates were evident from the data analysed by PHS. The results were 0.14 ± 0.05 , 0.02 ± 0.05 , 0.24 ± 0.10 and 0.04 ± 0.11 for the two-, three-, four- and five-year-old ewes, and the DDR equivalents were -0.02 ± 0.06 , 0.01 ± 0.09 and 0.03 ± 0.13 . The effect of selection was minor in magnitude. Most estimates in table 2.11 for heritability of NLW at 24-months are less than 0.1 (Young et al. 1963; Kennedy, 1967; More O'Ferrall, 1976; Eikje, 1975), but one value presented by More O'Ferrall (1976) of 0.16 is in good agreement with the two-year PHS value above. The three- and five-year-old values by PHS are negligible, as are all of the DDR results, but the four-year PHS estimate is higher than any

single-record heritability reviewed with the exception of one relating to fertility (0, 1) by Young et al. (1963). A possible bias could arise in DDR estimates where a ewe has no lambs during her lifetime as barrenness itself may have a genetic component. Ewes which have no ewe lambs would also be excluded.

The differences between age estimates of heritability are significant ($p < 0.05$) only for the PHS three-four comparison but form a definite pattern. If this cyclic effect was real, an explanation could be as follows: the two-year-old ewes entering the flock have all been similarly managed during their development, so that between-sire environmental differences should be non-existent at first lambing. At the second lambing, the expectation of the between-sire component due to the previous year NLW environment will not be zero as the sire groups will have reared different average numbers of lambs. The stress of raising larger average families at first lambing may decrease the propensity of the affected groups for multiple births at second lambing, thus reducing between-sire differences. The adverse environment will have reduced the 'better' groups ability to express their superiority at the second lambing. At the third lambing, the various sire groups will have experienced a more homogeneous NLW environment in the previous season, and differences between sire groups will again be expressed. The fourth lambing will be under similar circumstances to the second. High heritability could be expected whenever the previous season environment was relatively uniform for all sire groups.

This theory could be tested by computing the heritability of NLW for the ewes lambing as three-year-olds which were barren at

two-years and comparing with ewes which lambed at both ages. Unfortunately, only about 120 ewes fell into this category and the standard error of the heritability estimate would have been too large for the results to have been meaningful.

7. Fertility and Twinning

The estimates of heritability for fertility and twinning are all of low magnitude, and suggest that there is unlikely to be any appreciable response to mass selection. The heritability of twinning is higher at each age than the heritability of fertility, which indicates that retaining replacements from dams which produce twins at weaning may be more successful than selecting from progeny of dams which merely raise a lamb.

What selection pressure has been applied has been against barrenness, which raises the suspicion that the fertility estimates may be biased by the culling of dry ewes. The ewes were not culled until after recording and therefore at each age the only selection had been based on previous records. Considering that selection differentials never exceeded 0.20 of a standard deviation, and that the heritability was expected to be low, bias should be unimportant. However, if there is any bias present the early records should be virtually free of it.

Young et al. (1963) calculated the heritability of fertility based on NLW using a maximum likelihood procedure and reported estimates of 0.0 and 0.29 at two- and three-years of age. Their analysis of variance computations yielded heritabilities of 0.03 and 0.15 at the same respective ages and 0.09 for the sum of the two ages. The two-year estimates are similar to those recorded in table 5.13, but the

three-year estimates exceed those found here. However, the differences are not significant.

8. Conclusions

The heritabilities of all wool characteristics are medium to high according to the estimates presented in previous sections. The downwards bias in these estimates is generally not great enough to be considered as other than part of the random variation. It can be stated with some confidence that, based on this and other studies, the wool traits examined would respond well to selection.

The estimates were calculated after taking into account those interactions which contributed more than two percent to the total variance, but which were not excluded by other considerations. Table 5.14 contains the PHS heritabilities for the variables calculated from data which were corrected for interactions, as well as estimates where the data were uncorrected. The differences between methods were always small, and non-significant. No serious error would arise from calculating heritability estimates ignoring interactions where they contributed to variance to the extent of those analysed here.

Although differences were noted between heritability estimates computed by the PHS and DDR methods, the discrepancy only attained significance among quality number values which were discussed earlier. Differences between ages were seldom significant, but as a characteristic measured at different ages might not necessarily be the same trait genetically, the comparison may be irrelevant

The practical effect of low heritability for reproductive traits can be seen in tables 5.1 to 5.4, where the difference in NLW between ewes reared as singles and those reared as twins was only two to four

percent, dependent upon age. The NLW estimates suggest that selection for NLW at two- and four-years of age may be more accurate in increasing future lamb production than the same operation performed at three- or four-years of age.

Table 5.14 Comparative Heritability Estimates from Models Including and Excluding Important Interactions

Variable	Age	With Interaction		Without Interaction		Differences	
Quality number	2	0.22 ± 0.06		0.21 ± 0.06		0.01 ± 0.08	
Quality number	3	0.27	0.08	0.21	0.08	0.06	0.11
Fibre diameter	3	0.54	0.13	0.49	0.12	0.05	0.18
Staple length	5	0.71	0.18	0.69	0.18	0.02	0.25

B. Genetic Correlations

1. Between Wool Characteristics

The estimates of the genetic correlations between wool characteristics are presented with their standard errors in table 5.15.

Comparisons will be made with the published estimates of Mullaney et al. (1970) throughout this discussion. Their results were derived from Merino, Corriedale and Polwarth sheep of 30-months of age and are therefore most closely comparable with the two- and three-year-old estimates from this study. Any discussion contrasting their results with mature Perendale estimates will presuppose that only the two- and three-year-old ages are being considered.

The genetic correlations will be discussed under subheadings, following the format of table 5.15.

(a) Greasy Fleece Weight with Other Wool Characteristics

The results from this analysis indicate that greasy fleece weight is positively related to all of the other wool characteristics studied, except quality number, at all mature ages. The only inconsistency in sign in the estimates relates to the genetic correlation between greasy fleece weight and staple length, where the four-year-old value is negative by the daughter-dam (DD) method, but is negligible in magnitude and has a large standard error.

Antagonisms which may confuse selection policy are evident in some associations. Increased fibre diameter and decreased quality number in the next generation will result from selecting as replacements, the progeny of ewes which grow the heaviest fleeces. Fibre diameter will be most affected where progeny are selected from young

Table 5.15 Estimates of Genetic Correlations and Standard Errors.

		<u>Wool Traits.</u>			
		Age	PHS	DD	
(a) Greasy fleece weight					
- fibre diameter					
	2	0.57 ± 0.13		0.36 ± 0.08	
	3	0.54 ± 0.15		0.52 ± 0.08	
	4	0.28	0.27	0.23	0.23
	5		a		
- quality number					
	2	-0.22	0.17	-0.45	0.07
	3	-0.07	0.20	-0.29	0.08
	4	-0.49	0.22	-0.46	0.10
	5	-0.11	0.42		
- staple length					
	2	0.68	0.09	0.44	0.07
	3	0.71	0.10	0.49	0.08
	4	0.66	0.17	0.36	0.16
	5	0.69	0.22		
- wool character					
	2	0.60	0.12	0.28	0.11
	3	0.26	0.20	0.44	0.18
	4	0.46	0.30	-0.06	0.18
	5	0.17	0.37		
(b) Quality number					
- fibre diameter					
	2	-0.55	0.20	-0.64	0.08
	3	-0.31	0.21	-0.56	0.09
	4	-0.65	0.21	-0.39	0.15
	5	-0.62	0.22		
- staple length					
	2	-0.57	0.13	-0.67	0.07
	3	-0.56	0.15	-0.71	0.07
	4	-0.43	0.23	-0.36	0.13
	5	-0.62	0.22		
- wool character					
	2	0.21	0.19	0.01	0.12
	3	0.26	0.21	0.58	0.16
	4	0.49	0.30	0.26	0.14
	5	0.74	0.28		

Table 5.15 continued

(c) Fibre diameter					
- staple length					
	2	0.57	0.14	0.20	0.10
	3	0.69	0.14	0.28	0.13
	4	0.13	0.29	0.15	0.40
	5	0.17	0.28		
- wool character					
	2	0.20	0.18	-0.12	0.15
	3	-0.04	0.25	0.09	0.26
	4	-0.85	0.42	0.31	0.44
	5	-0.46	0.30		
(d) Staple length					
- wool character					
	2	0.37	0.15	0.19	0.12
	3	0.07	0.21	-0.33	0.22
	4	0.36	0.33	-0.08	0.24
	5	0.05	0.27		

a. Negative variance component (Greasy fleece weight)

dams. The strong association between greasy fleece weight and staple length and the weaker relationship between greasy fleece weight and wool character are favourable to selection objectives.

The genetic correlations of Mullaney et al. (1970) are identical as to sign to the mature Perendale estimates for all except the greasy fleece weight - wool character relationship, where their values differ among breeds. Elliott's (1975) Perendale hogget genetic correlations are in the same direction as for the older ewes of the same breed, with the exception of the greasy fleece weight-quality number estimate (DD) which was small and positive.

Differences between methods of estimation are evident for every genetic correlation, but are significant only for the correlation between greasy fleece weight and staple length at two-years of age. It is assumed that these differences are due to sampling as they are seldom consistent in direction, and the DD analysis was based on a smaller sample than the PHS calculations.

(b) Quality Number with Other Wool Characteristics

The genetic correlation^s_λ between quality number and fibre diameter and between quality number and staple length were always negative, while the association of quality number with wool character was positive at all ages in this analysis. Considering that quality number and fibre diameter are both assessments of fibre fineness, the magnitude of some of the genetic correlations between them are remarkably low, but all are in the expected direction.

Dams with the finest quality numbers will produce progeny with fleeces which are shorter in the staple according to the genetic correlations presented in table 5.15 and this is antagonistic to

common selection aims which would require an increase in both characteristics. The genetic association between quality number and wool character ensure that advantageous correlated selection responses would be observed.

Mullaney et al.'s (1976) estimate (table 2.12) agree as to sign with those in table 5.15 for the quality number-fibre diameter and quality number-staple length genetic correlations, but their results for quality number-wool character vary widely among breeds, with two out of three estimates being low negative while the third is greater than the low positive Perendale values. The Perendale hogget genetic correlations (Elliott, 1975) for quality number-wool character is opposite in sign to the mature estimates but very small. The remainder are in agreement with the mature estimates as to sign.

None of the differences between methods was significant for the genetic correlations examined in this section.

(c) Fibre Diameter with Other Wool Characteristics

Fibre diameter and staple length are positively genetically correlated according to the estimates in table 5.15, but the signs of the fibre diameter-wool character relationship are inconsistent among ages.

Selection for decreased fibre diameter will be at the expense of decreased staple length which is clearly antagonistic to selection aims. The correlations are particularly strong at the younger ages. The picture is not so clear for the fibre diameter-wool character association as there is not only a change in sign with age, but also between methods. The PHS estimates imply that selection against

fibre diameter at two-years will decrease wool character, but later selection will have the converse effect. The DD values suggest that the opposite effect will occur at each age, but the estimates are all smaller than their standard errors. Only the four-year-old estimates are significantly different between methods.

Mullaney et al. (1970) found that data on two breeds produced small positive genetic correlations between fibre diameter and staple length while the third yielded strongly negative values which makes comparisons with the present results difficult. Their fibre diameter-wool character genetic correlations were consistently negative. Elliott (1975) recorded positive correlations between fibre diameter and staple length, and fibre diameter and wool character by both PHS and DD methods.

(d) Staple Length with Wool Character

The final wool trait genetic correlation to be discussed shows wide variation both within and between methods. The estimates are all negligible or low, but vary in sign. None of the differences between methods is significant. Elliott's (1975) results show significant differences between methods, but both are positive. Variability in both sign and size of the genetic correlation coefficient is evident in the estimates reported by Mullaney et al. (1970) who recorded a small negative value for one breed and medium positive values for the other two breeds. The two-year PHS estimates from this study are within the order of their range of positive values, but none of the other values coincide, although the DD two-year Perendale correlation is only slightly lower than the Corriedale estimate.

2. Number of Lambs Weaned with Wool Characteristics

The estimates of the genetic correlations between NLW and fleece characteristics are listed in table 5.16. The DD analysis provided generally unsatisfactory results due to small or negative daughter-dam covariances. Several estimates by both methods have very large standard errors.

All genetic correlations between NLW and greasy fleece weight calculated by the PHS method were found to be negative in this analysis. A DD estimate which conflicts in sign with all others in table 5.16 has a standard error in excess of unity. The indications are that selecting for increased reproductive rate will cause a correlated response toward lower fleece weight in the following generation. Although the negative estimates in table 2.13 support this conclusion, those figures are not strictly comparable with the Perendale values as the ages in each table are different. Other workers have observed NLW and wool traits at different ages. Note that only the two-year estimate is significantly different from zero, but that the signs are consistent.

Turner (1972) stated that some published estimates of the genetic correlation between reproduction and fleece weight are biased by the failure to correct the ewes wool weight for reproductive status. The arguments to support the contention are that the environmental effect of NLW (or number of lambs born) will influence the ewe's fleece weight, and that a twin born ewe will raise more twins herself. A negative genetic correlation may then be obtained through the environmental effect. Several experiments were cited showing that both reproduction rate and fleece weight can be increased concurrently under selection. While conceding that the logic of the argument is

Table 5.1.6 Estimates of Genetic Correlations and Standard Errors.
Number of Lambs Weaned With Wool Traits.

	Age	PHS	DD	
NLW				
- greasy fleece weight	2	-0.40 + 0.19	a	
	3	-0.04 ^b 0.63	0.47	c
	4	-0.25 0.28	-0.02	0.55
	5	-0.54 ^b 1.00		
- fibre diameter	2	-0.23 0.22	a	
	3	c c	a	
	4	-0.38 0.35	c	c
	5	d		
- quality number	2	0.03 0.25	a	
	3	0.92 ^b c	-0.39	c
	4	0.19 0.31	0.25	0.56
	5	0.34 ^b 0.99		
- staple length	2	-0.43 0.20	a	
	3	-0.72 ^b c	-0.67	c
	4	-0.16 0.30	-0.23	0.74
	5	-0.95 ^b c		
- wool character	2	-0.06 0.22	a	
	3	0.30 ^b 0.85	- c	c
	4	0.24 0.36	-0.12	0.78
	5	0.37 ^b 0.91		

a Negative denominator covariance.

b Small variance component for NLW.

c Greater than the theoretical limit of genetic correlation coefficients.

d Negative variance component.

soundly based, it is submitted that it does not apply to this analysis as the necessary adjustments were made to the fleece weight data.

The genetic correlation between NLW and fibre diameter is negative according to the figures in table 5.16. Unfortunately, results were only achieved at two ages. Young et al. (1963) also found that the genetic association was negative, but their fibre diameter measurement was recorded on hoggets.

The positive genetic correlations between NLW and quality number are consistent with the NLW-fibre diameter negative relationship. The PHS values are compatible as to sign, but the DD estimates are not. However, the contradictory negative DD value has a standard error larger than theory permits.

The NLW-staple length correlations suggest that for this sample of Perendales, selecting for one will result in a decrease in the other regardless of the age at which selection is undertaken. Young et al. (1963) disagree but as mentioned they recorded hogget wool characteristics, which may help reconcile their positive NLW-staple length value.

NLW-wool character genetic correlations in table 5.16 are a mixture of positive and negative most of which are unreliable due to large standard errors. The smallest sampling variances were associated with the two- and four-year PHS estimates, the first of which is marginally negative while the second is low positive.

The genetic correlation estimates involving NLW have disappointingly large standard errors particularly at the ages where NLW is lowly heritable, but the PHS results in table 5.16 are compatible.

If the PHS evidence is accepted, selection for NLW at any age will be accompanied by a correlated response downwards for greasy fleece weight, fibre diameter and staple length, and upwards for quality number and wool character except possibly at two-years for the latter. The NLW-greasy fleece weight and NLW-staple length associations are particularly unfortunate as these are very important components of profitability.

(3) Conclusions

The genetic correlations were calculated separately for each age as each trait can be considered as a different characteristic at each age. This implies that the expression of a genotype in a particular environment may change with time. The expression of particular genes may be dependent upon the degree of maturity of the animal, and hence genetic variation and covariation may change with age.

Wide variation has been noted between the estimates of Mullaney *et al.* (1970) and the tabulated values in this thesis. Discrepancies could arise from sources such as sampling, breed, and age inequality.

Several antagonisms to selection objectives have been recorded, but the most serious involve the correlations between fleece weight and NLW, and fleece weight and quality number or fibre diameter. Fleece weight and NLW in particular are important components of productivity and therefore selection for these negatively correlated traits may best be achieved by use of a selection index. However, note that few of the genetic correlation estimates involving NLW significantly deviate from zero.

C. Phenotypic Correlations

1. Between Wool Characteristics

The phenotypic correlation estimates between the wool characteristics are listed in table 5.17. The discussion in this section will follow the format used for the genetic correlations.

(a) Greasy fleece Weight with Other Wool Characteristics

The signs of the phenotypic correlations between greasy fleece weight and the other wool characteristics are the same as for the genetic correlations, and show that the sheep with the heaviest fleeces are those whose wool is coarsest, has the longest staple and the highest wool character. Examination of table 2.20 confirms that this complex of relationships consistently go together. The hogget correlations of Elliott (1975) are always of the same sign as the mature Perendale estimates.

The phenotypic correlations in this section are generally more even in size than the genetic correlations except for the greasy fleece weight-staple length relationship where the latter vary little. The phenotypic associations are also usually smaller than the genetic equivalents.

As explained earlier the results of Mullaney et al. (1970) can at best be compared only with the two- and three-year estimates from this study. Only their greasy fleece weight-quality number correlations are greater than any of the greasy fleece weight relationships discussed. The remainder are approximately the same or less.

The correlation between greasy fleece weight and wool character decreased with age in these data, but was always negligible.

Table 5.17 Estimates of Phenotypic Correlations Between Wool Characteristics.

	Age	Correlation Coefficient
(a) Greasy fleece weight		
- fibre diameter	2	0.34
	3	0.45
	4	0.37
	5	0.34
- quality number	2	-0.21
	3	-0.22
	4	-0.28
	5	-0.27
- staple length	2	0.41
	3	0.45
	4	0.42
	5	0.35
- wool character	2	0.17
	3	0.11
	4	0.09
	5	0.04
(b) Quality number		
- fibre diameter	2	-0.37
	3	-0.38
	4	-0.42
	5	-0.41
- staple length	2	-0.43
	3	-0.39
	4	-0.40
	5	-0.37
- wool character	2	0.13
	3	0.24
	4	0.28
	5	0.30

Table 5.17 Continued(c) Fibre diameter
- staple length

2	0.22
3	0.25
4	0.20
5	0.15

- wool character

2	0.05
3	0.00
4	-0.05
5	-0.16

(d) Staple length
- wool character

2	0.09
3	-0.01
4	0.04
5	0.13

(b) Quality Number with Wool Characteristics

The phenotypic and genetic correlations involving quality number are of the same sign for each relationship. The phenotypic associations indicate that selecting for increased quality number will result in decreased fibre diameter and staple length and increased wool character in the current flock.

Again it is plain that quality number and fibre diameter cannot both accurately reflect fibre fineness as the correlation between them is at best medium in size.

The correlations between quality number and each other trait are similar among ages except two-year quality number-wool character which is noticeably smaller than at the other ages. Most of the correlations are smaller at the same age than their genetic equivalents.

Elliott's (1975) hogget figures have the same sign as the mature estimates and are of similar magnitude. The comparable Perendale ages yielded figures for each correlation involving quality number which were approximately equal to those of Mullaney et al. (1970) except that one of the Australian results was of opposite sign to the remainder.

No real age trends are apparent.

(c) Fibre Diameter with Other Wool Characteristics

Again the phenotypic relationships show less variability among ages than the genetic analogs, and are in the main of lower magnitude. The indications are that the sheep with finest wool also grow the shortest staple. The change with increasing age from positive to negative noted in the genetic correlation estimates is also perceptible in the phenotypic correlation figures, but less pronounced.

The detrimental effect of shorter staple associated with selection for quality number may be less harmful if fibre fineness selection is based on fibre diameter, as the staple length-fibre diameter relationship is less than the staple length-quality number correlation.

The hogget results for both associations were of the same sign, but larger than the two-year values. The fibre diameter-wool character estimates show a trend with age from 0.12 (hogget) to -0.16, but the consistently small values suggest that the trend may not be real.

Mullaney et al. (1970) figures for the fibre diameter-staple length correlation include the range for the estimates for the two similar ages here. They found all negative phenotypic correlations between fibre diameter and wool character.

(d) Staple Length and Wool Character.

Staple length and wool character have a phenotypic correlation of approximately zero at all ages except five-year-old according to the results in table 5.17. Mullaney et al. (1970) reported negligible values which were nevertheless larger than what were found for the Perendales at the two youngest mature ages. The hogget value was about the same as for the two-year-olds.

2. Number of Lambs Weaned and Wool Characteristics.

The consistent negative correlations between NLW and greasy fleece weight (table 5.18) for the Perendales is in agreement with the majority of published estimates in table 2.21, even though the ages at which the various traits were recorded are different for each data set. Most previous estimates are very small, being between 0.04 and -0.12, while values found in this analysis never exceeded -0.17.

Table 5.18 Estimates of Phenotypic Correlations
Number of Lambs Weaned With Wool Traits.

	Age	PHS
NLW		
- greasy fleece weight	2	-0.11
	3	-0.05
	4	-0.17
	5	-0.09
- fibre diameter	2	-0.01
	3	-0.01
	4	0.00
	5	0.04
- quality number	2	0.01
	3	0.05
	4	0.01
	5	-0.01
- staple length	2	-0.08
	3	-0.08
	4	-0.13
	5	-0.04
- wool character	2	-0.00
	3	0.01
	4	0.08
	5	-0.02

The negligible values of the NLW-fibre diameter, NLW-quality number and NLW-wool character phenotypic correlations suggest that there is probably no relationship between these variables. There is no evidence in table 2.21 to suggest otherwise.

NLW and staple length have a phenotypic correlation which, although small is invariably negative in these data. Although in disagreement with the few available mature published results, no other data set have included single-age comparisons, and none of the estimates have exceeded 0.06.

3. Conclusions

The same problems will be encountered with short term flock improvement as were found in genetic improvement. Selection for increased fleece weight will result in coarser wool, shorter in the staple and less lambs.

IV Between-age and Lifetime Study

A. Repeatability

1. Bartlett's Test of Homogeneity of Variance

The results of Bartlett's test of homogeneity of variance appear in table 5.19. Separate tests were carried out for mature records only, and for all records between one- and five-years of age, and were based on observations on all available animals at a particular age.

The results of the Bartlett's test show that the hypothesis that the variances of the mature records are the same should not be rejected, for all traits except staple length. When the hogget records were included, the test suggests rejection of hypothesis of no differences, except for fibre diameter. The variances listed in table 5.29 appear to be not greatly different one from the other and the regression of later on earlier records should be a reasonable approximation of the correlation between records.

There is a trend towards decreased variance with age among quality number and fibre diameter records which is not so apparent among the other traits, although smallest staple length variances appear at later ages. Fleece weight is less variable at the hogget measurement, while wool character is more variable at the same age. Only mature records are available for NLW, which shows little change in variability with time.

2. Repeatability Estimates.

The regression of later on earlier age are presented in table 5.20. There is frequently a trend among the estimates with the later values being less accurate. As there are differences between the

Table 5.19

Bartlett's Test of Homogeneity of Phenotypic Variance

Age	d. f.	Mean Squares					
		Quality Number	Wool Character	Staple Length	Fleece Weight	Fibre Diameter	NLW
1	2891 (2479)	3.62	1.19	2.48	0.16	5.68	-
2	1703 (1192)	3.39	0.95	2.78	0.26	4.98	0.30
3	1140 (865)	3.27	0.97	2.60	0.29	5.42	0.31
4	707 (505)	3.18	0.93	2.28	0.24	5.20	0.35
5	431 (292)	3.11	0.96	2.33	0.26	4.96	0.34
χ^2 (all records)		55.87 [†]	10.046*	61.095 [†]	222.763 [†]	1.762	-
χ^2 (mature records)		2.585	0.274	11.232**	6.313	1.932	6.569

* 0.025 < p < 0.050

** 0.010 < p < 0.025

† p < 0.010

Table 5.20 Regression of Later on Earlier Record,

Variable	Earlier Age	Later age			
		2	3	4	5
Quality Number	1	0.45 ± 0.02	0.41 ± 0.03	0.45 ± 0.04	0.31 ± 0.04
	2		0.53 ± 0.02	0.51 ± 0.03	0.42 ± 0.04
	3			0.63 ± 0.03	0.47 ± 0.04
	4				0.46 ± 0.04
			Average 0.46		
Wool Character	1	0.18 ± 0.03	0.18 ± 0.03	0.16 ± 0.03	0.14 ± 0.04
	2		0.20 ± 0.02	0.14 ± 0.03	0.08 ± 0.03
	3			0.29 ± 0.03	0.28 ± 0.04
	4				0.32 ± 0.04
			Average 0.18		
Staple Length	1	0.61 ± 0.02	0.53 ± 0.03	0.44 ± 0.04	0.44 ± 0.04
	2		0.58 ± 0.02	0.49 ± 0.03	0.42 ± 0.04
	3			0.56 ± 0.03	0.48 ± 0.04
	4				0.48 ± 0.04
			Average 0.50		
Fleece Weight	1	0.68 ± 0.03	0.69 ± 0.03	0.59 ± 0.04	0.55 ± 0.06
	2		0.70 ± 0.02	0.55 ± 0.03	0.54 ± 0.04
	3			0.64 ± 0.03	0.58 ± 0.04
	4				0.65 ± 0.04
			Average 0.62		
Fibre Diameter	1	0.67 ± 0.02	0.66 ± 0.03	0.61 ± 0.04	0.46 ± 0.05
	2		0.87 ± 0.02	0.80 ± 0.03	0.72 ± 0.05
	3			0.84 ± 0.03	0.74 ± 0.04
	4				0.73 ± 0.04
			Average 0.71		
Number of Lambs Weaned	2		0.05 ± 0.03	0.07 ± 0.04	0.09 ± 0.05
	3			0.11 ± 0.04	0.06 ± 0.05
	4				0.18 ± 0.04
			Average 0.09		

estimates, pooling is inappropriate, but Ercanbrack (1968) suggested that an average is valid. A weighted average may have biased the average estimate due to the systematic change in standard errors and estimates and therefore an unweighted average was calculated.

(a) Quality Number

The repeatability of adjacent records is generally higher than more widely spaced records. There is a tendency for later records to be more repeatable than earlier observations, although the regression of fifth on fourth is only marginally greater than the correlation between second and first, and is less than the other two adjacent records.

Mullaney et al. (1970) reported values of the correlation between 18- and 30-month records of three breeds of 0.60 to 0.71 with the repeatability based on various pairs of records at different ages ranging from 0.68 to 0.78. The average repeatability of 0.46 for Perendale quality number is substantially smaller than their estimates.

(b) Wool Character

The closer wool character measurements are related in time, the more repeatable they are, according to the results obtained. The conclusion from the figures in table 5.20 is that wool character observed at one age is not a good indicator of future wool character. Efforts to improve the trait in the current flock will not be very rewarding at the level of selection intensity which can be practically applied.

None of the correlations found by Mullaney et al. (1970) is as low as those found here for wool character.

(c) Staple Length

Adjacent staple length records become less repeatable as age increases, as shown by the results presented in table 5.20. The closer a pair of observations is in time the higher the repeatability.

The regression of later on earlier record computed in this study are within the range of repeatability estimates reported by other workers and derived by different methods (table 2.17). Gjedrem (1969) and Young et al. (1960) agreed that the smallest correlations between records involved earliest and latest ages. The former found an increasing association between records separated by one year, as the ewes grew older, which is the opposite to what was found in the Perendales.

The correlations found in the literature between pairs of records exceed those found here, including the average repeatability of 0.50.

(d) Fleece Weight

The trend in the relationship between records separated by one year is not quite so clear for fleece weight, although the tendency is for the regression to be higher at the younger ages. The average estimate was 0.62.

These results are in general agreement with many of those reviewed and tabulated in table 2.14 but derived by different methods. The correlations computed by various authors agree with the present observation that the more widely spaced records are less well correlated (Young et al. 1960; Wright and Stevens, 1953).

(e) Fibre Diameter

Fibre diameter is highly repeatable, but with a decreasing trend as the records become more widely separated in time. The older ages

are more highly correlated except that the regression of five- on four-year-old record does not conform to the pattern.

Both the magnitude and the general pattern of repeatability estimates are similar between Gjedrem's (1969) values and those in table 5.20. The size of the repeatabilities estimated by other authors (table 2.18) are generally lower than the average Perendale estimate of 0.71.

(f) Number of Lambs Weaned

Later records may be a better indicator of the following age performance than early records (table 5.20). Two-year records may be a better indicator of four- and five-year production than they are of three-year performance but the differences between the regressions are small. The implications of this trend will be discussed in the next section.

The average repeatability of 0.09 is in close agreement with most of the estimates in table 2.19. Rae and Ch'ang (1955) found the correlation between successive pairs of Romney records to vary between 0.12 and 0.25, which is higher than the range found here.

An upward trend with age was not recorded by Young et al. (1963) who reported that four-year repeatability was less than for two- or three-year-old ewes.

(g) Number of Lambs Weaned at Different Production Levels

The repeatability of the difference between one and two lambs was always higher than the difference between zero and one lamb (table 5.12). Improvement of current flock performance is unlikely to be successful where the only selection policy is to cull barren ewes. A more successful method of flock improvement may be to select for twinning.

Table 5.21 Regression of Later on Earlier Record, NLW at
Different Production Levels

Initial difference	Earlier age	Later age		
		3	4	5
Between zero and one lamb weaned				
	2	0.01 \pm 0.14	0.03 \pm 0.22	0.03 \pm 0.30
	3		0.02 \pm 0.17	-0.09 \pm 0.42
	4			0.08 \pm 0.35
		Average 0.01		
Between one and two lambs weaned				
	2	0.06 \pm 0.20	0.13 \pm 0.20	0.12 \pm 0.24
	3		0.14 \pm 0.14	0.12 \pm 0.22
	4			0.21 \pm 0.14
		Average 0.13		
One lamb (above pooled)				
	2	0.03 \pm 0.03	0.09 \pm 0.03	0.08 \pm 0.04
	3		0.11 \pm 0.04	0.08 \pm 0.08
	4			0.18 \pm 0.05
		Average 0.10		

Young et al. (1963) investigated the repeatability of the same differences examined here, and table 5.21 confirms that repeatability is dependent upon level of production and is non-linear.

Particular problems arise from the finding of low repeatabilities, particularly at younger ages. The practical breeder requires early information on the lambing potential of his flock to enable him to predict future performance and plan his improvement strategy. A low repeatability of barrenness means that most ewes barren at one age wean a lamb at consequent lambings. Edgar (1958) concluded on the basis of observations taken at Whatawhata Hill Country Research Station that barren two-year-olds had the same probability of lambing as three-year-olds as those which had reproduced at first lambing. Low repeatability of the difference between one and two lambs indicates that although retention of ewes which rear twins will increase later production, the improvement will be small. When considered on a flock basis the problem is particularly serious as intense selection is impracticable.

An unexpected result was that the repeatability of two-year twinning is higher at four-years than three-years. The difference between the estimates is small relative to the standard errors, but could nevertheless be real. If the physiological stress of twinning as a two-year-old was great enough to affect the ability of three-year-olds to raise a lamb, the repeatability of two-year performance would be low at the following lambing. The ewes which raised twins at first lambing would have recovered by the third lambing as a four-year-old and be able to better express their genotype for fertility, and repeatability expressed as the regression of four-or three-year performance would increase.

(h) Conclusions

Repeatability was estimated in this study as the regression of later on earlier record. As well as the advantages mentioned in an earlier section, regression estimators have a practical application in allowing quantitative prediction of future performance based on a unit of selection on a previous record.

The estimates of repeatability for quality number, staple length, fleece weight and fibre diameter show that lifetime gains in these wool traits are likely to be substantial. Wool character and NLW are liable to be relatively unrewarding as a selection target. The objectively measured wool traits (fleece weight, staple length and fibre diameter) showed higher repeatability than the subjectively assessed traits. This was not unexpected as the latter are prone to the problems associated with the repeatability between and within assessors.

Wool character and NLW are peculiar in that the repeatability calculated was lower than the heritability, which is one of its components. No explanation can be offered for this phenomenon, but it is interesting to observe that Turner (1968) accepted a similar relationship when constructing an index for ranking animals on their dams' reproductive performance.

Age differences in repeatability are apparent in all of the traits studied, showing that there are environmental factors in common among some pairs of records which are not present in other pairs.

The use of the intraclass correlation method for repeatability may have given biased results if applied to these data. One of the fundamental assumptions of the method is that all possible correlations between pairs of records are the same, but this is not the case in the

present data. In addition, use of intraclass correlation is not justified for NLW because of the non-linearity of differences between initial classes (table 5.21).

B. Heritability of Average Annual Performance.

The heritability of mean annual performance was calculated from data in which every animal had a complete set of records from two- to five-years of age. The results would have been identical had the sum of the four records been used instead, but would have been less meaningful with respect to quality number, wool character and fibre diameter than the mean, and therefore the latter was preferred. Only the PHS method was used as few daughter-dam pairs were available where both had a full set of records. Because there were a limited number of records for the analysis, the estimates have large standard errors. The estimate of approximate selection bias was calculated using the accumulated selection differentials calculated from table 5.12 for five-year-olds.

The estimates of heritability of average performance are listed in table 5.22 with their standard errors and approximate selection bias. The biases are all small relative to the standard errors for the wool characteristics, but Rönningens (1972a) method does not cater for negative estimates. However, selection bias would be virtually zero for an estimate as small as that calculated for average annual NLW.

The estimate of heritability for quality number (0.50 ± 0.18), wool character (0.61 ± 0.20) and staple length (0.84 ± 0.21) are all higher than the estimates calculated separately for each age and discussed earlier. The fleece weight (0.44 ± 0.18) and fibre diameter (0.49 ± 0.22) figures are within the range of the values calculated for the various ages, while the NLW heritability

Table 5.22 Heritability Estimates, Standard Errors and Approximate Biasses
Average Annual Performance

Trait	Estimate (PHS)	Bias
Quality Number	0.50 \pm 0.18	-0.10
Wool Character	0.61 0.20	-0.06
Staple Length	0.84 0.21	-0.14
Fleece Weight	0.44 0.18	-0.12
Fibre Diameter	0.49 0.22	-0.13
NLW	-0.01 0.12	-

(-0.01 ± 0.12) is lower than any of those for NLW in table 5.13.

These estimates indicate that the average mature lifetime performance is highly heritable for wool characteristics.

The heritability of average annual or total lifetime production records appear to have been largely ignored by other workers. Shelton and Menzies' (1968a,b) estimates for mean greasy fleece weight (table 2.11) slightly exceed the Perendale figure. The same authors studied lamb production and recorded 0.28 for lifetime NLW, and 0.28 and 0.25 for total NLW between three- and seven-years of age. Their NLW estimates are all considerably higher than those from this study.

C. Genetic Correlations Between Ages.

Lush (1945) developed the expression

$$\frac{nr}{1 + (n-1)r}$$

where n = number of records

r = repeatability

to allow the comparison of animals with different numbers of records. Ercanbrack (1968) discussed the failure of the assumptions fundamental to the derivation of the formula. Amended formulae were then presented for use when the assumptions do not hold.

The assumptions discussed by Ercanbrack include

- (i) the same genotype with the same genetic expression is exhibited in all records of the same animal
- (ii) the correlation between the additively genetic and phenotypic expressions of the trait is the same for each record
- (iii) there is a permanent environmental factor which, although different for each animal, has the same influence on all

records of the same animal

(iv) temporary environmental effects are random for each record.

It has previously been shown that the heritability is not necessarily the same at each age. The change in phenotypic correlation between pairs of records may also mean that environmental factors may be non-random, changing systematically with time. The genetic correlation between ages is a measure of the genes which are operating in common at different ages, and should test the first assumption.

The results of computing the genetic correlations between ages form table 5.23. NLW is not included as the trait yielded negative variance components at some ages. The standard errors are large as the calculations were carried out on a set of data in which each animal had completed five consecutive records beginning as a hogget.

If the same expression of the genotype was common to each age, then the expected genetic correlation would be unity. Therefore the hypothesis to be tested in deciding whether assumption (i) is breached is

$$H_0 : r_g = 1.0$$

The underlined estimates in the table are all significantly different from unity at the five percent level. Therefore it can be assumed that for quality number, wool character and fleece weight, the genetic expression is not the same at each age. For quality number and fleece weight, all significant estimates involve the hogget record, suggesting that genetic expression in the immature animal is different to that in the mature sheep; that is, these characteristics are genetically different traits at different ages. It is a reasonable assumption that physiological differences provide a different

Table 5.23 Genetic Correlations Between Ages and Between Each Age and Average Annual Performance,
With Standard Errors

Variate	Age	Age				
		2	3	4	5	Average
Quality Number						
	1	0.76 ± 0.25	0.37 ± 0.25	0.48 ± 0.25	0.43 ± 0.28	0.52 ± 0.21
	2		0.68 ± 0.26	0.84 ± 0.29	0.84 ± 0.29	0.87 ± 0.16
	3			0.92 ± 0.13	0.85 ± 0.17	0.93 ± 0.06
	4				1.00 ± 0.15	1.00 ± 0.06
	5					0.98 ± 0.07
Wool Character						
	1	a ± 0.32	0.84 ± 0.31	0.22 ± 0.45	0.33 ± 0.35	0.82 ± 0.26
	2		0.62 ± 0.26	0.88 ± 0.32	0.13 ± 0.30	0.77 ± 0.14
	3			0.64 ± 0.31	0.47 ± 0.26	0.83 ± 0.11
	4				0.94 ± 0.28	a ± 0.14
	5					0.73 ± 0.14
Staple Length						
	1 ^b	a ± a	a ± a	a ± a	a ± a	a ± a
	2		0.94 ± 0.12	0.97 ± 0.09	0.99 ± 0.11	0.98 ± 0.04
	3			0.91 ± 0.12	0.97 ± 0.14	0.95 ± 0.06
	4				a ± 0.11	1.00 ± 0.03
	5					1.00 ± 0.04
Fleece Weight						
	1	0.41 ± 0.25	0.34 ± 0.32	0.68 ± 0.20	0.57 ± 0.30	0.53 ± 0.23
	2		0.76 ± 0.17	0.78 ± 0.16	0.88 ± 0.21	0.92 ± 0.07
	3			0.89 ± 0.15	0.71 ± 0.26	0.89 ± 0.08
	4				a ± 0.17	0.98 ± 0.05
	5					0.98 ± 0.09

contd/...

Table 5.23 Continued

Fibre Diameter										
1	a	+ 0.44	0.92	+ 0.15	0.91	+ 0.17	0.83	+ 0.17	0.91	+ 0.14
2	b		a	0.36	a	0.35	a	0.53	a	0.33
3					0.77	0.15	0.92	0.11	0.94	0.06
4							1.00	0.08	0.96	0.04
5									1.00	0.04

a Greater than theoretical limit

b Small variance component

environment for the operation of the genotype in the hogget, due at least partially to females of this age not undergoing the stress of reproduction.

The significant deviations of the genetic correlations from unity for wool character both involve five-year-old records. The correlation estimate between hogget and five-year observations also approaches significance. In this case it is suggested that the older animals provide a physiologically different environment from the younger animals.

The genetic correlation between individual age records and average mature performance allows the assessment of the average response over all ages in the following generation. The relevant coefficients listed in table 5.23 pertain to the average mature production between two- and five-years of age. Therefore the later age observations are themselves part of the average, whereas hogget records are not. The results show that there is only a medium genetic correlation between hogget and mature average for quality number and greasy fleece weight, and therefore the first record may not be a good predictor of the average production in the next generation. For the other traits the genetic correlation involving the first record is high.

The mature ages are all highly correlated with their average performance, the coefficient in all cases approximating unity. There is no strong trend in the magnitude of the genetic correlation with age, but for the objectively measured traits, slightly higher figures were found for the oldest ewes. It can be concluded that no mature record better predicts average production than any other.

V Application and Concluding Discussion

A Some Aspects of Selection

The parameters estimated in this work are valuable in showing that they may not be assumed to be constant over ages, but that their values may change with age. They also have value in the selection of replacements for the flock. Where sequential selection is applied annually, it is apparent that the average genetic merit of the retained group will change. Bichard et al. (1973) examined the effects of retaining replacement progeny from parents of different ages and the implications of truncation selection amongst the parents. The consequence of the truncation of the distribution is that the probability of progeny selection is partially dependent upon parental age. Their development assumed that the difference in the means of progeny groups from parents of different ages was due entirely to the improvement resulting from parent selection. Bichard et al. (1973) studied three selection strategies:

- (i) Method I - selection of equal proportions of progeny from each parental age group, which ignores genetic differences between the age subclasses.
- (ii) Method II - phenotypic or mass selection, in which the highest ranking animals are retained regardless of the parental age. This will make partial use of the genetic differences between parental subclasses.
- (iii) Method III - selection based on the predicted breeding values of the progeny, which makes optimum use of genetic differences between parental age subclasses.

In method III candidates for selection with the same phenotypic value but from different parental age distributions will have unequal

expected breeding values. The method relies on the calculation of the truncation points in each parental age distribution at which the progeny expected breeding values are equal.

Although method II is the usual procedure for selecting replacements, it was shown that method III would give a greater rate of improvement.

If the difference between means of successive parental age distributions is d , then the distance between points of equal expected breeding value in the first and n th parent age group is

$$Y_n = \frac{(n-1)d(1-h^2)}{h^2}$$

It is apparent that a constant heritability value has been assumed for each age by Bichard et al. (1973). The formula could be generalized to incorporate different heritabilities at each age as

$$Y_n = d \sum \frac{(1-h_i^2)}{h_i^2}$$

where the summation is over $i=1\dots(n-1)$

If in addition, d varied between ages,

$$Y_n = \sum \frac{d_i(1-h_i^2)}{h_i^2}$$

Hence, where there are n parental age groups, the successive truncation points, where the first parity truncation point is C , would be

$$C, C + Y_1, C + Y_2, \dots, C + Y_n.$$

This method incorporates the policy of retaining an animal in the flock until its breeding value is exceeded by one of the candidates for selection.

Hopkins and James (1977) extended the concept to include the

genetic effects of own age among potential parents of possible entrants into the breeding population. They evaluated three strategies additional to those described by Bichard et al. and defined them as parent selection methods:

- (i) Method A - correct allowance for genetic effects of own age based on one record.
- (ii) Method B - phenotypic selection ignoring genetic effects of own age.
- (iii) Method C - correct allowance for genetic effects of own age based on the mean of records accumulated over the individual's lifetime; i.e., correction is made both for own age and number of records.

Two heritabilities were defined:

- (i) h^2 - the regression of breeding value on phenotype within a parental age progeny group.
- (ii) H - the regression of breeding value on phenotype over all parental age sub-groups within one distribution.

$$H = \frac{h^2 + V_B}{1 + V_B}$$

where V_B is the component of variance between parental age classes, and

$1 + V_B$ is the total phenotypic variance.

A degree of approximation is introduced into H by the assumption that h^2 is the same for all records.

Investigation of the comparative efficiencies of the methods showed that parental selection was more efficient in terms of response, than the progeny selection method discussed by Bichard et al. (1973). Within the parental selection methods, selection based on the mean of

accumulated records was more efficient than where single records were used, and both exceeded the phenotypic selection procedure in efficiency. Hopkins and James (1977) explained that the superiority of the parental compared to progeny selection was due to greater variability between the means and flatter distributions for the parent groups.

B. Selection Indices

Several genetic correlations were shown in earlier sections to be important in that they were antagonistic to selection objectives. Selection under these circumstances may best be achieved by the use of an index which combines the traits into an aggregate selection criterion. This emphasizes that overall productivity, and not particular components of it, is the required objective for efficiency.

Selection indices were calculated for hoggets using much of the variance-covariance structure presented by Elliott and Johnson (1976). Covariances involving NLW in the ewe, and hogget fleece traits were derived from the lifetime performance data set. Elliott and Johnson omitted wool character from their computations, but it was included here using hogget parameter estimates derived by Elliott (1975). The relative economic values (RE) listed by Elliott and Johnson (1976) were also used, except that quality number was given zero economic value as it was thought that their values for this trait and fibre diameter were alternatives rather than complimentary. This is particularly the case when emphasis is placed on objective wool measurement. Wool character was entered with zero value as there is no direct evidence to the contrary. A point of interest is that their assumed value of the heritability of NLW compared well with the mean value found in this work for the first three reproduction records. The parameters used

are listed in table 5.24a.

The indices constructed for two-year-old ewes included information on their dams reproductive performance, as well as their own NLW and wool production.

The aggregate genotype or breeding value (H) assumed for the two-year-old ewes was

$$H = a_1 g_{NLW} + a_2 g_{GFW} + a_3 g_{SL} + a_4 g_{FD} + a_5 g_{QN} + a_6 g_{WC}$$

where a_i = relative economic value of the i th trait

g = additive genetic value of the individual for the i th trait

The index had the form

$$I = b_1 NLWD + b_2 NLW + b_3 GFW + b_4 SL + b_5 FD + b_6 QN + b_7 WC$$

where the b_i are the weighting factors to be determined, and the

other abbreviations are defined at the foot of table 5.24.

The assumption was made in these computations that the selection objective involved maximizing overall merit, and therefore no indices were calculated for single trait selection. The parameters used in the two-year-old ewe indices form table 5.24b.

The indices are listed in table 5.25 and 5.26. The first index in each table includes all variates, while the remaining indices have different traits omitted. The following points will be helpful in interpreting the tables:

- (i) Value is defined as the percentage reduction in genetic gain resulting from the omission of the i th trait (Cunningham, 1969).
- (ii) SDI is the standard deviation of the index and describes the gain in economic units which could be expected from one standard deviation of selection on the index.

Table 5.24 Selection Index Parameters

(a) <u>Hogget</u>				Variate						
Variate	REV	σ_p	σ_g	NLWD	GFW	HBW	SL	QN	FD	WC
NLWD	700.0	0.57	0.20	0.12	0.00	0.00	-0.03	0.06	-0.03	-0.02
GFW	150.0	0.50	0.28	-0.01	0.32	-0.04	0.23	-0.13	0.21	0.08
HBW	0.0	3.96	2.06	0.18	0.77	0.27	-0.13	0.74	-0.07	-0.50
SL	25.0	1.54	1.08	0.00	0.34	0.79	0.49	-0.66	0.97	0.26
QN	0.0	1.90	0.97	0.02	-0.15	-0.23	-1.32	0.26	-0.75	-0.07
FD	-20.0	2.30	1.69	0.00	0.56	-1.37	1.20	-1.14	0.54	0.08
WC	0.0	1.12	0.52	0.00	0.12	0.00	0.17	0.27	0.30	0.22
(b) <u>Two-year ewes</u>				NLW	GFW	SL	QN	FD	WC	
NLW	700.0	0.55	0.20	0.14	-0.03	-0.10	0.01	-0.08	-0.01	
GFW	150.0	0.50	0.37	-0.03	0.53	0.27	-0.07	0.34	0.12	
SL	25.0	1.67	1.11	-0.07	0.34	0.44	-0.54	1.04	0.22	
QN	0.0	1.84	0.86	0.01	-0.19	-1.75	0.22	-0.78	0.18	
FD	-20.0	2.23	1.64	-0.01	0.38	0.82	-1.53	0.54	0.09	
WC	0.0	0.97	0.55	0.00	0.08	0.14	0.23	0.10	0.33	

Genetic covariances above the main diagonal, phenotypic below. Heritabilities on the diagonal.

σ_p = phenotypic standard deviation NLWD = dam's NLW record QN = quality number
 σ_g = genetic standard deviation GFW = greasy fleece weight FD = fibre diameter
 REV = relative economic value HBW = hogget body weight WC = wool character
 SL = staple length

- (iii) RE is the relative efficiency of the index. In this study all efficiencies are calculated relative to the first in each table; i.e., the index which includes all variates. The figure computed is the ratio of the SDI (Cunningham, 1969).
- (iv) r_{HI} is the correlation between the aggregate genotype and the index, which is maximized so that the index will predict the aggregate breeding value with maximum attainable accuracy.
- (v) r_{HI}^2 is a measure of the heritability of the index (Gjedrem, 1967).

Hogget Indices

Index 1a, table 5.25, shows that hogget body weight, staple length, quality number and wool character would each result in a reduction of less than five percent in genetic gain if omitted from the full index. When these four traits are not recorded (index 1i), the relative efficiency falls by 19 percent.

The reproductive record of the hogget's dam is the most important characteristic in the main index, and its value is increased if any wool trait is left out. There is a 25 percent reduction in the relative efficiency when this dam information is excluded from the index (1b). The exclusion of NLWD or greasy fleece weight decreases efficiency by considerably more than the removal of the four least important traits (1i). Of the other wool characteristics, quality number decreases relative efficiency by the greatest margin when it is left out of the index. The full index indicates selection against hogget body weight, wool character and fibre diameter. The latter is easily justified, but selection against the other two is contrary to popular belief. Advice is frequently given to breeders that they should retain their heaviest hoggets as flock replacements, but the weighting factors suggest that this may not be the

Table 5.25 Selection Index Solutions. Hogget.

Index	Detail	Variate							SDI	RE	r_{HI}^2	r_{HI}
		NLWD	GFW	HBW	SL	QN	FD	WC				
1a	Weight	104.4	101.7	-4.8	12.6	11.2	-13.6	-18.1				
	Value	17.8	19.9	3.9	3.1	4.3	9.0	4.8	63.4	100	0.32	0.56
1b	Weight	-	92.5	-3.2	-8.4	10.0	1.0	-29.7				
	Value	-	31.3	2.9	2.4	6.2	0.1	25.5	47.5	75	0.18	0.42
1c	Weight	105.9	-	0.4	0.3	10.3	8.1	-22.1				
	Value	33.4	-	0.0	0.0	6.1	6.3	12.7	49.0	77	0.19	0.44
1d	Weight	103.1	85.2	-	-8.7	8.7	0.9	-27.0				
	Value	19.7	18.0	-	1.6	2.9	0.0	12.5	59.8	94	0.28	0.53
1e	Weight	102.8	93.7	-5.0	-	11.8	0.1	-29.5				
	Value	18.3	19.9	4.4	-	6.2	0.0	14.2	61.5	97	0.30	0.55
1f	Weight	106.6	85.2	-4.7	3.7	-	-2.6	-25.9				
	Value	22.9	16.5	4.4	0.4	-	0.4	12.6	57.9	91	0.27	0.52
1g	Weight	103.1	79.8	-4.8	12.0	15.3	-	-30.5				
	Value	17.5	14.3	3.9	2.9	8.5	-	14.4	63.0	99	0.31	0.56
1h	Weight	107.9	92.5	-4.3	11.4	8.9	-13.9	-				
	Value	21.4	18.6	3.4	2.8	3.1	10.6	-	60.3	95	0.29	0.54
1i	Weight	109.3	75.7	-	-	-	-13.6	-				
	Value	32.1	24.8	-	-	-	6.9	-	51.5	81	0.21	0.46

best plan where overall improvement is the objective. Hogget body weight has no value in the index when greasy fleece weight is not part of the index, but increases in value above the full index when any of the other wool traits are not recorded. Selection against wool character is unlikely to be acceptable to the breeder, but the relative efficiency drops by five percent if it is not included. The reduction in genetic gain if wool character was deleted rises to be maintained at greater than 12 percent in indices 1b to 1g.

Two-year-old Ewe Indices

The reproductive record of a two-year-old ewe and its dam both have large positive weightings in every index in which they appear (table 5.26). Despite the high relative economic value of greasy fleece weight, it is strongly selected against at this age (index 2a). To test how much of this weighting is due to the medium negative genetic correlation (-0.40) between greasy fleece weight and NLW, the index was recalculated with this value halved (-0.20). The result (index 2i) was a much lower negative weighting on greasy fleece weight. Staple length would be affected similarly. It is not suggested that index 2i should be used as an alternative to 2a. The economic value of an extra lamb weaned compared with a unit increase in any other trait has a large effect on the index.

If no information was available on the NLW record of the dam of the two-year-old ewe, the efficiency of the index would drop by 23 percent (index 2b) indicating that for optimum progress recording of parental information is vital. The ewe's own record is generally of slightly greater value than its dam, except when greasy fleece weight is not included. The most essential characteristic in two-year ewe selection

Table 5.26 Selection Index Solutions. Two-year-old Ewes.

Index	Detail	Variate							SDI	RE	r_{HI}^2	r_{HI}
		NLWD	NLW	GFW	SL	FD	QN	WC				
2a	Weight	84.9	66.6	-78.3	-10.9	31.4	1.5	21.5				
	Value	8.0	12.8	9.2	2.0	26.4	0.0	3.7	73.86	100	0.44	0.66
2b	Weight	-	81.3	17.6	-16.3	-13.7	-14.0	23.7				
	Value	-	37.9	0.8	7.8	7.7	6.0	7.8	56.70	77	0.19	0.42
2c	Weight	100.3	59.6	-	24.5	6.5	39.4	-17.1				
	Value	11.5	10.2	-	10.5	1.4	32.8	2.4	72.65	98	0.43	0.66
2d	Weight	91.3	62.5	13.4	-	4.3	26.1	-11.1				
	Value	11.9	14.2	0.3	-	0.5	24.8	1.3	66.16	90	0.35	0.59
2e	Weight	97.2	60.3	22.6	14.9	-	32.7	-15.2				
	Value	12.4	12.1	1.2	4.3	-	27.5	2.1	68.75	93	0.38	0.62
2f	Weight	85.1	66.6	-69.7	-10.9	30.1	-	1.2				
	Value	8.8	14.1	7.9	3.1	29.6	-	0.0	70.79	96	0.40	0.63
2g	Weight	86.5	66.1	-70.4	-8.1	31.4	4.9	-				
	Value	9.0	13.7	8.1	1.2	28.9	0.5	-	71.12	96	0.41	0.64
2h	Weight	97.6	69.1	73.9	-	-13.3	-	-				
	Value	16.0	20.7	12.3	-	6.9	-	-	61.80	84	0.24	0.50
2i	Weight	98.9	72.4	-15.1	-11.4	22.7	1.1	17.3				
	Value	12.0	16.7	0.4	2.3	13.8	0.0	2.6	71.14	96	0.32	0.57

is the ewes own reproduction, and it was therefore considered irrelevant to produce an index in which this trait was omitted.

Although it has a high economic value, addition of greasy fleece weight to an index which already contains all of the other traits only increases efficiency by two percent (index 2c). Only if staple length or fibre diameter are deleted from the index, does the weighting on fleece weight become positive. Similarly, staple length is selected against in the presence of greasy fleece weight and/or fibre diameter.

Fibre diameter and quality number weights are the same sign whenever both are included in an index. Fibre diameter has much greater value in the main index and affects efficiency more when it is excluded than quality number. Selection for coarser wool is indicated by the fibre diameter weighting factor, due to the positive association it has with greasy fleece weight.

Unlike the situation in the hogget index, selection in the full two-year index is towards higher wool character. The effect on relative efficiency is similar at both ages.

The points which are likely to be difficult to justify to the Perendale sheep breeder arising from this selection index study are

- (i) Negative selection for hogget body weight.
- (ii) Positive selection for greasy fleece weight in hoggets, negative among two-year-old sheep.
- (iii) Selection for hogget staple length and against two-year staple length.
- (iv) Penalizing fine woolled two-year ewes while retaining fine woolled hoggets.
- (v) Selection against hogget wool character and for two-year wool

character.

The breeder would have to be convinced of the utility of the indices on the basis of an integrated selection policy. One of the reduced indices from each set may be more acceptable even though less efficient and resulting in a lower rate of genetic gain, as the breeder may then not have the conflict of what he should be selecting for, and what he believes he should favour in his selection policy.

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