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GENOTYPE-ENVIRONMENT INTERACTIONS
AND GENETIC PARAMETERS IN
NEW ZEALAND ROMNEY SHEEP

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ABSTRACT

Performance records of 1,113 New Zealand Romney ewe hoggets from two subflocks maintained on control (CSR) and intensive (HSR) stocking rates were analysed. The data represented the progeny of 34 sires and were collected between 1967 and 1974 inclusive which covered four consecutive two-year sire periods.

The traits investigated were hogget live-weight (HLW), greasy fleece weight (GFW), clean wool weight per unit area (WA), clean scoured yield (Y), staple length (SL), mean fibre diameter (MFD), standard deviation of the fibre diameter (SFD), quality number (QN), crimps per centimeter (CPC), total crimp number (TCN), character (CHG), tippiness (TG), handle (HG), lustre (LG), greasy colour (GCG), scoured colour (SCG), discoloured area (DAG), cotting (CG), cotted area (CAG) and soundness (SG).

Stocking rate had significant effect on all the traits excepting MFD, SFD, TCN and HG. HSR depressed the traits investigated excepting Y, SFD, QN, CPC, HG, GCG, SCG, CG and CAG. Year effects except in DAG were an important source of variation. The influence of birth-rank except on HLW, SFD, CHG and HG was small. Stocking rate x year interactions except in CPC, TCN, CHG, TG, HG, GCG and CAG were important. Sire x stocking rate interactions were significant in HLW, MFD, SFD, TCN and GCG only, whereas sire x year interactions were significant in HLW, GFW, HG and SCG.

Sire x stocking rate and sire x year interactions were included in different ways in some formulae for calculation of heritability estimates. These estimates were calculated from paternal half-sib analyses in CSR,

HSR and combined data. The various estimates for the different traits were in the following ranges:-

HLW 0.21 - 0.72,	GFW 0.38 - 0.61,	WA 0.31 - 0.49,
Y 0.19 - 0.53,	SL 0.54 - 0.63,	MFD 0.34 - 0.87,
SFD 0.35 - 0.66,	QN 0.46 - 0.72,	CPC 0.48 - 0.88,
TCN 0.65 - 1.09,	CHG 0.24 - 0.34,	TG 0.13 - 0.27,
HG 0.23 - 0.66,	LG 0.32 - 0.42,	GCG 0.22 - 0.44,
SCG 0.10 - 0.39,	DAG 0.04 - 0.21,	CG 0.12 - 0.67,
CAG 0.18 - 0.53,	SG 0.00 - 0.22.	

No significant differences between the estimates in the two stocking rates except in CG and SG were observed. The relevance of these comparisons is discussed in terms of sire x stocking rate and sire x year interactions.

Intra-trait genetic correlations between the two stocking rates were close to unity except in HLW ($P < 0.05$); Y, SFD, GCG, SCG ($0.05 < P < 0.1$).

Genetic correlations between traits were calculated by the paternal half-sib method. The correlation coefficients suggest that the HLW selection results in higher fleece weight, longer staples, better fleece character, increased variation in fibre diameter, higher quality number and crimping and more lustre. Selection for fleece weight would result in longer staples, less crotting and less susceptibility to break and increased mean fibre diameter. Correlated responses expected with selection for fineness are reduced staple length, more crotting and less sound wool. Selection for TCN results in favourable changes in HLW, GFW, TG, crotting, colour and soundness. Favourable changes in yield, crimping, discoloured area are expected following selection for whiteness of a midside sample, whereas GFW could decline.

Applications of the results are discussed with particular reference to the role played by sire x stocking rate and sire x year interactions in the genetic improvement of characters of economic importance in New Zealand Romney sheep.

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TABLE OF CONTENTS

<u>Chapter</u>		<u>Page</u>
	ABSTRACT	ii
	ACKNOWLEDGEMENTS	v
	LIST OF TABLES	x
	LIST OF FIGURES	xii
ONE	INTRODUCTION	1
TWO	REVIEW OF LITERATURE	4
	CLASSIFICATIONS OF GENOTYPE-ENVIRONMENT INTERACTIONS	4
	FALCONER'S CONCEPT OF GENETIC CORRELATIONS BETWEEN PERFORMANCE IN DIFFERENT ENVIRONMENTS	12
	Experimental evidence for Falconer's concept	13
	GENOTYPE-ENVIRONMENT INTERACTIONS IN SHEEP	20
	Growth characteristics	21
	Carcass characteristics	29
	Fleece characteristics	32
	Reproductive traits in ewes	41
	Others	45
	GENETIC PARAMETERS	46
	Heritability	46
	Genetic correlations	60
	GENERAL CONCLUSIONS	78
THREE	SOURCE OF DATA	79
	THE DATA	81

TABLE OF CONTENTS
(continued)

<u>Chapter</u>		<u>Page</u>
FOUR	STATISTICAL METHODS	86
	PRESENCE OF INTERACTION	86
	ANALYSIS OF VARIANCE	88
	Least squares and computing methods	88
	Fitting models to the data	90
	Estimation of mean squares, variance and covariance components	96
	LEAST SQUARES ESTIMATES	98
	POOLING OF THE SIRE GROUP PERIODS ANALYSES	98
	PARTITIONING THE VARIATION	99
	VARIANCE COMPONENT ESTIMATES	99
	GENETIC PARAMETERS	101
	Heritability	101
	Genetic correlations	103
FIVE	RESULTS AND DISCUSSION	105
	ESTIMATES OF NON-GENETIC FACTORS, INTERACTIONS AND VARIANCE COMPONENTS	105
	Hogget live-weight	110
	Greasy fleece weight	115
	Clean wool weight per unit area	118
	Clean scoured yield	120
	Staple length	121
	Mean fibre diameter	124
	Standard deviation of the fibre diameter	125
	Quality number	127
	Crimps per centimeter	128
	Total crimp number	130

TABLE OF CONTENTS
(continued)

<u>Chapter</u>	<u>Page</u>
Character grade	131
Tippiness grade	134
Handle grade	135
Lustre grade	137
Greasy colour grade	138
Scoured colour grade	140
Discoloured area grade	141
Cotting grade	143
Cotted area grade	144
Soundness grade	146
HERITABILITY ESTIMATES, INTRA-TRAIT GENETIC CORRELATIONS AND INTERACTION VARIANCE COMPONENTS	148
Hogget live-weight	152
Greasy fleece weight	155
Clean wool weight per unit area	156
Clean scoured yield	157
Staple length	158
Mean fibre diameter	159
Standard deviation of the fibre diameter	161
Quality number	162
Crimps per centimeter	163
Total crimp number	164
Character grade	165
Tippiness grade	167
Handle grade	168
Lustre grade	169
Greasy colour grade	170
Scoured colour grade	171
Discoloured area grade	172
Cotting grade	173
Cotted area grade	174
Soundness grade	176
INTER-TRAIT GENETIC CORRELATIONS	177

TABLE OF CONTENTS
(continued)

<u>Chapter</u>		<u>Page</u>
SIX	CONCLUDING DISCUSSION ON PRACTICAL IMPLICATIONS	185
	BIBLIOGRAPHY	194

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Some published estimates of heritability of live-weight, wool quantity and quality traits in sheep	48
2	Some published estimates of genetic correlations between various characteristics for live-weight, wool quantity and quality in sheep	64
3	Combined stocking rate analysis. Calculation of reductions in sums of squares and expectations of mean squares	94
4	Within stocking rate analysis. Calculation of reductions in sums of squares and expectations of mean squares	95
5	Percentage of total variance attributable to each factor for each variable from the combined stocking rate analysis pooled from the different Sire group periods	106
6	Least squares estimates and standard errors of environmental effects for HLW and GFW	111
7	Least squares estimates and standard errors of environmental effects for WA and Y	119
8	Least squares estimates and standard errors of environmental effects for SL and MFD	122
9	Least squares estimates and standard errors of environmental effects for SFD and QN	126
10	Least squares estimates and standard errors of environmental effects for CPC and TCN	129
11	Least squares estimates and standard errors of environmental effects for CHG and TG	132
12	Least squares estimates and standard errors of environmental effects for HG and LG	136
13	Least squares estimates and standard errors of environmental effects for GCG and SCG	139
14	Least squares estimates and standard errors of environmental effects for DAG and CG	142
15	Least squares estimates and standard errors of environmental effects for CAG and SG	145

LIST OF TABLES
(continued)

<u>Table</u>		<u>Page</u>
16	Heritability estimates and standard errors of various traits obtained from the pooled analyses by different methods	149
17	Intra-trait genetic correlations and standard errors of traits in two stocking rates	151
18	Genetic correlations and standard errors among various traits from the pooled analysis of variance and covariance	178

LIST OF FIGURES

<u>Fig.</u>	<u>Title</u>	<u>Page</u>
1	Illustration of genotype (A, B) x environment (X, Y) interactions as suggested by Haldane (1946) (after McBride, 1958)	5
2	Types of heredity x environment interaction (after Dunlop, 1962)	9
3	A classification of genotype x environment interactions specially designed for use in farm animals studies (after Pani, 1971)	11

CHAPTER ONE

INTRODUCTION

Genotype-environment interaction (GEI) occurs whenever a change from one environment to another results in different effects on the genotypes in the population. Thus if changing from environment 1 to environment 2 adds 10 units to one genotype and 15 units to another, GEI will be present. GEI implies that genotypic and environmental effects are not additive, i.e., instead of being able to assume that a trait x is the sum of a genotypic component and an environmental component, it is necessary to add an effect due to the joint interaction of genotype and environment. The presence of GEI could result in a change of ranking of the animals or at least in the magnitude of their differences. The latter type will bring a change of heritability and so will influence effectiveness of selection. This leaves no doubt that planning of a breeding programme depends on the magnitude of GEI as well as the estimated values of other genetic parameters.

A major problem of practical importance posed by the possible presence of GEI is the choice of environmental conditions under which to practice selective breeding. In planning a selection programme, a breeder has to decide the environmental circumstances under which the programme is conducted. This is a very important decision which becomes more critical as the range of environments in which the improved stock are used commercially, increases.

Should the breeder subject the animals among which selection is to be made to a 'good' environment which gives maximal expression to the desired character or should he rather subject them to conditions, whether

'good' or 'bad' under which the improved genotype is destined subsequently to live and perform? Falconer (1952) and Falconer and Latyszewski (1952) have discussed some aspects of the general problem of environment and selection. In particular they have criticized views, expressed by Hammond (1947), that environmental conditions if unfavourable, will prove to be a factor limiting the response to selection.

In the New Zealand Romney breed, it is common for ram-breeding flocks to be located in areas of favourable environmental conditions where rams are selected and bred under adequate levels of nutrition and in above-average husbandry and management to allow high individual performance to be achieved (Stevens, 1946; Rae, 1964). The progeny of the rams bred in these flocks, however, are expected to produce satisfactorily over a wide range of environmental conditions, usually much less favourable than those of the ram-breeding flocks. In a farming system which relies on pasture feeding, changing the stocking rate is the major method by which the level of nutrition supplied to the sheep can be varied. Therefore, as long as the current system of selection of breeding rams remains in practice, there is an obvious need to investigate the impact of genotype of sires x stocking rate and other important interactions on the effectiveness of selection. Clearly, if nutritional levels fluctuate violently, as they do, from low stocking rates to high stocking rates and if there are important genotype of sires x stocking rate interactions, the effectiveness of selection may be severely prejudiced. Little critical information is available on the importance of these interactions in sheep and on wool traits.

The purpose of this study was to investigate the possible interactions between the genotypes of sires within the New Zealand Romney breed of sheep and different levels of stocking rate. Thus, the work

was primarily concerned with detecting and evaluating the role played by the sire x stocking rate interactions with regard to the structure of heritability estimates in hogget live-weight, greasy fleece weight, clean wool weight per unit area, clean scoured yield, staple length, mean fibre diameter, standard deviation of the fibre diameter, quality number, crimps per centimeter, total crimp number, character, tippiness, handle, lustre, greasy colour, scoured colour, discoloured area, cotting, cotted area and soundness of wool. Sire x year interactions were also considered.

In order to obtain information and assess the practical implications of the observed interactions under investigation, the estimation of the genetic parameters and some environmental effects was considered to be necessary. As an outline of the scope of the thesis, three major topics may be mentioned.

1. Estimation of non-genetic factors and interaction effects on each character so that the appropriate adjustment of the data for the differences in the known environmental factors and interactions can be made prior to the genetic studies of variation and covariation.
2. Estimation of heritability estimates in different stocking rates and of intratrait genetic correlations to provide statistical evidence of sire x stocking rate interactions in the flock under study.
3. Estimation of inter-trait genetic correlations to describe what other characters are likely to change in future generations if one particular character is under selection.

CHAPTER TWO

REVIEW OF LITERATURE

CLASSIFICATIONS OF GENOTYPE-ENVIRONMENT INTERACTIONS

Classifications of GEI have been made by Haldane (1946), Mather and Jones (1958), McBride (1958), Dunlop (1962), Pani (1971) and others. Attempts have been made by several workers to take into account the extent of the changes in ranking of the same genotypes in different environments and the size of the differences between the environments and between the genetic effects.

Haldane (1946) classified the GEI which may occur when genotypes differing at a single locus are exposed to contrasting environments. Considering two genotypes (A, B) and two environments (X, Y) as an example, he tabulated six different types of interactions with the criterion that genotype A in an environment X has always the highest rank. He gave no attention to the types of differences between the environments and between genotypes. The six types of interactions are presented graphically in Fig. 1.

Mather and Jones (1958) described the differences among the four phenotypes given by two genotypes in each of the two environments in terms of three parameters, d_a measuring the average effect of genic differences, e_1 measuring the average effect of differences in environment and g_1 measuring the GEI. The quantity g_1 , the statistical interaction of d_a and e_1 is estimated by $(A : X + B : Y) - (A : Y + B : X)$ with sign ignored, i.e., taken as the amount added by the interaction to the phenotypes of A in environment X and B in environment Y, and deducted from the phenotypes of A in Y and B in X.

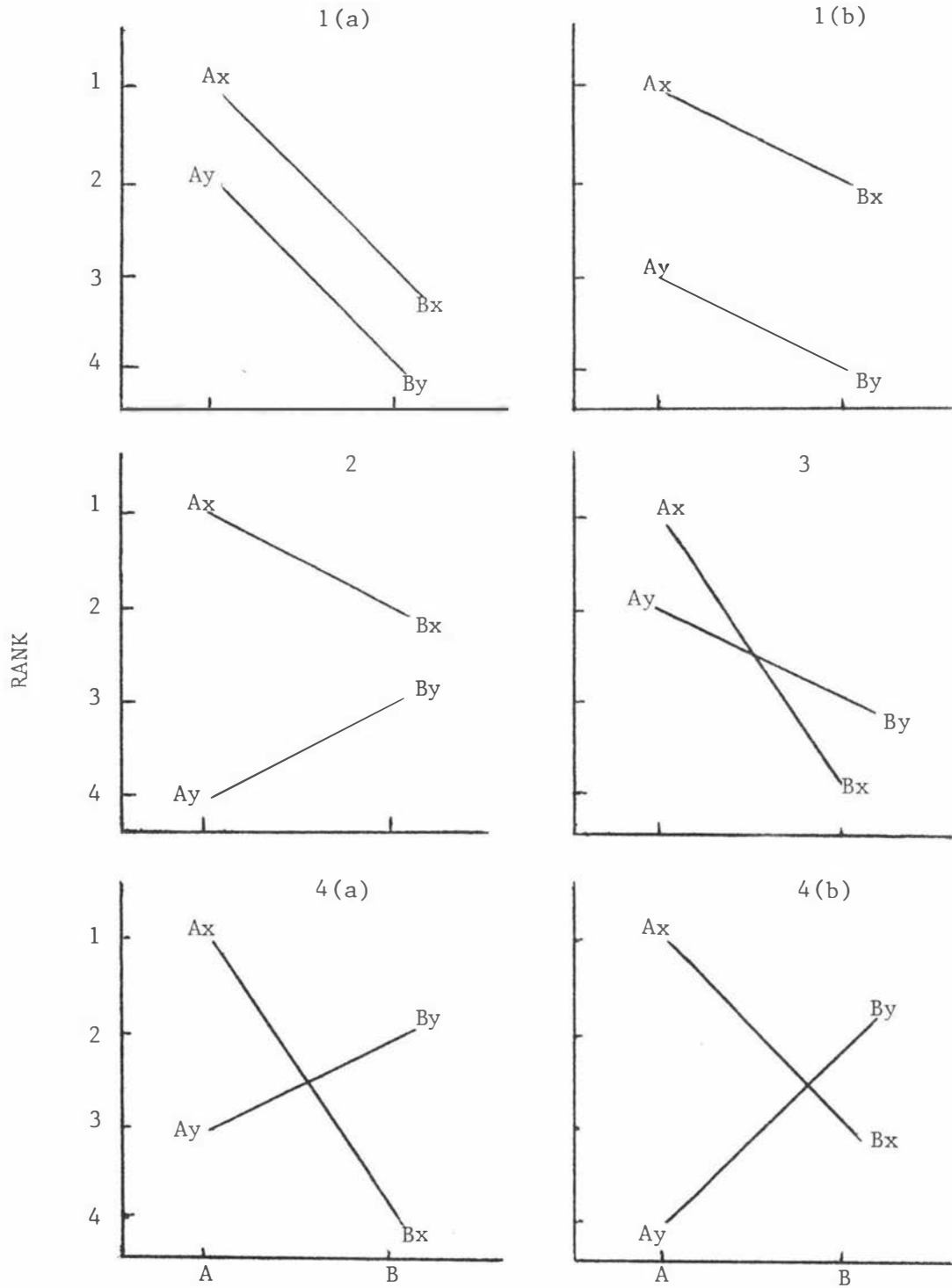


Fig. 1: Illustration of genotype (A, B) x environment (X, Y) interactions as suggested by Haldane (1946) (after McBride, 1958).

McBride (1958) proposed to classify GEI on the following basis:

1. Genetic differences as intra-population genotypes and inter-population genotypes.
2. Environmental differences as micro-environments and macro-environments.

Type A (intra-population, micro-environmental): This would involve interactions between those environmental factors which occur when all animals appear to be treated alike (i.e., are in a single general environment) and are from a single population genetically such as a single herd or flock.

Type B (intra-population, macro-environmental): These are interactions which might occur if the genetic differences of animals from a relatively homogenous genetic group were exposed to large environmental differences. The presence of type B interactions is of importance to plant and animal breeders concerned with selection within breeds or strains. The study of type B interactions has followed two lines; the static and dynamic. The static approach concerns the behaviour of different families within the normal range of genotypes compared in two or more contrasting environments. While the investigations of type B interactions in static populations may give some indication as to whether the environment is important in selection problems, these questions can be answered conclusively by selecting under different environmental conditions; i.e., by the dynamic approach to the problem. Falconer (1952), Falconer and Latyszewski (1952), Falconer (1960), Korkman (1961), Fowler and Ensminger (1960), Dalton (1967) and others conducted studies of this type.

Type C (inter-population, micro-environmental): Such interactions could be illustrated by an interaction of several lines, strains, breeds or crosses with environmental variability within flocks. The ideas on heterosis put forward by Robertson and Reeve (1952) suggest that the heterozygous genotypes are competent to handle a wider range of micro-environments than the homozygous genotypes and are thus less subject to environmental variation. Interpreting the results in view of the above suggests that the micro-environmental fluctuations cause some populations (the purebreds) to vary, yet they produce no effect on other populations (the hybrids). Heterosis, in this sense, is an example of type C interactions. However, type C interactions are not generally thought to be important in the field of applied genetics.

Type D (inter-population, macro-environmental): Type D interactions are found in genetic groups that show large varied responses to the different environments. The presence of type D interactions would influence important decisions in animal and plant breeding. Before the animal breeder can locate the breed or strain that will perform best in his environment, he must test for the presence of type D interactions. Having found the best strain for his particular conditions, he must then decide whether the conditions under which his selection is to be carried out are important; i.e., whether any type B interactions are present.

Haldane (1946) classified the GEI which may occur when genotypes differing at a single locus are exposed to contrasting environments, and Dunlop (1962) extended Haldane's classification to cover the types of interaction which may occur with groups of animals differing at many loci. A similar approach was adopted by McBride (1958). Dunlop identified four types of interaction according to magnitude of differences in

genotype and environment. He arbitrarily classified genetic differences as either large or small, defining small genetic differences as those occurring among individuals of a single population such as single flock or the related flocks of a breed or strain and large genetic differences as those between strains, breeds, species or even wider genetic division. Similarly, he defined small environmental differences as those occurring from individual to individual in a single general environment where differences due to such definable elements in the environment as field, age, sex, etc. are either non-existent or have been corrected for, and large environmental differences as those between different districts or regions or widely husbandry or nutritional regimes. His method of classification is illustrated in Fig. 2.

Interaction of type 1: small x small - This may occur in the usual model of sources of variation in a population where genotypes and environments are uncorrelated. These interactions are difficult to estimate; if present, a source of variation of unknown size could lead to a fall in the heritability and hence hinder progress by selection. This type of interaction corresponds to type A of McBride's (1958) classification.

Interaction of type 2: large x small - These may occur when there are large differences between genotypes and small differences between environments, such as several breeds in one area. These interactions are seldom important and are difficult to estimate.

Interaction of type 3: small x large - This class of interaction corresponds to type B of McBride's classification. Large interactions of this type are a hindrance to selection as the small genetic

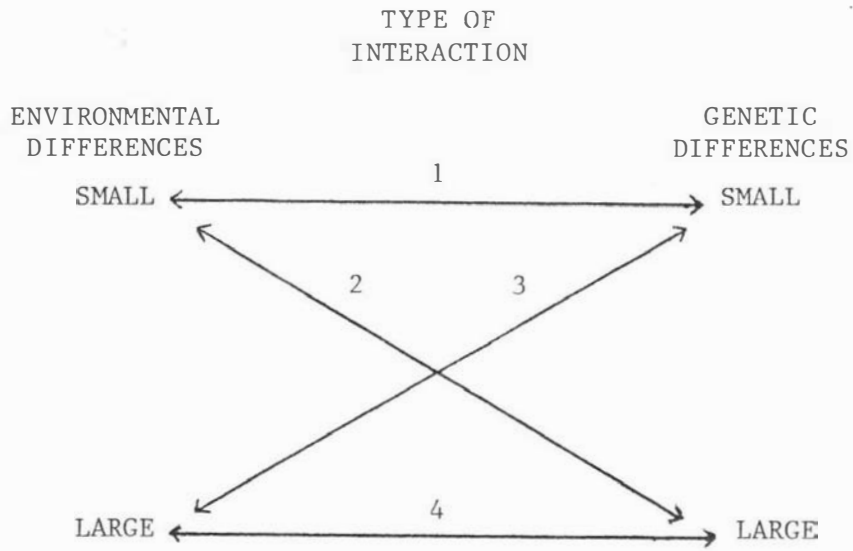


Fig. 2: Types of Heredity x Environment Interaction (after Dunlop, 1962)

differences are separated by large environmental differences. In many countries, sires are produced in stud flocks which are usually situated in good areas, the animals being treated to above-average husbandry practices; males are then distributed for use over a wide range of environments. Investigation of the magnitudes of type 3 interaction is therefore of considerable importance. If a common foundation stock were randomly divided into two distinct environments and then selected under these environments, the differences in the genotypes developed under these regimes would stem originally from this type of interaction, but it may well develop into type 4 interaction by the end of the experiment; i.e., genetic groups showing large differential response to the different environments. This has been recorded by Falconer and Latyszewski (1952) in selection for body weight in mice.

Interactions of type 4: large x large - Most likely to find interactions of greatest magnitude. Interactions of this type are of importance in choosing the class of organism suited to a particular environment. Type 4 can be described as strain x environment, the strain being existing or specifically developed.

Recently, Pani (cited by Pani and Lasley, 1972) attempted to classify the interaction in the context of breeding of animals for different environments. He based the classification on whether the rank of genotypes under consideration change from one environment to the other and also if the interaction effects are statistically significant. His classifications (type 1-4) are presented in Fig. 3. Type 3 in this case reflects the kind of interaction where a difference in heritability (difference in the magnitude of genetic width) but no change in rank was noted. In type 4, the estimate of heritability may or may not accompany the change in ranks.

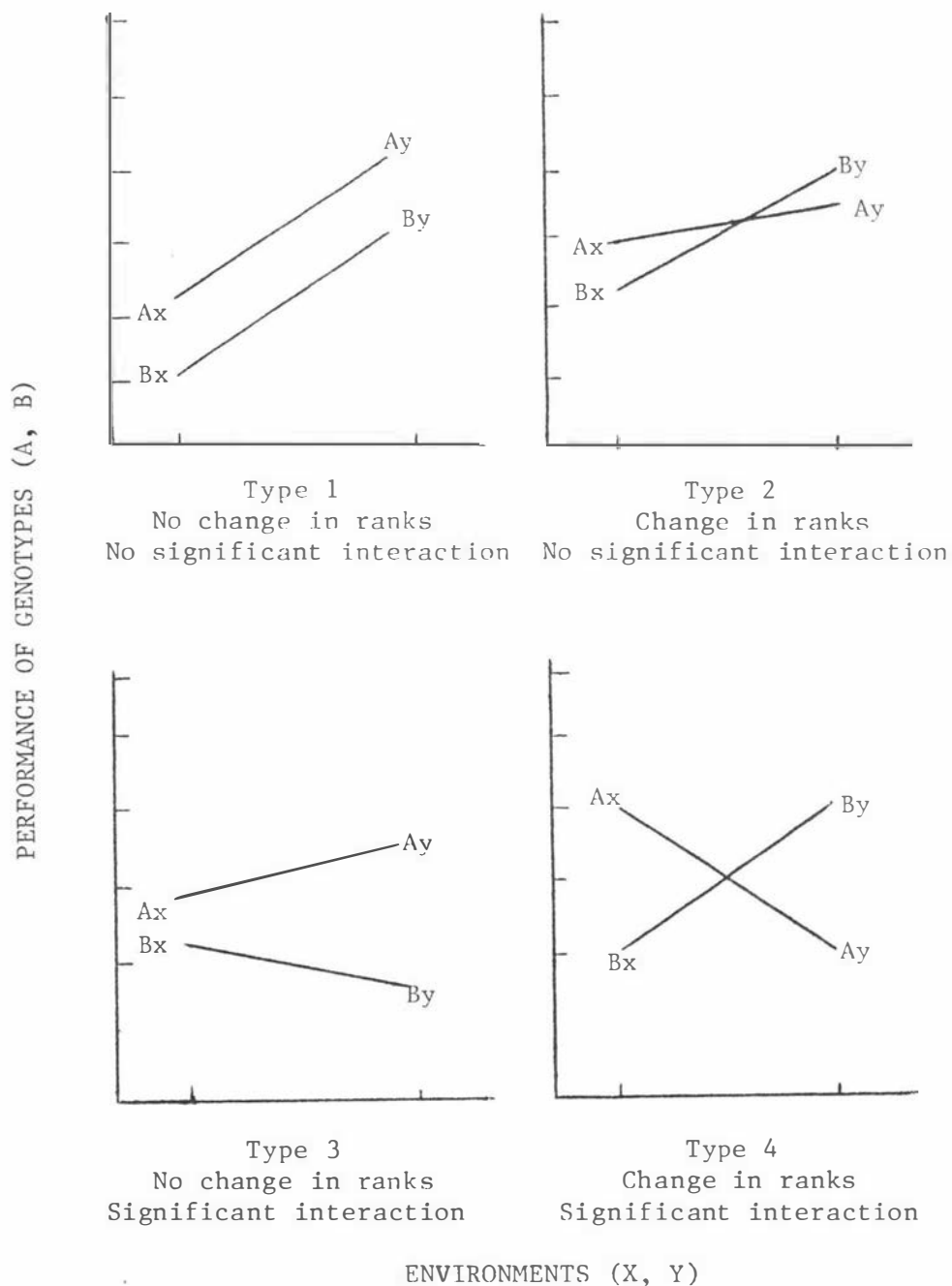


Fig. 3: A classification of genotype x environment interactions specially designed for use in farm animal studies (after Pani, 1971)

FALCONER'S CONCEPT OF GENETIC CORRELATIONS BETWEEN PERFORMANCE IN DIFFERENT ENVIRONMENTS

Geneticists and breeders are primarily interested in the transmitting ability of animals and plants. This interest is not confined to just one trait but to several traits which together make up total production and not just for the expression of these traits in one environment but in a range of environments.

Falconer (1952) made a considerable conceptual advance in handling of this subject when he considered the problem of performance under two environments as a case of two different correlated characters, thus extending the concept of genetic correlation (Hazel, 1943) to this situation. This concept allows one to estimate the relative progress that can be made from direct selection for performance in a given environment or from indirect selection practiced in a different environment. He argued that since performance in a favourable environment has a different genetic basis from performance in an unfavourable environment, a superior genotype in one environment could not be expected to be a superior in a different environment. The magnitude of the correlation coefficient (r_G) is a measure of the proportion of the genes which are common to both characters. If $r_G = 1$ then all of the genes are common to both and two characters can be regarded as one and no GEI occurring.

Falconer (1952) described the above concept by an application of the rules of path coefficients as follows: Let characters 1 and 2 stand for performance (expressed in standard deviations) of some trait under two environments. Direct selection for 1 will produce gain proportional to h_1^2 (since $\Delta G_1 = ih_1 \sigma_1$). Selection for 1 on the basis

of 2 will be (all else being equal) proportional to $h_2 r_{12}$ when $\Delta G =$ genetic change, $h^2 =$ heritability, $i =$ selection differential in standard deviation units, $\sigma =$ genetic standard deviation, $r =$ genetic correlation. When the quantity $h_2 r_{12}$ exceeds h_1 indirect selection is more efficient than direct selection. However, GEI reduces r_{12} and may make selection in one environment for performance in another inefficient. James (1961) developed the statistical aspect of the problem by extending Falconer's (1952) treatment to the case where genetic gain in both environments is desired, though the two environments may differ.

Falconer (1952) pointed out that if control of the environment involved only a reduction in environmental variance, the genetic correlation would be unity. If h_1^2 and h_2^2 are respectively the heritabilities of performance in controlled and uncontrolled economic environment and r_G is the genetic correlation between them, then if $h_1 r_G$ is greater than h_2 , selection should be carried out under the controlled environment.

Experimental evidence for Falconer's concept

The study of GEI based on the theory propounded by Falconer (1952) and further developed by Dickerson (1962) in general, has followed two lines - the dynamic and the static.

In the dynamic approach to GEI, the possible accumulations of differential responses are measured when selection is practised in different environments. It is possible to contrast the different behaviour of the genotypes in different environments when they are selected not only in their environment of selection but also in other environments. The published experiments in mammals are restricted

almost exclusively to growth rate on *ad libitum* and restricted feeding regimens for rats and mice. Estimation of GEI, as undertaken by Falconer and Latyszewski (1952) is impracticable in livestock because of the number of generations required and the necessity for avoiding temporal variations in environment. Since the estimation of the parameters with the required precision necessitates the measurement of a large number of individuals in each of the alternative environments, the cost appears to be prohibitive in farm animals. One such study reported so far by Fowler and Ensminger (1960) in pigs deserves mention.

An alternative to the dynamic approach is the static approach in which the relative performances of different genotypes are measured under different environments in factorially designed experiments and the interaction variance estimated. Ideally, one would wish to compare the performance of the same genotype over different environments. This is usually not possible with domestic animals. Hence groups of related individuals, i.e., paternal half-sibs, breeds, strains are commonly chosen for study. Considerably less resources are required for the static approach and a number of workers have applied it to the farm animals.

While the investigations of GEI in static populations may give indications as to whether the environment is important in selection problems, these questions can, in fact, only be answered conclusively by selecting under different environmental conditions.

Falconer and Latyszewski (1952) reported the result of a selection experiment in support of Falconer's (1952) contention. The effect of the plane of nutrition on improvement in body weight achieved by selection was studied in mice. Two strains derived from a single

foundation population were selected in exactly the same manner for weight at 6 weeks of age: one strain was fed *ad lib.* and the other was restricted to about 75% of the normal food intake between the ages of weaning and weighing - that is, between the ages of 3 to 6 weeks. The result of selection was however, different in each environment. Weight increased under selection in both strains; the average increase per generation in the full diet strain was 1.5% of the unselected weight, and 1.3% in the restricted strain. The heritability was higher in the restricted diet strain being 0.29 on restricted diet and 0.20 on full. Exchanges of nutritional level were made between the strains after 5, 7 and 8 generations of selection. When reared on the restricted diet, the restricted diet strain was superior in 6 week weight, the full diet strain showing no improvement over the unselected level. When reared on full diet, the full diet strain was superior but the restricted diet strain did not fall far short of it and showed a marked improvement over the unselected level for full diet. It is concluded that the results do not support Hammond's thesis.

Another experiment with mice selected on optimal and suboptimal diets was reported by Falconer (1960). Two-way selection was applied to one pair of lines for growth rate when individuals were reared on a high plane of nutrition and to another pair of lines when individuals were reared on a low plane of nutrition. The selected traits were high and low body weight gain from 21 to 42 days of age. The diets were normal and high fibre. The latter reduced growth from 21 to 42 days of age by 20%. Results of this experiment showed that 21 to 42 days body weight when measured on the optimal diet, was increased almost as much by selection on the suboptimal as on the optimal diet but growth on the suboptimal diet was not increased at all by selection on the

optimal diet. In this and the previous experiment by Falconer and Latyszewski (1952) selection on optimal diets improved only growth on the optimal diets but selection on suboptimal diets improved growth on both diets. Results of the two experiments indicate that it may be better to select under the worst conditions rather than the best conditions if the selected population is expected to perform over a range of environments. It is also of interest that the mice selected for increased growth on the suboptimal diet were less fat and were better mothers than those selected on the optimal diets. Falconer stated that the results in his experiment which refer to the final outcome of thirteen generations of selection, do not accord well with the theory of selection for correlated characters. Over the first few generations the results were in reasonably good agreement with the theory. The discrepancies probably arose from changes of the genetic parameters which took place during the course of selection. There are other studies of GEI on mice, *Drosophila* and *Tribolium*, similar to that of Falconer and Latyszewski (1952) and Falconer (1960).

Most of the work on mice is based on selection within different diets and on sire progeny groups studied in relation to the differences in quality and quantity of feed (Young, 1953; Korkman, 1961; Park *et al.* 1966; Dalton, 1967; Bateman 1971 and 1974; Kownacki and Gebler, 1972). Young (1953) examined the strain x diet interactions and observed the slower growth of C57 strain of mice on crushed oats than the CBA strain. The heritability estimates of body weight was lower (0.066) in a selection on a low plane and higher (0.218) in a selection on a higher plane of nutrition (Korkman, 1961).

Park *et al.* (1966) investigated the influence of feeding regime on the effects of selection for post-weaning gain in the rat and pointed to the desirability of selecting under the conditions in which it is expected the descendants are to be kept. When compared in each regime, the selection line developed in that regime tended to give a larger response than those developed in other regimes. Dalton (1967) observed that the indirect responses on either plane (full diet and diluted diet) were equal to the direct responses on the same plane. However, Dalton's findings do not so much contradict Falconer's recommendations as remove their limitations. Other studies cited by Bateman (1971, 1974) and Kownacki and Gebler (1972) also support Falconer's general thesis. Wilson *et al.* (1972) observed that there was no indication that selection could be increased by subjecting mice to temperature stress during the selective process.

Extensive studies relating to the problem of GEI have been made with the lab. insects. In a series of studies on the ecological genetics of *Drosophila* Robertson (1959, 1963) revealed the interdependency of genetic and environmental factors in determining the nature of quantitative variation. Lines selected for large and small body size in *Drosophila* showed relatively larger weight reduction when grown on suboptimal diets than did individuals from the unselected population. Druger (1962) found the magnitude of correlated response for wing-length under the temperature other than that of selection was influenced by both direction of selection and culturing temperature. However, the heritability estimates obtained under two divergent conditions (larval density) were very close in an experiment by Frahm and Kojima (1966). The 'correlated' response of a line was usually as large as the line's primary response.

In studies of growth of *Tribolium* cultured in different humidities, McNary and Bell (1962) and Bray *et al.* (1962) found GEI significantly influencing the responses to selection. Bell and McNary (1963) however, found that selection for growth in the suboptimal environment gave a correlated response in the optimum equal in both the replications to the direct response of selection under optimum conditions. Hardin and Bell (1967) reported that the maximum performance in a certain environment resulted from selection in that environment and the maximum average performances resulted from selection in the poor environment. Yamada and Bell (1969) observed in a selection experiment that the direct selection responses exceeded correlated responses under both levels of nutrition (Good and Poor) and average performance of lines selected for large larval size under 'Poor' exceeded average performance of lines selected for large size under 'Good'.

An experiment comparable to those of Falconer on mice was conducted by Fowler and Ensminger (1960) with swine and deserves mention. They randomly divided a crossbred population of swine into two lines. One was selected for increased average daily gain for weaning to 69 kg under a full feeding regime (H). The other line was selected for the same trait at a feeding level of 70% that of full feed group (L). The results obtained were quite similar to those of Falconer in that gain in weight occurred in lines selected within the high (H) and the low (L) nutritional planes. Also, when the stocks selected on the one plane were transferred to the other the L was equivalent in gain to H stock in the H regime but the H stock was inferior to the L stock on the L regime but apparently superior to the foundation stock. The L stock had higher efficiency in the utilisation of feed than the H stock on both regimes.

The approach of Falconer (1952) to the problem of GEI and the results of the other experiments reviewed above lead to the following main inferences.

One general principle which seems to emerge from the experiments on GEI is that they are most likely to be found where interpopulation genotypes and macroenvironments are involved. The generality of inferences possible from the above experiments are limited by the fact that the magnitude of differences between the environments and between the genetic effects vary in different situations. This leads us to the necessity of exploring the influence of a variety of environments and genotypes on each of the traits in which we have interest. The findings from the experiments reviewed above in general support Falconer's thesis. The results are in agreement in suggesting that progress from selection under unfavourable conditions approaches or equals that under favourable conditions when the objective is to improve performance in a favourable environment. However, selection under the unfavourable conditions consistently produced more response than did selection under favourable conditions when the objective is improvement in the unfavourable or average environments. In general, experimental information does not indicate that one can expect to enhance progress by selecting in an environment different from that in which the population is to be produced.

And finally, the consequences of GEI existing for two environments can be predicted from (1) the genetic correlation between the two environments for a trait; (2) the heritability estimates in the two environments; (3) the phenotypic variances of a trait in two environments. Since the value of the heritability depends on the

magnitude of all the components of variance, a change in any of these will affect it.

GENOTYPE-ENVIRONMENTAL INTERACTIONS IN SHEEP

A remarkable diversity is observed in sheep production systems throughout the world. Sheep are expected to live and produce a considerable variety of products; meat, wool and milk etc., over a wider range of environments than most farm animals. The prevailing farming practices do not permit as rigid a control of environments in raising sheep as is possible with the dairy cattle or poultry. Since optimum production is critical of any livestock enterprise, the existence of GEI and particularly of genotype x nutrition interactions and breed genotype x environment for components of production and reproduction in sheep are likely to be important.

Relatively little critical information is available on the importance of GEI in sheep. The static experimental approach, in which the relative performance of different genotypes are measured under different environments in factorially designed experiments and the interaction variance estimated, has been applied in most of the studies conducted in sheep. Considerably less resources are required for this approach. The choice of the genotypes and treatments, has, in general, been arbitrary creating a body of literature with a wide range of genotypes and treatments combinations. Interactions involving differences in nutritional status or levels have received more attention than research on any other environmental effects. A review of the reports on various traits of economic importance in sheep is presented below.

Growth characteristics

Genotype x nutrition

King and Young (1955) conducted an experiment showing the responses in body weight and body measurements exhibited by young ewes of the Blackface, Cheviot and Wiltshire breeds under two nutritional and two temperature treatments. The dilution of oats by chaff was adopted as a convenient method of restricting the diet. The warm environment consisted of pens in a heated animal-house kept at 60-65^oF. The cold environment consisted of pens erected in a very windy alley exposed to rigors of a cold winter.

Neither breed x environment nor breed x plane of nutrition was significant in yearling weight. Skeletal measurements such as length of hind-cannon and tibia; width of hind-cannon and heart-girth showed the presence of marked significant interactions due to more rapid growth of Blackface sheep on the high plane of nutrition. The negative results for characters which gave insignificant interactions were less informative, since they may be a reflection only of the small scale of the experiment. This experiment corresponds to Type 4 of Dunlop's classification; i.e., when genetic and environmental differences are both large.

Four breeds (Lincoln, Corriedale, Polwarth and Fine Merino) were maintained on two nutritional regimes by Daly and Carter (1955). Though the interactions were not specifically studied, they concluded that: "With few exceptions the absolute or relative values of the characters measured form a smooth series from the Fine Merino through the Polwarth and Corriedale to the Lincoln - either in the ascending or the descending order or show little or no difference between the breeds (e.g. body length and height, food intake per unit nett live weight;

total skin products per unit food intake). The relative positions of the breeds were generally maintained as food was progressively reduced". However, there was an indication of the GEI when examining the ratio of body weight at unrestricted intake to body weight at 20% of this intake, the Merino showing the greatest percentage response to changes in nutritional level.

Marston, Pierce and Carter (cited by Turner and Young, 1969) examined strain x environment interactions in Australia. Two Merino strains (strong wool and fine wool) were fed at two nutritional levels. The strong wool strain showed a greater body weight response to good nutrition.

King *et al.* (1959) studied the differential response of lambs of various breeds and crosses to different planes of nutrition. The lambs of two breeds and five crosses of sheep were wintered in high-high, high-low, low-high and low-low nutritional environments and subsequently brought to the same weight for slaughter. In body weight, the main feature of the experiment was the similarity of the response to different environments. Body measurements also showed conformity between breeds in response to environments.

Morley (1956) in an experiment involving the progeny of different Merino rams kept on a high and a low plane of nutrition found no interactions in body weight at 6 months but highly significant interactions were evident at 12 and 17 months body weight.

At the collective farm in Altai, U.S.S.R. Stakan *et al.* (1963) found that the heritabilities were lower under poor than good environmental conditions. Studies were conducted involving two groups

of lambs reared on two planes of nutrition, high and low; heritability estimates of 0.15 and 0.05 respectively were found for weight. Variation of this character was less in high plane than in low plane.

Effectiveness of selection of sheep of Kuchugury breed group under different feeding regimes was investigated by Anfinogenova (1970) in the U.S.S.R. Ewes were fed on an adequate diet or a diet 23% less than adequate. The genetic variance amounted to .12 and .30 respectively; the percentage of lambs classed grade 1 rose from 42 to 51% for progeny of grade 1 or grade 2 dams and from 7 to 43.2% for progeny of grade 4 dams when dams on inadequate diet were placed on adequate diet.

Ercanbrack and Price (1969) studied whether the effects of early weaning on growth rate was the same in Rambouillet, Targhee and Columbia lambs. All lambs were reared in the same flock to an average age of 75 days and half from each breed were weaned and placed in a dry lot, the remaining half stayed with their dams. Among inbred lambs (33% inbred), no significant interaction between breed and weaning response was observed though in the non-inbred group there was a significant interaction between breed and response. In the non-inbred group Targhees were superior in daily gain among lambs not weaned. Targhees also were superior among certified lambs but Columbias were superior among lambs having access to pasture.

In an interim report of a long term experiment to study the GEI in the components of lamb production, Joyce *et al.* (1976) reported the effects of mature body size and fertility on the level and efficiency of animal production. Four genotypes of sheep (Coopworth, Perendale and two Romney strains) were maintained on three different stocking rates (26 ewes/ha, 21 ewes/ha and 16 ewes/ha). There was no change in

the relative ranking of genotypes in terms of ewe live weights. Ewe mortality was similar for all genotypes and all stocking rates. Increasing stocking rate reduced lamb birth weight by 5%, the effect being more marked for multiple born lambs than for single born. Genotype x environment interactions have not been analysed as yet.

The heritability estimates of birth weight in two flocks were 0.58 to 0.76 and 0.52 to 0.76 respectively on the higher plane of nutrition. For sheep on the lower plane of nutrition the corresponding heritability estimates were 0.34 and 0.23 (Burdukovskaya and Timashev, 1971). These observations were made in an experiment to determine the effect of type of selection and level of nutrition on the heritability of birth weight in Soviet Merino sheep.

Breed x ration concentrate level on rate and efficiency of lamb growth was investigated by Glimp (1971). A significant ($P < 0.01$) interaction was observed. Suffolk and Hampshire lambs showed differential response to energy level for lamb growth. The trial was divided into three periods and six treatments representing six feeding schedules. Lambs from eight breeds were randomly divided into two lots per treatment group. Suffolk and Hampshire lambs gained faster when the ration energy level was increased above the level provided in the first two treatments while no differential response to energy level was observed among other breeds.

Testing and evaluation of progeny of sires under different environments was carried out by Gol'tsblat and Budanstev (1973) in U.S.S.R. Three sire groups totalling 70 young Précoce rams were each reared under different sets of management conditions; group 1 on pasture, group 2 and 3 at testing stations on group and individual feed

respectively. There were no significant GEI for growth or food conversion and sires ranked in the same order on three sets of test conditions for their progeny.

Hohenboken *et al.* (1976b) found no significant breed x environment interactions for birth weight. For weaning weight, sire x management system was highly significant. There were no significant dam breed x management interactions. These results were obtained from an experiment involving diallele cross among three breeds replicated over three years and two grazing management systems. Breeds were the Suffolk, Hampshire and Willamette and management systems were hill pastures vs irrigated pastures. The basic mathematical model included environmental effects (management systems, years, management x year interactions, age of dam, sex and birth and rearing type), breed and breed x environment interaction effects. In addition, sires nested within breed, management systems and year were included.

Genotype x location

The Canada Department of Agriculture and the Virginia Agricultural Station co-operatively studied GEI in sheep (Carter *et al.*, 1971a, 1971b, 1973). The experiment involved ewes of two breed crosses, North Country Cheviot (NC) rams x Canadian Leicester (L) ewes and Hampshire x (Hampshire x Rambouillet) backcrosses compared through five lamb crops (1961-65) at two locations; Ottawa, Ontario, Canada and Glade Spring, Virginia, U.S.A. The difference in latitude resulted in a considerable difference in the relative summer-winter day length and longer colder winters at Ottawa. The same Suffolk rams were used each season at both stations and the rams were replaced annually. Carter *et al.* (1971a) observed significant location x breed cross interactions for weight of

lambs weaned per ewe mated. The interaction approached significance ($0.05 < P < 0.10$) for body weight of the ewe at breeding time. The significant breed x location interaction for weight of lambs weaned per ewe mated may be possibly due to the differential fertility of two kinds of ewes at different locations. The magnitude of the interaction component in body weight of the ewes was small and probably not of economic significance.

Significant ewe breed cross x location interactions were evident for birth weight and adjusted 120 day weight but not for average daily gain from birth to weaning (Carter *et al.*, 1971b). Birth weight of lambs from NC x L ewes was heavier at both locations but the difference was much larger in Ottawa than in Virginia resulting in a significant breed x location interaction ($P < 0.05$). The situation was similar with respect to 120 day weight. A large and highly significant interaction was observed between ewe breed cross and type of birth for birth weight. While significant ewe breed cross x location interactions were present for birth and 120 day weight, the differences involved were relatively small.

Strain x location interactions in body traits were investigated by Dunlop (1963). In this experiment five strains of Australian Merino were compared at three locations with contrasting environments in New South Wales and Queensland. Rams were rotated between the locations to ensure similarity in the three sets of genotypes. The resulting data were analysed by separate year-age of ewe groups. Observations were made on body weight, body length, width of hips, width of shoulders, depth of chest and length of leg. No significant strain x year and strain x location interactions were observed for adult weights. With

one exception interactions among the main classes were not important sources of variation in body size. The exception was year x location interaction which was significant in over 60% of tests. These interactions between year and location were brought about by variability in pasture condition from one year to the next in any given location. His final conclusion was that the specific adaptations are not important when choosing an existing strain, at least for the range of environments, strains and production measures studied.

GEI and the effects of environments on phenotypic and genetic variation was studied by Osman and Bradford (1965) in an experiment conducted at two locations with Targhee-type sheep. The distance between locations was not great and the main difference appeared to be in nutrition with sheep at Hopland Field station having a lower plane of nutrition than at Davis. Eight Targhee-type rams were used on all ewes in both locations in order to ensure that the different groups in the experiment were genetically as similar as possible initially. Davis lambs received creep feed whereas Hopland lambs did not. The characters studied were birth and 120 day weight, gain from weaning to fall and from fall to shearing, 450 day weight and conformation score. For many traits mean level of performance was much higher at Davis. The phenotypic variance was higher in the 'good' (Davis) than the 'poor' (Hopland) environment with the result that the selection differential was also higher for the 'good' environment. Heritability estimates obtained from paternal half-sib for 120 day weight and yearling traits were higher in better environment. Sire x location interaction was negligible in birth weight though it was significant in one of the years. Sire x location effects were found to be highly significant (from pooled mean squares) for 450 days weight but were not

significant for 120 day weight. Studies of interaction involving blood group genotypes and locations by Stansfield *et al.* (1964) also indicated the absence of interaction effects on birth weight and weaning weight in sheep. Radomska (1965) investigated sire x flock (confounded with location) in the progeny of Merino rams. Birth weight, weight at 100 days (weaning), daily gain to 100 days and body weight at six and 12 months were studied. Interactions were found to be negligible for birth weight but the presence of sire x station (testing station vs flock) was noted for weaning weight.

Genotype x sex

Vesely and Robison (1970) studied sire x sex interactions in growth traits such as body weight, weaning weight, average daily gain, final weight, total gain and feed efficiency in Romnelet and Rambouillet. GEI were not significant for any of the traits. The heritabilities of the traits did not differ significantly between the two sexes. They concluded from the results that no significant differences in the ranking of sire groups existed. Genetic correlations between the two sexes were calculated to verify the conclusions. Very high genetic correlations were obtained. Only the correlation for birth weight in Rambouillet and feed efficiency in Romnelet appeared to deviate markedly from unity. Absence of significant sire-sex interactions, similarity of heritabilities in two sexes and very high genetic correlations suggested that the genotype-sex interactions were not important in the two populations of the study.

Brown *et al.* (1961) in the study of evaluation of factors affecting the growth of spring lambs found no significant line x sex interaction in birth weight and 120 day weight and weaning weight. There were no significant differences due to sex and line.

Genotype x year and others

Rae (1958) in a study of genetic variation and covariation in productive characters of New Zealand Romney sheep found the interaction of sires and years for body type of sheep was not significant.

No significant interaction for body weight between genetic origin and age were found by Diez *et al.* (1974) in Corriedales of three different origins kept in Peru at altitudes of 4260-5000m.

Peters and Heaney (1974) studied the interactions in factors influencing the growth of lambs reared artificially or with their dams. Included in the experiment were the lambs of Suffolk and Shropshire breeds and their reciprocal crosses and Ottawa synthetic origin. There were significant interactions of rearing system with breeds of lamb ($P < 0.01$), sex ($P < 0.05$), type of birth up to 70 days and rearing system with year ($P < 0.01$) in growth rate up to 140 days of age.

Carcass Characteristics

Genotype x nutrition

No significant interactions were observed between sire x ration for carcass traits (carcass weight, dressing percent, carcass grade, loin eye area and percent of fat in carcass) by Osman and Bradford (1967) in an experiment comparing grade Targhee lambs at two levels of nutrition.

King *et al.* (1959) observed no significant interactions for carcass weight, chest circumference, eye muscle (width x depth) and depth of fat over the eye muscle in an experiment to study differential response of lambs of various breeds and crosses to different planes of nutrition.

Significant genotype x nutrition and genotype x environment interactions were reported for growth, slaughter weight, dressing percentage, carcass composition and meat characteristics by Budanstev (1973) in an experiment of meat production of lambs sired by different rams and fattened under different conditions, i.e., indoors vs pasture.

GEI effects on lamb growth and carcass merit were reported by Hohenboken *et al.* (1976b) (see also p25) from a diallele cross among three breeds replicated over three years and two grazing management systems. In this study both genotype x environment and mating system x environment interactions for growth and carcass quality were studied. For carcass weight per day of age, breed of sire x management system was highly significant. Breed of sire x management system were also significant for finish score and USDA quality grade. Sire breed x year interactions were significant for finish score ($P < 0.01$), percent kidney fat and fat thickness ($P < 0.05$). Important breed rank changes did not occur for any of these interactions. The only significant dam breed x year effect was percent kidney fat ($P < 0.01$) in which breed of dam effects were more variable in some years than in others. No important rank changes occurred. Breed of sire x breed of dam interactions were absent for all measures of carcass merit while both breed effects and sire effects within breed were significant. No three factor interaction of sire breed x dam breed with management systems or with year was significant.

Genotype x location

Carter *et al.* (1973) (see also p25) examined the genotype-location interactions in the lamb carcass traits and found that the interaction was highly significant ($P < 0.01$) for carcass weight and carcass grade,

significant at $P < 0.05$ for weight of loin and at $P < 0.10$ for carcass yield (dressing-out percentage) and weight of shoulder. In Virginia, carcasses of lambs from H x HR ewes were slightly heavier (0.16 kg) than those from NC x L ewes. However, in Ontario those from NC x L ewes were 1.71 kg heavier. Breed x location interactions in these traits are another measure of the differential response of the ewe breed crosses and their lambs to the environments at two locations as expressed in lamb growth rate and size. There was no evidence of interactions in any carcass measurements when carcass weight was held constant. It was concluded that NC x L ewes were clearly superior under the environmental conditions in Ontario while the H x HR is adapted to Virginia.

Genotype x sex

Cramer and Marchello (1964) studied sire x sex interactions in the composition of subcutaneous fat from fat biopsies at 9 weeks of age to 18 months of age in Columbia ram-ewe twin lambs, but for the iodine number interactions were found not significant in any of the other traits (melting point, lauric acid, myristic acid, palmitic acid, stearic acid, oleic acid, linoleic acid and minor acids) studied.

In another investigation Kromann and Ray (1967) observed significant line of breeding x sex (wether and ram lambs) interactions for carcass weight, fat percent and protein percent but not for fat:protein ratio.

Genotype x year and others

Breed x year interactions were studied by Boylan *et al.* (1976a) while comparing the fatty acid composition of carcasses of Finnish crossbred, Suffolk, Targhee and Minnesota lambs. Interactions were

not found significant except for heptadecanoic acid among the various fatty acids (myristic, pentadecanoic, palmitic, stearic, oleic, linoleic) studied. In another study Boylan *et al.* (1976b) examined the breed x year and breed x type of birth and rearing interactions in the carcass traits of Finnish crossbred lambs. Interactions were significant only for the USDA yield grade and quality grade ($P < 0.05$) out of the various carcass traits (hind saddle weight, kidney and pelvic fat, Longissimus area, fat thickness over Longissimus) studied.

Fleece characteristics

Few analyses of interaction effects on wool traits have been carried out. As the magnitude of differences in the genotypes and the environments employed in the experiments which have been conducted varied widely, it is worthwhile to consider each study separately in this part of the review.

Genotype x nutrition

Whether the heritability of a trait is dependent on the plane of nutrition was studied by Morely (1956) in an experiment on interaction between genotype and plane of nutrition in fleece traits of Australian Merino. Interactions were not found significant in any of the traits studied (greasy fleece weight, yield, clean fleece weight, staple length and crimps/inch) in the half-sib progeny of different Merino rams kept on a high and low plane of nutrition. The ratio of genetic to total variance was not affected by the plane of nutrition in the experiment, contradicting Hammond's (1947) thesis that "... it is only possible to direct evolution by selection of genes for these characters under circumstances where the environmental conditions are optimal for the

development of the character in question". The intra-class correlation among half-sibs for fleece characters were similar in both plane of nutrition in this experiment.

Stakan *et al.* (1963) obtained heritability estimates of fleece as 0.20 and 0.19 in the 'high' and 'low' planes of nutrition respectively. An experiment involving sires of fine-wooled sheep and two planes of nutrition was carried out in the U.S.S.R. to test the effect of environment on genetic characters and their heritability. Variation was less in 'high' plane than in 'low' plane for fleece weight at 15 months of age.

Responses in wool weight and some of its components exhibited by young ewes of the Blackface, Cheviot and Wiltshire breeds were studied in two nutritional and two temperature treatments by King and Young (1955). The traits investigated were clean weight of all fibres on tattooed area, clean weight of wool fibres on tattooed area, density (fibres per unit area); density (non-medullated fibres per unit area); average length of all fibres; average length of wool fibres; average diameter of all fibres and average diameter of wool fibres. Significant effects were produced by different environments on all traits. Breed x nutrition interaction was significant only for the first two characters. The interaction in wool production was due to the outstanding ability of Blackface to increase the size of fibres in the medullated fraction of the fleece. Similar observations were reported by Kelly (1949) in an experiment in which strong wool and fine wool Merinos gave respectively 8.0 and 7.3 lb on a 'low plane' of nutrition and 18.4 and 13.3 lb on a 'high plane'. The increased difference between the strains can be attributed to a great extent to changes in the cross sectional area of the fibre.

King *et al.* (1959) examined differential reactions to four nutritional environments (high-high, high-low, low-high and low-low) in twin lambs of two breeds (Blackface and Welsh Mountain) and five crosses for greasy wool weight and fibre length. Neither interaction of cross x plane of nutrition nor the twin pairs within a cross x plane of nutrition was significant. However, Burdukovskaya and Timashev (1971) reported estimates of heritability for wool length in the progeny of rams having long wool as 0.30 to 0.52, and 0.17 to 0.25 in two flocks fed on higher and lower planes of nutrition respectively; for rams with wools of moderate length, the corresponding figures were 0.30 to 0.45 and 0.15 to 0.23.

In a study by Osman and Bradford (1967) grade Targhee ram and wether lambs by different sires were obtained and each sire family was divided at random into two groups. One half of each group was fed a high energy ration and the other half a low energy ration for 7 weeks (Period I). Subsequently animals from both groups were fed the high energy ration for another period of 7 weeks (Period II). The treatment groups were thus designated as HH and LH. Sire x plane of nutrition was significant ($P < 0.05$) for staple length (Period I) in the case of wether lambs and clean fleece weight (Period II) in the ram lamb data. If the magnitude of GEI bears a relationship to the magnitude of the main effects, then the traits which showed significant sire differences within environments, since ration effects were large, would be expected to show most interactions. This was found to be true for clean fleece weight in the case of rams. However, staple length of wethers and carcass weight of rams showed significant interaction even though the sire differences were not significant.

Ewes from three flocks, one selected for high clean wool weight, one selected for low clean wool weight, and a random control group were investigated by Williams and Winston (1965) for relative efficiency of conversion of feed to wool. Three nutritional levels were imposed. Flocks x levels of nutrition was found significant for clean wool production ($P < 0.05$) though it was not significant for efficiency (g wool: g food). On the high and intermediate planes the mean clean wool weights of the high wool weight group, relative to control (= 100) were 126 and 120 respectively, while on the low plane it was only 101. Similar figures for the low weight group were 87, 88 and 96. The interaction is evident in this case, but only when the nutritional differences become extreme, i.e., on the low level.

A group selected for high clean wool weight and a random control kept on two planes of nutrition, maintenance and *ad lib.* showed much smaller differences in the experiment conducted by Dolling and Piper (1968), the wool weight relative to control (= 100) being 114 on *ad lib.* and 110 on maintenance.

No significant interactions for efficiency of conversion of fodder to wool was observed by Dunlop *et al.* (1966) who fed three strains of Merino (fine wool, medium wool and strong wool) on two levels of nutrition, maintenance and 1.4 x maintenance. The clean wool weight in medium and strong wool strains was 122 and 137 on maintenance and 128 and 142 on the higher ration relative to the fine strain (= 100).

South (1965) studied the relative efficiency of wool growth in each of the two groups of sheep fed on diets of chaff and nuts in Merino, Corriedale and Romney breeds. One group was fed to gain weight and the other to lose weight. The most efficient group was the Merino group on low plane of nutrition while there was little difference between the other groups.

Differential response in wool growth was observed when two levels of feeding (limited and unlimited feeding) were imposed on sheep from flocks selected for high (fleece plus) and low (fleece minus) clean fleece weight and a random-bred flock (Williams, 1966). There was greater response in rate of wool growth of the rams of fleece plus flock relative to those of random and fleece minus flocks. Flocks x levels interaction was significant for wool growth, efficiency of conversion of food to wool and fibre cross-sectional area and efficiency, but not for fibre length. The decrease in efficiency of fleece plus rams as feeding level increased was relatively smaller than those for other flocks.

Significant interaction between genotype and dietary treatments for wool production was reported in a study by Williams (1976). The study was conducted on 2 year old Merino ewes from the fleece plus and fleece minus selection flocks kept on two dietary treatments. The results were in general agreement with Williams (1966) that the wool production per unit area of skin and wool production per sheep were greater in the flock selected for high clean fleece weight; the difference between the flocks was more pronounced as level of intake of food increased.

Breed x environment interactions for wool production were examined by Hohenboken (1976). The environmental variables were systems of pastoral management (dry land hill pastures and irrigated pastures) and years. Genotypes were all possible straightbreds and reciprocal cross-bred combinations among Hampshire, Suffolk and Willamette. Ewe-breed x management system interaction affected wool production significantly ($P < 0.01$). Ewe breed x management system interaction was expressed as greater breed differences in the more favourable environment for wool production than in the less favourable environment.

Genotype x location

Dunlop (1962) reported the results of strain x location interactions (Type 4) experiment in wool traits in which five strains of the Australian Merino were run as breeding groups in three wool-growing regions of Australia. The stations were chosen to represent a range of environments and only one was specifically the home environment of one strain. He examined the importance of interactions of strain and location with year as the preliminary analyses suggested variation in interaction terms from year to year. Each main effect was assumed to be a random variable.

Strain x location interactions were found to be significant in clean fleece weight, greasy fleece weight, percentage clean scoured yield, crimps/inch, fibre diameter, character, colour and staple length. Strain x location interactions in these traits were no doubt real but they were generally small and accounted for only a small fraction of the variance. Such interactions were not significant in fibres per mm², count, soundness and handle. Strain x year was significant only for clean scoured yield and fibre diameter. He suggested that the lack of importance of the strain x location interactions results in part from the variability from the year to year of climatic conditions within individual locations. This resulted in variation in quantity and quality of fodder available. The frequent significance of strain x location x year, particularly in subjectively assessed traits, supported this argument. So unless any additional environment tested had a much lower year to year variability than those at Armidale, Cunnamulla and Deniliquin, strain x location interaction might still remain undemonstrated.

In continuation of the above experiment Dunlop and Young (1966) analysed sire x station and sire x year interactions for clean wool weight in data from five Merino strains at three stations. During the experiment some rams were used in more than one year and in some cases at more than one station. The offspring of these rams produced three classes of data, i.e., sire x year (and age), sire x drop (and year) and sire x station in which sire x environment interactions were estimated on an intrastain basis. Sire x year (progeny age) and sire x drop interactions were found to be of negligible importance. Interaction terms for sire x station were found significant only on two occasions and were somewhat larger (on average about half as large as the ram component). They concluded that when clean wool weight is under selection, the interaction term of this size would be unimportant in the selection of ram in one environment for use in another. The much smaller interaction in sire x year and sire x drop analyses indicated that selection of a ram in one year for use in another is unlikely to hinder genetic progress and the decrease of heritability as a result of it will be of no consequence.

Stansfield *et al.* (1964) found no significant blood-group genotype (7 loci) x location interaction for various wool traits (side wool grade, thigh wool grade, staple length at weaning, greasy fleece weight, staple length and fleece grade of yearlings). Sheep representing five genetic backgrounds and three different environments were studied. The three environments were considerably different in climate, topography, season of lambing, planes of nutrition and levels of animal care.

Carter *et al.* (1971a) in the study referred to also on p 25 at Virginia in U.S.A. and Quebec in Canada, found the location x breed-cross interaction in greasy fleece weight approached statistical significance

while breed-cross x year was of negligible importance.

Staple length was the only trait in which sire x flock (location) was found significant (from pooled estimates) in the study by Osman and Bradford (1965) conducted at Davis and Hopland in California. The sire x location interactions for greasy fleece weight, fleece grade and face score were not significant. The heritability estimates for greasy fleece weight, staple length and fleece grade code and face cover score at Davis were 0.84 ± 0.33 , 0.53 ± 0.29 , 0.70 ± 0.31 and 0.21 ± 0.23 respectively, while the corresponding figures at Hopland were 0.50 ± 0.17 , 0.42 ± 0.16 , 0.58 ± 0.18 and 0.43 ± 0.16 respectively. Results of the several traits studied showed a very consistent pattern in favour of higher heritability in the more favourable environment at Davis and suggested strongly that this environment was more favourable for the expression of genetic differences. They concluded that the interactions, at least the kind leading to reversal of rank of genotypes between environment, were not of major importance in this material. This is in full agreement with the results reported by Dunlop (1962). It was suggested that more genetic progress would be made by selecting in a more favourable environment because of higher phenotypic variance in good environment; equal or higher heritability in the good environment and no large genotype-environment interactions, at least in the first few generations of selection.

The progeny of Merino rams (each from different flocks) were studied in flocks and at a progeny testing station by Radomska (1965). Observations were made on wool fineness at the second shearing, fleece weight and other fleece characters. Interactions due to different locations was found significant only for wool fineness at 2nd shearing.

The lack of the interaction in the case of other characters indicated that there was no disagreement between the progeny tests on the station and in flocks.

Dunlop and Hayman (1958) found strong evidence of interaction while comparing the incidence of fleece-rot for a number of strains of Merino sheep and locations in Australia. In three locations rainfall was sufficiently high to cause incidence of fleece-rot in the most susceptible sheep while in the other two locations conditions were such that its occurrence was either absent or negligible. They found that in the presence of sufficient rainfall to cause fleece-rot, the strong wool strain was most susceptible and the fine wool strain least susceptible. The fine strain was thus well adapted to high rainfall environments in terms of fleece-rot whereas the strong strain was not.

Genotype x sex

Genotype x sex interactions and the genetic correlations between sexes for greasy fleece weight, clean fleece weight, staple length, wool grade and wool yield were evaluated by Vesely and Robison (1970) in rams and ewes of Rambouillet and Romnelet sheep. No significant interactions ($P < 0.05$) were detected in any of the traits studied in either breeds. The heritabilities of the traits did not differ significantly between the two sexes. The heritabilities in Rambouillet males and females respectively were; greasy fleece weight 0.34 ± 0.17 , 0.46 ± 0.17 ; clean fleece weight 0.28 ± 0.16 , 0.28 ± 0.15 ; staple length 0.31 ± 0.16 , 0.19 ± 0.13 ; wool grade 0.19 ± 0.15 , 0.14 ± 0.13 ; yield 0.56 ± 0.19 , 0.45 ± 0.17 respectively. The corresponding figures in Romnelet were; greasy fleece weight 0.28 ± 0.16 , 0.18 ± 0.15 ; clean fleece weight 0.46 ± 0.18 , 0.29 ± 0.17 ; staple length 0.36 ± 0.17 , 0.36 ± 0.17 ; wool

grade 0.76 ± 0.21 , 0.23 ± 0.16 ; yield 0.33 ± 0.17 , 0.32 ± 0.17 . The genetic correlations of each trait between two sexes were calculated and only the correlations for greasy fleece weight and clean fleece weight deviated markedly from unity. It was thus concluded that no significant differences in ranking of sires existed between the two sexes.

Genotype x year and others

No significant interaction between sire x year was observed by Rae (1958) in wool traits (greasy fleece weight, staple length, quality number or count and hairiness) excepting fleece character ($P < 0.01$) in a flock of New Zealand Romney sheep. This single significant result could be due to genuine non-linear interaction between sires genotype and environmental conditions peculiar to each year or to differences between dam and sire x dam interaction or it could be an artefact of the subjective assessment. The exact cause was not established from the data.

Significant interactions between genetic origin and age in Corriedales were observed by Diez *et al.* (1974) for fleece weight, fibre diameter and staple length in a study involving sheep from three different genetic origins in Peru.

Reproductive traits in ewes

Genotype x nutrition

Ewes of two genotypes which differed with respect to potential fertility were subjected to three nutritional regimes to estimate the importance of GEI for various reproductive traits (Meyer, 1974). The two genotypes were Targhee (medium fertility) and Finnish Landrace x

Targhee characterised by high prolificacy. 'Low', 'Medium' and 'High' feed intake levels of alfalfa were the three nutritional treatments involved in the experiment. Interaction approached significance ($P \approx 0.09$) for preflushing, ovulation rate but was absent for ovulation rate measured after one cycle of flushing. No interaction effects were found for oestrus cycle length or lambing performance although there were indications of breed differences in the incidence of silent heats and ova success rate on the various treatments. The effect of this interaction in general were of limited importance for most reproductive traits measured suggesting that the introduction of genes from this high fertility breed into the existing sheep should improve reproductive rate over a fairly wide range of levels of nutrition. Genetic improvement originating in one nutritional requirement is likely to be expressed at least in part, in other nutritional environments.

Genotype x pasture interaction in the fertility of Romney ewes was studied by Ch'ang (1963). The differential response of ewes born as single or twins when grazed on oestrogenic red clover and a rye-grass/white clover association (control) was examined. Ewes grazed on oestrogenic red clover were lower in fertility than ewes grazed on control pastures. Effects due to interaction were not significant at 5% level for average date of lambing, but were significant in one year for percent barrenness (as a measure of lambing percentage).

Genotype and mating system x environment interactions for reproduction traits in ewes were reported by Hohenboken ^{et al} (1976a) from a diallel cross among three breeds of sheep replicated over three years and two grazing management systems (improved dry hill land pastures versus irrigated and heavily fertilized lowland pastures). Breeds were

Hampshire, Suffolk and Willamette. Sire breed x management was not significant for fertility, prolificacy and lamb survival. Sire breed x year approached significance for fertility and was significant for prolificacy. Both interactions involved rank changes among the sire breeds but in no case were the differences within years large or important. Dam breed x management interactions involving changes in rank of dam breeds did not differ, but there was a marked dam breed x environment interaction ($P < 0.05$) for fertility. Dam breed x years was not significant for any of the characters.

Significance testing for reproduction traits is fraught with difficulty because of the distribution problems. Dunlop (1963) remarked that even in weight of lambs born or weaned per ewe mated, the underlying effect of lamb numbers make the distribution partially discontinuous. Carter *et al.* (1971a) observed that the discontinuous nature and coarse classification of barren or lambing (0 or 1) as well as of lambs born or weaned per ewe (1, 2, 3, occasionally 4) brought about problems of distribution and tests of statistical significance.

Genotype x location

Strain x location, strain x sex and strain x age interactions on survival rate to weaning of Merino lambs were examined in two sets of data by Lax and Turner (1965). The strain trial involved five strains of Merino run without selection at each of three locations (Cunnamulla, Armidale and Deniliquin) with six age groups of ewes. The same five strains were later included in selection groups at Armidale with seven age groups of ewes. There was no significant location x strain interaction in the strain trial. Strain x age interaction ($P < 0.01$) was found significant, while strain x sex was found negligible in the

Armida selection group. However, Dunlop (1963) in a study of strain x location and strain x year interactions in reproductive performance found no significant interaction in Merinos for number of lambs born, number of lambs weaned, weight of lambs born and weight of lambs weaned. Strain x year interactions were virtually absent and strain x locations accounted for only a very small fraction of variation, while strain x location x year was of slight importance.

Similar results were obtained by De Hass and Dunlop (1969) while examining the importance of strain x location interactions in the reproductive traits of Merinos. Strain x location interactions were not large enough to suggest any differences in adaptation of strains to particular locations in reproductive traits of single births and multiple births.

Pattie (1965) also working with Merinos, reported that a random-bred flock and flocks selected in positive and negative directions for weaning weight did not interact significantly with years for wet ewes, lambs mothered, lambs weaned (all three expressed as percent of ewes joined), multiple births, ewes lambing and lost (both expressed as percent of wet ewes) and lamb deaths (mothering to weaning as percent of lambs mothered).

Location x breed (cross) of ewe interaction in sheep was studied by Carter *et al.* (1971a) (see also p25) for number of lambs born, lambs born alive, lambs weaned, lambing date and weight of lambs weaned. This interaction was highly significant ($P < 0.01$) for average lambing date suggesting a real difference in response to season of breeding as a part of two environments. It was also significant ($P < 0.05$) for weight of lambs weaned per ewe mated. The two kinds of ewes were in

reverse rank at two locations for weight of lambs weaned per ewe mated. The interaction approached significance ($0.05 < P < 0.1$) for ewes lambing per 100 ewes mated. None of the other interactions were close to significance.

Dun *et al.* (1966) also observed the significant interaction between strain of Merino ewe and season of joining for percentage of ewe lambing (expressed as a percentage of ewes joined) and twin births (as a percentage of lambing ewes) in a comparison of autumn and spring joining of Young Peppin and South Australian Merino ewes mated to Border Leicester rams.

The infertility of sheep resulting from GEI was investigated by Willham (1973). Two breeds of ewes, i.e., Welsh Mountain (WM) and Border Leicester (BL) were compared for reproductive attributes such as time of onset of the breeding season, mating percentage, lambing percentage and patterns of cyclic activity under two different photoperiods. Under the local ambient photoperiod at $51^{\circ} 43'N$ the breeds did not differ significantly but under a simulated equatorial photoperiod, 100% of WM ewes showed oestrus vs 37.5% of BL ewes. The WM ewes had 3 to 10 cycles and a high incidence of silent heats compared with 2 to 7 cycles and no silent heats in the BL ewes; 10 WM ewes mated and 9 lambed, but only 2 BL ewes mated and 1 lambed.

Others

Cresswell (1958) compared the distance travelled by New Zealand Romney and Cheviot sheep grazing on hill and lowland pastures. The difference between the breed means was statistically significant. In general, Cheviots covered more distance on the hill and the flat land

than the New Zealand Romney. The effect of switching two breeds from hill to flat land and from flat land to hill land were also studied. Romneys raised their mileage when transferred from hill to flat land and transference back from flat to hill actually raised their level of activity.

GENETIC PARAMETERS

Heritability

Heritability is arguably the most important single concept in the application of genetics to animal breeding (Hill, 1974). To this point, the prime concern in reviewing the literature for the effects of GEI has been limited to two main questions:

1. Is the heritability different in different environments, and
2. Is the ranking of animals on the basis of genetic merit the same in different environments?

Apart from the above effects of GEI on the ranking and correlated response, there is a specific effect of interaction on the estimates of heritability. Estimates of the heritability of a character are normally made within a single macroenvironment; it is assumed that the micro fluctuations operate independently of the genetic variations, and that the two combine their effects additively. It is usual, however, in estimating heritability to analyse records from several years, age groups, seasons, etc., particularly in farm animals where the number of animals per generation is small. While computing the estimates, the data may be corrected for known environmental sources of variation (and interactions) which would otherwise inflate the error term and bias the estimate of heritability downwards.

If GEI are important, the average genetic differences would be overestimated and the heritability estimates are inflated in the following way (Dickerson, 1963):

<u>Test</u>	<u>Performance of Progeny</u>	<u>Heritability</u>
One environment	Same environment	$\frac{\sigma_A^2 + \sigma_{GEI}^2}{\sigma_A^2 + \sigma_{GEI}^2 + \sigma_E^2}$
One environment	Other environments	$\frac{\sigma_A^2}{\sigma_A^2 + \sigma_{GEI}^2 + \sigma_E^2}$

Very little work has been undertaken for the purpose of obtaining information which might be used to produce valid and efficient estimates of genetic parameters in varying environments in sheep, especially for wool traits. Most of the published estimates of heritability obtained by paternal half-sib method are based on analysis of the sire effects nested within years which would include sire x year effects. This would inflate the heritability estimates in the presence of GEI.

Turner and Young (1969) classified the various traits of economic importance in sheep based on arbitrary limits of heritability estimates as follows:- values of 0.3 or more were regarded as high levels of heritability; those between 0.1 and 0.3 as intermediate and those below 0.1 as low.

Heritability estimates of some traits relevant to this work obtained by various workers on different breeds of sheep are presented in Table 1. Most of the heritabilities for the traits in sheep are estimated from paternal half-sib correlation or daughter-dam regression. No information was available on clean wool weight/unit skin area, total crimp number, tippiness grade, discoloured area grade, coting grade,

TABLE 1: Some published estimates of heritability of live-weight, wool quantity and quality traits in sheep

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Live-weight</u>				
0.64	16 m.o. F	DDR	Merino	Young <i>et al.</i> (1960)
0.58	16 m.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.53	1 y.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.36	10 m.o.	POR	Merino	Morley (1950)
0.36	-	POR	Merino	Morley (1955a)
0.09	-	PHS	Merino	Morley (1955a)
0.32	10 m.o.	PHS	N.Z. Romney	Baker <i>et al.</i> (1974)
0.38	10 m.o.	PHS	N.Z. Romney	Baker <i>et al.</i> (1974)
0.22	15 m.o.	PHS	N.Z. Romney	Baker <i>et al.</i> (1974)
0.22	15 m.o.	PHS	N.Z. Romney	Baker (1977)
0.39	10 m.o.	PHS	N.Z. Romney	Ch'ang and Rae (1970)
0.42	10 m.o.	DDR	N.Z. Romney	Ch'ang and Rae (1970)
0.51	14 m.o.	PHS	N.Z. Romney	Ch'ang and Rae (1970)
0.46	14 m.o.	DDR	N.Z. Romney	Ch'ang and Rae (1970)
0.45	18 m.o.	PHS	Rambouillet	Burfening <i>et al.</i> (1971)
0.36	1 y.o.	DDR	Navajo	Hall <i>et al.</i> (1964)
0.54	-	DDR	Merino	Beattie (1962)
0.65	16 m.o.	DDR	Merino	Brown and Turner (1968)
0.82	14 m.o. (adjusted)	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
0.85	14 m.o. (unadjusted)	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
0.02	10 m.o.	PHS	Romney Marsh	Radomska and Tyszka (1972)
0.14	1 y.o.	PHS	Romney Marsh	Radomska and Tyszka (1972)
0.11	-	-	Romney Marsh	Radomska and Klewicz (1975)
0.00	18 m.o.	PHS	Polish Mountain	Nawara and Duniec (1972)
0.43	10 m.o.	PHS	Polish Merino	Nawara (1971)

¹ m.o. = months old, y.o. = years old, F = female, M = male, S = Singles, T = Twins

² DDR = Daughter-dam regression, PHS = Paternal half-sib, POR = Parent-offspring regression, ISR = Intra-sire regression, ISC = Intra-sire correlation.

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Live-weight</u>				
0.41	1 y.o. (before shearing)	ISC	Corriedale	Katada and Takeda (1962)
0.55	1 y.o. (after shearing)	ISC	Corriedale	Katada and Takeda (1962)
0.79	1 y.o.	PHS	Fine wool sheep	Shelton and Manzies (1968)
0.40	1 y.o.	DDR	Rambouillet	Terrill and Hazel (1943)
0.39	18 m.o.	DDR	Welsh Mountain	Dalton (1962)
0.59	18 m.o.	POR	Welsh Mountain	Doney (1958)
0.46	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
0.42	15 m.o.	PHS	S.A. Romney	Bosman (1958)
0.13	1 y.o.	PHS	Columbia	Balch (1965)
0.31	1 y.o.	PHS	Kivircik	Ozcan (1971)
0.33	1 y.o.	ISR	Kivircik	Ozcan (1971)
0.39	1 y.o.	DDR	Kivircik	Ozcan (1971)
0.19	1 y.o.	PHS	Rahmani	Karam (1959)
0.27	14 m.o.	PHS	Perendale	Elliott (1975)
0.44	14 m.o.	DDR	Perendale	Elliott (1975)
1.06	15 m.o. (Good environment)	PHS	Targhee	Osman and Bradford (1965)
0.40	15 m.o. (Poor environment)	PHS	Targhee	Osman and Bradford (1965)
0.66	14 m.o.	DDR	Romney	Builov (1970)
<u>Greasy fleece weight</u>				
0.30	14 m.o. (unadjusted)	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
0.11	14 m.o. (adjusted)	PHS	Rambouillet	Basset <i>et al.</i> (1967)
0.42	16 m.o.	DDR	Merino	Brown and Turner (1968)
0.35	14 m.o.	DDR	N.Z. Romney	Rae (1946)
0.15	14 m.o.	DDR	N.Z. Romney	Rae (1948)
0.32	14 m.o.	PHS	N.Z. Romney	Rae (1958)
0.31	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.11	14 m.o.	DDR	N.Z. Romney	Rae (1958)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Greasy fleece weight</u>				
0.45	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.34	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.46	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.30	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.49	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.32	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.39	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.14	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.40	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.22	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.51	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.30	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.31	1 y.o.	PHS	Rambouillet	Vesely <i>et al.</i> (1970)
0.29	1 y.o.	PHS	Rommelet	Vesely <i>et al.</i> (1970)
0.34	1 y.o. M	PHS	Rambouillet	Vesely and Robison (1970)
0.46	1 y.o. F	PHS	Rambouillet	Vesely and Robison (1970)
0.28	1 y.o. M	PHS	Rommelet	Vesely and Robison (1970)
0.18	1 y.o. F	PHS	Rommelet	Vesely and Robison (1970)
0.45	16 m.o. F	DDR	Merino	Young <i>et al.</i> (1960)
0.43	16 m.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.33	1 y.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.35	-	DDR	Merino	Beattie (1962)
0.58	-	PHS	Rambouillet	Shelton and Menzies (1968)
0.39	1 y.o.	POR	Merino	Morley (1951)
0.67	1 y.o.	PHS	Merino	Morley (1951)
0.40	-	POR	Merino	Morley (1955a)
0.44	-	PHS	Merino	Morley (1955a)
0.84	15 m.o. (Good environment)	PHS	Targhee	Osman and Bradford (1965)
0.50	15 m.o. (Poor environment)	PHS	Targhee	Osman and Bradford (1965)
0.47	-	PHS	Awassi	Ghoneim <i>et al.</i> (1974)
0.16	-	DDR	Awassi	Ghoneim <i>et al.</i> (1974)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Greasy fleece weight</u>				
0.38	-	DDR	Dala	Eikje (1975)
0.47	-	DDR	Rygja	Eikje (1975)
0.48	-	DDR	Cheviot	Eikje (1975)
0.40	-	DDR	Spaelsau	Eikje (1975)
0.51	-	DDR	Steigar	Eikje (1975)
0.34	1 y.o.	DDR	Navajo	Hall <i>et al.</i> (1964)
0.28	1 y.o.	DDR	Rambouillet	Terrill and Hazel (1943)
0.10	1 y.o.	DDR	N.Z. Romney	McMahon (1943)
0.12	5 m.o.	PHS	Dala	Gjedrem (1969)
0.10	5 m.o.	DDR	Dala	Gjedrem (1969)
0.59	-	PHS	Texel	Kooistra <i>et al.</i> (1966)
0.00	1 y.o.	PHS	Romney Marsh	Radomska and Tyszka (1972)
0.32	2 y.o.	PHS	Romney Marsh	Radomska and Tyszka (1972)
0.37	3 y.o.	PHS	Romney Marsh	Radomska and Tyszka (1972)
0.07	-	-	Romney Marsh	Radomska and Klewick (1975)
0.47	1 y.o.	PHS	Polish Mountain	Nawara and Duniec (1972)
0.50	2 y.o.	PHS	Polish Mountain	Nawara and Duniec (1972)
0.37	3 y.o.	PHS	Polish Mountain	Nawara and Duniec (1972)
0.33	-	PHS	Polish Merino	Nawara (1971)
0.48	2 y.o.	PHS	Polish Merino	Nawara (1971)
0.35	1 y.o. F	ISC	Corriedale	Katada and Takeda (1962)
0.61	2 y.o.	POR	Welsh Mountain	Doney (1958)
0.43	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
0.23	14 m.o.	PHS	N.Z. Romney	Lundie (1971)
0.29	15 m.o.	PHS	N.Z. Romney	Baker <i>et al.</i> (1974)
0.57	15 m.o.	PHS	N.Z. Romney	Baker <i>et al.</i> (1974)
0.29	15 m.o.	PHS	N.Z. Romney	Baker (1977)
0.57	15 m.o.	DDR	N.Z. Romney	Baker (1977)
0.54	1 y.o.	PHS	Kivircik	Ozcan (1971)
0.68	1 y.o.	ISR	Kivircik	Ozcan (1971)
0.62	1 y.o.	DDR	Kivircik	Ozcan (1971)
0.32	14 m.o.	PHS	Perendale	Elliott (1975)
0.30	14 m.o.	DDR	Perendale	Elliott (1975)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Clean scoured yield</u>				
0.37	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.28	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.51	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.44	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.59	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.56	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.39	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.32	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.52	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.50	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.52	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.52	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.44	1 y.o.	PHS	Rambouillet	Vesely <i>et al.</i> (1970)
0.39	1 y.o.	PHS	Rommelet	Vesely <i>et al.</i> (1970)
0.56	1 y.o. M	PHS	Rambouillet	Vesely and Robison (1970)
0.45	1 y.o. F	PHS	Rambouillet	Vesely and Robison (1970)
0.33	1 y.o. M	PHS	Rommelet	Vesely and Robison (1970)
0.32	1 y.o. F	PHS	Rommelet	Vesely and Robison (1970)
0.49	16 m.o. F	DDR	Merino	Young <i>et al.</i> (1960)
0.44	16 m.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.50	1 y.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.39	-	POR	Merino	Morley (1955a)
0.75	-	PHS	Merino	Morley (1955a)
0.75	-	POR	Merino	Morley (1950)
0.40	-	DDR	Merino	Beattie (1962)
0.33	2 y.o.	PHS	Polish Merino	Nawara (1971)
0.49	15 m.o.	DDR	Merino	Brown and Turner (1968)
<u>Staple length</u>				
0.46	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
0.73	20 m.o.	POR	Welsh Mountain	Doney (1958)
0.38	20 m.o.	DDR	Welsh Mountain	Dalton (1962)
0.36	1 y.o.	DDR	Rambouillet	Terrill and Hazel (1943)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Staple length</u>				
0.16	14 m.o.	DDR	N.Z. Romney	Rae (1946)
0.21	-	DDR	N.Z. Romney	Rae (1948)
0.35	14 m.o.	DDR	N.Z. Romney	Rae (1950)
0.48	14 m.o.	PHS	N.Z. Romney	Rae (1958)
0.35	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.50	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.73	1 y.o.	PHS	Columbia	Balch (1965)
0.29	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.53	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.48	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.59	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.50	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.43	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.36	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.47	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.53	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.42	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.44	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.31	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.31	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.25	1 y.o.	PHS	Rambouillet	Vesely <i>et al.</i> (1970)
0.39	1 y.o.	PHS	Romnelet	Vesely <i>et al.</i> (1970)
0.31	1 y.o. M	PHS	Rambouillet	Vesely and Robison (1970)
0.19	1 y.o. F	PHS	Rambouillet	Vesely and Robison (1970)
0.36	1 y.o. M	PHS	Romnelet	Vesely and Robison (1970)
0.36	1 y.o. F	PHS	Romnelet	Vesely and Robison (1970)
0.37	16 m.o. F	DDR	Merino	Young <i>et al.</i> (1960)
0.35	16 m.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.31	1 y.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.44	2 y.o.	PHS	Polish Merino	Nawara (1971)
0.31	1 y.o.	PHS	Polish Mountain	Nawara and Duniec (1972)
0.45	2 y.o.	PHS	Polish Mountain	Nawara and Duniec (1972)
0.57	3 y.o.	PHS	Polish Mountain	Nawara and Duniec (1972)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Staple length</u>				
0.75	2 y.o.	PHS	Chokla	Bhasin and Desai (1966)
0.53	15 m.o. (Good environment)	PHS	Targhee	Osman and Bradford (1965)
0.42	15 m.o. (Poor environment)	PHS	Targhee	Osman and Bradford (1965)
0.23	1.y.o. F	DDR	Navajo	Hall <i>et al.</i> (1964)
0.69	1 y.o.	PHS	Columbia	Balch (1965)
0.36	1.y.o.	DDR	Rambouillet	Terrill and Hazel (1943)
0.67	1 y.o.	DDR	Rambouillet	Shelton <i>et al.</i> (1954)
0.43	5 m.o. S	PHS	Dala	Gjedrem (1969)
0.54	5 m.o. T	PHS	Dala	Gjedrem (1969)
0.37	5 m.o.	DDR	Dala	Gjedrem (1969)
0.44	5 m.o. M	PHS	Dala	Gjedrem (1969)
0.42	5 m.o. M	PHS	Dala	Gjedrem (1969)
0.46	5 m.o. F	PHS	Dala	Gjedrem (1969)
0.50	-	DDR	Merino	Beattie (1962)
0.43	-	DDR	Merino	Brown and Turner (1968)
0.49 (unadjusted)	1 y.o.	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
0.46 (adjusted)	1 y.o.	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
0.37	1 y.o.	ISC	Corriedale	Katada and Takeda (1962)
0.69	1 y.o.	PHS	Kivircik	Ozcan (1971)
0.59	1 y.o.	ISR	Kivircik	Ozcan (1971)
0.67	1 y.o.	DDR	Kivircik	Ozcan (1971)
0.49	14 m.o.	PHS	Perendale	Elliott (1975)
0.35	14 m.o.	DDR	Perendale	Elliott (1975)
0.22	-	POR	Merino	Morley (1950)
0.21	-	POR	Merino	Morley (1951)
0.24	1 y.o.	PHS	Merino	Morley (1951)
0.56	-	POR	Merino	Morley (1955a)
0.52	-	PHS	Merino	Morley (1955a)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Mean fibre diameter</u>				
0.47	16 m.o.	DDR	Merino	Brown and Turner (1968)
0.70	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.46	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.59	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.49	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.64	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.46	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.44	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.30	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.56	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.44	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.62	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.49	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.45	16 m.o. F	DDR	Merino	Young <i>et al.</i> (1960)
0.12	16 m.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.34	1 y.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.35	1 y.o. F	DDR	Navajo	Hall <i>et al.</i> (1964)
0.35	-	DDR	N.Z. Romney	McMahon (1943)
0.34	5 m.o. S	PHS	Dala	Gjedrem (1969)
0.47	5 m.o. T	PHS	Dala	Gjedrem (1969)
0.53	5 m.o.	DDR	Dala	Gjedrem (1969)
0.39	5 m.o.	PHS	Dala	Gjedrem (1969)
0.45	5 m.o. M	PHS	Dala	Gjedrem (1969)
0.38	5 m.o. F	PHS	Dala	Gjedrem (1969)
0.57	-	DDR	Merino	Beattie (1962)
0.48	2 y.o.	PHS	Polish Merino	Nawara (1971)
0.52	-	DDR	Merino	Schinckel (1958)
0.23	-	DDR	Merino	Seitanova (1966)
0.33	2 y.o.	PHS	Chokla	Bhasin and Desai (1966)
0.17	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
0.29	-	PHS	S.A. Romney	Bosman (1958)
0.52	1 y.o.	PHS	Kivircik	Ozcan (1971)
0.61	1 y.o.	ISR	Kivircik	Ozcan (1971)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Mean fibre diameter</u>				
0.65	1 y.o.	DDR	Kivircik	Ozcan (1971)
0.54	14 m.o.	PHS	Perendale	Elliott (1975)
0.47	14 m.o.	DDR	Perendale	Elliott (1975)
<u>Standard deviation of the fibre diameter</u>				
0.41	5 m.o.	DDR	Dala	Gjedrem (1969)
0.42	5 m.o.	PHS	Dala	Gjedrem (1969)
0.54	5 m.o. M	PHS	Dala	Gjedrem (1969)
0.31	5 m.o. F	PHS	Dala	Gjedrem (1969)
0.61	5 m.o. S	PHS	Dala	Gjedrem (1969)
0.48	5 m.o. T	PHS	Dala	Gjedrem (1969)
<u>Quality number</u>				
0.60	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.36	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.51	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.38	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.43	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.35	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.54	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.36	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.39	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.37	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.33	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.32	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.44	-	PHS	Texel	Kooistra <i>et al.</i> (1966)
0.26	14 m.o.	PHS	Perendale	Elliott (1975)
0.31	14 m.o.	DDR	Perendale	Elliott (1975)
0.37	14 m.o.	DDR	N.Z. Romney	Rae (1946)
0.41	14 m.o.	DDR	N.Z. Romney	Rae (1948)
0.27	14 m.o.	DDR	N.Z. Romney	Rae (1950)
0.47	14 m.o.	PHS	N.Z. Romney	Rae (1958)
0.27	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.34	14 m.o.	DDR	N.Z. Romney	Rae (1958)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Crimps per inch/centimeter</u>				
0.40	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.16	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.27	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.34	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.35	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.13	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.24	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.22	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.21	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.25	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.22	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.09	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.36	16 m.o. F	DDR	Merino	Young <i>et al.</i> (1960)
0.51	16 m.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.43	1 y.o. M	DDR	Merino	Young <i>et al.</i> (1960)
0.40	-	POR	Merino	Morley (1950)
0.28	-	PHS	Merino	Morley (1955a)
0.47	-	POR	Merino	Morley (1955a)
0.57	-	DDR	Merino	Beattie (1962)
0.16	-	PHS	Polish Merino	Nawara (1971)
0.45	16 m.o.	DDR	Merino	Brown and Turner (1968)
0.40	-	DDR	Merino	Schinckel (1958)
0.24	2 y.o.	PHS	Chokla	Bhasin and Desai (1966)
0.72	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
0.31	-	PHS	S.A. Merino	Bosman (1958)
<u>Character grade</u>				
0.49	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.78	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.45	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.41	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.54	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.43	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Character grade</u>				
0.39	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.39	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.44	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.37	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.42	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.32	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.38	-	PHS	Merino	Morley (1955b)
0.66	1 y.o.	PHS	Columbia	Balch (1965)
0.23	14 m.o.	PHS	Perendale	Elliott (1975)
0.23	14 m.o.	DDR	Perendale	Elliott (1975)
0.16	14 m.o.	DDR	N.Z. Romney	Rae (1946)
0.15	14 m.o.	DDR	N.Z. Romney	Rae (1946)
0.27	14 m.o. (side)	DDR	N.Z. Romney	Rae (1948)
0.20	14 m.o. (fore quarter)	DDR	N.Z. Romney	Rae (1948)
0.38	14 m.o. (hind quarter)	DDR	N.Z. Romney	Rae (1948)
0.12	14 m.o.	PHS	N.Z. Romney	Rae (1958)
0.22	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.16	14 m.o.	DDR	N.Z. Romney	Rae (1958)
0.25	14 m.o.	DDR	N.Z. Romney	Rae (1958)
<u>Handle grade</u>				
0.10	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.27	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.25	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.10	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.14	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.37	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.35	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.25	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.28	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.08	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)

TABLE 1: (continued)

Estimate	Age and remarks ¹	Method of estimation ²	Breed	Reference
<u>Handle grade</u>				
0.28	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.56	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.44	14 m.o.	DDR	N.Z. Romney	Rae (1948)
0.30	-	PHS	Merino	Morley (1955b)
<u>Lustre grade</u>				
0.27	14 m.o.	DDR	N.Z. Romney	Rae (1948)
<u>Greasy colour grade</u>				
0.38	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.36	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.37	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.41	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.40	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.28	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.24	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.27	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.29	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.34	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.32	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.29	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
0.00	14 m.o.	DDR	N.Z. Romney	Rae (1948)
0.63	-	PHS	Merino	Morley (1955b)
<u>Scoured colour grade</u>				
0.20	16 m.o.	-	Merino	Jackson (1973)

cotted area grade and soundness grade in wool. Only one reference each on lustre grade and scoured colour grade of wool by Rae (1948) and Jackson (1973) respectively were available. It appears that all quantitative and qualitative wool traits reported in Table 1 have moderately high heritability and estimates range between 0.2 and 0.6 in most cases.

Heritability, being a function of genetic variance, could change its value with any change in gene frequency as a consequence of selection. Periodic re-estimation of heritability for traits of economic importance particularly for flocks under artificial selection is thus useful. However, Hill (1974) remarked that gene effects have to be very large in relation to the phenotypic standard deviation before genetic variances are likely to change markedly in the first few generations. He stated that the general impression is that predictions based on present estimates are useful for, say, five generations. A reasonable degree of linearity of response is thus assumed in the first few generations. No appreciable change in heritability of clean wool weight in Merinos was observed by Brown and Turner (1968) in the flocks which has been under selection for this trait for 12 years. Contrary to this, Pattie and Barlow (1974) reported realized heritability of 0.53 and 0.11 for ewes in the first two, and subsequent three generations respectively in a flock at Trangie Agricultural Research Station, selected for high clean fleece weight. The corresponding figures for rams were 0.65 and 0.02.

Genetic correlations

Intra-trait genetic correlations

Since Falconer (1952, 1960) extended the concept of genetic correlation between two traits (Hazel, 1943), to the genetic correlation

between phenotypes for the same trait expressed in two environments, the idea has been widely recognized by quantitative geneticists. Dickerson (1962) pointed out that the problems posed by consideration of more than one character and more than one environment in selection programmes are quite similar. He equated, in fact, the number of characters to the number of environments and the correlation between characters within individuals to correlation between the phenotypic expression of the same trait in different environments.

On the basis of Falconer's (1952) thesis, Robertson (1959) presented formulae in terms of mean squares for estimating the genetic correlation of the performance of the same genotype in two or more environments and Dickerson (1962) presented a similar method for estimating genetic correlation in terms of genetic and genotype-environment interaction variance components obtained from the analysis of variance.

The appropriate product moment estimates of genetic correlation can be obtained from genetic components of variance and covariance for any pair of environments. However, when large numbers of environments are involved, it would be more convenient to estimate the average degree of genetic correlation from the ordinary components of variance for genotypes (σ_G^2 across environments) and for interaction (σ_{GEI}^2) by the intraclass method. It was, however, observed that GEI is likely to be somewhat overestimated and the genetic repeatability or correlation between environments is underestimated, in any analysis of actual performance data, because any genetic or environmental effects that are not strictly additive (i.e., multiplicative or proportional deviations from additive effects) will contribute to the estimates of interaction

variance. Dickerson (1962) and Yamada (1962) worked out the necessary algebra for adjusting the interaction components of variance in random and mixed statistical models respectively so that the use of adjusted value in the intraclass correlation makes this correlation identical with the average produce moment coefficient between the same genotype in each of the macroenvironments. The adjustment is made for any important variation between environments in the scale of genetic effects.

There are not many reports of magnitudes of genetic correlations between environments for characters of economic importance in sheep and these have been discussed individually in the previous section. The correlations reported did not deviate markedly from unity. Robertson (1959) explained that the estimate of the genetic correlation between performance in two or more environments as a quantitative expression of GEI is of value in giving a measure of practical rather than statistical significance. He suggested that an estimate of r_G around 0.8 would be of biological or agricultural importance and no results would be worth considering unless a genetic correlation of 0.6 or less which is significantly different from unity, is detected.

Inter-trait genetic correlations

To this point, in the review of literature the concept of genetic correlation has been limited to the performance of the same genotypes for a trait in sheep in two different environments as a quantitative expression of GEI.

However, genetic association among different characters are important in formulating selection plans. These are an outcome of pleiotropic effects of genes and to a minor degree of linkage or selection with varying emphasis on the different characters in many interbreeding

groups of a population. Turner (1977) stated that genetic correlations are used in development of breeding plans to indicate what other characteristics are likely to change in future generations besides those under selection, to decide what counter selection might be needed to prevent such changes and to decide whether an easily-measured character can be used as a selection criteria to obtain genetic gains instead of one more difficult (or more expensive) to measure.

The genetic correlations as reported by various workers among the traits relevant to this work for different breeds of sheep are presented in Table 2. They are mostly estimated from daughter-dam or half-sib covariances. Genetic correlations among traits of interest in this work have not been as thoroughly investigated as have heritabilities. Table 2 gives the information for the traits that have been studied extensively. No information was available on genetic correlations for clean wool weight/unit skin area, total crimp number, tippiness grade, lustre grade, scoured colour grade, discoloured area grade, coting grade, cotted area grade and soundness grade in wool.

Genetic correlations, as in the case of heritability, may change under selection. Not only the degree but the direction may change. Turner and Young (1969) emphasised that in any selection programme re-estimates should be made at intervals of a few years. Changes in some genetic correlations in groups of Australian Merinos under selection for high clean wool weight for 12 years were observed by Brown and Turner (1968). The genetic correlation between clean wool weight and fibre number decreased from +0.4 to 0 while r_G for clean wool weight and body weight increased from 0.2 to 0.5. Two negative genetic correlations also increased in magnitude; fibre number x fibre diameter from -0.6 to -0.8 and fibre number x fibre volume from -0.5 to -0.9.

TABLE 2: Some published estimates of genetic correlations between various characteristics for live-weight, wool quantity and quality in sheep

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
LW x GFW	-0.03	-	PHS	Merino	Morley (1955a)
	-0.11	-	POR	Merino	Morley (1955a)
	0.77	14 m.o.	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
	0.45	-	PHS	Rambouillet	Burfening <i>et al.</i> (1971)
	-0.07	1 y.o.	DDR	Navajo	Hall <i>et al.</i> (1964)
	-0.20	-	DDR	Merino	Beattie (1962)
	0.26	16 m.o.	DDR	Merino	Brown and Turner (1968)
	-0.07	14 m.o.	PHS	Perendale	Elliott (1975)
	0.18	14 m.o.	DDR	Perendale	Elliott (1975)
	0.41	5 m.o.	PHS	Dala	Gjedrem (1969)
	0.44	-	PHS	Merino	Nawara (1971)
	0.54	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
LW x Y	-0.08	-	POR	Merino	Morley (1955a)
	0.44	-	PHS	Merino	Morley (1955a)
	0.11	-	DDR	Merino	Beattie (1962)
	0.09	16 m.o.	DDR	Merino	Brown and Turner (1968)
LW x SL	0.65	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.28	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.11	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.16	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)

¹ LW = Live-weight, GFW = Greasy fleece weight, Y = Clean scoured yield, SL = Staple length, MFD = Mean fibre diameter, SFD = Standard deviation of the fibre diameter, CV = Coefficient of variation of fibre diameter, QN = Quality number, CPC = Crimps per centimeter, CPI = Crimps per inch, TCN = Total crimp number, CHG = Character grade, HG = Handle grade, GCG = Greasy colour grade, SCG = Scoured colour grade

² m.o. = months old, y.o. = years old

³ DDR = Daughter-dam regression, PHS = Paternal half-sib, POR = Parent-offspring regression

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
LW x SL	-0.15	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.07	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-1.11	-	POR	Merino	Morley (1950)
	-0.25	-	PHS	Merino	Morley (1955a)
	-0.26	-	POR	Merino	Morley (1955a)
	-0.06	16 m.o.	DDR	Merino	Brown and Turner (1968)
	0.52	14 m.o.	PHS	Rambouillet	Basset <i>et al.</i> (1967)
(unadjusted)					
	0.47	14 m.o.	PHS	Rambouillet	Basset <i>et al.</i> (1967)
(adjusted)					
	-0.06	14 m.o.	PHS	Perendale	Elliott (1975)
	0.22	14 m.o.	DDR	Perendale	Elliott (1975)
	0.09	5 m.o.	PHS	Dala	Gjedrem (1969)
	0.21	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
LW x MFD	-0.16	1 y.o.	DDR	Navajo	Hall <i>et al.</i> (1964)
	-0.01	5 m.o.	PHS	Dala	Gjedrem (1969)
	0.00	-	DDR	Merino	Beattie (1962)
	0.12	16 m.o.	DDR	Merino	Brown and Turner (1968)
	-0.02	14 m.o.	PHS	Perendale	Elliott (1975)
	0.00	14 m.o.	DDR	Perendale	Elliott (1975)
	0.16	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
LW x SFD	0.27	5 m.o.	PHS	Dala	Gjedrem (1969)
LW x CV	0.18	-	DDR	Merino	Beattie (1962)
LW x QN	0.37	14 m.o.	PHS	Perendale	Elliott (1975)
	-0.10	14 m.o.	DDR	Perendale	Elliott (1975)
LW x CPC/ CPI	0.12	-	POR	Merino	Morley (1950)
	-0.02	-	PHS	Merino	Morley (1955a)
	0.05	-	POR	Merino	Morley (1955a)
	0.15	-	DDR	Merino	Beattie (1962)
	0.07	16 m.o.	DDR	Merino	Brown and Turner (1968)
	-0.05	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
LW x CHG	0.21	-	PHS	Merino	Morley (1955b)
	-0.47	14 m.o.	PHS	Perendale	Elliott (1975)
	-0.31	14 m.o.	DDR	Perendale	Elliott (1975)
LW x HG	-0.09	-	PHS	Merino	Morley (1955b)
LW x GCG	0.11	-	PHS	Merino	Morley (1955b)
GFW x Y	-0.09	16 m.o.	DDR	Merino	Schinckel (1958)
	0.06	-	DDR	Merino	Beattie (1962)
	-0.22	-	PHS	Merino	Morley (1955a)
	-0.05	-	POR	Merino	Morley (1955a)
	0.03	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.75	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.40	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.18	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.27	30 m.o.*	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.25	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.49	1 y.o.	PHS	Rambouillet	Vesely <i>et al.</i> (1970)
	0.30	1 y.o.	PHS	Rommelet	Vesely <i>et al.</i> (1970)
	GFW x SL	0.40	14 m.o.	DDR	N.Z. Romney
0.45		5 m.o.	DDR	Dala	Gjedrem (1969)
0.08		1 y.o.	DDR	Navajo	Hall <i>et al.</i> (1964)
0.40		15 m.o.	PHS	Targhee	Osman and Bradford (1965)
0.17		-	PHS	Merino	Morley (1955a)
-0.02		-	POR	Merino	Morley (1955a)
0.56		1 y.o.	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
(unadjusted)					
0.75		1 y.o.	PHS	Rambouillet	Bassett <i>et al.</i> (1967)
(adjusted)					
0.20		18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
0.47		18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.29		30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
0.13	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)	

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
	0.17	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.18	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.25	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	0.60	14 m.o.	PHS	N.Z. Romney	Rae (1958)
	0.21	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	0.26	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.38	1 y.o.	PHS	Rambouillet	Vesely <i>et al.</i> (1970)
	0.70	1 y.o.	PHS	Romnelet	Vesely <i>et al.</i> (1970)
	0.70	-	DDR	Merino	Beattie (1962)
	0.29	16 m.o.	DDR	Merino	Brown and Turner (1968)
	0.76	14 m.o.	PHS	Perendale	Elliott (1975)
	0.44	14 m.o.	DDR	Perendale	Elliott (1975)
GFW x MFD	0.14	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.19	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.08	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.40	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.47	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.43	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.19	-	PHS	Chokla	Bhasin <i>et al.</i> (1968)
	-0.10	1 y.o.	PHS	Navajo	Hall <i>et al.</i> (1964)
	0.23	5 m.o.	PHS	Dala	Gjedrem (1969)
	0.19	-	DDR	Merino	Beattie (1962)
	0.13	16 m.o.	DDR	Merino	Brown and Turner (1968)
	0.43	14 m.o.	PHS	Perendale	Elliott (1975)
	0.44	14 m.o.	DDR	Perendale	Elliott (1975)
	0.58	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
GFW x SFD	0.35	5 m.o.	PHS	Dala	Gjedrem (1969)
GFW x CV	0.15	-	DDR	Merino	Beattie (1962)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
GFW x QN	-0.49	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.55	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.66	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.75	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.53	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.48	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.47	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.62	14 m.o.	PHS	N.Z. Romney	Rae (1958)
	-0.47	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.49	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.48	14 m.o.	PHS	Perendale	Elliott (1975)
	0.09	14 m.o.	PHS	Perendale	Elliott (1975)
	-0.42	-	PHS	Texel	Kooistra <i>et al.</i> (1966)
GFW x CPC/ CPI	-0.61	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.67	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.79	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.99	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.77	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.35	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.56	-	POR	Merino	Morley (1955a)
	-0.06	-	PHS	Merino	Morley (1955a)
	-0.38	-	PHS	Chokla	Bhasin <i>et al.</i> (1968)
	-0.87	-	DDR	Merino	Beattie (1962)
	-0.20	16 m.o.	DDR	Merino	Brown and Turner (1968)
	-0.13	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
GFW x CHG	0.09	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.32	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.43	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.29	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.54	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.27	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.16	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	0.09	14 m.o.	DDR	N.Z. Romney	Rae (1958)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
GFW x CHG	0.08	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	0.27	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.06	-	PHS	Merino	Morley (1955b)
	0.52	14 m.o.	PHS	Perendale	Elliott (1975)
	0.32	14 m.o.	DDR	Perendale	Elliott (1975)
GFW x HG	0.08	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.87	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.08	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.70	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.47	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.53	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.15	-	PHS	Merino	Morley (1955b)
GFW x GCG	-0.30	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.70	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.10	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.42	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.35	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.45	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.28	-	PHS	Merino	Morley (1955b)
Y x SL	0.36	16 m.o.	DDR	Merino	Brown and Turner (1968)
	0.54	-	DDR	Merino	Beattie (1962)
	0.66	-	PHS	Rambouillet	Vesely <i>et al.</i> (1970)
	0.32	-	PHS	Romnelet	Vesely <i>et al.</i> (1970)
	0.57	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.27	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.42	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.36	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.23	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.41	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.63	-	POR	Merino	Morley (1955a)
	0.27	-	PHS	Merino	Morley (1955a)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
Y x MFD	0.15	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.01	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.03	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.24	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.23	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.27	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.03	-	DDR	Merino	Beattie (1962)
	0.12	16 m.o.	DDR	Merino	Brown and Turner (1968)
Y x CV	0.09	-	DDR	Merino	Beattie (1962)
Y x QN	-0.46	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.66	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.37	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.24	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.32	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.53	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
Y x CPC/ CPI	-0.54	16 m.o.	DDR	Merino	Brown and Turner (1968)
	-0.15	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.58	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.69	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.14	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.20	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.53	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.49	-	POR	Merino	Morley (1955a)
	-0.37	-	PHS	Merino	Morley (1955a)
	-0.47	-	DDR	Merino	Beattie (1962)
Y x CHG	0.30	-	PHS	Merino	Morley (1955b)
	0.26	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.49	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.09	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.26	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.06	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.28	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
Y x HG	0.14	-	PHS	Merino	Morley (1955b)
	-0.16	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.30	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.08	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.16	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.51	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.18	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
Y x GCG	0.31	-	PHS	Merino	Morley (1955b)
	0.57	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.76	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.82	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.67	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.65	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.59	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
SL x MFD	-0.35	-	PHS	Chokla	Bhasin <i>et al.</i> (1968)
	0.15	1 y.o.	DDR	Navajo	Hall <i>et al.</i> (1964)
	0.53	14 m.o.	PHS	Perendale	Elliott (1975)
	0.31	14 m.o.	DDR	Perendale	Elliott (1975)
	0.44	-	DDR	Merino	Schinckel (1958)
	-0.19	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.63	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.01	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.09	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.26	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.29	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.01	5 m.o.	PHS	Dala	Gjedrem (1969)
	-0.11	-	DDR	Merino	Beattie (1962)
	0.03	16 m.o.	DDR	Merino	Brown and Turner (1968)
0.68	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)	
SL x CV	0.04	-	DDR	Merino	Beattie (1962)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
SL x SFD	0.19	5 m.o.	PHS	Dala	Gjedrem (1969)
SL x QN	-0.43	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.47	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.66	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.57	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.61	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.65	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.73	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.76	14 m.o.	PHS	N.Z. Romney	Rae (1958)
	-0.63	14 m.o.	PHS	Perendale	Elliott (1975)
	-0.41	14 m.o.	DDR	Perendale	Elliott (1975)
SL x CPC/ CPI	-0.75	-	DDR	Merino	Beattie (1962)
	-0.18	-	POR	Merino	Morley (1950)
	-0.34	-	POR	Merino	Morley (1955a)
	-0.66	-	PHS	Merino	Morley (1955a)
	0.25	-	PHS	Chokla	Bhasin <i>et al.</i> (1968)
	-0.57	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.27	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.60	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.59	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.55	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.53	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.76	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
SL x CHG	0.31	-	PHS	Merino	Morley (1955b)
	0.13	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	0.74	14 m.o.	PHS	N.Z. Romney	Rae (1958)
	0.44	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.40	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.16	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.20	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.23	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
SL x CHG	0.23	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.47	14 m.o.	PHS	Perendale	Elliott (1975)
	0.03	14 m.o.	DDR	Perendale	Elliott (1975)
SL x HG	0.40	-	PHS	Merino	Morley (1955b)
	0.65	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.28	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.11	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.16	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.15	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.07	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
SL x GCG	0.40	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.86	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.22	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.23	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.52	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.30	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.43	-	PHS	Merino	Morley (1955b)
MFD x SFD	0.11	-	DDR	Merino	Beattie (1962)
	0.69	5 m.o.	PHS	Dala	Gjedrem (1969)
MFD x QN	-0.46	14 m.o.	PHS	Perendale	Elliott (1975)
	-0.27	14 m.o.	DDR	Perendale	Elliott (1975)
	-0.30	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.47	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.30	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.50	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.69	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.75	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
MFD x CPC/ CPI	-0.11	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.82	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.41	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.52	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.73	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.82	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.17	-	DDR	Merino	Beattie (1962)
	-0.10	16 m.o.	DDR	Merino	Brown and Turner (1968)
	-0.17	-	DDR	Merino	Schinckel (1958)
	-0.36	-	PHS	Chokla	Bhasin <i>et al.</i> (1968)
	-0.63	14 m.o.	DDR	N.Z. Romney	Tripathy (1966)
MFD x CHG	0.09	14 m.o.	PHS	Perendale	Elliott (1975)
	0.10	14 m.o.	DDR	Perendale	Elliott (1975)
	-0.33	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.13	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.46	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.63	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.06	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.17	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
MFD x HG	-0.70	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.85	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.59	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.85	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.19	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.50	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
MFD x GCG	-0.32	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.32	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	-0.08	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.14	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.11	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.26	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
SFD x CPC/ CPI	-0.42	-	DDR	Merino	Beattie (1962)
QN x CPC/ CPI	1.00	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.96	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	1.39	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	1.11	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	1.05	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.94	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
QN x CHG	-0.13	14 m.o.	PHS	Perendale	Elliott (1975)
	0.44	14 m.o.	DDR	Perendale	Elliott (1975)
	0.21	14 m.o.	DDR	N.Z. Romney	Rae (1958)
	-0.41	14 m.o.	PHS	N.Z. Romney	Rae (1958)
	0.08	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.21	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.26	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.55	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.01	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.27	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
QN x HG	0.20	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.34	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.53	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.80	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.56	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.10	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
QN x GCG	-0.62	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.33	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.03	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.08	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.05	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.27	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
CPC/CPI x CHG	-0.28	-	PHS	Merino	Morley (1955b)
	0.33	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.20	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.37	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.30	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.15	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.08	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
CPC/CPI x HG	-0.32	-	PHS	Merino	Morley (1955b)
	-0.05	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.33	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.67	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.66	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.57	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.41	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
CPC/CPI x GCG	0.29	-	PHS	Merino	Morley (1955b)
	-0.08	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	-0.42	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.09	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.27	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.16	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	-0.10	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
CHG x HG	1.08	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.91	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.65	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.95	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.73	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.84	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.86	-	PHS	Merino	Morley (1955b)
CHG x GCG	0.18	-	PHS	Merino	Morley (1955b)

TABLE 2: (continued)

Traits ¹	Estimate	Age ²	Method of estimation ³	Breed	Reference
HG x GCG	0.31	-	PHS	Merino	Morley (1955b)
	0.09	18 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.48	30 m.o.	DDR	Polwarth	Mullaney <i>et al.</i> (1970)
	0.43	18 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.34	30 m.o.	DDR	Merino	Mullaney <i>et al.</i> (1970)
	0.09	30 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)
	0.36	18 m.o.	DDR	Corriedale	Mullaney <i>et al.</i> (1970)

GENERAL CONCLUSIONS

From the above review, it is evident that the majority of factorial experiments to study GEI in sheep have been either of the breed x environment (location) or the sire x environment (nutritional level) type. Both of these interactions have significance in relation to selection, the first in connection with the choice of breed or strain and the second in relation to within flock selection. The general conclusion is that although significant Type 3 and Type 4 interactions (Dunlop's classification) are sometimes found with sheep, they are unimportant in relation to sheep breeding plans in reducing the expected gains except when very wide differences in environment (rainfall, temperature, photoperiods, nutrition) exist. The reports of intra-trait genetic correlations between environments for characters of economic importance in sheep also reveal that the correlations do not in general, deviate markedly from unity and the environments have to differ considerably for rank order changes to be important.

CHAPTER THREE

SOURCE OF DATA

A long-term experiment was designed at Massey University in 1966 to investigate possible interaction between the genotype of sire within the New Zealand Romney breed of sheep and different levels of stocking. The data used in this study, covering a period of 8 years from 1967 to 1974 inclusive, were obtained from the two subflocks of a randomly-bred flock maintained at Massey University. This flock has been used for many years as a source of data for calculation of genetic parameters.

The origin and the earlier management of the flock has been described elsewhere (Rae, 1958; Ch'ang, 1967). This flock since its establishment in 1944 has been maintained by a system of random breeding and random selection of female replacements. No artificial selection has been practised within the flock. Young rams were obtained from various Romney ram-breeding flocks as well as from a selection flock which has subgroups which are selected for higher greasy fleece weight and for open faces. There was little likelihood of inbreeding occurring in the flock.

The randomly-bred flock was split into two subflocks in March, 1966. Each age group of the flock was divided at random into two parts, one part allocated to each subflock. These subflocks are subsequently referred to as the high stocking rate flock (HSR) and control stocking rate flock (CSR).

The grazing units and their management has been described by Sumner (1969). However, it is necessary to outline certain aspects of the structure of the experiment and data collection relevant to this study.

HSR:- Approximately 220 mixed-age Romney ewes and their replacement hoggets were grazed on 10.12 hectares area of land divided into eight approximately equal-sized paddocks. In 1966 the ewes were grazed over the whole area. Subsequently female replacements were also grazed on the area. The young ewes to enter the breeding flock were selected at random from the stock born and bred on the unit. The stocking rate of the unit for the years reported in this study was kept at approximately 26 ewe equivalents per hectare (assuming 1 hogget = 0.6 ewe equivalents). No cattle were run on the unit and hay was cut and saved during the summer for winter feeding.

CSR:- The mixed-aged ewes and their replacement hoggets were grazed on the adjoining 17.40 hectares area of land at a normal stocking rate of 16 ewe equivalents per hectare. This flock was slightly larger and of similar age structure to HSR. Like the HSR unit this unit was self supporting except for rams. Wether lambs were removed from the experimental area at weaning or soon after. Occasionally cattle were used to control excess pasture growth.

Pastures on both units were predominantly a ryegrass-white-clover association. All routine farm operations such as drenching against parasites, dipping, care of feet, crutching and shearing were carried out as nearly alike as possible on both units.

The same rams were used for both the units. Each group of rams were used for two years thus allowing the records used in this study to investigate the possible occurrence of sire x year interaction also. Each ram was hand mated to approximately 22 ewes in the HSR and to 25 ewes in the CSR unit. In all years the ewes were randomised to each sire group. The mating season started between 15 and 25 March in each

year and the duration of mating period varied only a little from year to year, being not less than 51 days or more than 58 days. During mating, vasectomised rams, equipped with harnesses carrying tuppung crayons, were run with the ewes. As ewes came into their heat period they were marked by the teaser rams. Ewes recognised as being in oestrus were put into a pen with the appropriate ram. The breeding ewes remained for four lambing seasons in the flock until cast for age as five and a half year olds. The lambs were born in August and September and weaning took place towards the end of November or early in December. All wether lambs were sold after weaning but ewe lambs were retained in their respective units. Hogget shearing occurred in October, ewe shearing occurred one month later while lambs were shorn in January.

THE DATA

The data used in this study represented the female progeny of 34 New Zealand Romney sires. As mentioned, sires used in the previous year were retained for further mating in a second year. Two groups of 10 sires each were used in years 1968/69 and 1970/71 but in 1966/67 and 1972/73 the loss of some rams meant that the data from the progeny of only 7 sires were satisfactory for analysis. The data available for the present analysis were therefore based on those collected over four consecutive two-year sire periods. These sire groups are subsequently referred to as follow in the study.

<u>Group</u>	<u>Sires</u>	<u>Year of Data</u>
Sire group 1	7	1967/68
Sire group 2	10	1969/70
Sire group 3	10	1971/72
Sire group 4	7	1973/74

The data from daughters of those sires which were not used in the second year have been excluded.

For the purpose of the investigation data on hogget live-weight (HLW), greasy fleece weight (GFW), clean wool weight per unit area (WA), clean scoured yield (Y), staple length (SL), mean fibre diameter (MFD), standard deviation of the fibre diameter (SFD), quality number (QN), crimps per centimeter (CPC), total crimp number (TCN), character (CHG), tippiness (TG), handle (HG), lustre (LG), greasy colour (GCG), scoured colour (SCG), discoloured area (DAG), cotting (CG), cotted area (CAG) and soundness (SG) of wool were analysed.

The HLW used in this study is the post-shearing weight of hoggets at 14-15 months of age. The measurement was made initially to the nearest pound but later measurements were recorded to the nearest 0.5 kg. The earlier records were converted to kilogrammes.

Wool weight per unit area was measured from the mid-side position prior to shearing. The samples were scoured and the clean wool weight per square centimetre was calculated. The details of sampling and scouring methods have been described elsewhere by Sumner (1969). The samples were scoured by a four bowl detergent and scouring method. The data for this trait recorded in Sire group 3 period were incomplete and were not analysed.

GFW was recorded immediately after shearing and was measured to the nearest 0.05 kg. The belly-wool weight was included in this weight. The measurement of GFW represented only the growth of about 9-10 months between lamb shearing and hogget shearing in October of each year.

For calculation of Y, the mid-side samples were weighed greasy after being conditioned to 68°F and 65% relative humidity for 48 hours. Sampling and scouring methods have been described by Sumner (1969). The scoured samples were again allowed to condition for 48 hours before reweighing. Y was calculated as percent clean fleece weight of the greasy wool weight of the sample.

The SL of the greasy sample from the mid-side region was measured to the nearest 0.5 cm. Since the tip of the staple in Romneys tapers towards a point, the measurement was made from the base of the staple to a position midway between the point where the staple starts to taper and the tip, taking care not to stretch the staple unduly.

MFD was measured on the scoured mid-side sample. One hundred and fifty fibres from each sample were measured by projection microscope. The mean and standard deviation (in micrometers) was calculated from these observations. The data for MFD and SFD in Sire group 2 and Sire group 4 periods were not analysed as it was incomplete.

QN is a visual appraisal of the spinnability and hence fineness of wool. It is based mainly on staple crimp frequency and lustre (Henderson, 1965; Wickham and Bigham, 1973). This assessment can be affected by observer variation. The standards generally in use in New Zealand (which are similar to those in world trade) were used.

The number of crimps were counted over the whole length of a staple from the greasy mid-side sample of wool. CPC were calculated from TCN in a staple and SL. Since the data for both these traits were incomplete in Sire group 3 period, it was not analysed for that group.

CHG, TG, HG, LG, GCG, CG and SG of wool were subjectively graded on greasy mid-side samples. These were graded on a one to nine scale. In all cases nine grades were used, the score of 9 being allotted to the expression considered most desirable, 1 to the least desirable. The system of the grading was designed so that the distribution tended to follow a normal curve. Sumner (1969) has described this grading system.

CHG reflects clarity and evenness of staple crimp, absence of tapering tip and medullation. Where crimps were well defined throughout the staple a high score was given. Lower grades reflected poorly defined crimping.

TG ranged from absolutely flat and blocky (9) to extremely tapering tip (1).

HG was assessed without regard to QN with the sample screened from the view of the assessor. Soft wool was given high grades.

LG was graded without reference to fineness. High grades were like Lincoln wool.

The lowest GCG were given to samples which were most discoloured.

CG reflected the degree of fibre entanglement on the mid-side position with high grades being free of entanglement.

SG was based on freedom of wool from tenderness or break. Samples were evaluated by placing 'standard sized' staples under hand tension with sound staples being given high grades. The data for SG in the Sire group 1 period were not analysed as it was incomplete.

Following scouring all samples were assessed for the SCG using the same standards as for GCG of wool.

CAG and DAG of the fleece were assessed on the whole fleece at the time of shearing. These whole-fleece characteristics were also subjectively graded on a scale of 1 (inferior) to 9 (superior). CAG of the whole fleece was dependent on the degree and extent of entanglement over the whole fleece while DAG was estimated mainly on the basis of how far the discolouration extends over the fleece with the account taken of severity of discolouration. The data for DAG in the Sire group 1 and Sire group 2 periods were not analysed as they were incomplete.

Inaccuracies of grading in all the above subjectively graded traits could result from observer variation, as well as other uncontrolled environmental factors.

CHAPTER FOUR

STATISTICAL METHODS

PRESENCE OF INTERACTION

The detection and evaluation of GEI by different techniques: ranking of genotypes in each environment (Haldane, 1946); differences in response of each of the genotypes in two environments (Osborne, 1951); regression of measurements of a trait on environmental levels for each genotype (Yates and Cochran, 1938); orthogonal comparison of subclasses (Mather and Jones, 1958); factorial analysis of variance (Sprague and Federer, 1951); genetic correlation of the same trait in two environments estimated from variance and covariance analysis (Falconer, 1952); selection in two environments (Falconer, 1952); differences in the magnitudes of heritability and experiments with identical twins, have been reported by various workers. Statistical methods available for analysis of interactions in general and GEI in particular were reviewed by Freeman (1973).

If the GEI is significant, the next step is frequently to try to describe this interaction in terms of biologically meaningful parameters. To find whether interactions are present and then to consider their importance, it is sometimes not enough to estimate the components of variation attributable to the main effects and to look for the structure underlying the observed non-additivity. Following Falconer's (1952) extension of the concept of genetic correlation to the study of GEI, the use of factorial analysis of variance techniques in estimating the importance and testing for significance of GEI has received much attention in animal breeding. On the basis of Falconer's (1952) concept, Robertson (1959) presented formulae in terms of mean squares with their

appropriate variances for estimating the genetic correlation of the performance in two or more environments. He showed the composition of the component of variance for GEI to be:

$$\sigma_{\text{GEI}}^2 = \frac{1}{2} (\sigma_{G1} - \sigma_{G2})^2 + \sigma_{G1}\sigma_{G2} (1 - r_g)$$

where σ_{G1} and σ_{G2} refer to the genetic standard deviations in environment 1 and 2 respectively and r_g is the genetic correlation between the performance in the two environments.

Dickerson (1962) discussed the subject of quantitative estimation of GEI in terms of variance components and suggested that, in general, the standard analysis of variance is a satisfactory method of estimating GEI and intra-class genetic correlation provided

- (1) adjustment is made for any important variation between environments in the scale of genetic effects (i.e., for inter-environmental variance in the intra-environmental σ_{Gi}) and
- (2) the variance component for average genetic ranking across all environments is interpreted as the average covariance for the same genotype in different environments (i.e., $\sigma_G^2 = \bar{\sigma}_{Gij}$), to include the real possibility of negative genetic correlation.

Yamada (1962) presented formulae for both random and mixed models to estimate genetic correlations between performance in two or more environments after adjusting the interaction component of variance so that the use of the adjusted value in the intra-class correlation makes this correlation identical with the average product-moment coefficient between the same genotype in each of the macroenvironments.

In the framework of this experiment concerned with comparison of paternal half-sib groups, the analysis of variance technique is employed in detecting and evaluating GEI and the role played by GEI with regard to the structure of heritability estimates.

ANALYSIS OF VARIANCE

Least squares and computing methods

The estimates of genetic parameters are made more accurate if the identifiable environmental sources of variation (and interactions) in the data are adequately removed. Since the inclusion of the factors in the model used for studying genetic variation and covariation depend upon whether or not the terms included in the model are statistically significant, preliminary analyses of variance were carried out. The preliminary analyses formed the basis of the decision for the appropriate models to be fitted in the subsequent analyses to calculate proportion of the observed variance controlled by the various factors (and interactions) in the model.

For the preliminary analysis of variance, a subset of the data in which each record had observations on all measured and subjectively assessed traits included in the study was selected and analysed. The distribution of numbers of observations in the subclasses was non-orthogonal. Hence the method of least squares procedures was used. The principles of least squares analyses and the detailed steps used in the estimation process have been discussed by Kempthorne (1952) and Harvey (1960).

Solutions to the least squares equations

A general mathematical model can be written in the matrix notation as:

$$Y = Xb + e$$

where

Y is a known Nx1 vector of observations

(N is the total number of observations)

X is an Nxp incidence matrix of known values

(p is the number of factors in the model)

b is a px1 vector of unknown parameter values to be estimated

e is an Nx1 vector of random error effects $E(e) = 0$

$$E(ee') = \sigma^2 I_N$$

where I is NxN identity matrix

Derivation of least squares estimator of b follows minimization of the sum of squares of the observations from their expected values.

Since $E(e) = 0$ and hence $E(y) = Xb$

then

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

Choosing as the estimator \hat{b}^* that value of b which minimizes $e'e$ involves differentiating $e'e$ with respect to elements of b and equating partial derivatives to zero. The resulting normal equations are

$$X'X \hat{b} = X'y$$

Provided $(X'X)^{-1}$ exists, the normal equations have the unique solution

for \hat{b}

$$\hat{b} = (X'X)^{-1} X'y$$

* $\hat{}$ is used to indicate an estimate

The solution of normal equations requires that the matrix $X'X$ is of full rank. If $X'X$ is not of full rank, it has no inverse and no unique solution. If $(X'X)^{-1}$ does not exist, a solution can be obtained by using a generalised inverse of $X'X$ (Searle, 1971).

Alternatively, Harvey (1960) discussed the types of restrictions which may be imposed on the estimates of parameters to obtain a solution. The two types of restrictions used for reducing normal equations to full rank in the preliminary analysis and the analyses for estimating the genetic parameters in this work respectively are:

(1) That for each factor in a model, one of the effects equals zero.

and (2) That for each factor in a model, the sum of the constant estimates equals zero.

Corresponding to the above restrictions applied in the analyses, the ordinary least squares and the use of generalised inverse methods give identical solutions for the estimable functions of the unknown parameters.

A computer subroutine was available for inverting square matrices of order less than 35×35 . Larger inverse matrices were obtained through the use of matrix partitioning procedures as described by Searle (1966).

Fitting models to the data

A general model fitted in testing for the significance of the main effects and interactions for HLW and wool traits in the Sire group 2 and Sire group 3 periods was:

$$Y_{ijklmn} = \mu + s_i + r_j + t_k + b_l + a_m + (sr)_{ij} + (st)_{ik} + (rt)_{jk} + (rb)_{jl} + (srt)_{ijk} + e_{ijklmn}$$

where

μ = mean of all records of a character when equal frequencies exist in each subclass.

s_i = the effect of the i th sire.

$i = 1$ to 10 (Sire group 2 records)

$i = 1$ to 7 (Sire group 3 records)

r_j = the effect of the j th stocking rate.

$j = 1, 2$ ($j = 1$ implies HSR, $j = 2$ implies CSR)

t_k = the effect of the k th year.

$k = 1, 2$

The 'year' effect is a measure of the variation in the data caused by environmental conditions peculiar to each year such as differences in the amount and distribution of the rainfall, mean monthly temperature, feed supply, and other less tangible factors which make up the yearly environment. The year effects will also be partly due to year to year inconsistency of grading of subjective traits. Different graders were assessing the traits in different years.

b_l = the effect of the l th birth rank.

$l = 1$ or 2, specifying ewe hoggets born as a single or ewe hoggets born as a twin respectively. The very few born as triplets were included with the twins.

a_m = the effect of the m th age of dam.

$m = 1$ or 2, specifying age of dam as 2 year old or older respectively.

$(sr)_{ij}$ = the effects of interaction between sire and stocking rate.

$(st)_{ik}$ = the effects of interaction between sire and year.

$(rt)_{jk}$ = the effects of interaction between stocking rate and year.

$(rb)_{j1}$ = the effects of interaction between stocking rate and birth rank.

$(srt)_{ijk}$ = the effects of interaction between sire, stocking rate and year.

Y_{ijklmn} = the observation on the n th individual born in the l th birth rank, maintained on j th stocking rate in the k th year, daughter of a ewe in the m th age group and the i th sire.

e_{ijklmn} = is the random error peculiar to the $ijklmn$ th observation and follows NID $(0; \sigma^2)$.

All effects in the model were regarded as fixed except s_i , $(sr)_{ij}$, $(st)_{ik}$ and $(srt)_{ijk}$ which are random sets of effects (other than e_{ijklmn}). Other interactions not included in the model were not considered important. Sire group 2 and 3 periods data were analysed separately. Formal F-tests of significance were carried out on the factors included in the model. The term used as denominator was the error except where two- or three-term interactions were significant. Where a three-term interaction was significant, the relevant two-term interactions were tested against it. The main effects were tested against relevant two-term interactions in case of random interactions being significant.

Following the exclusion of effects of age of dam, interaction between stocking rate and birth rank, interaction between sire, stocking rate and year which were found to have no significant effect ($P < 0.05$) on the trait concerned, procedures were applied to derive suitable models for estimating population parameters and evaluation of GEI.

A general model describing a datum for which every significant effect was fitted in the combined stocking rate analysis is:

$$Y_{ijklm} = \mu + s_i + r_j + t_k + b_l + (sr)_{ij} + (st)_{ik} + (rt)_{jk} + e_{ijklm}$$

where the terms are as described previously except the following

s_i = the effect of the i th sire.

$i = 1$ to 7 (Sire group 1 records)

$i = 1$ to 10 (Sire group 2 records)

$i = 1$ to 10 (Sire group 3 records)

$i = 1$ to 7 (Sire group 4 records)

Y_{ijklm} = the observation on the m th individual born under l th birth rank, maintained on j th stocking rate in the k th year, daughter of the i th sire.

e_{ijklm} = is the random error peculiar to the $ijklm$ th observation and follows NID $(0; \sigma^2)$.

All effects in the model were regarded as fixed except s_i , $(sr)_{ij}$, $(st)_{ik}$ which are random sets of effects. If the genotypes are regarded as random and environments as fixed, the interactions effects are also random (Harvey, 1960). The data in all the four Sire group periods were analysed separately. Formal F-tests were carried out in accordance with the procedure explained earlier. The expectations of mean squares for the above model are shown in Table 3.

The model used to represent a datum for within stocking rate (HSR and CSR) analyses can be written as:

$$Y_{iklm} = \mu + s_i + t_k + b_l + (st)_{ik} + e_{iklm}$$

TABLE 3: Combined Stocking Rate Analysis
Calculation of Reductions* in Sums of Squares (S.Sqs)
and Expectations of Mean Squares (EMS)

Source	Reduction	EMS
Sire	$R (s u, r, t, b, sr, st, rt)$	$\sigma_e^2 + k_9 \sigma_s^2$
Stocking rate	$R (r u, s, t, b, st, rt)$	$\sigma_e^2 + k_7 \sigma_{sr}^2 + k_8 q_r^2$
Year	$R (t u, s, r, b, sr, rt)$	$\sigma_e^2 + k_5 \sigma_{st}^2 + k_6 q_t^2$
Birth-rank	$R (b u, s, r, t, sr, st, rt)$	$\sigma_e^2 + k_4 q_b^2$
Sire x stocking rate	$R (sr u, s, r, t, b, st, rt)$	$\sigma_e^2 + k_3 \sigma_{sr}^2$
Sire x year	$R (st u, s, r, t, b, sr, rt)$	$\sigma_e^2 + k_2 \sigma_{st}^2$
Stocking rate x year	$R (rt u, s, r, t, b, sr, st)$	$\sigma_e^2 + k_1 q_{rt}^2$
Error	$y'y - R (u, s, r, t, b, sr, st, rt)$	σ_e^2

q^2 = quadratic term (fixed effect)

* The terminology for reductions in sums of squares given by Searle (1971) will be used throughout the text in this work.

$R (.)$ 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.

TABLE 4: Within Stocking Rate Analysis
Calculation of Reductions in Sums of Squares (S.Sqs)
and Expectations of Mean Squares (EMS)

Source	Reduction	EMS
Sire	$R (s u, t, b, st)$	$\sigma_e^2 + k_5\sigma_s^2$
Year	$R (t u, s, b)$	$\sigma_e^2 + k_3\sigma_{st}^2 + k_4q_t^2$
Birth-rank	$R (b u, s, t, st)$	$\sigma_e^2 + k_2q_b^2$
Sire x year	$R (st u, s, t, b)$	$\sigma_e^2 + k_1\sigma_{st}^2$
Error	$y'y - R (y, s, t, b, st)$	σ_e^2

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

where the terms are as described previously except the following:

Y_{iklm} = the observation on mth individual in the kth year,
daughter of ith sire and born under lth birth rank.

e_{iklm} = is the random error peculiar to the iklm th observation
and follows NID $(0; \sigma^2)$.

All effects in the model were regarded as fixed except s_i and $(st)_{ik}$ which are random sets of effects. The data in all the four Sire group periods were analysed separately. Formal F-tests were carried out in accordance with the procedure explained earlier. The expectations of mean squares for above model are shown in Table 4.

Estimation of mean squares, variance
and covariance components

The direct method of Harvey (1960) was used in computing sums of squares from which mean squares were calculated. An abbreviated form of the direct method of computing sums of squares is:

$$\hat{\beta}' Z^{-1} \hat{\beta}$$

where

$\hat{\beta}'$ = a row vector of least squares estimates for a given
set of equations.

Z^{-1} = the inverse of square segment of the inverse of the
variance covariance matrix corresponding, by row and
column to this set of estimates.

and $\hat{\beta}$ = a column vector of the least squares estimates for the
given set of equations.

The above simplified procedure of calculating sums of squares of the various effects in the respective models used is equivalent to fitting submodels (Harvey, 1960; Searle, 1966; Cunningham, 1970). The expectations of mean squares for both the models used in the investigation were obtained under assumptions of mixed models in accordance with the procedures described by Henderson (1954) and Harvey (1960).

The general theory involved in the use of least squares procedures with unequal subclass frequencies for the estimation of variance and covariance components with the mixed models has been discussed by Henderson (1953), Searle and Henderson (1961) and Searle (1968). Three methods of estimating variance components are described in Henderson (1953). Since Method 1 is appropriate for random models only, it was not used in this study. Method 2 was also found inappropriate in this study because of the necessity to analyse interactions between random and fixed effects. Method 3 was applied for this investigation as it was not subject to any of the limitations of the other two methods. Variance components were required from mixed models and random interactions of sire x stocking rate and sire x year were also included in the models. Method 3 is based on the method of fitting constants. It uses reductions in sums of squares due to fitting different subgroups of factors in the model. The estimation of variance components is done by equating each computed reduction to its expected value. Compared to Method 1 and Method 2, this method is far more appropriate for the mixed model, since it yields variance component estimators that are relatively unaffected and uncomplicated by the fixed effects. Its 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 full matrix less the effect of interest is required.

Computer programmes were written following Harvey (1960, 1970) to compute the variance and covariance components by Method 3. The k coefficients in Tables 3 and 4 were computed by the direct and indirect procedures described by Harvey (1960).

LEAST SQUARES ESTIMATES

The least squares estimates of the main effects regarded as fixed and various interactions included in the model for the combined stocking rate analysis were computed for all the Sire group periods separately by solving the least squares equations (Harvey, 1960). The standard errors of the least squares estimates were calculated for all the four Sire group periods separately according to the following formula as suggested by Harvey (1960).

$$s_{\hat{c}_i} = \sqrt{C^{ii} \hat{\sigma}_e^2}$$

where C^{ii} is the corresponding diagonal inverse element for that constant and $\hat{\sigma}_e^2$ is the error mean square.

POOLING OF THE SIRE GROUP PERIODS ANALYSES

In order to pool the results of the analyses over all the Sire group periods, the method suggested by Cunningham (1970) was used. In this method, the sums of squares and degrees of freedom are added for all the sources of variation. The variance components coefficients are obtained by averaging, weighting each by its corresponding number of degrees of freedom.

PARTITIONING THE VARIATION

The proportion of variance accounted for each factor in the pooled analyses for the combined data was calculated from the positive variance components (including fixed effect quadratic components) and then converted to a percentage. For example, variance due to stocking rate ($\% V_r$) for a trait might be

$$\% V_r = \frac{q_r^2}{\sigma_s^2 + q_r^2 + q_t^2 + q_b^2 + \sigma_{sr}^2 + \sigma_{st}^2 + q_{rt}^2 + \sigma_e^2} \times 100$$

VARIANCE COMPONENT ESTIMATES

The variance components estimates of sire, sire x stocking rate and sire x year interactions derived from the least squares analysis of data in the combined stocking rate and within stocking rate analyses for all the four Sire group periods individually and the pooled analyses were used in determining the importance of GEI for the traits under investigation.

Using the notation specified earlier for the effects in the model, the following intra-class relationships were obtained:

1. The relative magnitudes of the interaction variance components (individually or combined) to the total variance were calculated as follows:

(a) combined stocking rate analysis

$$(i) \frac{\sigma_{sr}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2}$$

$$(ii) \frac{\sigma_{st}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2}$$

$$(iii) \frac{\sigma_{sr}^2 + \sigma_{st}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2}$$

(b) Within stocking rate analysis

$$\frac{\sigma_{st}^2}{\sigma_s^2 + \sigma_{st}^2 + \sigma_e^2}$$

2. The proportions which the sire x stocking rate interaction and sire x year interaction variance components (individually or combined) contribute to the total genetic variances were calculated as follows:

(a) Combined stocking rate analysis

$$(i) \frac{\sigma_{sr}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2}$$

$$(ii) \frac{\sigma_{st}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2}$$

$$(iii) \frac{\sigma_{sr}^2 + \sigma_{st}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2}$$

(b) Within stocking rate analysis

$$(i) \frac{\sigma_{st}^2}{\sigma_s^2 + \sigma_{st}^2}$$

3. A comparison of the relative magnitude of the two parts of the genetic variance (i.e., the interaction and the between-sire components) was made as follows:

(a) Combined stocking rate analysis

$$\frac{\sigma_{sr}^2 + \sigma_{st}^2}{\sigma_s^2}$$

(b) Within stocking rate analysis

$$\frac{\sigma_{st}^2}{\sigma_s^2}$$

If the ratio is large, the performance of a genotype would be less repeatable over all environments and *vice versa*.

GENETIC PARAMETERS

Heritability

Estimates of heritability were obtained from paternal half-sib correlations. The estimates of heritability derived from paternal half-sib correlations using the sire component does not contain variance due to dominance, to epistasis involving dominance deviation or to maternal effects (Turner and Young, 1969). Since the between-sire component is the variance between the means of half-sib families, it estimates the phenotypic covariance of half-sibs, $Cov(HS)$, which is $\frac{1}{4} V_A$ (Falconer, 1960a) where V_A is an abbreviation for additive genetic variance. Thus in a population mating at random $4 \sigma_S^2$ estimates the genetic variance of the population. But in this study as the random interactions (i.e., sire x stocking rate and sire x year) were found to be significant, the size of the variance for random interactions were estimated to make allowance for its presence.

In the present study, heritability estimates were pooled over all the Sire group periods analysed both in the combined stocking rate and within stocking rate analyses by the method suggested by Cunningham (1970), i.e., by adding the sums of squares and degrees of freedom for between and within sires. Gregory *et al.* (1978) showed that the use of this procedure was more accurate than combining half-sib estimates by weighting each estimate by the reciprocal of its variance, a method which may bias the pooled estimate downwards towards zero.

With the notation used earlier in the analyses of variance, the heritability for each trait was estimated as follows:

(a) Combined stocking rate analysis

$$h^2 = \frac{4 \sigma_s^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2}$$

(b) Within stocking rate analysis

$$h^2 = \frac{4 \sigma_s^2}{\sigma_s^2 + \sigma_{st}^2 + \sigma_e^2}$$

Most of the published estimates obtained by the paternal half-sib method are based on analyses of the sire effects nested within years and hence would include sire x year interactions as part of the sire effect. Also most estimates are for sheep at the same stocking rate. To study the effects of these facets of the normal methods of obtaining genetic parameters, the heritability estimates were also obtained by the following formulae:

(c) Combined stocking rate analysis

$$h^2 = \frac{4 (\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2)}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2}$$

(d) Within stocking rate analysis

$$h^2 = \frac{4 (\sigma_s^2 + \sigma_{st}^2)}{\sigma_s^2 + \sigma_{st}^2 + \sigma_e^2}$$

Precision of Heritability

A large sample variance of heritability using mean squares rather than variance components as described by Kempthorne (1957) was adapted in this study to calculate the approximate standard errors of the estimated heritabilities.

Using large sample theory for a balanced situation, if

$$\hat{\theta} = \frac{u_1A + u_2B + u_3C + \dots}{v_1A + v_2B + v_3C + \dots} = \frac{X}{Y}$$

where u_i and v_i are constants and A, B, C etc. are mean squares, then large sample variance of $\hat{\theta}$ is:

$$V(\hat{\theta}) = \frac{V(X)}{Y^2} - \frac{2 X \text{Cov}(XY)}{Y^3} + \frac{X^2}{Y^4} V(Y)$$

where $V(X) = u_1^2V(A) + u_2^2V(B) + u_3^2V(C) + \dots$

$V(Y) = v_1^2V(A) + v_2^2V(B) + v_3^2V(C) + \dots$

$\text{Cov}(XY) = u_1v_1V(A) + u_2v_2V(B) + u_3v_3V(C) + \dots$

Since the denominators of the heritability estimates in this study contain the interaction variance components, the large-sample variance of heritability derived by Swiger *et al.* (1964) was found inappropriate.

Genetic correlations

Inter-trait genetic correlations

Harvey (1970) showed that variance and covariance components can be estimated simultaneously. Coefficients for covariance components in the expectation of mean products are the same as for corresponding variance components when all dependent variables are available for all observations. Variance and covariance components were estimated by Henderson's Method 3 for all the traits under investigation in the pooled analysis for the combined stocking rate analysis. In a population mating at random, the covariance components between sires equals one fourth of the covariance between the additive deviations caused by genes in the two characters.

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

$$r_{g_{xy}} = \frac{\text{Cov } a_x a_y}{[\sigma_{a_x}^2 \times \sigma_{a_y}^2]^{1/2}} = \frac{4 \text{ Cov } s_x s_y}{[4 \sigma_{s_x}^2 \times 4 \sigma_{s_y}^2]^{1/2}}$$

where

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

The formula of Tallis (1959) was adapted to estimate approximate sampling errors of the genetic correlations. This formula is a modification of that given by Robertson (1959) which is applicable only to the cases where the heritabilities for the two traits are the same.

Intra-trait genetic correlations

Formula presented by Yamada (1962) for mixed models and two environments was adapted for estimating the genetic correlations between performance in two stocking rates as a quantitative expression of sire-stocking rate interaction.

$$r_g = \frac{\sigma^2_s - \frac{1}{2}\sigma^2_{sr}}{\sigma^2_s + \frac{1}{2}\sigma^2_{sr} - \frac{1}{2}(\sigma_{s_1} - \sigma_{s_2})^2}$$

where s refers to the sire component and σ_{s_1} and σ_{s_2} refer to genetic standard deviations in stocking rate HSR and CSR respectively. The above formula of r_g is not subject to any of the limitations suffered by Dickerson's (1962) formula which was derived under the assumption of the same genetic variance in each of the environments. The approximate standard errors of the intra-trait genetic correlation coefficients were estimated by Robertson's (1959) formula.

CHAPTER FIVE

RESULTS AND DISCUSSION

ESTIMATES OF NON-GENETIC FACTORS, INTERACTIONS AND VARIANCE COMPONENTS

The records of the various productive traits such as live-weight and the wool traits of hoggets are affected by a variety of environmental factors such as age of dam, type of birth, sex, nutrition and year of record. Some of these factors are easily identifiable and recorded. Their effects can be removed statistically from the performance records so that the accuracy of selection is improved.

In the present study, as indicated in Chapter 4, the known environmental factors considered likely to be of importance in the data and included in the statistical model were: stocking rate (CSR or HSR), age of dam (2 year old or older), type of birth (single or twin), effect of the year in which the record was made and the relevant interactions between the main effects. The preliminary analyses of variance of the effects of age of dam, stocking rate x birth rank and sire x stocking rate x year interactions indicated that in all instances, these three effects were statistically non-significant ($P < 0.05$).

Analyses of variance for other main effects and interactions were completed in each Sire group period separately and pooled according to the procedure explained in the earlier chapter. The statistical models to describe the computation procedures involved in these analyses have been described previously. The proportion of the total variation attributable to each factor for each variable in the combined stocking rate analysis pooled from the different Sire group periods is shown in Table 5 together with the statistical significance of each factor.

TABLE 5: Percentage of total variance attributable to each factor for each variable from the combined stocking rate analysis pooled from the different Sire group periods

Factor	HLW	GFW	WA	Y	SL
Sire	1.9**	3.3**	7.5**	4.5**	10.9**
Stocking rate	63.8**	37.3**	10.3**	2.6**	18.2**
Year	6.9**	24.9**	9.0**	14.4**	3.7**
Birth-rank	0.8**	-	0.3	-	0.2
Sire x Stocking rate	1.3**	0.4	-	1.6	-
Sire x year	1.2**	1.3**	2.2	0.5	1.0
Stocking rate x Year	1.5**	4.5**	4.1**	19.6**	2.1*
Error	22.6	28.3	66.6	56.8	63.9

Statistical significance of mean squares

* P<0.05

** P<0.01

TABLE 5: (continued)

Factor	MFD \checkmark	SFD	QN	CPC	TCN
Sire	10.2**	6.1**	10.2**	8.3**	10.9**
Stocking rate	2.4	1.7	3.4**	3.6**	-
Year	1.6**	11.6**	12.0**	44.2**	38.2**
Birth-rank	-	1.4**	0.5	0.5	-
Sire x Stocking rate	2.7*	3.9**	0.6	0.2	1.8*
Sire x Year	0.7	1.5	-	-	0.2
Stocking rate x Year	13.2**	15.4**	6.7**	0.3	-
Error	69.2	58.4	66.6	42.9	48.9

TABLE 5: (continued)

Factor	CHG	TG	HG	LG	GCG
Sire	4.7**	5.4**	4.5**	5.8**	3.3**
Stocking rate	3.7**	1.4*	0.1	0.8*	12.4**
Year	28.9**	4.0**	19.1**	21.3**	28.2**
Birth-rank	1.3**	-	2.1**	1.0	-
Sire x Stocking rate	0.2	-	0.6	1.4	1.4*
Sire x Year	0.3	-	2.9*	-	1.3
Stocking rate x Year	1.3	-	1.2	3.2**	1.1
Error	59.6	89.2	69.5	66.5	52.3

TABLE 5: (continued)

Factor	SCG	DAG	CG	CAG	SG
Sire	2.0	2.1	5.0**	3.4**	1.8**
Stocking rate	5.6**	5.6**	3.7**	4.9**	25.4**
Year	8.1**	0.5	8.0**	39.0**	12.8**
Birth-rank	-	-	0.5	-	-
Sire x Stocking rate	1.3	-	-	0.7	-
Sire x Year	2.7*	-	-	-	-
Stocking rate x Year	6.1**	7.4**	2.5**	0.7	17.5**
Error	74.2	84.4	80.3	51.3	42.5

The estimates of the main environmental effects in the different Sire group periods analysed, expressed as deviations from the overall mean, together with their standard deviations derived from the error mean square are presented in Tables 6-15.

The analytical results for each trait studied are presented as follows:

Hogget live-weight

HLW in this study represents the post-shearing live-weight at 14-15 months of age.

The overall averages of HLW for each Sire group period and the least squares effects for different subclasses obtained by the method of fitting constants are listed in Table 6.

In all the four Sire group periods, the least squares effects show that there was a pronounced stocking level effect on HLW at shearing with the HLW being depressed in the HSR group. The above results are in close agreement with Sumner (1969). The nutrition of the HSR animals was severely restricted in the early part of the spring as a result of confining the animals to a limited area. This practice, though enabling the lambing ewes to have an access to more pasture, retarded the body growth of the hoggets.

Live-weight gain is proportional to intake in excess of the maintenance requirements. When stocking rates are increased, intake per sheep falls but intake in excess of maintenance shows a greater proportionate change. As a result live-weight gain per hectare is more sensitive to increasing the stocking rate than is wool production

TABLE 6: Least squares estimates and standard errors of environmental effects for HLW and GFW

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
HLW (kg)	Stocking rate				
	CSR	5.11 ± 0.23	5.34 ± 0.24	3.12 ± 0.26	3.51 ± 0.30
	HSR	-5.11 ± 0.23	-5.34 ± 0.24	-3.12 ± 0.26	-3.51 ± 0.30
	Year				
	1	2.12 ± 0.23	1.73 ± 0.23	-0.38 ± 0.24	0.76 ± 0.28
	2	-2.12 ± 0.23	-1.73 ± 0.23	0.38 ± 0.24	-0.76 ± 0.28
	Birth-rank				
	Single	0.38 ± 0.22	0.69 ± 0.26	0.77 ± 0.33	0.55 ± 0.41
	Twin	-0.38 ± 0.22	-0.69 ± 0.26	-0.77 ± 0.33	-0.55 ± 0.41
	General mean	32.93 ± 0.23	35.12 ± 0.24	30.14 ± 0.29	34.18 ± 0.39
	Standard deviation	3.94	4.03	3.67	3.64
GFW (kg)	Stocking rate				
	CSR	0.32 ± 0.03	0.60 ± 0.04	0.17 ± 0.03	0.38 ± 0.04
	HSR	-0.32 ± 0.03	-0.60 ± 0.04	-0.17 ± 0.03	-0.38 ± 0.04
	Year				
	1	0.55 ± 0.03	0.25 ± 0.03	0.07 ± 0.03	0.13 ± 0.04
	2	-0.55 ± 0.03	-0.25 ± 0.03	-0.07 ± 0.03	-0.13 ± 0.04
	Birth-rank				
	Single	0.03 ± 0.03	0.03 ± 0.04	0.06 ± 0.04	-0.01 ± 0.06
	Twin	-0.03 ± 0.03	-0.03 ± 0.04	-0.06 ± 0.04	0.01 ± 0.06
	General mean	3.56 ± 0.03	3.28 ± 0.03	3.00 ± 0.03	3.17 ± 0.05
	Standard deviation	0.48	0.59	0.43	0.49

(Langlands and Bennett, 1973). Differences in the plane of nutrition due to stocking level may have variable interactions with the incidence or severity of the disease. While increasing the stocking rate may increase the incidence of disease associated with increasing physical contact between animals (Spedding, 1965), there is only limited information on the effect of stocking rate on nematode infection. Under Australian conditions it appears there is little effect with the mature sheep (McManus and Arnold, 1965; Southcott *et al.*, 1967) although substantial worm burdens may build up in young sheep at higher levels of stocking possibly due to their poor immunity status or nutrition (McManus and Arnold, 1965).

The animals born as singles are superior in their growth rate to animals born as twins, attaining a heavier body weight at hogget stage in this study. Similar observations were made by Rae (1950), Ch'ang (1967), Tripathy (1966) and Baker *et al.* (1974) in New Zealand Romneys. Rae (1950) observed that the single born New Zealand Romney hoggets were 3.02 kg heavier than twins. The magnitude of birth rank effect was however, lower in this study on HLW than reported by these workers. Terrill *et al.* (1947) noted that the type of birth had an important effect on body weight accounting for 7 and 13% of the total variation in Columbia and Targhee ewes respectively.

Between-year effects are caused by factors such as nutrition, climate and management peculiar to each year. The trend in this study suggests that the HLW is easily affected by environmental conditions peculiar to each year such as differences in the amount and distribution of the rainfall.

The main source of environmental variation in HLW, as identified by the analysis of variance and quantified by proportioning the variance, was stocking rate. Table 5 shows that this accounts for 63.8% in the pooled variance analysis and it ranges from 51.1% to 66.8% in the individual Sire group periods. The 'year' effect contributed 6.9% ($P < 0.01$) to the total observed variance. Birth-rank though significant ($P < 0.01$) accounted for only 0.8% of the variance in the pooled analysis while it contributed 2.6% in the Sire group 3 period.

The importance of the significant interactions was evaluated by variance components analysis from the pooled analysis of variance and the individual Sire group analyses of variance. Sire x stocking rate, sire x year and stocking rate x year interactions were significant ($P < 0.01$) in the pooled analysis of variance for HLW. HLW is important from a selection standpoint, and the presence of random interactions would hamper the genetic progress unless properly accounted for.

Interactions of sire x stocking rate are of prime interest in this investigation. Sire x stocking rate interaction contributed 1.3% of the total observed variance in the pooled variance analysis while it contributed 2.3% of the total variability in Sire group 3 period. Morley (1956) reported highly significant sire x nutrition interactions at 12 and 17 months body weight. In these, the interaction components were large and highly significant. The difference between the planes of nutrition in his experiment was more extreme than commonly encountered in practice. Osman and Bradford (1965) also found highly significant sire x nutrition interactions (from pooled mean squares) for 450 day weight in sheep. Carter *et al.* (1971b) observed significant interactions for 120 day body weight. Significant genotype x nutrition interactions

were reported for growth and slaughter weight by Budanstev (1973). However, in Dunlop's (1963) study strain x location interactions for adult weights in sheep were non-significant.

Sire x year interactions contributed 1.2% to the total variability for HLW in the pooled variance analysis. Although the size of interactions variance component was about 2% in the Sire group 2 period, no sire x year interactions were observed in Sire group 4 period. Possible causes of sire x year interactions have been discussed by Rae (1958). The fact that the sire x year interactions are significant though small in the pooled analysis has considerable selection implications.

Ch'ang (1967) studied the sire x year interaction in HLW and found it to be a negligible source of variation. Dunlop (1963) observed non-significant strain x year interactions for adult weight. King and Young (1955) reported non-significant breed x environment interactions in yearling weight. Rae (1958) found the sire x year interactions for body type to be not significant.

A further step taken to assess the practical implications of the observed significant random interactions and the role played by these interactions with regard to the structure of heritability estimates shall be discussed in the next section.

Stocking rate x year interactions were significant ($P < 0.01$) and contributed 1.5% of the total observed variance in HLW from the pooled analysis while in Sire group 3 period it contributed about 8% of the total variation. Such interactions were also reported as significant by Dunlop (1963) for adult weights.

Greasy fleece weight

The overall averages and least squares constants for GFW for 9-10 months wool growth between lamb and hogget shearing for each of the Sire group periods analysed are presented in Table 6.

In all the four Sire group periods, CSR animals had higher GFW than the HSR animals. The magnitude of stocking rate effects in Sire group 2 period was more pronounced than in the other Sire group periods probably because of summer drought conditions prevailing during those two years. HLW showed similar trends during this period. There is considerable evidence that the fleece weight is inversely related to the stocking rate and is approximately proportional to herbage intake.

Bublath (1969) reported that the Romney wethers at low stocking rates grew significantly ($P < 0.01$) more wool as compared with those grazing at high stocking rates. Joyce *et al.* (1976) observed that the sheep stocked at highest rates produced 11% less wool than those at the lowest rates. McManus (1961) referred to some work carried out in Victoria, Australia with stocking rates of two, four and six sheep per acre. The average fleece weights per sheep decreased successively as follows: 13.8, 12.3 and 11.3 lb. Results similar to those reported in the present study were obtained by Sumner (1969) in the same flock used in this study.

The response to nutritional level is also reflected by changes in both the diameter of fibres and their length growth rate. A reduction in the feeding level will reduce the fibre length growth effectively and will also reduce the diameter of fibres. As a prolonged period of severe under-nutrition is required to reduce the total fibre population

(Allden, 1968), the response in fleece weight to a change in stocking rate will almost always be due to a change in fibre-volume. Kelly (1949) in an experiment in which strong wool and fine wool Merino gave respectively 8.0 and 7.3 lb on a 'Low Plane' of nutrition and 18.4 and 13.3 lb on a 'High Plane' of nutrition, attributed the increased difference of GFW between the strains mainly to the changes in the cross-sectional area of the fibres, since the difference in mean diameter increased from 3.6 μ on the 'Low Plane' to 8 μ on the 'High Plane'.

The signs of the birth rank effects on GFW in this study are consistent with those for Romney data reported by Tripathy (1966) and Baker *et al.* (1974) but the magnitude was lower than reported by these workers.

Between 'year' effects could take into account a wide array of combinations of at least temperatures, rainfall, photoperiods and system of management. Adverse environmental conditions during the year could depress the GFW indirectly through the rate of growth in HLW and the development of secondary follicles.

The results of the pooled analysis of variance for GFW are presented in Table 5. Stocking rate and year effects were significant ($P < 0.01$) and account for 37.3% and 24.9% of the total variance.

Sire x stocking rate interactions contributed only 0.4% (NS) to the total observed variance in the pooled analysis of variance. It contributed 1.1% ($P < 0.05$) only to the total observed variation in the Sire group 1 period while in other Sire group periods it was non-significant. The practical importance of its being significant in Sire group 1 period would be negligible in view of the small number of

degrees of freedom available for the analysis. Similar results were obtained by Morley (1956) who reported non-significant genotype x nutrition interactions for GFW. Neither interactions of breed cross x plane of nutrition nor the twin pairs within a cross x plane of nutrition were significant for GFW in a study conducted by King *et al.* (1959). The effects of these interactions on GFW were also found non-significant by Osman and Bradford (1965). Strain x stations interactions for GFW, though significant, in a study by Dunlop (1962) were generally small and accounted for only a minor fraction of the variance.

Sire x year interactions were significant ($P < 0.01$) in this study and contributed 1.3% of the total variance in the pooled analysis of variance. No significant sire x year interactions for GFW were observed by Rae (1958). Dunlop (1962) also reported strain x year interactions for the trait were non-significant. The small size of variance component account by those interactions indicate that selection of rams in one year for use in another is unlikely to hinder genetic progress in GFW.

Stocking rate x year interactions were found significant ($P < 0.01$) and contributed 4.5% to the total variability in the pooled analysis of variance as against 21.6% in the Sire group 4 period in which it was observed as highly significant. Dunlop (1962) reported station x years interactions were highly significant ($P < 0.01$) for GFW. High significance of stocking rate x year in this study suggests that to some extent the lack of importance of sire x stocking rate interactions results from the year to year variability of climate and hence variation in quantity and quality of fodder available within individual stocking rates.

Clean wool weight per unit area

Rate of wool growth is measured as the weight of clean (dry) wool in grams per square centimeter of skin over a specified period of time. The overall averages of WA for three Sire group periods analysed are presented in Table 7 together with the least squares estimates of the main effects in the model.

Differences between stocking rate suggest that the WA is depressed in the HSR. The stocking rate effect contributed 10.3% to the total variability and was significant ($P < 0.01$) in the pooled analysis of variance. The stocking rate effect was more pronounced in the Sire group 2 period probably because of the summer drought conditions prevailing during those two years and reduced feed intake. The above results are in agreement with Bublath (1969). He reported that the New Zealand Romney sheep grew more wool per unit area at a low stocking rate as compared to the sheep in the high stocking rate.

Between-year effects were also highly significant and contributed 9% of variability in the pooled analysis of variance. Variation in wool production between years was probably associated with reduced pasture growth and hence feed intake.

Sire x stocking rate interactions were non-significant for this trait in the pooled analysis of variance and the individual Sire group periods. Thus the sires ranked consistently in the same order.

King and Young (1955) however, reported significant breed x plane of nutrition interactions for clean weight of wool fibres on a tattooed area and clean weight of all fibres on the tattooed area.

TABLE 7: Least squares estimates and standard errors of environmental effects for WA and Y

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
WA (gms/cm ²)	Stocking rate				
	CSR	-0.009 ± 0.003	0.022 ± 0.003	-	0.012 ± 0.006
	HSR	0.009 ± 0.003	-0.022 ± 0.003	-	-0.012 ± 0.006
	Year				
	1	-0.015 ± 0.003	0.017 ± 0.003	-	0.003 ± 0.005
	2	0.015 ± 0.003	-0.017 ± 0.003	-	-0.003 ± 0.005
	Birth-rank				
	Single	0.002 ± 0.003	-0.004 ± 0.003	-	-0.011 ± 0.008
	Twin	-0.002 ± 0.003	0.004 ± 0.003	-	0.011 ± 0.008
	General mean	0.366 ± 0.003	0.308 ± 0.003	-	0.365 ± 0.007
	Standard deviation	0.05	0.05	-	0.07
Y (percent)	Stocking rate				
	CSR	-0.24 ± 0.23	-0.91 ± 0.23	-0.07 ± 0.31	1.24 ± 0.38
	HSR	0.24 ± 0.23	0.91 ± 0.23	0.07 ± 0.31	-1.24 ± 0.38
	Year				
	1	0.40 ± 0.24	1.29 ± 0.22	-2.15 ± 0.30	2.02 ± 0.35
	2	-0.40 ± 0.24	-1.29 ± 0.22	2.15 ± 0.30	-2.02 ± 0.35
	Birth-rank				
	Single	0.21 ± 0.23	-0.23 ± 0.25	-0.45 ± 0.41	-0.13 ± 0.51
	Twin	-0.21 ± 0.23	0.23 ± 0.25	0.45 ± 0.41	0.13 ± 0.51
	General mean	77.14 ± 0.22	76.39 ± 0.22	78.37 ± 0.35	76.81 ± 0.48
	Standard deviation	4.07	3.83	4.49	4.53

Sire x year interactions though non-significant in the pooled analysis contributed slightly more than 2% of the variance. Variations in sampling may have contributed to the sire x year interactions in the Sire group 2 period where it ($P < 0.05$) accounted for 4.4% of the total variability.

Stocking rate x year interactions were significant in the pooled analysis of variance.

Clean scoured yield

The least squares effects for each of the four Sire group periods for yield are listed in Table 7. The stocking rate effects differ for the various Sire group periods. This could be attributed to the sampling variation. Sumner (1969) reported higher means for Y in the CSR animals group. Morley (1956) also observed higher Y in the 'High Plane' animals as compared to 'Low Plane' animals though the difference was not significant. Between stocking rate effects on Y in the pooled analysis of variance though significant, contributed only 2.6% to the total variability while the between years effect accounted for 14.4% and was highly significant. Between years effects could be due to the difference in rainfall and other climatic factors. Differing degrees of contamination with mud and dust could be important.

Sire x stocking rate interactions contributed less than 2% to the total observed variance and was non-significant in the pooled variance component analysis. It was significant ($P < 0.05$) and accounted for 4.5% to the total variability in the Sire group 3 period. The result obtained from the pooled analysis of variance agrees with Morley (1956) who reported that sire x nutrition interactions were non-significant.

Dunlop (1962) however, observed significant strain x station interactions though the size of the interactions term was not large.

In the pooled variance component analysis sire x year interactions were found non-significant and relatively of less importance. Significant interaction ($P < 0.05$) between sire and year was, however, observed in the Sire group 3 period and it contributed slightly over 4% to the total variation. Dunlop (1962) also observed significant strain x year interactions in the trait though it accounted for just over 1% of the total variability. Stocking rate x year interactions contributed major portion of variation due to interactions.

Staple length

Staple length in this study reduced with high stocking rate though the extent of response differed in different Sire group periods. Staple length has been observed by various workers to lower with increased stocking rate (Sharkey *et al.*, 1962; Sumner, 1969; Canon, 1972; Lipson and Bacon-Hall, 1974; White and McConchie, 1976). Between stocking rates SL differed more markedly during the Sire group 2 period as 1969 and 1970 had summer droughts which could depress wool growth through nutritional deprivation. In the pooled analysis of variance 18.2% of the variation was between stocking rates while this component increased to 34.8% in the Sire group 2 period.

In this study singles have slightly shorter SL than the twins in all the four Sire group periods. This is in agreement with Lax and Brown (1967) and Elliott (1975). Lowered total follicle number of twins could perhaps explain these results. Longer fibres may be produced by sheep with lower follicle population (Fraser, 1952; Schinckel and Short,

TABLE 8: Least squares estimates and standard errors of environmental effects for SL and MFD

Trait	Factor	Sire group 1 1967/68	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
SL (cm)	Stocking rate				
	CSR	0.27 ± 0.09	1.02 ± 0.09	0.36 ± 0.13	0.48 ± 0.12
	HSR	-0.27 ± 0.09	-1.02 ± 0.09	-0.36 ± 0.13	-0.48 ± 0.12
	Year				
	1	-0.12 ± 0.10	0.68 ± 0.09	-0.25 ± 0.12	0.59 ± 0.11
	2	0.12 ± 0.10	-0.68 ± 0.09	0.25 ± 0.12	-0.59 ± 0.11
	Birth-rank				
	Single	-0.13 ± 0.09	-0.13 ± 0.10	-0.02 ± 0.16	-0.26 ± 0.16
	Twin	0.13 ± 0.09	0.13 ± 0.10	0.02 ± 0.16	0.26 ± 0.16
	General mean	14.63 ± 0.10	13.90 ± 0.09	13.58 ± 0.14	13.25 ± 0.15
Standard deviation	1.66	1.57	1.82	1.45	
MFD (µm)	Stocking rate				
	CSR	0.53 ± 0.15	-	0.11 ± 0.19	-
	HSR	-0.53 ± 0.15	-	-0.11 ± 0.19	-
	Year				
	1	0.37 ± 0.16	-	0.30 ± 0.18	-
	2	-0.37 ± 0.16	-	-0.30 ± 0.18	-
	Birth-rank				
	Single	0.09 ± 0.15	-	-0.17 ± 0.24	-
	Twin	-0.09 ± 0.15	-	0.17 ± 0.24	-
	General mean	35.46 ± 0.16	-	35.02 ± 0.21	-
Standard deviation	2.66	-	2.67	-	

1961). Lax and Brown (1967) observed an increased ($P < 0.01$) number of fibres per mm^2 for singles. Sumner and Wickham (1970), however, observed no significant effect of birth rank on the S_f/P_f ratio at the hogget shearing in the same flock as under study.

Differences between year accounted for 3.7% ($P < 0.01$) of the total variation in the pooled analysis of variance though it explained 17.7% in the Sire group 3 period. Variation between years could be due to the climatic conditions prevailing or management decisions such as time between shearings. A short alteration between the shearing times could be instrumental (Wickham and Bigham, 1973) particularly when the wool growth is approaching its maximum, i.e., during November (Henderson, 1968).

Sire x stocking rate interactions were non-significant both in the pooled analysis of variance and from the four Sire group periods analyses.

These results are in agreement with Morley (1956) who reported non-significant sire x nutrition interactions for this trait. Similar results were reported by King and Young (1955) and King *et al.* (1959) for average fibre length. Stansfield *et al.* (1964) also observed no significant genotype x location interactions for SL. Dunlop (1962) however, indicated small significant strain x location interactions. Nevertheless the interactions for this trait in his experiment accounted for only a very minor (less than 1%) fraction of the variation. Sire x flock interactions were observed significant for SL from the pooled estimates only by Osman and Bradford (1965).

Sire x year interactions explained only 1% (NS) in the pooled variance component analysis. Similar observations for sire x year interactions were reported for the trait in the New Zealand Romney sheep

by Rae (1958). Dunlop (1962) also studied strain x year interactions and found no such interactions as significant for the trait.

Stocking rate x year interactions though significant ($P < 0.05$) account for only 2.1% in the pooled analysis of variance.

In general, interactions were not important for the trait and accounted for only a very minor fraction of the variance components. Stocking rates were the most important source of variation.

Mean fibre diameter

Results recorded in the study under investigation in both the Sire group periods analysed suggested that MFD decreases with increased stocking rate. There is considerable evidence that the MFD decreases with the increased stocking rate (Sharkey *et al.*, 1962; Sumner and Wickham, 1969; Canon, 1972; Lipson and Bacon-Hall, 1974; White and McConchie, 1976). As a prolonged period of decreased level of nutrition is required to reduce the total fibre population of non-breeding sheep (Allden, 1968), the lower fleece weight with increased stocking rate will normally be due to a reduced fibre-volume. Ryder (1956) and Coop (1953) have suggested that the length and diameter of fibre are affected equally by poor nutrition.

Between year effects though significant ($P < 0.01$) contributed only 1.6% of the total variation in the pooled variance components analysis.

Sire x stocking rate interactions were significant ($P < 0.05$) for MFD and explained 2.7% of the total variation in the pooled variance component analysis. Dunlop (1962) also reported significant strain x location interactions of moderate size in MFD. Flocks x level of nutrition interactions were found significant for fibre cross-sectional

area by Williams (1966). King and Young (1955) however, did not observe any significant breed x nutrition interactions for the average diameter of wool fibre.

Sire x year interactions were of no significance in the population under study and accounted for less than 1% of the total variation in the pooled analysis of variance. The results obtained are supported by observations on such interactions for MFD by Dunlop (1962). Stocking rate x year interactions were found highly significant ($P < 0.01$) and were the main source of variation in this trait.

Standard deviation of the fibre diameter

The stocking rate effect was not statistically significant and contributed less than 2% of the total observed variation. SFD was however, higher in the HSR than CSR in both the Sire group period analysed though the difference was not significant. Year differences were highly significant and contributed 11.6% to the total observed variation. The birth rank effect was also found significant ($P < 0.01$). Variation in fibre diameter could be from fibre to fibre within a site or from point to point along the fibre.

Significant sire x stocking rate ($P < 0.01$) and sire x year (NS) interactions explained about 4 and 1.5% of the variation respectively. Variation due to interactions could be in part due to nutritional level x fibre interactions and also the differences between years in seasonal availability of feed.

TABLE 9: Least squares estimates and standard errors of environmental effects for SFD and QN

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
SFD (μm)	Stocking rate				
	CSR	-0.18 \pm 0.06	-	-0.08 \pm 0.07	-
	HSR	0.18 \pm 0.06	-	0.08 \pm 0.07	-
	Year				
	1	-0.35 \pm 0.05	-	-0.28 \pm 0.07	-
	2	0.35 \pm 0.05	-	0.28 \pm 0.07	-
	Birth-rank				
	Single	0.03 \pm 0.05	-	-0.24 \pm 0.09	-
	Twin	-0.03 \pm 0.05	-	0.24 \pm 0.09	-
	General mean	8.91 \pm 0.06	-	8.48 \pm 0.08	-
Standard deviation	0.96	-	1.02	-	
QN (unit)	Stocking rate				
	CSR	-0.12 \pm 0.09	-0.18 \pm 0.10	-0.54 \pm 0.13	-0.21 \pm 0.14
	HSR	0.12 \pm 0.09	0.18 \pm 0.10	0.54 \pm 0.13	0.21 \pm 0.14
	Year				
	1	0.04 \pm 0.09	-0.24 \pm 0.10	0.14 \pm 0.12	-1.19 \pm 0.13
	2	-0.04 \pm 0.09	0.24 \pm 0.10	-0.14 \pm 0.12	1.19 \pm 0.13
	Birth-rank				
	Single	0.04 \pm 0.08	0.17 \pm 0.11	0.08 \pm 0.17	0.36 \pm 0.18
	Twin	-0.04 \pm 0.08	-0.17 \pm 0.11	-0.08 \pm 0.17	-0.36 \pm 0.18
	General mean	48.22 \pm 0.09	48.53 \pm 0.10	48.60 \pm 0.15	49.40 \pm 0.17
Standard deviation	1.50	1.71	1.86	1.64	

Quality number

QN which has been used to indicate fineness and spinning characteristics, is subjectively assessed mainly on crimp frequency with lustre another important factor (Wickham and Bigham, 1973). Other factors such as length, and handle are considered to affect the assessment of QN, though the variation in these attributes does not necessarily equate with the changes in fibre diameter.

In all the four Sire periods analysed, QN was higher in HSR sheep; the variation due to stocking rate agrees with these changes in CPC. Similar results were obtained in New Zealand Romney hoggets by Bublath (1969). The softness of handle is closely related to the fineness of fibres and longer staples to be marked down in QN, probably of the belief that they must be therefore coarser. The effect of stocking rate on QN has been examined by Joyce *et al.* (1976). The observations made in this study are in agreement with these workers. Sumner and Wickham (1969) however, in analyses of QN reported that the fleeces were judged to be coarser at the higher stocking rate in the New Zealand Romney ewes. This was perhaps due to the wool grown at the high stocking rate being more lustrous than that grown at the low stocking rate. X

The effect of years accounted for the major fraction of the total observed variation in the trait and was highly significant. A part of this variation could be due to variations in the standards due to varying emphasis placed on the component attributes by the observers during the years under study.

Sire x stocking rate interactions were found non-significant for the traits in the pooled and the individual Sire group periods analyses

of variance. Osman and Bradford (1965) also reported sire x flock interactions as non-significant in this trait.

Dunlop (1962) observed that strain x location interactions for the trait accounts for only a negligible fraction of the variance and are non-significant.

Sire x year interactions were non-significant for the trait in this investigation and were not important in the pooled or the individual Sire group period analyses. Rae (1958) and Dunlop (1962) also reported that genotype x year interactions were not significant for the trait. As a cause of variability of QN, stocking rate x year interactions appears to be more important than CPC in this investigation.

Crimps per centimeter

Staple crimp is used in assessing wool quality because of the approximate inverse relationship between the CPC and MFD (Ryder and Stephenson, 1968), though with some wools, at least, crimp is not a good indicator of the fibre cross-sectional area (Roberts and Dunlop, 1957).

The effect of stocking rate on the trait explained 3.6% ($P < 0.01$) of the total observed variation in the pooled variance components analysis. A tendency for CPC to increase with increased stocking rate was noted in all the three Sire group periods analysed. Results similar to this study have been reported by Sumner (1969). An increase in fibre length caused by nutrition could result in a decrease of CPC, if crimp is a periodic function of time. Robards *et al.* (1974) studied the differences in intake of food on crimp frequency and observed no significant effect.

TABLE 10: Least squares estimates and standard errors of environmental effects for CPC and TCN

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
CPC (unit)	Stocking rate				
	CSR	-0.02 ± 0.01	-0.08 ± 0.01	-	-0.05 ± 0.03
	HSR	0.02 ± 0.01	0.08 ± 0.01	-	0.05 ± 0.03
	Year				
	1	0.17 ± 0.01	0.02 ± 0.01	-	-0.01 ± 0.02
	2	-0.17 ± 0.01	-0.02 ± 0.01	-	0.01 ± 0.02
	Birth-rank				
	Single	0.01 ± 0.01	0.03 ± 0.02	-	0.04 ± 0.04
	Twin	-0.01 ± 0.01	-0.03 ± 0.02	-	-0.04 ± 0.04
	General mean	1.06 ± 0.01	1.14 ± 0.01	-	1.44 ± 0.03
Standard deviation	0.23	0.23	-	0.32	
TCN (unit)	Stocking rate				
	CSR	0.10 ± 0.16	0.05 ± 0.15	-	0.05 ± 0.23
	HSR	-0.10 ± 0.16	-0.05 ± 0.15	-	-0.05 ± 0.23
	Year				
	1	-2.28 ± 0.16	1.06 ± 0.15	-	0.68 ± 0.21
	2	2.28 ± 0.16	-1.06 ± 0.15	-	-0.68 ± 0.21
	Birth-rank				
	Single	0.12 ± 0.15	0.24 ± 0.16	-	0.19 ± 0.31
	Twin	-0.12 ± 0.15	-0.24 ± 0.16	-	-0.19 ± 0.31
	General mean	15.14 ± 0.16	15.59 ± 0.15	-	18.74 ± 0.29
Standard deviation	2.73	2.56	-	2.75	

On the published evidence (Roberts and Dunlop, 1957) CPC is little, if at all, affected by nutrition.

Between year differences were the major source of variation and accounted for 44.2%. This could result from the differences in climatic conditions such as rainfall in particular during the years, inaccuracies of measurements and technician variation. Wickham and Bigham (1973) suggested that the staple crimp can be affected by disorientation of crimp-waves of individual fibres which results from several environmental conditions such as weathering and brushing of the fleece against objects.

None of the interactions was significant sources of variation in the pooled analysis of variance. However, sire x stocking rate and sire x year interactions contributed 3.2 and 2.7% of the total observed variation respectively in Sire group 2 period. Dunlop (1962) found the interactions between strains and locations though significant on occasions, accounted for a negligible fraction of the variation. Strain x years and location x year interactions were reported as non-significant. Non-significant genotype x plane of nutrition interactions were reported for the trait by Morley (1956).

Total crimp number

TCN was not affected by the stocking intensity in all the three Sire group periods analysed. Swart and Kotze (1937) suggested that total number of crimps in the fibres of a lock was not constant, although there was a correlation of +0.9 between crimp size and fibre length indicating that the total number of crimps is independent of fibre length.

The major and only important source of variation in the trait was the year effect. It explained 38.2% of the total observed variation in the pooled variance components analysis. As in CPC this could have resulted from the various environmental sources of variation which make up the yearly environment in addition to the variations due to the technician and inaccuracies of measurements.

Sire x stocking rate were the only significant interactions ($P < 0.05$) and contributed slightly less than 2% to the total observed variation. However, it contributed 5.9% of the total variation, though statistically non-significant in the Sire group 4 period when the degrees of freedom were low. This could be due to the change of ranking of sires in the two stocking rates.

Character grade

CHG is an assessment based on staple crimp clarity and evenness, staple formation, blockiness of the staple tip and freedom from medullation (Wickham and Bigham, 1973).

CHG was lower in HSR sheep. Results obtained from the study were in general agreement with Bublath (1969), Langlands and Bennett (1973) and Joyce *et al.* (1976). Increased stocking levels will lead to a poorer character, partly as a result of wool becoming more tippy (Sumner, 1969). The between stocking rates effect was highly significant and explained 3.7% ($P < 0.01$) of the total variation in the pooled variance components analysis. Ryder and Stephenson (1968) pointed out that CHG seems to become worse only after prolonged and severe nutritional stress, although CHG is badly affected by copper deficiency.

TABLE 11: Least squares estimates and standard errors of environmental effects for CHG and TG

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
CHG (grade)	Stocking rate				
	CSR	0.02 ± 0.06	0.27 ± 0.07	-0.09 ± 0.06	0.27 ± 0.07
	HSR	-0.02 ± 0.06	-0.27 ± 0.07	0.09 ± 0.06	-0.27 ± 0.07
	Year				
	1	0.66 ± 0.06	0.59 ± 0.06	0.05 ± 0.06	-0.11 ± 0.07
	2	-0.66 ± 0.06	-0.59 ± 0.06	-0.05 ± 0.06	0.11 ± 0.07
	Birth-rank				
	Single	0.05 ± 0.06	0.20 ± 0.07	0.08 ± 0.07	-0.08 ± 0.10
	Twin	-0.05 ± 0.06	-0.20 ± 0.07	-0.08 ± 0.07	0.08 ± 0.10
	General mean	4.95 ± 0.05	5.22 ± 0.06	5.49 ± 0.06	5.69 ± 0.09
	Standard deviation	1.03	1.09	0.83	0.90
TG (grade)	Stocking rate				
	CSR	0.03 ± 0.07	-0.08 ± 0.05	-0.21 ± 0.07	-0.03 ± 0.06
	HSR	-0.03 ± 0.07	0.08 ± 0.05	0.21 ± 0.07	0.03 ± 0.06
	Year				
	1	0.15 ± 0.07	-0.09 ± 0.05	0.15 ± 0.07	-0.25 ± 0.06
	2	-0.15 ± 0.07	0.09 ± 0.05	-0.15 ± 0.07	0.25 ± 0.06
	Birth-rank				
	Single	0.09 ± 0.06	-0.01 ± 0.05	0.003 ± 0.096	0.12 ± 0.08
	Twin	-0.09 ± 0.06	0.01 ± 0.05	-0.003 ± 0.096	-0.12 ± 0.08
	General mean	6.88 ± 0.06	6.43 ± 0.04	5.38 ± 0.08	5.18 ± 0.08
	Standard deviation	1.14	0.81	1.06	0.75

Between years differences were highly significant and accounted for the major fraction, i.e., 28.9% of the total variation in the pooled variance components analysis for the trait. Chapman (1964) associated dogginess in wool with increasing rainfall.

As "wool character" may have different meaning to different observers, variations between observers may contribute to year to year variation in this trait.

Twin-born hoggets in general had lower CHG than the single-borns. Similar observations on CHG due to birth-rank were recorded by Elliott (1975) in the Perendale hoggets.

None of the interactions analysed were significant and they contributed only a negligible fraction of the variation to the total variation in the pooled variance components analysis.

Sire x stocking rate interactions though non-significant contributed 4% to the total variation in the Sire group 3 period. Dunlop (1962) recorded significant station x strain interactions ($P < 0.05$) of moderate size for the trait.

Sire x year interactions though non-significant explained 1.9 and 2.2% in the Sire group 3 and 4 periods respectively. Rae (1958) recorded significant sire x year interactions ($P < 0.01$) for CHG in a flock of New Zealand Romney sheep. He suggested that this could be due to the genuine non-linear interactions between the sire genotype and environmental conditions peculiar to each year or the differences between dams and sire x dam interactions. It could also be an artefact of the subjective assessment. Strain x years interactions, however, were found non-significant in a study by Dunlop (1962).

Tippiness grade

TG is subjectively assessed with wool having a rather pointed 'tip' protruding beyond the bulk of staple being graded low and wool with 'square tipped' staples getting high grades.

Henderson (1968) attributed this trait to two main factors (1) high variability of fibre lengths and diameter (2) wide differences in fibre diameter between the tip and butt of the staple. A thin and 'wispy' tip in the Merino can be caused by poor nutrition at the time of shearing, whereas tippiness in British breeds is due to more rapid growth of the coarser fibres (Ryder and Stephenson, 1968). When it is present this fault becomes more evident in sheep with relatively low fibre number and little yolk.

The least squares estimates presented in Table 11 suggest that TG is better in the HSR group of sheep. However, the between stocking rate effect though significant ($P < 0.05$) contributed only a negligible fraction of the variation in the pooled variance components analysis.

The between year effect was found highly significant ($P < 0.01$) and contributed 4% to the variation in the pooled variance components analysis. 'Year' differences could arise from differences in the climatic conditions, especially rainfall, as TG may be affected by wetting and drying of the staple. Since this trait is subjectively graded, variations in scoring by different observers could also contribute to the variation due to this source.

None of the interactions contributed to the total observed variation in the pooled variance components analysis. Sire x stocking rate and sire x year interactions though found non-significant contributed over 3% in the Sire group 2 period. Stocking rate x year interactions were

however, unimportant as a source of variation in all the Sire group periods analysed.

Handle grade

The stocking rate effects on handle grade were small and non-significant. There was a tendency for the HSR wools to be softer handling.

Between year effects were highly significant and explained 19.1% of the variation in the pooled analysis. Since weathering is one of the major causes of harshness, differences in the yearly environments because of climatic conditions may have contributed to this source of variation. Other factors such as variations in the standards of scoring and the subjective assessment of the trait might have also contributed to the 'year' effects.

Single-born hoggets displayed relatively higher HG than the twin-borns. This effect was highly significant and explained 2.1% in the pooled variance components analysis.

Sire x stocking rate interactions were not significant and contributed only 0.6% in the pooled variance components analysis. Dunlop (1962) also reported strain x locations interactions (NS) were a negligible source of variations for the trait.

Sire x year interactions were found significant ($P < 0.05$) and explained 2.9% of the total variation in the pooled variance components analysis. Highly significant interactions were observed in the Sire group 3 period. It contributed 11.7% of the variation. This could be real or an artefact of the grading system.

TABLE 12: Least squares estimates and standard errors of environmental effects for HG and LG

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
HG (grade)	Stocking rate				
	CSR	-0.10 ± 0.05	-0.03 ± 0.04	0.03 ± 0.06	-0.11 ± 0.06
	HSR	0.10 ± 0.05	0.03 ± 0.04	-0.03 ± 0.06	0.11 ± 0.06
	Year				
	1	-0.37 ± 0.05	-0.39 ± 0.04	0.15 ± 0.05	-0.08 ± 0.05
	2	0.37 ± 0.05	0.39 ± 0.04	-0.15 ± 0.05	0.08 ± 0.05
	Birth-rank				
	Single	0.07 ± 0.05	0.15 ± 0.05	0.10 ± 0.07	0.15 ± 0.07
	Twin	-0.07 ± 0.05	-0.15 ± 0.05	-0.10 ± 0.07	-0.15 ± 0.07
	General mean	6.50 ± 0.05	6.28 ± 0.04	5.83 ± 0.06	6.13 ± 0.07
Standard deviation	0.92	0.73	0.80	0.67	
LG (grade)	Stocking rate				
	CSR	0.08 ± 0.06	-0.12 ± 0.04	0.04 ± 0.04	-0.03 ± 0.06
	HSR	-0.08 ± 0.06	0.12 ± 0.04	-0.04 ± 0.04	0.03 ± 0.06
	Year				
	1	-0.46 ± 0.05	0.29 ± 0.04	0.002 ± 0.04	0.10 ± 0.06
	2	0.46 ± 0.05	-0.29 ± 0.04	-0.002 ± 0.04	-0.10 ± 0.06
	Birth-rank				
	Single	-0.02 ± 0.05	0.11 ± 0.04	0.06 ± 0.06	-0.16 ± 0.08
	Twin	0.02 ± 0.05	-0.11 ± 0.04	-0.06 ± 0.06	0.16 ± 0.08
	General mean	5.68 ± 0.06	5.93 ± 0.03	5.53 ± 0.05	5.08 ± 0.08
Standard deviation	0.91	0.62	0.63	0.76	

Stocking rate x year interactions were non-significant and contributed very little of the variation.

Lustre grade

LG was subjectively graded without reference to fineness. High grades were very lustrous. The overall averages of LG of hogget wool for each Sire group period analysed are presented in Table 12. The least squares constants for different subclasses of the main effects are listed in Table 12.

The stocking rate effect though significant ($P < 0.05$) contributed only 0.8%, a negligible fraction of the total variation in the pooled variance components analysis. The significance of stocking rate appears largely an artefact of the method of statistical analysis since the ranking of the two stocking rates was non-consistent. An analysis of variance with all years included as a cross-classification would probably result in most of the variance being ascribed to the stocking rate x year interactions. The birth rank effect was only 1% (NS) of the total variation.

The year effect was the major source of variation and accounted for 21.3% of the total variation in the pooled variance components analysis. Variations in the standards of scoring by different observers is probably the major cause of this.

Sire x stocking rate and sire x year interactions were non-significant in the pooled variance components analysis. However, in Sire group 4 period, it was found to be highly significant and contributed 7% of the observed variation. This response could be due to genuine non-linear interactions between the sire genotype and stocking level. Sire x year

interactions were however, unimportant in all the four Sire group periods analysed.

Stocking rate x year interactions explained 3.2% of the total variation and was observed to be highly significant in the pooled variance components analysis. However, the apparent importance of these interactions may be largely an artefact of the grading system associated with the difficulty of maintaining consistent standards.

Greasy colour grade

GCG was better in the HSR wool in all the Sire group periods analysed. The response of GCG to stocking rate was in accord with the findings by Bublath (1969), Sumner (1969), Langlands and Bennett (1973), and Joyce *et al.* (1976). This may have been due to fewer pigments secreted by skin glands (Ryder and Stephenson, 1968). The difference between stocking rates explained about 12.4% ($P < 0.01$) of the variation in the pooled variance components analysis.

The year effect was highly significant and was the major source of variation accounting for 28.2% of the variation in the pooled variance components analysis. Variations in climatic conditions are important in causing year to year differences in wool colour. The causes of discolouration are complex but it appears that prolonged wetting, particularly in the warm conditions, tends to be associated with high levels of discolouration. Problems of subjective assessment may also contribute to this source of variation.

Sire x stocking rate interactions accounted for 1.4% ($P < 0.05$) of the total variation in the pooled variance components analysis.

TABLE 13: Least squares estimates and standard errors of environmental effects for GCG and SCG

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
GCG (grade)	Stocking rate				
	CSR	-0.33 ± 0.05	-0.23 ± 0.03	-0.07 ± 0.03	-0.01 ± 0.04
	HSR	0.33 ± 0.05	0.23 ± 0.03	0.07 ± 0.03	0.01 ± 0.04
	Year				
	1	0.55 ± 0.05	-0.02 ± 0.03	-0.25 ± 0.03	-0.22 ± 0.05
	2	-0.55 ± 0.05	0.02 ± 0.03	0.25 ± 0.03	0.22 ± 0.05
	Birth-rank				
	Single	0.05 ± 0.05	0.03 ± 0.03	-0.01 ± 0.04	0.05 ± 0.06
	Twin	-0.05 ± 0.05	-0.03 ± 0.03	0.01 ± 0.04	-0.05 ± 0.06
	General mean	6.56 ± 0.05	6.35 ± 0.03	6.15 ± 0.03	6.37 ± 0.06
Standard deviation	0.88	0.53	0.46	0.53	
SCG (grade)	Stocking rate				
	CSR	-0.17 ± 0.04	-0.11 ± 0.04	-0.19 ± 0.04	0.02 ± 0.08
	HSR	0.17 ± 0.04	0.11 ± 0.04	0.19 ± 0.04	-0.02 ± 0.08
	Year				
	1	-0.25 ± 0.04	0.06 ± 0.04	-0.11 ± 0.04	-0.21 ± 0.07
	2	0.25 ± 0.04	-0.06 ± 0.04	0.11 ± 0.04	0.21 ± 0.07
	Birth-rank				
	Single	-0.06 ± 0.04	-0.04 ± 0.04	0.06 ± 0.05	-0.01 ± 0.10
	Twin	0.06 ± 0.04	0.04 ± 0.04	-0.06 ± 0.05	0.01 ± 0.10
	General mean	6.21 ± 0.04	6.38 ± 0.03	6.13 ± 0.04	5.62 ± 0.10
Standard deviation	0.70	0.65	0.56	0.94	

Significant differences ($P < 0.01$) in GCG due to these interactions were observed in Sire group 1 period wherein it contributed 2.8% of the observed variation. Dunlop (1962) reported significant strain x station interactions, though the average size of the interactions term was small.

Sire x year interactions contributed only a little over 1% of the variation and were non-significant. Similar results of strain x year interactions in the trait were reported by Dunlop (1962). It was however, significant in three of the four Sire group periods analysed and explained slightly over 2% of the variation in each analysis.

Stocking rate x year interactions were unimportant as a source of variation.

Scoured colour grade

SCG of wool was subjectively assessed following scouring, using the same standards as for GCG of wool. Like GCG of wool, SCG was higher in HSR wool as compared to CSR wool. These results are in agreement with Sumner (1969). Stocking rate accounted for 5.6% ($P < 0.01$) of the total variation in the pooled analysis. The year effect though highly significant and a major source of variation was comparatively less important than in GCG.

Interactions in general were important sources of variation and contributed about 10% of the total variation. Sire x year interactions were observed to be significant ($P < 0.05$) and contributed 2.7% in the pooled variance components analysis. The extent of the response clearly differed between Sire group periods, the greatest variation due to sire x

year interactions being in Sire group 3 period when it contributed 6% of the variation. As a cause of variability Sire x stocking rate interactions were less important than the sire x year interactions and accounted for a little over 1% of the observed variation in the pooled analysis. It was found equally unimportant as a source of variability in the Sire group periods analysed individually and shows a good resemblance to those estimated in the GCG. Stocking rate x year interactions were highly significant and explained 6.1% of the total observed variation in the pooled analysis.

Discoloured area grade

DAG was assessed at the time of shearing mainly on the basis of how far the discolouration extended over the whole fleece with account taken of the severity of discolouration. The overall averages of DAG of fleece for each Sire group period analysed are presented in Table 14. DAG was better in the CSR fleeces, a finding similar to that of Sumner (1969). Wickham and Bigham (1973) suggested that the very high stocking rate appears to result in increased discolouration perhaps as a result of increased dirt contamination or slower drying of more cotted wool. Differences due to stocking rate in the trait were found to be highly significant and accounted for 5.6% of the total observed variation in the pooled variance components analysis. The year effect was found to be non-significant and contributed a small fraction to the total variability in the pooled analysis.

Both sire x stocking rate and sire x year interactions were found to be non-significant and did not contribute to the total variation in DAG. However, in Sire group 4 period, sire x stocking rate and sire x year

TABLE 14: Least squares estimates and standard errors of environmental effects for DAG and CG

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
DAG (grade)	Stocking rate				
	CSR	-	-	0.09 ± 0.04	0.15 ± 0.05
	HSR	-	-	-0.09 ± 0.04	-0.15 ± 0.05
	Year				
	1	-	-	-0.05 ± 0.04	0.06 ± 0.05
	2	-	-	0.05 ± 0.04	-0.06 ± 0.05
	Birth-rank				
	Single	-	-	-0.06 ± 0.05	0.04 ± 0.07
	Twin	-	-	0.06 ± 0.05	-0.04 ± 0.07
	General mean	-	-	6.31 ± 0.04	5.28 ± 0.07
Standard deviation	-	-	0.57	0.63	
CG (grade)	Stocking rate				
	CSR	-0.06 ± 0.04	0.10 ± 0.02	-0.08 ± 0.03	0.11 ± 0.05
	HSR	0.06 ± 0.04	-0.10 ± 0.02	0.08 ± 0.03	-0.11 ± 0.05
	Year				
	1	0.19 ± 0.04	-0.08 ± 0.02	0.004 ± 0.03	-0.11 ± 0.05
	2	-0.19 ± 0.04	0.08 ± 0.02	-0.004 ± 0.03	0.11 ± 0.05
	Birth-rank				
	Single	0.06 ± 0.03	0.04 ± 0.03	0.03 ± 0.04	-0.04 ± 0.07
	Twin	-0.06 ± 0.03	-0.04 ± 0.03	-0.03 ± 0.04	0.04 ± 0.07
	General mean	6.88 ± 0.03	6.89 ± 0.02	6.02 ± 0.03	6.57 ± 0.06
Standard deviation	0.63	0.40	0.41	0.59	

interactions contributed 3.3% (NS) and 1.4% (NS) of the total observed variation respectively. As a cause of variability in the trait, stocking rate x year interactions were a major factor.

Cotting grade

Wickham and Bigham (1973) attributed the cotting of the fleece mainly to two events: shedding of fine fibres; the migration of the shed fibres to entangle with other fibres in the fleece. Wetness and drying of the fleece may aid the process. Cotting is seldom severe in hogget fleeces.

Differences in CG between stocking rates were highly significant ($P < 0.01$, 3.7% of the variation) but inconsistent in ranking. Bublath (1969), Sumner and Wickham, (1969) and Langlands and Bennett (1973) reported that CG increased with the stocking rate. Joyce (1961) observed that the low plane nutrition more than doubled the incidence of CG.

The 'year' effect was highly significant and was the major source of variation in the pooled analysis. The climatic differences between the years, especially the rainfall, could be a major factor in this source of variation. Joyce (1961) found that the incidence of CG was affected by season, breed, age, reproductive performance and nutrition. As in other subjectively graded traits, the observer variation could also contribute to the 'year' effect in the trait.

Both sire x stocking rate and sire x year interactions were non-significant and did not contribute to the total variation in the pooled analysis. Though non-significant, the sire x stocking rate interactions were responsible for 2.7 and 1.8% of variation in the Sire group 2 and 3 periods respectively. Sire x year interactions were not of any importance.

Stocking rate x year interactions were significant in the pooled analysis and this was reinforced by the inconsistency of the stocking rate effects between periods. It was of particular importance in Sire group 4 period where it contributed over 10% to the total observed variation.

Cotted area grade

CAG was subjectively assessed on the degree and extent of entanglement of the wool fibres over the whole fleece. In all fleeces there is some evidence of entanglement of wool fibres but it is only when it is severe enough to cause difficulty in dividing the fleece that a fleece is given the description "cotted" or "matted" (Henderson, 1968). CAG was generally more severe in the HSR fleeces. These results are in agreement with Joyce (1961), Sumner (1969) and Langlands and Bennett (1973). Sumner and Wickham (1969) observed that increased stocking rate tends to result in a greater amplitude of the seasonal rhythm of wool growth and fibre diameter with the trough of the rhythm occurring later in the year. This can result in increased cotting. It is believed that poor feeding or any other stress which is likely to reinforce or prolong the normal winter depression will cause shedding of more fibres and may result in more cotting. Cotting tends to be more severe on the regions having the greatest variability of fibre diameter.

Stocking rate was observed to be significant ($P < 0.01$) and contributed 4.9% to the total variation in the pooled analysis.

The 'year' effect was highly significant and explained 39%, a very high proportion of the total variation in the pooled variance components analysis. Climatic differences and grading difficulties have probably both contributed to the effect.

TABLE 15: Least squares estimates and standard errors of environmental effects for CAG and SG

Trait	Factor	Sire group 1 1967/1968	Sire group 2 1969/1970	Sire group 3 1971/1972	Sire group 4 1973/1974
CAG (grade)	Stocking rate				
	CSR	-0.05 ± 0.04	0.27 ± 0.04	0.04 ± 0.03	0.04 ± 0.06
	HSR	0.05 ± 0.04	-0.27 ± 0.04	-0.04 ± 0.03	-0.04 ± 0.06
	Year				
	1	-0.50 ± 0.04	-0.19 ± 0.04	-0.09 ± 0.03	0.59 ± 0.05
	2	0.50 ± 0.04	0.19 ± 0.04	0.09 ± 0.03	-0.59 ± 0.05
	Birth-rank				
	Single	-0.03 ± 0.03	-0.04 ± 0.05	0.00 ± 0.04	-0.05 ± 0.08
	Twin	0.03 ± 0.03	0.04 ± 0.05	0.00 ± 0.04	0.05 ± 0.08
	General mean	6.62 ± 0.04	6.72 ± 0.04	6.85 ± 0.03	6.11 ± 0.07
Standard deviation	0.61	0.71	0.44	0.68	
SG (grade)	Stocking rate				
	CSR	-	0.46 ± 0.07	-0.11 ± 0.09	1.25 ± 0.10
	HSR	-	-0.46 ± 0.07	0.11 ± 0.09	-1.25 ± 0.10
	Year				
	1	-	0.63 ± 0.07	0.42 ± 0.09	-0.09 ± 0.09
	2	-	-0.63 ± 0.07	-0.42 ± 0.09	0.09 ± 0.09
	Birth-rank				
	Single	-	0.10 ± 0.08	0.09 ± 0.11	-0.07 ± 0.13
	Twin	-	-0.10 ± 0.08	-0.09 ± 0.11	0.07 ± 0.13
	General mean	-	6.31 ± 0.07	5.88 ± 0.10	5.49 ± 0.13
Standard deviation	-	1.21	1.27	1.15	

None of the interactions was significant in the pooled analysis. Sire x stocking rate interactions, though non-significant explained 2.7% in the Sire group 2 period. In other periods it was found to be of negligible importance. Stocking rate x year interactions were significant in the Sire group 1 period where it explained 2.1% only of the total observed variation.

Soundness grade

Stocking rate was highly significant and contributed 25.4% of the total variation in the pooled analysis.

Henderson (1968) attributed the unsoundness in wool to the decrease in cross-sectional area of a region of the fibres, shedding and the fundamental structural weakness of the fibres, - these effects acting singly or in combination.

Wickham (1968) examined the various factors causing the lack of strength in the fibres and pointed out that increasing stocking-rates can result in the higher levels of unsoundness. Other possible causes are seasonal differences in wool growth rate, pregnancy, lactation, lambing and other stresses accentuating the fundamental seasonal effect.

Brown (1971) suggested that sudden changes in feed such as sudden introduction of sheep to an all hay or all crop diet or the sheep from dry feed to lush green feed could also be a factor in the break of wool.

Analyses of SG appraisals indicate that SG was generally lower in the HSR fleeces. These results are in conformity with Bublath (1969) and Langlands and Bennett (1973). However, Sumner (1969) obtained variable results; the hogget wool in 1967 was sounder in HSR while in the ewe fleeces in 1966 the HSR group had sounder wool, the position was reversed in 1967.

'Year' explained 12.8% of the total observed variation and was found highly significant. Year to year differences could be due to the climatic conditions such as rainfall, parasitic infections, or any other stresses contributing to the fundamental seasonal effect. Variations in the standards of scoring may also have contributed to this source of variation.

Both sire x stocking rate and sire x year interactions were non-significant, the estimates are extremely small and cause only a small fraction of the variance in the analyses. Dunlop (1962) also reported strain x location and strain x year interactions were not significant for soundness.

Stocking rate x year interactions contributed 17.5% to the total observed variation and were highly significant in the pooled variance components analysis.

HERITABILITY ESTIMATES, INTRA-TRAIT GENETIC CORRELATIONS AND INTERACTION VARIANCE COMPONENTS

To this point, the discussion of sire x stocking rate and sire x year interactions has been largely confined to the conclusions that interactions have or have not been detected. The impact of these interactions, with particular regard to the structure of heritability estimates for various traits, needs further consideration.

The heritability estimates of the traits for the CSR, HSR and the combined data analyses from the pooled variance components analyses by two different methods are listed along with their standard errors in Table 16. The two methods used are NEI (interaction variance components excluded in the numerator of the heritability expression) and NII (interaction variance components included in the numerator of the heritability expression). The significance of differences between the various heritability estimates were assessed by calculating the standard error of the difference and examining the change in the estimates in terms of this standard error.

When comparing the estimates of heritability in the present study with the estimates from other studies, it must be remembered that the basic model assumed is frequently different. Most estimates of heritability are based on models which lead to estimates similar to those of NII type of Table 16. When interactions are important sources of variance, selection responses calculated from these types of estimates may well be higher than the responses likely to be achieved in practice.

The genetic correlations of each trait between the two stocking rates were calculated as a quantitative expression of the sire x stocking rate

TABLE 16: Heritability estimates and standard errors of various traits obtained from the pooled analyses by different methods*

Method	CSR		HSR		COMBINED	
	NEI	NII	NEI	NII	NEI	NII
Trait	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$
HLW	0.46 ± 0.17	0.72 ± 0.24	0.21 ± 0.11	0.47 ± 0.22	0.27 ± 0.10	0.64 ± 0.20
GFW	0.38 ± 0.15	0.38 ± 0.15	0.61 ± 0.21	0.61 ± 0.21	0.39 ± 0.13	0.60 ± 0.17
WA	0.41 ± 0.19	0.47 ± 0.19	0.31 ± 0.16	0.31 ± 0.16	0.40 ± 0.15	0.49 ± 0.17
Y	0.53 ± 0.19	0.53 ± 0.19	0.19 ± 0.11	0.19 ± 0.11	0.28 ± 0.10	0.42 ± 0.12
SL	0.54 ± 0.19	0.57 ± 0.20	0.55 ± 0.20	0.56 ± 0.18	0.57 ± 0.17	0.63 ± 0.18
MFD	0.81 ± 0.34	0.87 ± 0.33	0.34 ± 0.20	0.46 ± 0.26	0.49 ± 0.20	0.66 ± 0.25
SFD	0.57 ± 0.26	0.58 ± 0.25	0.47 ± 0.24	0.58 ± 0.27	0.35 ± 0.15	0.66 ± 0.24

* For CSR and HSR data

$$\frac{\text{NEI}}{h^2} = 4 \left[\frac{\sigma_s^2}{\sigma_s^2 + \sigma_{st}^2 + \sigma_e^2} \right]$$

$$\frac{\text{NII}}{h^2} = 4 \left[\frac{\sigma_s^2 + \sigma_{st}^2}{\sigma_s^2 + \sigma_{st}^2 + \sigma_e^2} \right]$$

* For Combined data

$$\frac{\text{NEI}}{h^2} = 4 \left[\frac{\sigma_s^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2} \right]$$

$$\frac{\text{NII}}{h^2} = 4 \left[\frac{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2}{\sigma_s^2 + \sigma_{sr}^2 + \sigma_{st}^2 + \sigma_e^2} \right]$$

The notation used in the above expression have been described earlier in Chapter 3.

TABLE 16: (continued)

Method	CSR		HSR		COMBINED	
	NEI	NII	NEI	NII	NEI	NII
Trait	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$	$h^2 \pm \text{S.E.}$
QN	0.46 \pm 0.17	0.46 \pm 0.17	0.59 \pm 0.20	0.72 \pm 0.25	0.52 \pm 0.16	0.56 \pm 0.17
CPC	0.48 \pm 0.20	0.56 \pm 0.21	0.75 \pm 0.28	0.88 \pm 0.26	0.64 \pm 0.22	0.66 \pm 0.22
TCN	0.65 \pm 0.25	0.81 \pm 0.27	0.86 \pm 0.31	1.09 \pm 0.29	0.70 \pm 0.24	0.83 \pm 0.26
CHG	0.24 \pm 0.12	0.28 \pm 0.13	0.31 \pm 0.14	0.32 \pm 0.13	0.29 \pm 0.10	0.34 \pm 0.12
TG	0.13 \pm 0.09	0.26 \pm 0.17	0.27 \pm 0.12	0.27 \pm 0.12	0.22 \pm 0.09	0.22 \pm 0.09
HG	0.30 \pm 0.13	0.66 \pm 0.22	0.48 \pm 0.11	0.48 \pm 0.11	0.23 \pm 0.09	0.42 \pm 0.15
LG	0.42 \pm 0.16	0.42 \pm 0.16	0.32 \pm 0.14	0.32 \pm 0.14	0.32 \pm 0.11	0.39 \pm 0.12
GCG	0.31 \pm 0.10	0.31 \pm 0.10	0.34 \pm 0.14	0.44 \pm 0.16	0.22 \pm 0.09	0.41 \pm 0.15
SCG	0.19 \pm 0.11	0.39 \pm 0.20	0.12 \pm 0.09	0.36 \pm 0.15	0.10 \pm 0.06	0.30 \pm 0.13
DAG	0.04 \pm 0.07	0.21 \pm 0.17	0.20 \pm 0.17	0.20 \pm 0.17	0.10 \pm 0.08	0.10 \pm 0.08
CG	0.39 \pm 0.15	0.67 \pm 0.23	0.12 \pm 0.10	0.12 \pm 0.10	0.23 \pm 0.09	0.23 \pm 0.09
CAG	0.37 \pm 0.15	0.53 \pm 0.18	0.18 \pm 0.11	0.27 \pm 0.13	0.23 \pm 0.09	0.29 \pm 0.11
SG	0.22 \pm 0.13	0.22 \pm 0.13	0.00 \pm 0.00	0.00 \pm 0.00	0.16 \pm 0.08	0.16 \pm 0.08

TABLE 17: Intra-trait genetic correlations and standard errors of traits in two stocking rates

Trait	r_G	S.E.	Trait	r_G	S.E.
HLW	0.58	0.20	CHG	0.92	0.13
GFW	0.90	0.10	HG	0.90	0.16
Y	0.74	0.17	LG	0.80	0.15
MFD	0.93	0.09	GCG	0.65	0.21
SFD	0.52	0.27	SCG	0.57	0.37
QN	0.95	0.07	CAG	0.96	0.15
CPC	1.03	0.18	SG	1.06	0.20
TCN	0.87	0.09			

interactions to examine its practical significance in selection. These intra-trait genetic correlations along with their standard errors are presented in Table 17. The significance of deviation of the intra-trait correlations from unity was tested.

The relative magnitudes of the sire x stocking rate and sire x year variance components to the total variance and total genetic variance were computed to illustrate the importance of these random interactions in the traits under investigation.

Hogget live-weight

The heritability estimates of HLW computed by NEI and NII methods in the pooled analyses were 0.46 ± 0.17 and 0.72 ± 0.24 in the CSR; 0.21 ± 0.11 and 0.47 ± 0.22 in the HSR; 0.27 ± 0.10 and 0.64 ± 0.20 in the combined data respectively. The estimates by NEI method in general are similar to the other estimates of the heritability of HLW in the New Zealand Romney (0.46 Tripathy, 1966; 0.51 Ch'ang and Rae, 1970; 0.22 Baker *et al.*, 1974). The estimates by NII method in this study though at the upper limit are well within the range of estimates for the other breeds reported in the literature.

Although the heritabilities calculated from the CSR data were higher than those for the HSR, there were no significant differences between these estimates. As a result of large standard errors, there were no significant differences in all the three analyses between the estimates by NEI and NII methods.

Significant sire x year interactions ($P < 0.05$) contributed 6.4 and 6.5% in the CSR and HSR respectively to the total variance and formed a

very substantial proportion of the total genetic variance in both the analyses. In HSR, while comparing the relative magnitude of sire x year interactions and between sire variance components, the ratio was exceedingly large indicating that the performance of the progeny of a sire would not be highly repeatable over the years. The ranking of sires may be very different in various years.

In the combined data analysis, sire x stocking rate and sire x year interactions were significant ($P < 0.01$), contributed 4.6 and 4.5% respectively to the total variance and formed 29.1 and 28% respectively of the total genetic variance. The ratio of sire x stocking rate and sire x year interactions to the between-sire variance was about 1.3, indicating the importance of these random interactions in this trait. The same trend was observed in the individual Sire group periods. The difference between the estimates by two methods approached significance ($0.05 < P < 0.10$). Evidence of genotype x nutrition interactions being important in this trait has been provided by various workers (Morley, 1956; Osman and Bradford, 1965; Carter *et al.*, 1971b; Budanstev, 1973). In Dunlop's (1963) work, the lack of large and consistent genotype x location interactions in HLW were attributed to the presence of year x location interactions of some importance.

The intra-trait genetic correlation between the two stocking rates for HLW was estimated to be 0.58 ± 0.20 , significantly ($P < 0.05$) different from unity. Robertson (1959) suggested that an estimate of r_G around 0.6 would be of consequence in selection.

Falconer (1952) stated that the ratio of the 'correlated response' ($\Delta'G_1$) in environment 1 to the 'direct response' (ΔG_1) is

$$\frac{\Delta'G_1}{\Delta G_1} = \frac{h_2}{h_1} r_G \dots\dots\dots (1)$$

where h_2 and h_1 are the square roots of the heritability in environment 2 and 1 respectively and r_G is the intra-trait genetic correlation between the two environments. An assumption of equal intensity of selection was made in deriving the equation. From the above expression it follows, that an advantage of selection in the secondary environment would accrue only through an increase of heritability. The increase in heritability would have to be great enough to offset the loss of efficiency through selection being made in one environment that has not exactly the same genetic basis as the other environment, i.e., $h_2 r_G$ must be greater than h_1 .

The observed heritabilities in this investigation were 0.46 and 0.72 in the CSR; 0.21 and 0.47 in the HSR by NEI and NII methods respectively. With the value of r_G being 0.58, the above ratios (equation 1) worked out to be about 0.87 and 0.72 with NEI and NII respectively. Thus no advantage would be obtained by selecting sheep in the CSR for use in the HSR. The direct selection in the individual stocking rates will yield better results since the increase of heritability in the CSR was not great enough to offset the loss caused by r_G between the two stocking rates.

The presence of sire x year interactions may have some implications in commercial breeding practice as the rams selected for breeding are normally used over several years and their progeny are exposed to year to year variations in environment.

Greasy fleece weight

Values calculated for heritability of GFW by NEI and NII methods in the pooled analyses were 0.38 ± 0.15 and 0.38 ± 0.15 in the CSR; 0.61 ± 0.21 and 0.61 ± 0.21 in the HSR; 0.39 ± 0.13 and 0.60 ± 0.17 in the combined data respectively. The estimates though somewhat higher compare well with other estimates of the heritability of GFW in New Zealand Romney hoggets (0.35 Rae, 1946; 0.32 Rae, 1958; 0.43 Tripathy, 1966; 0.29 and 0.57 Baker *et al.*, 1974). The heritabilities obtained in this study are also well within the range of estimates reported for the other breeds in the literature.

No significant differences between the heritability estimates obtained in the CSR and in the HSR were observed. The estimates were identical by two methods in the CSR and in the HSR, as sire x year interactions (NS) did not contribute to the total variation in the trait. Similar observations were recorded in the individual Sire group periods.

In the combined data analysis, sire x stocking rate interactions (NS) contributed only 1% to the total variance and formed about 7% of the total genetic variance. Genotype x nutrition interactions in GFW have also been observed as non-significant and of little importance by other workers (Morley, 1956; King *et al.*, 1959; Osman and Bradford, 1965; Carter *et al.*, 1971a). The difference in the heritability estimates (NS) between the values obtained by two methods, could largely be attributed to the significant ($P < 0.01$) sire x year interactions (4% of the total variance and 27.5% of the total genetic variance).

Since the heritabilities of GFW did not differ significantly between the two stocking rates and since no significant sire x stocking rate

interactions were detected in the combined data analysis, it seems that no meaningful differences in the ranking of sires existed.

No particular advantage would accrue by selecting sheep in the HSR (higher heritability) for use in CSR (lower heritability) despite r_G being 0.90.

Clean wool weight per unit area

Estimates for WA heritability computed in the pooled analyses by NEI and NII methods were 0.41 ± 0.19 and 0.47 ± 0.19 in the CSR; 0.31 ± 0.16 and 0.31 ± 0.16 in the HSR; 0.40 ± 0.15 and 0.49 ± 0.17 in the combined data respectively.

Although the heritability estimates were higher in the CSR than in the HSR, the differences were not significant. The two estimates of the heritability were identical in the HSR. The difference in the two heritability estimates in the CSR were non-significant. Sire x year interactions contributed 1.5% to the total variance and formed 12.7% of the total genetic variance in the CSR. These interactions were important only in the Sire group 2 period where it accounted for over 10% of the total variance but it did not contribute to the total variation in the Sire group 3 period.

In the combined data analysis, sire x stocking rate interactions (NS) did not contribute to the total variation. Identical results were recorded in the individual Sire group period analyses. Significant breed x plane of nutrition interactions for clean weight of wool fibres and clean weight of all fibres on the tattooed area were reported by King and Young (1955) from studies on a small sample of breeds and environments.

Sire x year interactions (NS) contributed slightly more than 2% of the total variance and formed about 19.1% of the total genetic variance in the combined data analysis. The difference (NS) between the two estimates by NEI and NII were due to the presence of sire x year interactions.

The absence of significant sire x stocking rate, sire x year interactions and the non-significant difference in the heritability estimates between the two stocking rates suggest that interactions are not likely to be important for WA in the flocks under study.

The high estimates for heritability in WA indicate that selection is likely to be effective if there was sufficient justification to include this as a selection criterion.

Clean scoured yield

The heritability estimates for Y obtained by two methods in the pooled analyses were 0.53 ± 0.19 and 0.53 ± 0.19 in the CSR; 0.19 ± 0.11 and 0.19 ± 0.11 in the HSR; 0.28 ± 0.10 and 0.42 ± 0.12 in the combined data respectively. There are no comparable reports for the New Zealand Romney. However, these estimates compare well with those in the literature at 1-2 years of age in other breeds (Morley, 1955a; Young *et al.*, 1960; Vesely and Robison, 1970; Mullaney *et al.*, 1970).

The heritability estimate was lower with large standard errors in the HSR when compared to the estimate in the CSR but no significant difference was observed between the two estimates. The heritability estimates were identical by NEI and NII methods both in the CSR and HSR. Sire x year interactions (NS) did not contribute to the total variance

in both the analyses. However it contributed 4.0 and 16.0% in the Sire group 1 period in the CSR (NS) and HSR ($P < 0.01$) respectively.

In the combined data analysis sire x stocking rate (NS) accounted for 2.6% of the total variance and formed a substantial fraction (24.6%) of the total genetic variance. The above results agree with Morley (1956), who reported that sire x nutrition interactions were non-significant in this trait. Dunlop (1962) however, observed significant strain x station interactions though the size of the interactions term was not large. Sire x year interactions (NS) in this analysis were relatively less important and contributed a negligible fraction to the total variance. The difference (NS) in the estimates by NEI and NII was thus largely attributable to the sire x stocking rate interactions.

The intra-trait genetic correlation calculated was 0.74 ± 0.17 (deviation from unity, $0.05 < P < 0.1$). The observed heritabilities were 0.53 and 0.19 in the CSR and HSR respectively. The ratio of the 'correlated' to the 'direct' response estimated was 1.24 suggesting that no distinct advantage would be achieved by selecting sheep in the CSR for use in the HSR.

Staple length

The heritability estimates of SL computed by NEI and NII were 0.54 ± 0.19 and 0.57 ± 0.20 in the CSR; 0.55 ± 0.20 and 0.56 ± 0.18 in the HSR; 0.57 ± 0.17 and 0.63 ± 0.18 in the combined data respectively. These estimates in general compare well with the estimates of the heritability of SL in New Zealand Romney hoggets (0.50, 0.35, 0.48 Rae, 1958; 0.46 Tripathy, 1966) and other breeds listed in Table 1.

The heritability estimates of SL in the CSR and in the HSR were almost similar. Osman and Bradford (1965) while examining genotype x location interactions in SL also did not observe any significant difference of the heritability estimates in two locations. The estimates of heritability by two methods were alike both in the CSR and HSR. Sire x year interactions (NS) were small and formed less than 1% of the total variance both in the CSR and HSR. It however, contributed over 4.1% in the Sire group 1 period in the HSR and 4.8% in the Sire group 3 period in the CSR respectively to the total variation.

Sire x stocking rate interactions (NS) did not contribute to the total variance in the combined data analysis. Similar results were obtained in the individual Sire group periods analyses. Evidence of genotype x nutrition interactions being unimportant in SL has been provided by other workers (Morley, 1956; Dunlop, 1962; Osman and Bradford, 1965). King and Young (1955) and King *et al.* (1959) also reported similar results for average fibre length. Sire x year interactions (NS) too, as in the CSR and HSR analyses were extremely small (1.3% of the total variance) in the combined data analysis. Rae's (1958) and Dunlop's (1962) observations for such interactions in SL support the results obtained for sire x year interactions in the study.

Mean fibre diameter

The heritability estimates of MFD in the pooled analyses by NEI and NII methods were 0.81 ± 0.34 and 0.87 ± 0.33 in the CSR; 0.34 ± 0.20 and 0.46 ± 0.26 in the HSR; 0.49 ± 0.20 and 0.66 ± 0.25 in the combined data respectively. The only other estimate, 0.17 ± 0.10 (DDR) for MFD

in New Zealand Romney hoggets, was reported by Tripathy (1966). It was low when compared to the values reported in the other breeds. The values derived from this study are quite comparable to Elliott's (1975) PHS (0.54 ± 0.01) and DDR (0.47 ± 0.02) in Perendales. The sampling errors were large in the present investigation because of the small number of observations available.

Although the heritabilities were comparably higher in the CSR than in the HSR, differences between the estimates were not significant. The genetic variance was reduced by the higher stocking rate resulting in the lower estimates of heritability in the HSR. It suggests that CSR is more favourable for the expression of genetic differences in this trait.

The heritability estimates were somewhat higher by NII method as compared to by NEI. However, there were no significant differences in all the three analyses between the two estimates. Sire x year interactions (NS) contributed about 1.4 and 2.9% to the total variance in the CSR and HSR respectively.

In the combined data analysis significant sire x stocking rate interactions ($P < 0.05$) accounted for 3.2% of the total variance and formed 19.7% of the total genetic variance confirming the importance of these interactions. Such observations were also made by Williams (1966) and Dunlop (1962) for MFD in experiments of similar nature. The difference (NS) between the heritability estimates by two methods in the present study was largely due to the presence of significant sire x stocking rate interactions. Sire x year interactions (NS) contributed less than 1% of the total variance and were unimportant, a similar finding to that of Dunlop (1962).

The heritabilities in this study by NEI and NII methods respectively were 0.81 and 0.87 in the CSR; 0.34 and 0.46 in the HSR. With the value of intra-trait genetic correlation being 0.93 ± 0.09 , the ratio of the 'correlated' to the 'direct' response in the HSR worked out to be 1.44 and 1.28 by NEI and NII respectively.

The high heritability estimates for MFD indicate that there is an advantage in selection for MFD as compared to the selection for the relatively less-heritable subjectively-assessed quality numbers as a criterion of fineness. If selection for finer wool was justified measuring diameter to use in the final stages of ram selection particularly in nucleus flocks could be worthwhile.

Standard deviation of the fibre diameter

The heritability estimates of SFD were 0.57 ± 0.26 and 0.58 ± 0.25 in the CSR; 0.47 ± 0.24 and 0.58 ± 0.27 in the HSR; 0.35 ± 0.15 and 0.66 ± 0.24 in the combined data respectively. There are no comparable reports for SFD in the New Zealand Romney. However, the estimates of the same magnitudes for SFD are given by Kyle and Terrill (1953), Beattie (1962) and Gjedrem (1969). Kyle and Terrill (1953) reported a heritability of intermediate magnitude for diameter variability and Beattie (1962) found a heritability of 0.43 for C.V. of fibre diameter. Heritability estimates for SFD reported by Gjedrem (1969) range between 0.31 - 0.61.

No significant differences were observed between the estimates of heritability in the CSR and HSR owing to the large standard errors.

Sire x year interactions (NS) accounted for 2.7% of the total variance in the HSR while it was negligible (0.22%) in the CSR. However, the difference (0.11) between the estimates by NEI and NII methods in the HSR was non-significant.

In the combined data analysis, sire x stocking rate interactions ($P < 0.01$) accounted for 5.5% of the total variation and 33.4% of the total genetic variation. Sire x year interactions (NS) though relatively less important, accounted for 2.4% of the total variance and were slightly over 14% of the total genetic variance.

In the combined data analysis, the ratio of sire x stocking rate and sire x year interactions to the between-sire variance was 0.91 indicating the importance of these random interactions. The large difference of the heritability estimates in the combined data analysis (0.35 vs 0.66) was however, non-significant.

The intra-trait genetic correlation between the two stocking rates was 0.52 ± 0.27 (deviation from unity, $0.05 < P < 0.1$). By selecting in CSR (heritability being 0.57) for use in the HSR (heritability being 0.47), the genetic progress for fibre variability would be at almost half of the rate of improvement obtained by direct selection.

Quality number

Estimates for QN heritability computed in the pooled analyses were 0.46 ± 0.17 and 0.46 ± 0.17 in the CSR; 0.59 ± 0.20 and 0.72 ± 0.25 in the HSR; 0.52 ± 0.16 and 0.56 ± 0.17 in the combined data respectively. These estimates are somewhat higher than the other estimates of QN in New Zealand Romney hoggets (0.25, 0.34, 0.35, 0.47 Rae, 1958; 0.35 - 0.40 McMahon, 1943) but are well within the range of estimates for other breeds reported in the literature.

The heritabilities obtained were higher in the HSR than in the CSR but the differences between the estimates were non-significant.

Sire x year interactions (NS) did not contribute to the total variance in the CSR while it formed slightly over 3% of the total variance in the HSR. The difference (0.13) between the estimates by NEI and NII methods in the HSR was however, non-significant.

In the combined data analysis, sire x stocking rate interactions (NS) contributed less than 1% of the total variance. In the individual Sire group periods as well, such interactions were unimportant. Dunlop (1962) demonstrated that strain x location interactions in QN accounted for only a negligible fraction of the variance. Sire x year interactions (NS) were not of any importance both in the pooled and individual Sire group periods. Evidence of genotype x year interactions being unimportant in this trait was provided by Rae (1958) and Dunlop (1962). The heritabilities by two methods were quite similar.

The absence of significant interactions, the similarity of heritabilities in the two stocking rates and the very high (0.95 ± 0.07) intra-trait genetic correlation indicate that sire x stocking rate and sire x year interactions are not important for QN in these groups of sheep.

Crimps per centimeter

Values calculated for heritability of CPC were 0.48 ± 0.20 and 0.56 ± 0.21 in the CSR; 0.75 ± 0.28 and 0.88 ± 0.26 in the HSR; 0.64 ± 0.22 and 0.66 ± 0.22 in the combined data respectively. The values derived from the present analyses compare well with the heritability estimate of 0.72 in New Zealand Romney hoggets by Tripathy (1966) and the estimates for other breeds.

Estimates obtained in the HSR were higher than the estimates in the CSR suggesting that HSR was more favourable for the expression of the genetic differences. However, the differences between the estimates were non-significant. The intra-trait genetic correlation calculated between the two stocking rates was 1.03 ± 0.18 .

Sire x year interactions (NS) accounted for 2.0 and 3.0% of the total variation in the CSR and HSR respectively.

The two estimates of heritability derived in the combined data analyses were similar. Sire x stocking rate interactions (NS) contributed little (0.3%) to the total variance. Morley (1956) and Dunlop (1962) also reported such interactions to be of no consequence in the trait. Sire x year interactions (NS) did not contribute to the total variance, a finding similar to that of Dunlop (1962).

Total crimp number

Estimates of the heritability were 0.65 ± 0.25 and 0.81 ± 0.27 in the CSR; 0.86 ± 0.31 and 1.09 ± 0.29 in the HSR; 0.70 ± 0.24 and 0.83 ± 0.26 in the combined data respectively. No published estimates are available on the New Zealand Romney and other breeds with which to compare the estimates obtained in this study.

Although the heritabilities obtained were higher in the HSR than in the CSR, the differences between the estimates were not significant. The intra-trait genetic correlation between the two stocking rates was close to unity (0.87 ± 0.09).

Sire x year interactions ($P < 0.05$) contributed 4.0 and 5.7% to the total variance in the CSR and HSR respectively. However, no significant differences were observed between the estimates both in the CSR and HSR analyses.

In the combined data analysis significant sire x stocking rate interactions ($P < 0.05$) accounted for 2.9% of the total variance and formed 13.8% of the genetic variance. Sire x year interactions (NS) contributed little (0.3%) to the total variation. The difference between the two estimates in the combined data was largely due to the presence of significant sire x stocking rate interactions. However, this difference was observed to be non-significant.

The present study revealed that TCN is a highly heritable trait and could be considered as a possible selection criterion for genetic improvement in some traits.

Character grade

The heritability estimates of CHG computed by NEI and NII methods were 0.24 ± 0.12 and 0.28 ± 0.13 in the CSR; 0.31 ± 0.14 and 0.32 ± 0.13 in the HSR; 0.29 ± 0.10 and 0.34 ± 0.12 in the combined data analyses respectively. These estimates in general compare well with Rae's (1958) tabulated values (DDR) 0.25 ± 0.10 , 0.16 ± 0.12 , 0.22 ± 0.07 and (PHS) 0.12 in New Zealand Romney hoggets. The heritability (0.25) calculated from the regression of hogget measurement of daughter on mature measurement of dam in his work differed non-significantly from the heritability (0.16) calculated from the hogget measurement of daughter on hogget measurement of dam. The heritability estimate of 0.12 computed from PHS correlation in Rae's (1958) work were based on

few sire degrees of freedom. The estimates derived from the present study are well within the range of estimates for other breeds reported in the literature.

There were no significant differences between the heritability estimates obtained in the CSR and HSR. The intra-trait genetic correlation calculated between the two stocking rates was close to unity (0.92 ± 0.13).

Sire x year interactions (NS) contributed little (1.2 and 0.2% in the CSR and HSR respectively) to the total variation. However, they contributed slightly over 7 and 4% in the CSR and HSR respectively to the total variation in the Sire group 3 period. No significant differences were observed in the estimates by two methods both in the CSR and HSR analyses.

In the combined data analyses sire x stocking-rate interactions (NS) contributed less than 1% to the total variation. Sire x year interactions (NS) also accounted for a negligible percentage (less than one) of the total variation, a result similar to that of Dunlop (1962). Contrary to the above results, Rae (1958) reported significant sire x year interactions in the trait. In the present investigation there were no significant differences between the heritability estimates obtained by two methods.

It has been assumed that selection for CHG in New Zealand Romney is an inefficient way of using selection potential since the heritability estimates reported so far are of low magnitude (Wickham, 1973). However, the higher estimates of intermediate magnitude in this study suggest that there is a possibility of achieving some genetic improvement in CHG by selection.

Tippiness grade

Values calculated for heritability of TG were 0.13 ± 0.09 and 0.26 ± 0.17 in the CSR; 0.27 ± 0.12 and 0.27 ± 0.12 in the HSR; 0.22 ± 0.09 and 0.22 ± 0.09 in the combined data analyses respectively. No published estimates are available for comparison.

There were no significant differences between the estimates in the CSR and HSR. Sire x year interactions (NS) explained 3.2% of the total variation in the CSR. These interactions were absent in the HSR. The difference (0.13) between the estimates obtained by NEI and NII methods in the CSR was non-significant.

None of the interactions (sire x stocking rate and sire x year interactions) contributed to the total variation in the combined analysis, although in the Sire group 3 period, sire x stocking rate and sire x year interactions explained over 3% each of the total variance. The heritability estimates obtained from the pooled data were similar by the NEI and NII methods.

In the past tippiness has generally been assumed to be largely determined by genetic factors although proof of this was lacking (Henderson, 1968). Contrary to the above, the estimates of heritability obtained in this study suggests that it is a lowly heritable fault and there is not much scope for improvement of TG through selection. It seems that tippiness in these flocks of sheep was more a result of weathering and not because of inherited variability of fibre growth rate.

Handle grade

The heritability estimates of HG computed in the pooled analyses were 0.30 ± 0.13 and 0.66 ± 0.22 in the CSR; 0.48 ± 0.11 and 0.48 ± 0.11 in the HSR; 0.23 ± 0.09 and 0.42 ± 0.15 in the combined data analyses respectively. The values derived from the present analyses compare well with the heritability estimate of 0.44 in the New Zealand Romney by Rae (1948) and are well within the range of the estimates for other breeds reported in the literature.

There were no significant differences between the estimates obtained in the CSR and HSR. The intra-trait genetic correlation between the two stocking rates was 0.90 ± 0.16 . The difference (0.30 vs 0.66) between the estimates by NEI and NII methods in the CSR approached significance ($0.05 < P < 0.1$). Significant sire x year interactions ($P < 0.05$) explained over 9% of the total variation in the CSR. Such interactions were not apparent in the HSR data.

In the combined data analysis sire x stocking rate interactions (NS) formed a negligible fraction (0.8%) of the total variation, a finding similar to that of Dunlop (1962). Such interactions were equally unimportant in the individual Sire group period analyses.

Significant sire x year interactions ($P < 0.05$) accounted for 3.8% of the total variation in the pooled analysis for the combined data. The difference (0.23 vs 0.42) of the heritability by two different methods was largely attributable to the presence of significant sire x year interactions in the combined data analysis. However, there was no significant difference between the two estimates. HG depends greatly on subjective grading and this is probably a major factor limiting the

heritability. To some extent the subjectivity of these grades may be a factor in the sire x year interactions since the graders changed between years and different graders may have emphasised slightly different facets of handle.

Lustre grade

The corresponding estimates of heritability for LG in the pooled analyses were 0.42 ± 0.16 and 0.42 ± 0.16 in the CSR; 0.32 ± 0.14 and 0.32 ± 0.14 in the HSR; 0.32 ± 0.11 and 0.39 ± 0.12 in the combined data respectively. These estimates are slightly higher than the value of 0.27 reported by Rae (1948) in New Zealand Romney. There are no other published estimates.

There were no significant differences between the estimates of heritability obtained in the CSR and HSR. The intra-trait genetic correlation calculated between the two stocking rates was 0.80 ± 0.15 .

Sire x year interactions were absent both in the CSR and HSR analyses. Such interactions were unimportant in the individual Sire group periods except in Sire group 3 period wherein it explained 6.7% of the total variation. However, sire x year interactions could not influence the heritability estimates both in CSR and HSR pooled analyses.

In the combined data analysis sire x stocking rate interactions (NS) accounted for 1.9% of the total variation; in Sire group 4 period it explained 7.3% of the total variation. Sire x year interactions were unimportant. The small difference in the two heritability estimates from the combined data analysis was due to the effect of sire x stocking rate interactions, which was not significant however.

The heritability estimates of intermediate magnitude in LG point to the possibility of improving LG by selection (if the lustre is sufficient to justify consideration in selection plans).

Greasy colour grade

Heritabilities of GCG in the pooled analyses were 0.31 ± 0.10 and 0.31 ± 0.10 in the CSR; 0.34 ± 0.14 and 0.44 ± 0.16 in the HSR; 0.22 ± 0.09 and 0.41 ± 0.15 in the combined data analyses respectively. The only other New Zealand study in Romney sheep indicated that GCG was not heritable (Rae, 1948). A small number of sheep were involved in Rae's study. Mullaney *et al.* (1970) found GCG to have medium heritability (Merino 0.29 - 0.40, Corriedale 0.29 - 0.41, Polwarth 0.24 - 0.38). Morley (1955b) reported an estimate of 0.63 for GCG in the Australian Merino.

The heritability estimates of GCG in the CSR and HSR by NEI method were almost identical. The difference of the estimates (0.31 vs 0.44) by NII method in the CSR and HSR was non-significant. The intra-trait genetic correlation calculated between the two stocking rates was 0.65 ± 0.21 (deviation from unity, $0.05 < P < 0.1$). Progress from GCG in CSR (lower heritability) by selecting in HSR (higher heritability) with NII method would be only three quarters the rate of improvement obtained by direct selection.

Sire x year interactions were unimportant in the CSR. The two heritability estimates in the CSR were identical. In the HSR analysis, sire x year interactions (NS) explained 2.5% of the total variation and 23% of the total genetic variance. The difference between the two heritability estimates however, was non-significant.

In the combined data analysis, sire x stocking rate interactions ($P < 0.05$) explained 2.4% of the total variance and formed 23.7% of the total genetic variance. Sire x year interactions (NS) also accounted for 2.2% of the total variance and 21.7% of the total genetic variance. These findings are similar to those of Dunlop (1962). The difference of the heritabilities (0.22 vs 0.41) by two different methods was non-significant.

Medium heritability estimates of GCG in this study indicate the possibility of achieving more whiteness in Romney wool by selection of GCG. The indirect selection for GCG in wool would not yield worthwhile results because of its weak genetic associations with other wool traits considered to be of importance in selection plans.

Scoured colour grade

The heritability estimates of SCG were 0.19 ± 0.11 and 0.39 ± 0.20 in the CSR; 0.12 ± 0.09 and 0.36 ± 0.15 in the HSR; 0.10 ± 0.06 and 0.30 ± 0.13 in the combined data analyses respectively. There are no comparable estimates in the New Zealand Romney. Jackson (1973) has reported an estimate of 0.20 in Australian Merinos (the only other study reported in the literature). The estimates obtained for SCG are lower than the heritability estimates for GCG, presumably because of a genetically influenced coloured contaminant being washed out during scouring or because of greater difficulty in maintaining standards during the visual grading of scoured wool.

Although the heritability estimates were higher in the CSR than in the HSR, the difference between the estimates were non-significant. The genetic variance was reduced by the higher stocking rate effect resulting in the lower estimates of heritability in the HSR. The

intra-trait genetic correlation between the two stocking rates was 0.57 ± 0.37 (deviation from unity, $0.05 < P < 0.1$). The observed heritabilities by NEI methods were 0.19 and 0.12 in the CSR and HSR respectively. The ratio of the 'correlated' to the 'direct' response estimated was 0.72 suggesting that indirect selection would be less efficient than the direct selection in HSR.

Sire x year interactions ($P < 0.05$) in the HSR explained 6.1% of the total variation and 67% of the total genetic variance. The corresponding figures for sire x year interactions ($P < 0.05$) in the CSR were 5 and 51% respectively. The ranking of sires may be very different in various years indicating that the performance of the progeny of a sire would not be highly repeatable.

In the combined data analysis, sire x stocking rate interactions (NS) accounted for 1.6% of the total variation and 20.9% of the total genetic variance. The corresponding figures for significant ($P < 0.05$) sire x year interactions were 3.4 and 45.7% respectively. The heritability estimates by NEI and NII methods were not significantly different.

The results in this study revealed that response to selection for SCG is likely to be slow.

Discoloured area grade

Values calculated for heritability of DAG by NEI and NII methods were 0.04 ± 0.07 and 0.21 ± 0.17 in the CSR; 0.20 ± 0.17 and 0.20 ± 0.17 in the HSR; 0.10 ± 0.08 and 0.10 ± 0.08 in the combined data respectively. The sampling errors were large because of the small number of observations available. There are no other published estimates.

There were no significant differences between the estimates obtained in the two stocking rates. Sire x year interactions (NS) contributed slightly over 4% to the total variation in the CSR whereas they were absent in the HSR. As a consequence, the two estimates of heritability were different (NS) in CSR.

Widely differing heritability estimates were evident from the data in the two individual Sire group periods analysed. The estimates though positive had large standard errors in the Sire group 3 period both in the CSR (0.09 ± 0.17) and HSR (0.42 ± 0.32). The corresponding estimates in the Sire group 4 period were -0.32 ± 0.35 and -0.09 ± 0.12 . A similar trend was observed in the individual Sire group periods for the combined data. The values of heritability computed from the individual Sire group periods are of limited reliability since small degrees of freedom (9 and 6 in the Sire group 3 and 4 periods respectively) were available on which to base an estimate of variance among genetic values of the sires.

It is often thought that scourable diffuse yellow discolourations in wool are inherited (Henderson, 1968) and this fault could be controlled by breeding methods. No worthwhile examination of the genetics of the trait has been made so far. Low heritability estimates for DAG in this study suggest that little genetic improvement can be made by selection on this criterion.

Cotting grade

The estimates of heritability for CG were 0.39 ± 0.15 and 0.67 ± 0.23 in the CSR; 0.12 ± 0.10 and 0.12 ± 0.10 in the HSR; 0.23 ± 0.09 and 0.23 ± 0.09 in the combined data. There are no comparable estimates in the literature.

The estimates of heritability differed widely. There were significant differences ($P < 0.05$) between the estimates by NII method in the CSR and HSR but such differences were non-significant between the estimates by NEI method.

Significant sire x year interactions ($P < 0.05$) accounted for 6.9% of the total variation and 41.5% of the total genetic variation in the CSR. This resulted in the difference (0.28) of the heritability estimates by two methods. This difference was however, non-significant because of the large standard errors. Sire x year interactions were absent in the HSR data.

In the combined data, sire x stocking rate and sire x year interactions were absent. In the individual Sire group analyses, the interactions were equally unimportant excepting Sire group 3 and 4 periods where they were small in magnitude.

Cotting is assumed to be a fault associated with heredity, fibre variability being a heritable trait of the sheep and with the environment through poor nutrition and the presence of moisture (Henderson, 1955). The low to medium size of heritability estimates of CG in this study suggest that very limited genetic improvement is likely to be achieved by selection to control cotting.

Cotted area grade

The heritability estimates of CAG computed in the pooled analyses were 0.37 ± 0.15 and 0.53 ± 0.18 in the CSR; 0.18 ± 0.11 and 0.27 ± 0.13 in the HSR; 0.23 ± 0.09 and 0.29 ± 0.11 in the combined data. No published estimates are available for CAG in the New Zealand Romney and other breeds with which to compare the results obtained in this study.

Although the heritability estimates were higher in the CSR than in the HSR, no significant differences between the estimates were observed. The genetic variance was lower at the higher stocking rate and this resulted in the lower estimates of heritability in the HSR.

Sire x year interactions (NS) contributed 4.6% to the total variation and formed 34.3% of the total genetic variance in the CSR. The corresponding figures in the HSR for such interactions were 2.3 and 33.5% respectively. The heritability estimates in the CSR and HSR by NEI and NII methods differed non-significantly. The intra-trait genetic correlation was close to unity.

In the combined data analysis, sire x stocking rate interactions (NS) contributed 1.2% to the total variation and 16.3% to the total genetic variance. Sire x year interactions were absent both in the pooled as well as the individual Sire group periods. The difference of the heritability estimates (0.23 vs 0.29) by two methods was non-significant.

It is observed that the heritability estimates for CG and CAG are comparably lower in the HSR. The genetic variance was reduced by the higher stocking rate effect resulting in the lower estimates of heritability. Since CG and CAG do not respond greatly, it seems that direct selection for these traits is an inefficient way of using selection potential.

Soundness grade

All estimates of the heritability of SG were low, the estimates being 0.22 ± 0.13 and 0.22 ± 0.13 in the CSR; 0.16 ± 0.08 and 0.16 ± 0.08 in the combined data. The equivalent results in the HSR data indicated that SG was not heritable. There are no other comparable estimates.

Environmental variations were of considerable importance in the pooled HSR analysis (reducing the genetic differences to almost zero). The ratio of the genetic to total variance was much higher in the CSR, suggesting that CSR was more favourable for the expression of the genetic differences. Similar trends were recorded in the individual Sire group periods analyses.

The intra-trait genetic correlation calculated between the two stocking rates was 1.06 ± 0.20 . With the observed heritabilities of 0.22 in the CSR and 0.00 in the HSR, the selection response of SG could only be obtained when selecting the sheep in the CSR.

Sire x year interactions were absent in all the three pooled analyses. Similar trend was observed in the individual Sire group periods analyses. Sire x stocking rate interactions were of no consequence in the combined data. However, they contributed slightly over 4% to the total variation in the Sire group 4 period while it was absent in the other two periods.

Low estimates of heritability in SG reveal that there is a little likelihood of alleviating the major factors inducing unsoundness in wool by selecting for SG.

INTER-TRAIT GENETIC CORRELATIONS

The estimates of the genetic correlations obtained in the pooled analysis for the combined data are presented in Table 18. The literature contains little information on the genetic basis of covariation among the various traits investigated in this study. Since no other published estimates are available for comparison with the present values of genetic correlations for clean wool weight per unit area, total crimp number, tippiness grade, lustre grade, scoured colour grade, discoloured area grade, cotting grade, cotted area grade and soundness grade of wool, the following discussion is mainly confined to the results in this study. Some of the genetic correlations obtained in this study exceeded the theoretical limiting value of unity; sampling errors no doubt have contributed to these results. Although the uncertainty about the real value (large standard errors because of small number of observations) do not allow definite conclusions to be drawn from the present estimates, an outline of the general pattern of direct and correlated response to selection with reference to genetic improvement of hogget live-weight, fleece weight, fineness, whiteness, cotting and soundness of wool can be sketched. The heritability results used for this purpose are those obtained from the pooled analysis for the combined data by NEI method presented in Table 16.

The information available on the genetic correlations among HLW and wool traits in sheep, though of considerable significance (extent and direction of the correlated responses expected with HLW selection), is scanty in the literature. As HLW is one of the important traits in selection plans for the Romney sheep, it is worthwhile to discuss what wool traits may change in the Romney flocks as a result of selection for HLW.

TABLE 18: Genetic correlations¹ and standard errors² among various traits from the pooled analysis of variance and covariance

Traits	HLW	GFW	WA	Y	SL	MFD	SFD	QN	CPC	TCN	CHG	TG	HG	LG	GCG	SCG	DAG	CG	CAG	SG
HLW		0.11	0.22	0.06	0.50	0.02	0.55	0.37	0.43	0.53	0.44	0.07	0.02	0.29	0.30	0.26	-0.26	0.15	0.14	0.20
GFW	0.25		0.98	0.14	0.58	0.81	0.21	0.02	0.25	0.69	0.24	0.03	-0.84	-0.20	-0.19	-0.11	-0.79	0.50	0.53	0.74
WA	0.25	0.01		0.89	0.66	0.88	-0.23	-0.02	0.04	0.43	0.18	0.19	-0.86	0.01	0.13	-0.22	-0.02	0.66	0.58	>1
Y	0.26	0.24	0.05		0.03	0.33	-0.62	-0.43	-0.32	-0.36	0.15	-0.18	0.02	0.50	0.67	0.44	<-1	0.10	0.22	0.36
SL	0.23	0.15	0.13	0.23		0.41	0.29	-0.53	-0.44	0.07	-0.28	-0.61	-0.48	0.21	-0.06	-0.23	0.22	-0.10	0.02	0.46
MFD	0.48	0.09	0.12	0.23	0.21		0.53	-0.09	0.40	0.93	0.54	0.36	<-1	-0.09	0.43	0.30	-0.88	0.77	0.75	0.46
SFD	0.36	0.23	0.44	0.17	0.23	0.21		0.26	>1	>1	0.34	0.45	-0.73	-0.77	-0.07	0.13	<-1	0.08	0.40	-0.47
QN	0.12	0.23	0.24	0.19	0.15	0.25	0.24		>1	>1	0.61	0.97	-0.16	-0.84	0.02	0.27	0.50	0.58	0.57	-0.35
CPC	0.21	0.22	0.25	0.22	0.18	0.22	a	a		0.86	0.33	0.88	-0.31	-0.87	0.12	0.40	0.31	0.71	0.68	0.14
TCN	0.18	0.12	0.21	0.22	0.22	0.18	a	a	0.06		0.54	0.72	-0.66	<-1	0.08	0.25	0.32	0.77	0.78	0.32
CHG	0.20	0.16	0.06	0.24	0.21	0.19	0.24	0.14	0.22	0.17		0.74	0.13	0.25	0.57	0.20	0.36	0.63	0.60	0.01
TG	0.27	0.26	0.27	0.26	0.16	0.25	0.24	0.02	0.06	0.13	0.12		-0.29	<-1	0.21	0.26	0.89	0.77	0.78	<-1
HG	0.27	0.07	0.06	0.26	0.19	a	0.13	0.24	0.23	0.14	0.26	0.26		0.54	0.02	0.08	-0.06	-0.50	>1	-0.57
LG	0.24	0.23	0.25	0.18	0.22	0.26	0.11	0.07	0.06	a	0.23	a	0.18		-0.02	-0.43	-0.47	-0.44	-0.71	0.08
GCG	0.25	0.25	0.27	0.15	0.25	0.23	0.29	0.25	0.26	0.26	0.18	0.28	0.28	0.27		0.85	>1	0.37	0.65	-0.47
SCG	0.31	0.31	0.32	0.26	0.28	0.11	0.13	0.28	0.27	0.30	0.31	0.33	0.34	0.26	0.10		0.34	0.35	0.67	-0.44
DAG	0.36	0.13	0.38	a	0.32	0.09	a	0.26	0.25	0.33	0.32	0.08	0.39	0.29	a	0.43		0.17	0.44	-0.19
CG	0.26	0.19	0.15	0.26	0.24	0.11	0.29	0.16	0.13	0.10	0.16	0.12	0.21	0.21	0.24	0.30	0.38		0.99	0.21
CAG	0.26	0.18	0.18	0.25	0.24	0.12	0.24	0.17	0.14	0.10	0.17	0.12	a	0.13	0.16	0.19	0.40	0.01		-0.99
SG	0.29	0.13	a	0.26	0.22	0.25	0.25	0.24	0.29	0.26	0.29	a	0.21	0.29	0.25	0.33	0.43	0.30	0.01	

¹ Genetic correlations above diagonal

² Standard errors below diagonal

a Greater than theoretical limiting value of unity

Slight positive correlated responses would be expected in GFW with HLW selection because of the low (0.11) genetic correlations among these traits. The only other Romney estimate is much higher at 0.54 (Tripathy, 1966). The range reported in the review for Merinos is -0.03 to +0.26 which is more in agreement. Small positive responses in body-weight during selection for fleece weight have been reported by Dun (1958) and Brown and Turner (1968) confirming a small positive genetic correlation between HLW and GFW. Elliott (1975) reported estimates at 0.18 in Perendales.

A medium-sized positive genetic correlation (0.50) was found for HLW with SL and is in general agreement with Mullaney *et al.* (1970) in Polwarth and Bassett *et al.* (1967) in Rambouillet. The only estimate available in Romney was 0.21 (Tripathy, 1966). Most of the other estimates in the literature were either low positive or negative. If the correlation obtained in this study is real, then it would be useful to rely on HLW selection for longer staples. Selection for HLW is a common way of using selection potential and returns can be made in terms of both HLW and SL. Conversely selection for increased staple length would improve HLW at about two-thirds the rate achieved by direct selection.

This study provides evidence that selection for increased hogget live-weight would result in better fleece character. Morley (1955b) also obtained positive genetic correlations of intermediate magnitude between HLW and CHG. Other effects of HLW selection suggested by the estimates in this study are increased variation in fibre diameter, increased quality number and crimping and more lustre.

Clean wool weight is the commercial criterion of quantity of wool and selection should have improvement of clean fleece weight as an objective. But the estimation of clean wool weight entails extra cost and efforts in collecting and measuring a sample for percentage clean yield. Greasy fleece weight is a more easily measured criterion and its genetic and phenotypic correlations with clean wool weight are both positive (0.8 to 0.9) as reviewed by Turner (1977).

High positive genetic correlations between GFW x SL (0.58) and WA x SL (0.66) were found. Selection for higher GFW would result in longer staples while selection for staple length would improve fleece weight at two-thirds the rate achieved by direct selection. The estimates for GFW x SL genetic correlations for New Zealand Romney are within the range (0.21 - 0.60) of the previous estimates reported by Rae (1958) and Tripathy (1966). Estimates of 0.70 and 0.76 have been reported respectively by Beattie (1962) in Merinos and Elliott (1975) in Perendales.

Very high negative genetic correlations for GFW x HG (-0.84) and WA x HG (-0.86) suggest that selection for higher fleece weight would result in harsh handle of wool. Estimates of similar magnitude for GFW x HG were also reported by Mullaney *et al.* (1970) in Polwarth (-0.87), Merinos (-0.47, -0.70) and Corriedale (-0.53).

Other correlated responses to be expected in the wool with fleece weight selection are less crotching and lesser susceptibility to break. Selection for GFW could result in higher degree of yellowness in wool because of its negative genetic associations with GCG, SCG and DAG. Negative genetic correlations of intermediate magnitude for GFW x GCG have also been reported by Morley (1955b) and Mullaney *et al.* (1970).

Selection for SL may result in more tippiness in wool. This is evident from the high negative genetic correlations (-0.61) between SL x TG. Other important correlated responses expected with SL selection are decrease in QN and harsher handle of wool. The negative genetic correlations of intermediate magnitude exist for SL x QN (-0.53) and SL x HG (-0.48). Rae (1958) reported the estimates for SL x QN at -0.73 (DDR) and -0.76 (PHS) in the New Zealand Romney.

If selection for fineness in wool was to be considered, the very high positive genetic correlations for MFD x GFW (0.81) and MFD x WA (0.88) would hinder progress. These are in contrast to very small genetic correlations of QN with GFW (0.02) and WA (-0.02). Tripathy (1966) and Elliott (1975) reported values of MFD x GFW at 0.58 in New Zealand Romney and 0.44 in Perendales respectively. The negative genetic correlations between QN and MFD was surprisingly small (-0.09).

A medium-sized positive genetic correlation (0.41) was found for MFD x SL. Genetic correlations of similar magnitude were reported by other workers (Schinckel, 1958; Tripathy, 1966; Elliott, 1975). A negative genetic correlation of intermediate magnitude (-0.53) between QN and SL supports the estimate obtained for MFD x SL.

The genetic correlations reported here show the antagonism for attainment of a combination of heavier fleece weight and longer staples with finer wool.

MFD has a very high negative genetic correlation with HG, a finding similar to that of Mullaney *et al.* (1970). This indicates the possibility of improving fineness by selecting for softer handle. The progress would however, be 1.5 times as rapid if selection is based on measured fibre diameter.

Other adverse correlated responses expected with reduced MFD selection includes higher degree of fibre entanglement and less sound wool.

QN is positively correlated (0.37) with HLW suggesting the possibility of positive correlated responses with HLW selection. Elliott (1975) obtained similar genetic correlations in Perendales by the PHS method. But the indirect response through HLW would be almost one-quarter as efficient as direct selection for QN.

As expected a very high positive genetic correlation was found between QN and TCN.

SFD is positively correlated (0.53) with MFD. Gjedrem (1969) also obtained a very high (0.69) genetic correlation between SFD and MFD thus supporting the estimate obtained in this study.

SFD has been observed to be very highly correlated with TCN, indicating the possibility of improving SFD through indirect selection for reduced TCN. SFD is also negatively correlated with HG (-0.73) and LG (-0.77).

The other correlated responses expected with selection for reduced variability are higher yield, more sound and less discoloured wool.

Post-scouring colour (degree of whiteness) is stated by manufacturers to be important since pure white wool can be dyed to any other colour. SCG is very highly positively correlated (0.85) with GCG, thus indicating the possibility of improving SCG by selecting for GCG. If the genetic correlation between the SCG and GCG is real (the heritabilities for SCG and GCG being 0.10 and 0.22 respectively), the 'correlated' response would be slightly more, i.e., 1.3 times the direct response.

The correlations of SCG, excepting with Y (0.44), CPC (0.40) CAG (0.67), SG (-0.44) and LG (-0.43) are low with other traits.

Morley (1955b) reported estimates at 0.31 and 0.29 for GCG x Y and GCG x CPI respectively. Mullaney *et al.* (1970) observed high genetic correlations (0.59 - 0.82) for GCG x Y.

A very high positive genetic correlation was found for GCG x DAG. Since the heritability for DAG is low (0.10), it can be changed more readily through indirect selection for GCG.

Despite positive genetic correlation of intermediate magnitudes between GCG x CHG (0.57), no worthwhile genetic improvement would be possible in GCG through indirect selection for CHG (the heritability of CHG being 0.29). Morley (1955b) however, observed a low genetic correlation at 0.18 between GCG x CHG.

Lack of tensile strength in fibres and entanglement of fibres are factors contributing to fibre breakage during processing; the reduced fibre length can be of considerable processing significance (Wickham, 1973). CG, CAG, SG, have a high positive genetic correlation with GFW (0.50 - 0.74) and WA (0.58 - 1.0). Selection for GFW or WA would result in less crotting and more sound wool by indirect selection. Since the heritabilities of CG (0.23), CAG (0.23) and SG (0.16) are comparatively lower than GFW or WA, not much advantage would be obtained by direct selection for the traits. Selection for fleece weight could be relied on to improve the traits indirectly.

High positive genetic correlations exist between CG x CHG (0.63) and CAG x CHG (0.60) but there is no correlation between SG x CHG. Selection for CHG would no doubt result in a small positive correlated response for less crotting but it would be about three-quarters as efficient as direct selection.

CG and CAG are negatively correlated genetically (-0.44 and -0.71) with LG, and there are indications of improving cotting indirectly by selecting for lower LG.

There are indications that freedom from cotting can be improved indirectly by selecting for CPC or TCN as the genetic correlations for CG and CAG with CPC and TCN both are high (the heritabilities for CPC and TCN being 0.64 and 0.70 respectively). If the correlations between the traits are real, the ratio of the 'correlated' response through TCN selection to the direct response is about 1.36. From the genetic correlations it appears that selection for TCN would also result in favourable changes in HLW, GFW, WA, TG, colour and soundness but yield, lustre and softness would decline. Surprisingly both the mean and variation in fibre diameter would increase while the quality number, CPC and LG would suggest that the wool was getting finer.

Since CG, CAG and SG are all positively correlated (0.46 - 0.77) with MFD, selection for finer mean diameter would adversely affect these traits but selection for reduced SFD would improve soundness (the genetic correlation being -0.47 between SFD and SG). CG and CAG are positively correlated (0.58 and 0.57) with QN whereas a negative correlation of medium size (-0.35) exists with SG.

CHAPTER SIX

CONCLUDING DISCUSSION ON PRACTICAL IMPLICATIONS

Genetic gains from selection within a flock or within a breed depend mainly on the heritability of the characteristics under selection, on the number of them considered in the selection objective (the greater the number of characteristics considered, the less the progress in any one of them) and the genetic correlations between them. Estimates of heritability of a character are normally made within a single macro-environment; it is usually assumed that the micro-fluctuations operate independently of the genetic variations, and that the two combine their effects additively.

In New Zealand, it is common practice to breed and select rams on stud farms which provide relatively good environmental conditions, above average husbandry and management and operate at low stocking rates to ensure adequate levels of feeding. The progeny of these rams are expected to produce satisfactorily over a wide range of environments and stocking rates but usually at lower levels of feeding and poorer husbandry. Rams selected for breeding are normally used over several years and their progeny are exposed to year-to-year variations in environment. The presence of sire x stocking rate and sire x year interactions thus have implications in commercial breeding. The usual heritability estimates based on the analyses of sire-effects nested within years and at one particular stocking level are thus not entirely appropriate for use in the formulation of selection plans; the average genetic differences can be overestimated thus reducing the effectiveness of selection. This may limit the rate of genetic improvement.

Therefore the heritability estimates applicable under the commercial conditions may well require consideration of these random interactions to increase the effectiveness of selection. The concept of predicting breeding values accurately when sire x stocking rate or sire x year interactions are present thus needs consideration before discussing the application of the results in the study.

Suppose the mathematical model underlying the analysis of the data is:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + e_{ijk}$$

where, assuming for simplicity equal subclass numbers

$$i = 1, 2, \dots, a \quad j = 1, 2, \dots, b \text{ and } k = 1, 2, \dots, n$$

μ = mean of all records of a character

α_i = the effect of i th sire

β_j = the effect of j th stocking rate or j th year

$(\alpha\beta)_{ij}$ = the effects of interaction between sire and stocking rate or sire and year

Y_{ijk} = the observation on the k th individual maintained on j th stocking rate or j th year and daughter of the i th sire

e_{ijk} = is the random error peculiar to ijk th observation and follows NID $(0; \sigma^2)$

It will be assumed that β_j are fixed effects whereas α_i and $(\alpha\beta)_{ij}$ are random effects with variances σ_α^2 and $\sigma_{\alpha\beta}^2$

The prediction of breeding values by best linear unbiased prediction assuming the variance components are known, is worked out on the following basis:

1. When $\sigma_{\alpha\beta}^2 = 0$, the regression coefficient in the prediction of α_i , given the sample is as follows

$$\frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \frac{\sigma_e^2}{bn}} = \frac{nb\sigma_{\alpha}^2}{\sigma_e^2 + nb\sigma_{\alpha}^2}$$

2. When $\sigma_{\alpha\beta}^2 \neq 0$ and it is required to rank the sires according to knowledge of their likely use over the stocking rates. If, for example, the sires are to be used equally over all stocking rates, one would rank on the basis of prediction of $\alpha_i + \frac{1}{b} \sum_j (\alpha\beta)_{ij}$, where $\frac{1}{b}$ represents the fraction of the future progeny in the j th stocking rate. In the case of data with unequal subclass numbers, the ranking of sires is based on $\alpha_i + \sum_j \lambda_j (\alpha\beta)_{ij}$, where λ_j represents the fraction of future progeny in the j th environmental situation.

The regression coefficient in the prediction of $\alpha_i + \frac{1}{b} \sum_j (\alpha\beta)_{ij}$, given the sample is as follows

$$\frac{\sigma_{\alpha}^2 + \frac{\sigma_{\alpha\beta}^2}{b}}{\sigma_{\alpha}^2 + \frac{\sigma_{\alpha\beta}^2}{b} + \frac{\sigma_e^2}{bn}} = \frac{nb\sigma_{\alpha}^2 + n\sigma_{\alpha\beta}^2}{\sigma_e^2 + n\sigma_{\alpha\beta}^2 + bn\sigma_{\alpha}^2}$$

The use of the above regression coefficient assumes that the environmental effects (i.e., stocking rates) which occurred in the sample were the same as those for which the sires are to be selected.

3. When $\sigma_{\alpha\beta}^2 \neq 0$ and in contrast to the 2. above if the β_j represent the 'year' effects and the selected sires are to be used in another set of 'years'. As the 'years' and sire x year effects which will occur in the future are unpredictable, the sires can only be ranked on their general combining ability (α_1). In most ram breeding flocks, it is very difficult to predict the stocking rates at which

the progeny of rams sold from the flock would be expected to perform, this procedure would apply to stocking rates as well as years.

The regression coefficient in the prediction of α_i , given the sample is as follows

$$\frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \frac{\sigma_{\alpha\beta}^2}{b} + \frac{\sigma_e^2}{bn}} = \frac{nb\sigma_{\alpha}^2}{\sigma_e^2 + n\sigma_{\alpha\beta}^2 + bn\sigma_{\alpha}^2}$$

The above regression coefficients in 2. and 3. above may be written in terms of heritabilities. The heritabilities by two methods (NEI and NII) given earlier in chapter 5 are in the present situation as follows

$$h_1^2 = \frac{4\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\alpha\beta}^2 + \sigma_e^2} \quad \text{and} \quad h_2^2 = \frac{4(\sigma_{\alpha}^2 + \sigma_{\alpha\beta}^2)}{\sigma_{\alpha}^2 + \sigma_{\alpha\beta}^2 + \sigma_e^2}$$

Now the regression coefficient for 2. above is as follows

$$\frac{bn h_1^2 + n(h_2^2 - h_1^2)}{1 + (n - 1) h_2^2 + (bn - n) h_1^2}$$

The second term in the numerator of the regression coefficient given above exists because of the assumption that β_j stocking rate effects are fixed and these same effects are present for which the sires are to be selected. But when the β_j represents 'year' effects and sires are to be selected for use in another set of years, the second term in the numerator should be deleted in computing regression coefficients.

The present study was undertaken with the major objectives of detecting and evaluating the role played by sire x stocking rate and sire x year interactions on various estimates of heritability of characters of economic importance (i.e., HLW, wool quantity and quality traits) in New Zealand Romney hoggets. However, in the application of these results to field conditions, it is above all, necessary to assume

that genetic and environmental relationships in other Romney flocks are similar to those in the present flock.

Before discussing the practical applications of these findings on the sheep and wool improvement in the New Zealand Romney, it is necessary to define the present objectives and the relevant selection criteria involved. The selection objectives in a particular selection group of sheep depend on the end use of the product. In the New Zealand Romney, a dual purpose sheep, HLW and fleece weight are important selection objectives. Good colour is desired in the general purpose wools. The other selection criteria considered important for the improvement of wool quality include soundness and freedom from cotting. No value is attached to changing fibre diameter (NZSAP, 1974).

The evidence presented in this study suggests strongly that sire x stocking rate interactions are real for HLW. Such interactions however, are of no importance in traits concerned with wool production. Significant sire x stocking rate interactions were found both for mean and variation in fibre diameter, TCN and GCG of wool. Sire x stocking rate interactions were however, unimportant in other wool quality traits.

Sire x year interactions were highly significant both for HLW and GFW. Such interactions were also observed significant in SCG. The only other wool quality trait (measured or subjectively assessed) affected by this random source of variation was HG.

The presence of sire x stocking rate and sire x year interactions in HLW has clear implications in commercial breeding practice. The results from the study suggested that the low (CSR) stocking rate is more favourable for the expression of the genetic differences in HLW.

The genetic variance was reduced by the high stocking rate thus resulting in the lower estimates of heritability. The importance of this interaction was further demonstrated by the low intra-trait genetic correlation between the two stocking rates. The study further substantiated that direct selection in the individual stocking rate would yield better genetic gains (13% by NEI and 28% by NII methods respectively in HSR) than indirect selection in other stocking rate. This means that the current policy of selecting breeding rams at the stud breeder's farm at low stocking rate and in above-average husbandry and management for use over a wide range of high stocking rates would severely reduce the effectiveness of selection. No doubt, the only safe course is to select the rams at the 'commercial' stocking rate but this has practical problems and limitations. It is thus suggested that while estimating heritability for use in the formulation of selection plans, it is essential to take into account the impact of the sire x stocking rate interactions in HLW. The average reduction in expected gains would be of much consequence in selection because of the decrease in heritability.

Sire x stocking rate interactions are of very small magnitude for GFW. These results are supported by the absence of such interactions in characters closely related to fleece weight. Further evidence of this observation was provided by a very large intra-trait genetic correlation between the two stocking rates. The much smaller sire x stocking rate interactions in GFW indicate that selection of rams in one stocking rate for use in the other is unlikely to hinder genetic progress and the decrease in heritability as a result of it will be of no consequence.

Sire x year interactions controlled over 4% of the total variations in HLW and GFW. Under the conditions, as the sires selected are used over a number of years, it is not feasible to narrow down the environmental fluctuations that make up the yearly environment. The only practical measure suggested by the finding of significant sire x year interactions is consideration of its effect on the heritability estimates and prediction of breeding values while formulating selection plans for HLW and GFW.

Sire x stocking rate interactions of moderate magnitude have been found significant for MFD, SFD and TCN. In the New Zealand Romney as selection for fibre fineness is seldom practiced (because of virtually no price differential for fineness in wool coarser than $33\mu\text{m}$) such interactions are of no economic importance. The low stocking rate (CSR) was more favourable for the expression of the genetic differences. Sire x year interactions were relatively less important in these traits.

Sire x year interactions of intermediate magnitude in subjectively assessed traits of wool in SCG, GCG and HG could result from the problems of subjective assessment. Difficulty in maintaining standards of visual grading from year to year and technician variation are the likely causes of such interactions. Graders changed between years and different graders may have put emphasis on slightly different facets of colour and handle. Sire x stocking rate interactions were relatively unimportant for the subjectively assessed traits (excepting GCG) in wool. Such interactions in GCG, no doubt real, contribute very little to the total variation. The decrease in heritability will be small.

A more complete assessment of the applicability of the results requires consideration of the heritability estimates and the genetic

correlations among the traits studied. It may be noted that most of the subjectively assessed traits in wool are of low to moderate heritability.

Although the heritability estimates in this study for SCG were of intermediate magnitude by NII method, the presence of significant sire x year interactions (over 5% of the total variation) reduced the average genetic differences to a great extent. The evidence presented in the study suggests that there is some possibility of achieving more whiteness in the New Zealand Romney wool by selecting for GCG whereas the response to selection for SCG is relatively very low. As SCG is very highly correlated with GCG, the 'correlated' response to selection for SCG would be slightly more, i.e., 1.3 times the direct response. It is, as well, easier to use GCG as selection criteria for wool colour.

CG, CAG and SG do not respond much to direct selection. Thus the major factors inducing cotting and lack of strength in wool cannot be alleviated easily by direct selection. Selection for fleece weight could be relied on to improve these traits indirectly. These traits are best dealt with changes in management chiefly by time of shearing in New Zealand Romney.

Fleece character is frequently considered in selection by sheep farmers, many of whom believe it to be highly heritable. The present estimates reinforces earlier observations that it is only of low to moderate heritability. Similarly tippiness, one of the components of fleece character, has heritability estimates of similar magnitude.

The high heritability estimates obtained for TCN deserves mention. The evidence presented in this study has suggested that selection for

TCN would result in favourable changes in HLW, fleece weight, colour, coting and soundness - a desirable combination in the New Zealand Romney hoggets.

BIBLIOGRAPHY

- Allden, W.G. (1968). Under-nutrition of the Merino sheep and its sequelae. II. The influence of finite periods of arrested growth on the subsequent wool growth, fleece development and utilization of feed for wool production of lambs. *Aust. J. agric. Res.*, 19 : 639-648.
- Anfinogenova, V.T. (1970). Effectiveness of selection of sheep of Kuchugury breed group under different feeding regimes. *Anim. Breed. Abstr.*, 40 : No.3226.
- Baker, R.L. (1977). Breeding for improved productivity in Romney sheep - Waikite. *Anim. Breed. Abstr.*, 45 : No.541.
- Baker, R.L., Clarke, J.N. and Carter, A.H. (1974). Sources of variation for wool, body weight and oestrus character in Romney hoggets. *Proc. N.Z. Soc. Anim. Prod.*, 34 : 23-28.
- Balch, D.J. (1965). Estimates of genetic and phenotypic parameters in Columbia and Columbia x Southdown sheep. *Diss. Abstr.*, 25 : 5508-5509. ¹⁹⁻²²
- Bassett, J.W., Cartwright, T.C., Van Horn, J.L. and Willson, F.S. (1967). Estimates of genetic and phenotypic parameters of weanling and yearling traits in range Rambouillet ewes. *J. Anim. Sci.*, 26 : 254-260.
- Bateman, N. (1971). Selection of mice for growth on constant and on changing milk diets. *Anim. Prod.*, 13 : 425-440.
- Bateman, N. (1974). Growth in mice after selection on maize-milk diets. *Anim. Prod.*, 19 : 233-248.
- Beattie, A.W. (1962). Relationship among productive characters of Merino sheep in N.W. Queensland. 2. Estimates of genetic parameters with particular reference to selection for wool weight and crimp frequency. *Qd. J. agric. Sci.*, 19 : 17-26.
- Bell, A.E. and McNary, H.W. (1963). Genetic correlation and asymmetry of the correlated response from selection for increased body weight of *Tribolium* in two environments. *Proc. XI Intern. Congr. Genet.*, 1 : 256.
- Bhasin, N.R. and Desai, R.N. (1966). Studies on inheritance of characters concerning quality of wool fibre in Chokla strain of sheep. *Indian vet. J.*, 43 : 133-137.
- Bhasin, N.R., Desai, R.N. and Kapri, R.D. (1968). Genetic inter-relationship between fibre quality attributes and their relationship with quantity of fleece in Chokla breed of sheep. *Indian J. vet. Sci.*, 38 : 626-631.

- Bosman, S.W. (1958). Heritabilities and genetic correlations between characters in Merino sheep. *Anim. Breed. Abstr.*, 28 : No.746.
- Boylan, W.J., Berger, Y.M. and Allen, C.E. (1976a). Carcass merit of Finnsheep crossbred lambs. *J. Anim. Sci.*, 42 : 1413-1420.
- Boylan, W.J., Berger, Y.M. and Allen, C.E. (1976b). Fatty acid composition of Finnsheep crossbred lamb carcasses. *J. Anim. Sci.*, 42 : 1421-1426.
- Bray, D.F., Bell, A.E. and King, S.C. (1962). The importance of genotype by environment interaction with reference to control populations. *Genet. Res.*, 3 : 282-302.
- Brown, C.J., Bangus, C.A. and Sabin, S. (1961). Evaluation of factors affecting the growth of spring lambs. *Anim. Breed. Abstr.*, 30 : No.316.
- Brown, G.H. and Turner, H.N. (1968). Response to selection in Australian Merino sheep. II. Estimates of phenotypic and genetic parameters for some production traits in Merino ewes and analysis of the possible effects of selection on them. *Aust. J. agric. Res.*, 19: 303-322.
- Brown, T.H. (1971). The effect of three factors on the incidence of tender wool in deferred grazing management. *Aust. J. exp. Agric. Anim. Husb.* 11 : 607-617.
- Bublath, A.G. (1969). Some effects of pastures species and stocking rate on sheep and pasture production. Thesis, *Degree of Master of Agricultural Science, Massey University.*
- Budanstev, V.P. (1973). Meat production of lambs sired by different rams and fattened under different conditions. *Anim. Breed. Abstr.*, 43 : No.1734.
- Builov, S.V. (1970). Inheritance of production characters of Romney Marsh sheep. *Anim. Breed. Abstr.*, 39 : No.3430.
- Burdukovskaya, T.K. and Timashev, I.Z. (1971). The effect of type of selection and level of nutrition on the heritability of fleece weight of Soviet Merino sheep. *Anim. Breed. Abstr.*, 40 : 4638.
- Burfening, P.G., Van Horn, J.L. and Blackwell, R.L. (1971). Genetic and phenotypic parameters including occurrence of oestrus in Rambouillet ewe lambs. *J. Anim. Sci.*, 33 : 919-922.
- Canon, D.J. (1972). The influence of rate of stocking and application of superphosphate on the production and quality of wool and on the gross margin from Merino wethers. *Aust. J. exp. Agric. Anim. Husb.*, 12 : 348-354.
- Carter, R.C., Carman, G.M., McClaugherty, F.S. and Haydon, R.S. (1971a). Genotype-environment interaction in sheep. I. Ewe productivity. *J. Anim. Sci.*, 33 : 556-560.

- Carter, R.C., Carman, G.M., McClaugherty, F.S. and Haydon, R.S. (1971b). Genotype-environment interaction in sheep. II. Lamb performance traits. *J. Anim. Sci.*, 33 : 732-735.
- Carter, R.C., Carman, G.M. and McClaugherty, F.S. (1973). Genotype-environment interaction in sheep. III. Lamb carcass traits. *J. Anim. Sci.*, 36 : 617-621.
- Ch'ang, T.S. (1963). Genotype-pasture interaction in the fertility of Romney Marsh ewes. *Proc. N.Z. Soc. Anim. Prod.*, 23: 100-106.
- Ch'ang, T.S. (1967). The genetic basis of growth, oestrus behaviour and fertility in Romney Marsh ewes. Thesis, *Doctor of Philosophy in Animal Science, Massey University*.
- Ch'ang, T.S. and Rae, A.L. (1970). The genetic basis of growth, reproduction and maternal environment in Romney ewes. I. Genetic variation in hogget characters and fertility of the ewe. *Aust. J. agric. Res.*, 21 : 115-129.
- Chapman, R.F. (1964). A study of changes in staple crimp within the Australian wool clip. *J. Aust. Inst. agric. Sci.*, 30: 169-180.
- Coop, I.E. (1953). Wool growth as affected by nutritional and climatic factors. *J. agric. Sci., Camb.*, 43 : 456-472.
- Cramer, D.A. and Marchello, J.A. (1964). Seasonal and sex patterns in fat composition of growing lambs. *J. Anim. Sci.*, 23 : 1002-1010.
- Cresswell, E. (1958). Energy metabolism, ranging behaviour and haematological studies with Romney Marsh and Cheviot sheep. Thesis, *Doctor of Philosophy, Massey University*.
- Cunningham, E.P. (1970). A program for large-scale non-orthogonal analysis of variance and covariance. *J. Roy. Stat. Soc. (C)*, 19 : 160-172.
- Dalton, D.C. (1962). Characters of economic importance in Welsh Mountain sheep. *Anim. Prod.*, 4 : 269-278.
- Dalton, D.C. (1967). Selection for growth in mice on two diets. *Anim. Prod.*, 9 : 425-434.
- Daly, R.A. and Carter, H.B. (1955). The fleece growth of young Lincoln, Corriedale, Polwarth and Fine Merino maiden ewes under housed conditions and unrestricted and progressively restricted feeding on a standard diet. *Aust. J. agric. Res.*, 6 : 476-513.
- De Hass, H.J. and Dunlop, A.A. (1969). The effects of some variables on the components of reproduction rate in the Merino. *Aust. J. agric. Res.*, 20 : 549-559.
- Diez, J., Quijandria, B. and Calle, R. (1974). Genetic and environmental effects on body weight and wool in Corriedales. *Anim. Breed. Abstr.*, 43 : No.1124.

- Dickerson, G.E. (1962). Implications of genetic-environmental interaction in animal breeding. *Anim. Prod.*, 4 : 47-63.
- Dickerson, G.E. (1963). Biological interpretation of the genetic parameters of populations. *Statistical genetics and Plant Breeding NAS-NRC Publication 982*.
- Dolling, C.H.S. and Piper, L.R. (1968). Efficiency of conversion of food to wool. III. Wool production of ewes selected for high clean wool weight and of random control ewes on restricted and unrestricted food intakes in pens. *Aust. J. agric. Res.*, 19 : 1009-1028.
- Doney, J.M. (1958). The role of selection in the improvement of Welsh Mountain sheep. *Aust. J. agric. Res.*, 9 : 819-829.
- Druger, M. (1962). Selection and body size in *Drosophila pseudoobscura* at different temperatures. *Genetics, Austin, Tex.*, 47 : 209-222.
- Dun, R.B. (1958). The influence of selection and plane of nutrition on the components of fleece weight in Merino sheep. *Aust. J. agric. Res.*, 9 : 802-818.
- Dun, R.B., Alexander, R. and Smith, M.D. (1966). An interaction between strain of Merino ewe and season of joining. *Proc. Aust. Soc. Anim. Prod.*, 6 : 66-68.
- Dunlop, A.A. (1962). Interactions between heredity and environment in the Australian Merino. I. Strain x location interactions in wool traits. *Aust. J. agric. Res.*, 13 : 503-531.
- Dunlop, A.A. (1963). Interactions between heredity and environment in the Australian Merino. II. Strain x location interactions in body traits and reproductive performance. *Aust. J. agric. Res.*, 14 : 690-703.
- Dunlop, A.A. and Hayman, R.H. (1958). Differences among Merino strains in resistance to fleece rot. *Aust. J. agric. Res.*, 9 : 260-266.
- Dunlop, A.A. and McMahon, P.R. (1974). The relative importance of sources of variation in fibre diameter for Australian Merino sheep. *Aust. J. agric. Res.*, 25 : 167-181.
- Dunlop, A.A. and Young, S.S. (1966). Interactions between heredity and environment in the Australian Merino. III. Sire x environment interactions. *Aust. J. agric. Res.*, 17 : 227-235.
- Dunlop, A.A., Dolling, C.H.S. and Carpenter, M.T. (1966). Efficiency of conversion of fodder to wool at two nutritional levels by three Merino strains. *Aust. J. agric. Res.*, 17 : 81-89.
- Eikje, E.D. (1975). Studies on sheep production records. VII. Genetic, phenotypic and environmental parameters for productivity traits of ewes. *Acta Agric. Scand.*, 25 : 242-252.

- Elliott, K.H. (1975). A study of inheritance of some productive traits in Perendale sheep. Thesis, *Degree of Master of Agricultural Science, Massey University.*
- Ercanbrack, S.K. and Price, D.A. (1969). Genetic and environmental interactions in growth rate of lambs. *J. Anim. Sci.*, 28 : 853, *Abstr.*
- Falconer, D.S. (1952). The problem of environment and selection. *Amer. Nat.*, 86 : 293-298.
- Falconer, D.S. (1960). Selection of mice for growth on high and low planes of nutrition. *Genet. Res.*, 1 : 91-113.
- Falconer, D.S. (1960a). *Introduction to Quantitative Genetics.* Oliver and Boyd, Edinburgh, 365 pp.
- Falconer, D.S. and Latyszewski, M. (1952). The environment in relation to selection for size in mice. *J. Genet.*, 51 : 67-80.
- Fowler, S.H. and Ensminger, M.E. (1960). Interactions between genotype and plane of nutrition in selection for rate of gain in swine. *J. Anim. Sci.*, 19 : 434-449.
- Frahm, R.R. and Kojima, K. (1966). Comparison of selection response on body weight under divergent larval density conditions in *Drosophila pseudoobscura*. *Genetics, Austin, Tex.*, 54 : 625-637.
- Fraser, A.S. (1952). Growth of wool fibres in sheep. *Aust. J. agric. Res.*, 3 : 419-434.
- Fraser, A.S. (1954). Development of skin follicle population in Merino sheep. *Aust. J. agric. Res.*, 5 : 737-744.
- Freeman, G.H. (1973). Statistical methods for analysis of genotype-environment interactions. *Heredity, Lond.*, 31 : 339-354.
- Ghoneim, K.E., Taha, A.H., Kazzal, N.T. and Abdallah, R.K. (1974). Effects of nongenetic factors and estimation of genetic parameters on fleece weight of Awassi sheep in Iraq. *Anim. Breed. Abstr.*, 42 : No.1798.
- Gjedrem, T. (1969). Phenotypic and genetic parameters for fleece weight and some wool quality traits. *Acta. Agric. Scand.*, 19 : 103-115.
- Glimp, H.A. (1971). Effect of breed, ration energy level and their interactions on rate and efficiency of lamb growth. *J. Anim. Sci.*, 33 : 157-160.
- Gol'tsblat, A.E. and Budantsev, V.P. (1973). Testing and evaluation of progeny of sires under different environments. *Anim. Breed. Abstr.*, 42 : No.5326.

- Gregory, I.P., Roberts, E.M. and James, J.W. (1978). Genetic importance of meat sheep. V. Heritability of post weaning weight and gain in Dorset and Border Leicester sheep. *Aust. J. exp. Agric. Anim. Husb.*, 18 : 63-69.
- Haldane, J.B.S. (1946). The interaction of nature and nurture. *Ann. Eugen. (Lond.)*, 13 : 197-205.
- Hall, T.H., Ruttle, J.L. and Sidwell, G.M. (1964). Some genetic and phenotypic parameters in Navajo crossbred yearling ewes. *J. Anim. Sci.*, 23 : 485-489.
- Hammond, J. (1947). Animal breeding in relation to nutrition and environmental conditions. *Biol. Rev.*, 22 : 195-213.
- Hardin, R.T. and Bell, A.E. (1967). Two way selection for body weight in *Tribolium* on two levels of nutrition. *Genet. Res.*, 9 : 309-330.
- Harvey, W.R. (1960). Least-squares analysis of data with unequal subclass numbers. *U.S.D.A., ARS 20-8*, 157 pp.
- Harvey, W.R. (1970). Estimation of variance and covariance components in the mixed model. *Biometrics*, 26 : 485-504.
- Hazel, L.W. (1943). The genetic basis for constructing selection indexes. *Genetics*, 28 : 476-490.
- Henderson, A.E. (1955). Faults in New Zealand Wool. *Lincoln College technical publication, No.12*.
- Henderson, A.E. (1965). "Wool and Woolclassing". A.H. and A.W. Reed, Dunedin.
- Henderson, A.E. (1968). "Growing Better Wool". A.H. and A.W. Reed, Wellington, 108 pp.
- Henderson, C.R. (1953). Estimation of variance and covariance components. *Biometrics*, 9 : 226-252.
- Henderson, C.R. (1954). Analysis of variance in complex balanced multiple classifications. *Cornell University, Ithaca, (NY)*, mimeo notes.
- Hill, W.G. (1974). Heritabilities : Estimation problems and the present state of information. *Proc. 1st Wld. Cong. on Genetics applied to Livestock Production, Madrid, 7-11 October, 1974, III* : 343-351.
- Hohenboken, W.D. (1976). Genetic, environmental and interaction effects in sheep. III. Wool production and gross income per ewe. *J. Anim. Sci.*, 42 : 317-323.
- Hohenboken, W.D., Corum, K. and Bogart, R. (1976a). Genetic, environmental and interaction effects in sheep. I. Reproduction and lamb production per ewe. *J. Anim. Sci.*, 42 : 299-306.

- Hohenboken, W.D., Kennick, W.H. and Bogart, R. (1976b). Genetic, environmental and interaction effects in sheep. II. Lamb growth and carcass merit. *J. Anim. Sci.*, 42 : 307-316.
- Jackson, N. (1973). *Proc. Conf. Aust. Merino Stud Breeders*. (as cited by Turner, 1977).
- James, J.W. (1961). Selection in two environments. *Heredity*, 16 : 145-152.
- Joyce, J.P. (1961). Cotting in wool and ways of reducing it. *N.Z. Jl. agric. Res.*, 103 : 335-339.
- Joyce, J.P., Clarke, J.N., Maclean, K.S., Lynch, R.J. and Cox, E.H. (1976). The effect of level of nutrition on the productivity of sheep of different genetic origin. *Proc. N.Z. Soc. Anim. Prod.*, 36 : 170-178.
- Karam, H.A. (1959). Birth, weaning and yearling weights of Rahmani sheep. I. Effects of some environmental factors. II. Heritability estimates and correlations. *Empire J. exp. Agric.*, 27 : 313-323.
- Katada, A. and Takeda, I. (1962). Genetic correlations between body weights, greasy fleece weight and staple length in Corriedale yearling sheep. *Anim. Breed. Abstr.*, 31 : No.2140.
- Kelly, R.B. (1949). *Principles and Methods of Animal Breeding*. Sydney : Angus and Robertson.
- Kempthorne, O. (1952). *The Design and Analysis of Experiments*. John Wiley and Sons, New York.
- Kempthorne, O. (1957). *An Introduction to Genetic Statistics*. John Wiley and Sons, New York.
- King, J.W.B. and Young, G.B. (1955). A study of three breeds of sheep wintered in four environments. *J. agric. Sci., Camb.*, 45 : 331-338.
- King, J.W.B., Watson, J.H. and Young, G.B. (1959). Genotype-environment interactions in the wintering of lambs. *J. agric. Sci., Camb.*, 53 : 156-171.
- Kooistra, D., Vos, M.P.M. and Politick, R.D. (1966). Effect of genetic factors and some environmental factors in fleece weight and wool quality in Texel sheep. *Anim. Breed. Abstr.*, 34 : No.2161.
- Korkman, N. (1961). Selection for size in mice in different nutritional environments. *Hereditas.*, 47 : 342-356.
- Kownacki, M. and Gebler, E. (1972). Genotype-environment interaction exemplified in mice. *Genet. pol.*, 13 : 185-191.
- Kromann, R.P. and Ray, E.E. (1967). Energy metabolism in sheep as influenced by interactions among nutritional and genetic factors. *J. Anim. Sci.*, 26 : 1379-1384.

- Kyle, W.H. and Terrill, C.E. (1953). Heritabilities and repeatabilities of fleece and body traits of Rambouillet, Targhee and Columbia sheep born in 1951. *J. Anim. Sci.*, 12 : 896 Abstr.
- Langlands, J.P. and Bennett, I.L. (1973). Stocking intensity and pastoral production. III. Wool production, fleece characteristics and the utilisation of nutrients for maintenance and wool growth by Merino sheep grazed at different stocking rates. *J. agric. Sci., Camb.*, 81 : 211-218.
- Lax, J. and Brown, G.H. (1967). The effects of inbreeding, maternal handicap and range in age on 10 fleece and body characteristics in Merino rams and ewes. *Aust. J. agric. Res.*, 18 : 689-706.
- Lax, J. and Turner, H.N. (1965). The influence of various factors on survival rate to weaning of Merino lambs. I. Sex, strain, location and age of ewe for single-born lambs. *Aust. J. agric. Res.*, 16 : 981-995.
- Lerner, I.M. (1958). *The Genetic Basis of Selection*. John Wiley and Sons, New York.
- Lundie, R.S. (1971). Studies of productive traits in a New Zealand Romney flock : the effect of some environmental factors, heritabilities and repeatabilities. Thesis, *Degree of Master of Agricultural Science, Massey University*.
- Lipson, M. and Bacon-Hall, R.E. (1974). Influence of stocking rate on the manufacturing performance and textile properties of wool. *J. Aust. Inst. agric. Sci.*, 40 : 71-73.
- Mather, K. and Jones, R.M. (1958). The interaction of genotype and environment in continuous variation. I. Description. *Biometrics*, 14 : 343-359.
- McBride, G. (1958). The environment and animal breeding problems. *Anim. Breed. Abstr.*, 26 : 349-358.
- McMahon, P.R. (1943). The inheritance of multifactor characters in sheep. *Proc. N.Z. Soc. Anim. Prod.*, 3 : 70-80.
- McManus, W.R. (1961). Stocking rate and animal production. *Wool Technol. Sheep Breed.*, 8 : 69-72.
- McManus, W.R., Arnold, G.F. (1965). Worm burdens of adult and young sheep at different stocking rates. *Aust. Vet. J.*, 41 : 364-365.
- McNary, H.W. and Bell, A.E. (1962). The effect of environment on response to selection for body weight in *Tribolium castaneum*. *Genetics*, 47 : 969-970.
- Meyer, H.H. (1974). Genotype-environment interactions for reproduction traits in ewes. *Diss. Abstr.*, 34(2) : 548.
- Morley, F.H.W. (1950). Selection for economic characters in Merino sheep. *Anim. Breed. Abstr.*, 20 : No.1704.
- Morley, F.H.W. (1951). Selection for economic characters in Australian Merino sheep. 1. Estimates of phenotypic and genetic parameters. *Sci. Bull. Dept. Agric. N.S.W. No.73*.

- Morley, F.H.W. (1955a). Selection for economic characters. V. Further estimates of phenotypic and genetic parameters. *Aust. J. agric. Res.*, 6 : 77-90.
- Morley, F.H.W. (1955b). Selection for economic characters in Australian Merino sheep. VI. Inheritance and interrelationship of some subjectively graded characteristics. *Aust. J. agric. Res.*, 6 : 873-881.
- Morley, F.H.W. (1956). Selection for economic characters in Australian Merino sheep. VII. Interactions between genotype and plane of nutrition. *Aust. J. agric. Res.*, 7 : 140-146.
- Mullaney, P.D., Brown, G.H., Young, S.S.Y. and Hyland, P.G. (1970). Genetic and phenotypic parameters for wool characteristics in Fine-wool Merino, Corriedale and Polwarth sheep. II. Phenotypic and genetic correlations, heritability, and repeatability. *Aust. J. agric. Res.*, 21 : 527-540.
- Nawara, W. (1971). Heritabilities of main production traits in Polish Merino sheep. *Anim. Breed. Abstr.*, 42 : No.1086.
- Nawara, W. and Duniec, H. (1972). Heritability of the main production traits in Polish Mountain sheep. *Anim. Breed. Abstr.*, 41 : No.2144.
- NZSAP. (1974). Guidelines for wool production in New Zealand. *N.Z. Soc. Anim. Prod., Occasional publication, No.3.*
- Osborne, R. (1951). Sexual maturity in Brown Leghorns. The interactions of genotype and environment. *Proc. Roy. Soc. Edinb., B*, 64: 445-455.
- Osman, A.H. and Bradford, G.E. (1965). Effects of environments on phenotypic and genetic variation in sheep. *J. Anim. Sci.*, 24 : 766-774.
- Osman, A.H. and Bradford, G.E. (1967). Genotype-environment interaction and compensatory growth in sheep. *J. Anim. Sci.*, 26 : 1239-1243.
- Ozcan, H. (1971). The heritabilities of live weight, greasy fleece weight, staple length, and fibre diameter and the relationship among these wool characters in Kivircik yearling sheep at Inanli. *Anim. Breed. Abstr.*, 40 : No.4648.
- Pani, S.N. (1971). Genotype x environment interaction in sire evaluation. Thesis, *Doctor of Philosophy, University of Missouri, Columbia, Mo., U.S.A.*
- Pani, S.N. and Lasley, J.F. (1972). Genotype x environment interactions in animals. *Bull. Coll. Agric. Univ. Missouri, Columbia, No.992.*

- Park, Y.I., Hansen, C.T., Chung, C.S. and Chapman, A.B. (1966). Influence of feeding regime on the effects of selection for post weaning gain in the rat. *Genetics*, 54 : 1315-1327.
- Pattie, W.A. (1965). Selection for weaning weight in Merino sheep. II. Correlated responses in other production characters. *Aust. J. exp. Agric. Anim. Husb.*, 5 : 361-368.
- Pattie, W.A. and Barlow, R. (1974). Selection for clean fleece weight in Merino sheep. I. Direct response to selection. *Aust. J. agric. Res.*, 25 : 643-655.
- Peters, H.F. and Heaney, D.P. (1974). Factors influencing the growth of lambs reared artificially or with their dams. *Can. J. Anim. Sci.*, 54 : 9-18.
- Radomska, M.J. (1965). Comparative studies of some methods of progeny testing rams. 1. Analysis of methods. *Anim. Breed. Abstr.*, 34 : No.3049.
- Radomska, M.J. and Tyszka, A. (1972). I. Phenotypic and genetic correlations of some traits in Romney Marsh sheep, *Anim. Breed. Abstr.*, 41 : No.1137.
- Radomska, M.J. and Klewicz, J. (1975). Comparative analysis of certain Romney Marsh flock. II. Genetic parameters. *Anim. Breed. Abstr.* 44 : No.1201.
- Rae, A.L. (1946). Some aspects of progeny testing of New Zealand Romney Marsh rams. *University of New Zealand, Thesis Degree of Master of Agricultural Science, Massey Agricultural College, Library.*
- Rae, A.L. (1948). Some aspects of progeny testing in sheep. *Proc. N.Z. Soc. Anim. Prod.*, 8 : 97-104.
- Rae, A.L. (1950). Genetic variation and covariation in productive characters of New Zealand Romney Marsh sheep. Thesis, *Doctor of Philosophy, Iowa State Coll., Ames.*
- Rae, A.L. (1958). Genetic variation and covariation in productive characters of New Zealand Romney Marsh sheep. *N.Z. Jl. agric. Res.*, 1 : 104-123.
- Rae, A.L. (1964). Genetic problems in increasing sheep production. *Proc. N.Z. Soc. Anim. Prod.*, 24 : 111-129.
- Robards, G.E., Williams, A.J. and Hunt, M.H.R. (1974). Selection for crimp frequency in the wool of Merino sheep. II. Efficiency of conversion of food to wool. *Aust. J. exp. Agric. Anim. Husb.*, 14 : 441-448.
- Roberts, N.F. and Dunlop, A.A. (1957). Relation between crimp and fineness in Australian Merinos. *Aust. J. agric. Res.*, 8 : 524-546.

- Robertson, A. (1959). The sampling variance of the genetic correlation co-efficient. *Biometrics*, 15 : 469-485.
- Robertson, F.W. (1959). Gene-environment interaction in relation to the nutrition and growth of *Drosophila*. *Bio. Contributions*, the University of Texas, Austin, Texas, Pub., No.5914.
- Robertson, F.W. (1963). The ecological genetics of growth in *Drosophila*.
1. Body size and developmental time on different diets. *Genet. Res.*, 1 : 288-304.
- Robertson, F.W. and Reeve, E.C.R. (1952). Heterozygosity, environmental variation and heterosis. *Nature, Lond.*, 170 : 286.
- Ryder, M.L. (1956). Observations of nutritional and seasonal changes in the fleeces of Masham sheep. *J. agric. Sci., Camb.*, 47 : 129-144.
- Ryder, M.L. and Stephenson, S.K. (1968). *Wool Growth*. Academic Press Inc. (London) Ltd.
- Schinckel, P.G. (1958). Inter-relationship of fleece and body characters and the determination of fleece structure. *Proc. Conf. Sheep and Wool Extension Officers, Hawkesbury Agricultural College, N.S.W., C.S.I.R.O. (Australia) mimeo*.
- Schinckel, P.G. and Short, B.F. (1961). The influence of nutritional level during pre-natal and early post-natal life on adult fleece and body characters. *Aust. J. agric. Res.*, 12 : 176-202.
- Searle, S.R. (1966). *Matrix Algebra for the Biological Sciences*. John Wiley and Sons, New York.
- Searle, S.R. (1968). Another look at Henderson's methods of estimating variance components. *Biometrics*, 24 : 749-787.
- Searle, S.R. (1971). *Linear Models*. John Wiley and Sons, New York.
- Searle, S.R. and Henderson, C.R. (1961). Computing procedures for estimating components of variance in a 2-way classification, mixed model. *Biometrics*, 17 : 607-616.
- Seitanova, D. (1966). The co-efficient of heritability of some basic wool characters of Mutton Merino sheep. *Anim. Breed. Abstr.*, 35 : No.2635.
- Sharkey, M.J., Davis, I.F. and Kenny, P.A. (1962). The effect of previous and current nutrition on wool production in southern Victoria. *Aust. J. exp. Agric. Anim. Husb.*, 20 : 160-169.
- Shelton, M. and Menzies, J.W. (1968). Genetic parameters of some performance characteristics of range fine-wool ewes. *J. Anim. Sci.*, 27 : 1219-1223.
- Shelton, M., Miller, J.C., Magee, W.T. and Hardy, W.T. (1954). A summary of four years work in ram progeny and performance testing. *J. Anim. Sci.*, 13 : 215-228.

- Short, B.F., Fraser, A.S. and Carter, H.B. (1958). Effect of level of feeding on the variability of fibre diameter in four breeds of sheep. *Aust. J. agric. Res.*, 9 : 229-236.
- South, A.C. (1965). The efficiency of wool growth in Merino, Corriedale and Romney sheep. Thesis, *Degree of Master of Agricultural Science, Lincoln College*.
- Southcott, W.H., Heath, D.D. and Langlands, J.P. (1967). Relationship of nematode infection to efficiency of wool production. *J. Br. Grassld. Soc.*, 22 : 117-120.
- Spedding, C.R.W. (1965). Grazing management for sheep. *Herb Abstr.* 35 : 77-84.
- Sprague, G.F. and Federer, W.T. (1951). A comparison of variance components in corn yield trials. II. Error, year x variety, location x variety, and variety components. *Agron. J.* 43 : 535-541.
- Stakan, G.A., Soskin, A.A. and Vovocenko, F. Ja. (1963). The heritability of some characters in fine-wooled sheep. *Anim. Breed. Abstr.*, 34 : No.369.
- Stansfield, W.D., Bradford, G.E., Stormont, C. and Blackwell, R.L. (1964). Blood groups and their associations with production and reproduction in sheep. *Genetics, Austin, Tex.*, 50 : 1357-1367.
- Stevens, P.G. (1946). Breeding of sheep in New Zealand. *Proc. N.Z. Soc. Anim. Prod.*, 6 : 33-45.
- Sumner, R.M.W. (1969). A comparative study of the effects of two stocking levels on wool follicle development and wool production of the N.Z. Romney sheep. Thesis, *Degree of Master of Agricultural Science, Massey University*.
- Sumner, R.M.W. and Wickham, G.A. (1969). Some effects of increased stocking level on wool growth. *Proc. N.Z. Soc. Anim. Prod.*, 29 : 208-217.
- Sumner, R.M.W. and Wickham, G.A. (1970). A comparison of follicle development of N.Z. Romney lambs at two stocking levels. *N.Z. Jl. agric. Res.*, 13 : 395-400.
- Swart, J.C. and Kotze, J.J.J. (1937). Crimp in Merino wool as a periodic function of time? *Empire J. exp. Agric.*, 5 : 69-74.
- Swiger, L.A., Harvey, W.R., Everson, D.O. and Gregory, K.E. (1964). The variance of intra-class correlation involving groups with one observation. *Biometrics*, 20 : 818-826.
- Tallis, G.M. (1959). Sampling errors of genetic correlation coefficients calculated from analysis of variance and covariance. *Aust. J. Stat.*, 1(2) : 35-43.

- Terrill, C.E. and Hazel, L.N. (1943). Heritability of yearling fleece and body traits of Rambouillet ewes. *J. Anim. Sci.*, 2 : 358. *Abstr.*
- Terrill, C.E., Sidwell, G.M. and Hazel, L.N. (1947). Effects of some environmental factors on yearling traits of Columbia and Targhee ewes. *J. Anim. Sci.*, 6 : 115-122.
- Tripathy, L.P. (1966). Estimation of some important genetic and phenotypic parameters of some productive traits in N.Z. Romney Marsh sheep. Thesis, *Degree of Master of Agricultural Science, Massey University.*
- Turner, H.N. (1977). Australian sheep breeding research. *Anim. Breed. Abstr.*, 45 : 9-31.
- Turner, H.N. and Young, S.S.Y. (1969). "Quantitative Genetics in Sheep Breeding". McMillan, Australia, 331 pp.
- Vesely, J.A. and Robison, O.W. (1970). Genotype-sex interaction in sheep. *J. Anim. Sci.*, 31 : 273-277.
- Vesely, J.A., Peters, H.F., Slen, S.B. and Robison, O.W. (1970). Heritabilities and genetic correlations in growth and wool traits of Rambouillet and Romnelet sheep. *J. Anim. Sci.*, 30 : 174-181.
- White, D.H. and McConchie, B.J. (1976). Effect of stocking rate on fleece measurements and their relationship in Merino sheep. *Aust. J. agric. Res.*, 27 : 163-174.
- Wickham, G.A. (1968). Break and tenderness in wool. *Sheepfarming Annual 1968* : 73-78.
- Wickham, G.A. (1971). Some aspects of the relation of fibre fineness estimates. *Wool*, 5(3) : 33-37.
- Wickham, G.A. (1973). Selection criteria for wool improvement by sheep breeding. *N.Z. Soc. Anim. Prod. Wool Study Group Discussion Paper, 1973.* 32 pp.
- Wickham, G.A. and Bigham, M.L. (1973). The effects of sheep management on wool characteristics. *N.Z. Soc. Anim. Prod. Wool Study Group Discussion Paper, 1973.* 29 pp.
- Willham, H.L. (1973). The infertility of sheep resulting from genotype-environment interaction. *Anim. Breed. Abstr.*, 42 : No.3775.
- Williams, A.J. (1966). The efficiency of conversion of feed to wool during limited and unlimited feeding of flocks selected on clean fleece weight. *Aust. J. exp. Agric. Anim. Husb.*, 6 : 90-95.
- Williams, A.J. (1976). Metabolism of cystine by Merino sheep genetically different in wool production. IV. Rates of entry of cystine into plasma, measured with a single intravenous injection of L- ^{35}S cystine and subsequent incorporation of ^{35}S into wool fibres. *Aust. J. Biol. Sci.*, 29: 513-524.

- Williams, A.J. and Winston, R.J. (1965). Relative efficiencies of conversion of feed to wool at three levels of nutrition in flocks genetically different in wool production. *Aust. J. exp. Agric. Anim. Husb.*, 5 : 390-395.
- Wilson, S.P., Doolittle, D.P., Dunn, T.G. and Malven, P.V. (1972). Effect of temperature stress on growth, reproduction, and adrenocortical function of mice. *J. Hered.*, 63 : 324-330.
- Yamada, Y. (1962). Genotype by environment interaction and genetic correlation of the same trait under different environments. *Jap. J. Genet.*, 37 : 498-509.
- Yamada, Y. and Bell, A.E. (1969). Selection for larval growth in *Tribolium* under two levels of nutrition. *Genet. Res.*, 13 : 175-195.
- Yates, F. and Cochran, W.G. (1938). The analysis of group of experiments. *J. agric. Sci., Camb.*, 28 : 556-580.
- Young, G.B. (1953). A study of genotype-environment interaction in mice. *J. agric. Sci., Camb.*, 43 : 218-222.
- Young, S.S.Y., Turner, H.N. and Dolling, C.H.S. (1960). Comparison of estimates of repeatability and heritability for some production traits in Merino rams and ewes. II. Heritability. *Aust. J. agric. Res.*, 11 : 604-617.