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ESTIMATION OF IMPORTANT GENETIC AND PHENOTYPIC  
PARAMETERS OF SOME PRODUCTIVE TRAITS IN  
THE NEW ZEALAND ROMNEY MARSH SHEEP

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## A C K N O W L E D G E M E N T S

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"The qualitative, or enumeration data, are classified on the 'passed' or 'failed' basis. The little Victorian servant girl, who confided to her mistress that she was just a tiny bit pregnant, would fall straight into the 'pregnant' class. In quantitative data, every individual has a class, or measurement of its own."

- H.H. Holman (1962)

# CHAPTER I

## INTRODUCTION

## Chapter I

### I N T R O D U C T I O N

Early in the 1920's, Fisher, Wright and Haldane provided the theoretical basis for studies in quantitative inheritance which was later extensively applied to animal breeding problems by Lush (1937), Dickerson and Hazel (1944) and others. The pioneering work of these authors led to the basic concept of modern animal breeding in which the objective is to change the mean value of a 'population' instead of putting emphasis on obtaining an ideal 'individual' as was common in the Mendelian era. With the occurrence of this shift of emphasis from individuals to populations, the measurements suitable for non-discrete variation had to be designed so that the production figures could be averaged and subjected to various statistical analysis. The importance of measurement in animal breeding has been discussed by McBride (1954) and Turner (1964).

Most of the economically important characters in farm animals are quantitative, and in most cases their inheritance is polygenic. The phenotypic manifestation of such characters is subject to considerable modifications by environmental influences. It is therefore customary in animal breeding experiments to try to account for environmental differences when making a genetic assessment of a certain character. The differences may be eliminated by using estimates of the effects of known components of environmental variation and adjusting the records accordingly or by design-

ing the experiments in such a way that the comparisons can be made on an equivalent basis.

The breeder of livestock is confronted with the problem of choosing between alternative breeding methods and it is therefore important for him to have the knowledge of various genetic and phenotypic parameters to guide him in predicting the responses due to a particular breeding system.

Morley (1951) emphasized the importance of these parameters, especially as applied to the sheep breeding industry in which the breeder has to satisfy a market which fluctuates considerably in its relative emphasis on meat and wool.

Rae (1958a) indicated the lack of such information in the New Zealand Romney Marsh sheep despite the importance of this breed in the sheep industry of New Zealand.

Groenewold (1963), pointed out the ever present danger of deterioration of a trait while the other traits are being improved, and suggested the desirability of selection based on the knowledge of interrelationships between the different performance traits.

Rae (1964), in outlining the genetic problems in increasing sheep production in New Zealand, has emphasized the importance of breeding of rams under the present stratification of the sheep industry where there are a relatively small number of Stud farms supplying the breeding rams, and where increase in sheep numbers is sought through higher stocking rates, thus reducing the opportunity of ewe culling.

Thus theoretical considerations as well as practical necessity

justify any investigations that provide information on different genetic and phenotypic parameters for productive traits, especially in dual-purpose sheep such as New Zealand Romney Marsh, where index selection combining various wool and mutton characters, as suggested by Lush (1945), Terrill and Hazel (1953), Karam et al. (1953) and Groenewold (1963), can be the most efficient way of increasing over-all productivity.

Lush (1945), pointed out that the following information was needed for constructing an index:-

1. Heritability of each trait.
2. Relative economic importance of each trait.
3. Phenotypic and Genetic Correlations between the traits.
4. Standard deviations of each trait.

This study provides information on the magnitude of various genetic and phenotypic parameters for greasy fleece weight, hairiness, and staple length of Romney Marsh sheep which may be compared with the estimates published by Rae (1958a). A considerable amount of data has accumulated at Massey University since his work was published, and records for hogget live-weight, mean fibre diameter and crimps per inch were also available for analysis. Therefore, it is also intended to obtain parameters for these additional traits for which no information pertaining to Romney Marsh sheep of New Zealand appears to have been published.

The summary of the scope of this work is outlined below.

1. Characters under consideration -
  - (a) Greasy fleece weight ( $Y_1$ ).
  - (b) Hogget live-weight ( $Y_2$ ).
  - (c) Hairiness ( $Y_3$ ).

- (d) Mean fibre diameter ( $Y_4$ ).
- (e) Staple length ( $Y_5$ ).
- (f) Crimps per inch ( $Y_6$ ).

2. Environmental factors -

- (a) Year of birth.
- (b) Age of dam.
- (c) Type of birth.
- (d) Regression on date of birth

3. Estimates of phenotypic parameters -

- (a) Means.
- (b) Variances.
- (c) Correlations.

4. Estimates of Genetic parameters -

- (a) Heritability.
- (b) Genetic correlations.

A brief review of literature, method of analysis, results and discussions are included and are presented as shown in the Table of Contents.

CHAPTER II

REVIEW OF LITERATURE

## Chapter II

### REVIEW OF LITERATURE

#### A. INTRODUCTION

When the obvious causes of variation have been removed, we expect that the phenotypic average of a group of animals would also be its genetic average since the plus and minus deviations of the environment would cancel each other out.

There is an abundance of estimates of various environmental effects especially for American breeds of sheep such as Rambouillet, Columbia, Targhee etc., reported throughout the literature. (Hazel and Terrill, 1945; Hazel, 1946; Terrill et al., 1947, 1948; Karam et al., 1953; Cassard et al., 1953 and others).

Morley (1951), Rae (1956), Turner (1956) and Terrill (1958) have made extensive reviews of the literature on sheep breeding and have given the magnitude of different environmental effects, heritabilities, genetic and phenotypic correlations for various productive traits of different breeds of sheep.

Heritability, defined as the proportion of the phenotypic variance due to the average effects of genes, is the fundamental genetic parameter. Combined with the selection differential it provides an estimate of the permanent genetic improvement to be expected among the



progeny.

Information on genetic and phenotypic associations among the important economic characters are especially valuable in sheep improvement where selection for the simultaneous improvement of two or more characters is the rule rather than an exception.

The present review is intended, mainly, to deal with environmental factors such as year of birth, age of dam, type of birth and regression on age. The estimates of heritabilities and genetic and phenotypic correlations reported in the literature have been presented in Tables 1, 2 and 3. A brief outline of these will be given separately for each trait.

## B. GREASY FLEECE WEIGHT

### 1. Environmental effects

Turner (1956) noted that in the Australian Merino, the American Rambouillet and allied breeds, the coefficient of phenotypic variation of greasy fleece fell in the range of 10 - 17 percent. Though exact figures for the environmental component of this variation is not known, the literature is suggestive of the fact that it is quite significant.

Apart from variations caused by suint, dirt, moisture etc., the less obvious causes such as variations in shearing technique and errors in measurement and recording are likely to make significant contributions toward environmental variations (Freney and Turner, 1938; Morley, 1951).

TABLE 1

Some estimates of heritability of the traits under study

Traits	Breed	Heritability	Remarks	Reference
Greasy Fleece wt	N.Z. Romney	0.31	Dam-dtr. regr.	Rae (1958)
		0.32	Paternal $\frac{1}{2}$ -sib cor.	
	Rambouillet	0.28	1622 Dam-off-spring pairs	Terrill & Hazel (1943)
	Aust. Merino	0.40	Parent-off-spring regr.	Morley (1955)
		0.44	Paternal $\frac{1}{2}$ -sib cor.	
	S.Afr. Merino	0.09-0.47	Dam-offspring cor. Paternal $\frac{1}{2}$ -sib cor.	Beattie (1962) Bosman (1958)
Hogget Live wt	N.Z. Romney	-	-	-
	Rambouillet	0.40	1622 Dam-off-spring pairs	Terrill & Hazel (1943)
	Aust. Merino	0.36	Parent-off-spring regr.	Morley (1951)
		0.09	Paternal $\frac{1}{2}$ -sib cor.	
		0.54	Dam-offspring cor.	Beattie (1962)
	S.Afr. Merino	0.42-0.54	Paternal $\frac{1}{2}$ -sib cor.	Bosman (1958)
Hairiness	N.Z. Romney	0.68	Dam-dtr. regr.	Rae (1958)
		0.34	Paternal $\frac{1}{2}$ -sib cor.	
Mean Fibre Diameter	N.Z. Romney	-	-	-
	Rambouillet	0.57	Paternal $\frac{1}{2}$ -sib cor.	Shelton et al., (1954)
	Aust. Merino	0.57	Dam-offspring cor.	Beattie (1962)
	S.Afr. Merino	0.29-0.34	Paternal $\frac{1}{2}$ -sib cor.	Bosman (1958)
Staple Length	N.Z. Romney	0.35	Dam-dtr. regr.	Rae (1958)
		0.48	Paternal $\frac{1}{2}$ -sib cor.	
	Rambouillet	0.36	1622 Dam-off-spring pairs	Terrill & Hazel (1943)
	Aust. Merino	0.56	Parent-off-spring regr.	Morley (1955)
		0.52	Paternal $\frac{1}{2}$ -sib cor.	
		0.50	Dam-offspring cor.	Beattie (1962)
	S.Afr. Merino	0.45-0.52	Paternal $\frac{1}{2}$ -sib cor.	Bosman (1958)
Crimps per inch	N.Z. Romney	-	-	-
	Aust. Merino	0.47	Parent-off-spring regr.	Morley (1955)
		0.28	Paternal $\frac{1}{2}$ -sib cor.	
		0.57	Dam-offspring cor.	Beattie (1962)
	S.Afr. Merino	0.32-0.41	Paternal $\frac{1}{2}$ -sib cor.	Bosman (1958)

TABLE 2

Some estimates of genetic correlations reported in the literature

	Greasy Fleece wt	Hogget Live wt	Hairiness	Mean Fibre Diameter	Staple Length	Crimps per inch
Greasy Fleece wt	-	.20 $\pm$ .24 (Beattie, 1962) -.11 (Morley, 1955)	.28 $\pm$ .16 (Rae, 1958)	.19 $\pm$ .20 (Beattie, 1962)	.25 $\pm$ .19 (Rae, 1958) .70 $\pm$ .17 (Beattie, 1962) -.02 (Morley, 1955) .30 (Doney, 1956)	-.87 $\pm$ .20 (Beattie, 1962) -.56 (Morley, 1955)
Hogget Live wt			-	-.00 $\pm$ .16 (Beattie, 1962) .68 (Bosman, 1958)	.01 $\pm$ .17 (Beattie, 1962) -.26 (Morley, 1955) -.09 (Bosman, 1958)	.15 $\pm$ .18 (Beattie, 1962) .05 (Morley, 1955)
Hairiness				-	.41 $\pm$ .12 (Rae, 1958)	-
Mean Fibre Diameter					-.11 $\pm$ .14 (Beattie, 1962) -.42 (Bosman, 1958)	-.17 $\pm$ .13 (Beattie, 1962) .19 (Bosman, 1958)
Staple Length						.18 (Morley, 1951) -.75 $\pm$ .12 (Beattie, 1962) -.34 (Morley, 1955) -.73 (Bosman, 1958)
Crimps per inch						

TABLE 3

Some estimates of phenotypic correlations reported in the literature

	Greasy Fleece wt	Hogget Live wt	Hairiness	Mean Fibre Diameter	Staple Length	Crimps per inch
Greasy Fleece wt		0.36 (Morley, 1955)	0.04 (Rae, 1958)	0.15 (Morley, 1951)	0.45 (Rae, 1958) 0.30 (Morley, 1955)	-0.21 (Morley, 1955)
Hogget Live wt			-	0.15 (Morley, 1951) 0.46 (Bosman, 1958)	0.10 (Morley, 1955) 0.30 (Bosman, 1958)	0.05 (Morley, 1955)
Hairiness				-	0.11 (Rae, 1958)	-
Mean Fibre Diameter					0.03 (Morley, 1951) 0.09 (Bosman, 1958)	-0.30 (Morley, 1951) -0.07 (Bosman, 1958)
Staple Length						-0.22 (Morley, 1951) -0.23 (Bosman, 1958)
Crimps per inch						

These sources of variation, however, can probably be considered to be unimportant, because the repeatability of greasy fleece weight has been reported to be high (Morley, 1951; Wright and Stevens, 1953; Blackwell and Henderson, 1955; Doney, 1955; and Young et al., 1960). Most figures reported lie in the vicinity of 0.60.

Yearly differences have been reported to be the most important environmental source of variation in greasy fleece weight in American Columbia and Targhee sheep (Terrill et al., 1947). Years accounted for 16 and 14 percent of the total variation in these breeds. Terrill et al. (1948) found significant year effects on greasy fleece weight in Rambouillet sheep. Price et al. (1953) reported that 2.5 percent of the total variation in Navajo and Navajo crossbred ewes' fleece production was due to the differences in years.

Type of birth, age of dam, and regression on age have all been shown to have significant effect upon greasy fleece weight.

Rae (1950) showed that in the New Zealand Romneys, fleeces from those hoggets born as singles were 0.18 pounds heavier than fleeces from twins, and twins reared singly produced 0.22 pounds more greasy fleece than singles. His results also show that hoggets born from 3-year-old dam surpassed the fleece production of hoggets born from 2-year-old dam by 0.16 pounds.

In a recent paper, Brown et al. (1966) observed that in the Australian Merino, greasy and clean fleece weight reached a maximum at  $3\frac{1}{2}$  years, then declined by 0.3 - 0.2 pounds per year. Twin-born ewes cut 0.21 pounds (4.2% of the mean) less clean wool per year over their life-time than single-born ewes, while the progeny of 2-year old ewes

cut 0.32 pounds (6.4% of the mean) less than the progeny of adults.

## 2. Estimates of parameters

In general, the estimates of heritability for fleece weight fall within the range of 0.3 - 0.5 for most breeds (see Table 1). Heritability for this character in the New Zealand Romneys has been found to be generally low as compared with other breeds. Rasmussen (1942), McMahon (1943), and Rae (1948, 1950) have all reported the heritability of greasy fleece weight in Romney ranging from 0.10 - 0.17. Possible reasons for this discrepancy were put forward by Morley (1951). Rae (1956) has made some critical comments on Morley's hypothesis in deferring the possible cause of this until further information became available. In his later work with Romneys however, Rae (1958a) reported the heritability of 0.31 and 0.32 for greasy fleece weight as determined by regression of offspring on hogget record of dam and paternal half-sib method respectively, but the sampling errors of these estimates were high.

Reports on phenotypic and genetic correlations between greasy fleece weight and other characters are few in the literature. No figures are available on the New Zealand Romneys for comparison with the phenotypic correlations obtained by Morley (1951, 1955) except for the phenotypic correlation between greasy fleece weight and staple length in which case Rae's (1958a) figure of 0.45 compares favourably with Morley's 0.30 (Table 3).

As would be obvious from the Table 2, Morley (1955) and Beattie (1962) have reported contrasting figures for genetic correlations between

greasy fleece weight and other characters, although Morley's low figures are fairly within the range of sampling errors of Beattie's estimates except that the correlation between greasy fleece weight and staple length by Morley ( $-0.02$ ) appears to be too low.

The only comparable estimate of genetic correlation between greasy fleece weight and the characters under present investigation in Romney sheep is a correlation of  $0.25 \pm 0.19$  between greasy fleece weight and staple length reported by Rae (1958a).

There does not seem to be any other work published on genetic correlations of greasy fleece weight with hairiness and fibre diameter, for which Rae (1958a) and Beattie (1962) have reported the figures of  $0.28 \pm 0.16$  and  $0.19 \pm 0.20$  respectively.

Bosman (1958), in his study of heritabilities and genetic correlations between characteristics in the South African Merino sheep, reported the phenotypic correlations of greasy fleece weight only with clean fleece weight (0.85) and staple formation score (0.35). Unfortunately, he excluded from his study the genetic correlations between greasy fleece weight and other characteristics.

O'Ferrall and Vial (1962) working with four different breeds of Irish sheep, found a positive body weight-fleece weight relationship for all breeds with the exception of Oxford Downs and two of eight groups of Galways which gave slightly negative results.

### 3. Summary

The evidence available so far indicates that response to selection for greasy fleece weight will be fairly rapid on account of

its high heritability in most breeds, and that with the exception of negative genetic and phenotypic correlations between greasy fleece weight and crimps per inch, other correlation figures do not show any major antagonism to preclude selection for greasy fleece weight in combination with other characters.

### C. HOGGET LIVE WEIGHT

#### 1. Environmental effects

Studies carried out over a number of years demonstrate that body weight at weaning and yearling stages are definitely influenced by some non-genetic sources of variation. Hazel and Terrill (1945), in emphasizing the importance of environmental effects such as age of dam, type of birth, year of birth, sex and age of the animal, pointed out that the selection effectiveness was reduced to one-half when the records for weaning weight were not adjusted for these effects.

In American Columbia and Targhee yearling ewes, Terrill et al. (1947) noted that type of birth had an important effect on body weight, accounting for 7 and 13 percent of the total variation in Columbias and Targhees respectively. Single ewes weighed 7.12 pounds more than twins and 2.37 pounds more than twins raised singly in Columbia breed. The corresponding differences for Targhees were 4.70 pounds and 7.42 pounds respectively. With farm flocks, a tendency towards a gradual disappearance of type of birth effect as the age of sheep advanced has been reported by Phillips and Dawson (1940). Phillips et al. (1940), however,



found that in range sheep, singles were heavier than twins throughout the first year. In a more recent publication, Harrington et al. (1958) showed that differences in lamb weights due to type of birth and rearing in different Rambouillet crossbred lambs became relatively less important as the lambs grew older.

Working with yearling and mature Rambouillet rams, Terrill et al. (1948) demonstrated that the environmental factors accounted for 44 percent of the total variance, this being greater than for any other trait in their studies. Years, age of dam, and type of birth were all shown to exert significant influence on body weight.

Sidwell and Grandstaff (1949) studied the environmental effects on weaning weight, whereas Price et al. (1953) made observations on yearling body weight for Navajo and Navajo crossbred sheep. In both cases, the effects of age of dam and type of birth were significant, the magnitude of the effects being greater for weaning weight.

Rae's (1950) work with the New Zealand Romney Marsh sheep revealed that 15 percent of the total variance for yearling body weight was caused by environmental differences, this being the largest value compared with the percentage of environmental influences on the other traits studies by him. Single-born hoggets weighed 6.65 pounds heavier than twin-born ones, while twins raised singly weighed 2.24 pounds less than those born single. The offspring from 3-year old dams were heavier by 1.38 pounds compared with those born from 2-year old dams.

## 2. Estimates of parameter

Heritability estimates for yearling body weight have been

reported by various workers (Terrill and Hazel, 1943; Morley, 1955; Bosman, 1958; Young et al., 1960, and Beattie, 1962).

In the Australian Merino, the estimates obtained by Young et al. (1960) for their control group of 15 - 16 month old ewes is unusually high at 0.72, but the lower limit of their estimate, 0.52 compares favourably with the estimate of 0.36 by Morley (1955) and 0.54 by Beattie (1962). Terrill and Hazel's (1943) estimate of 0.40 for Rambouillet and Bosman's (1958) 0.42 for his Stud-A (plain-bodied) South African Merino are quite consistent with other figures reported.

The genetic and phenotypic correlations between hogget live weight and greasy fleece weight have already been discussed in the previous section.

Turner (1956) has reviewed the work on phenotypic correlations between body weight and other characters. She observed that the values for phenotypic correlations between body weight and staple length and between body weight and fibre diameter, though reported to have a wide range of -0.18 to +0.34 and -0.17 to +0.23, respectively, were predominantly positive in sign. Bosman's results in 1958 support this trend. A low phenotypic correlation of 0.05 between body weight and crimps per inch has been reported for the Australian Merino (Morley, 1955). It appears that no further information on this correlation has been published to provide a comparison.

In general, the genetic association of yearling body weight with other characters under consideration has been found to be fairly consistent. Negative correlations have been reported between body

weight and staple length (see Table 2). Beattie (1962) found a negligible genetic correlation between these characters.

### 3. Summary

Apart from a minor genetic antagonism between hogget live weight and staple length, the high heritability estimates and mostly positive phenotypic and genetic correlations suggest that hogget live weight selected singly or together with other characters under study will show positive response to selection.

## D. HAIRINESS

### 1. Environmental effects

Quite a lot of work has been done on the inheritance of birth coat characters, especially after Duerden's discovery of sickle-tip fibres in Merino in 1927 and later, the full classification of birth-coat fibres by Dry (1933, 1934). Rae (1956) has outlined, in detail, the inheritance of halo hair abundance and mode of action of the N and nr genes. Referring to the work of Dry (1940) in which he discovered a major gene affecting the abundance of halo hairs in the lamb, Rae (1956) has warned against the too facile acceptance of the techniques of population genetics which are applied under the assumption that the inheritance of a quantitative character is polygenic.

The information on environmental effects, especially for later kemp and non-kemp hairiness, is scanty.

Grandstaff and Wolf (1947) found that difference between ages, years, lambs within years, and also the interaction of years x ages were highly significant for both Navajo and Navajo crossbred sheep. They sampled the fleece of these sheep at 28 day intervals from birth to one year of age and found a reduction of 5.9 percent of kemp and 20.7 percent of other medullated fibres in the fleeces of Navajo lambs. The reduction was slightly greater for both types of fibres for the crossbred lambs. Their results showed that a major part of the change occurred between the ages of 28 and 84 days. Earlier, Grandstaff and Blunn (1944) had reported that the average amount of kemp in the fleeces of Navajo lambs decreased from 15 percent at 28 days of age to 4.5 percent at 84 days, then maintained a fairly constant level until the lambs reached yearling age. Pohle et al. (1945) observed a rapid decrease in percentage medullation of hairy-fleeced lambs of the Rambouillet, Targhee, Corriedale and Columbia breeds, between 2 and 5 months of age.

Wilson et al. (1959), in studying the effects of environments on the birth coats of Rambouillet, Targhee, and Columbia lambs, noted that males had significantly less hair and wool at birth than females. Single Rambouillet and Columbia lambs were more hairy than twins but type of birth had no significant effect on wool covering. In general, the offspring of younger dams exhibited significantly less hair and wool than the offspring of older dams, but Targhee lambs from 6-year old dams exhibited significantly more wool than lambs from 7-year old dams.

Goot (1945a) demonstrated that variations in the amount of hairiness in the fleece of New Zealand Romney Marsh sheep were due to

level of hairiness or individuality (51%), age (17%), season (4%) and various interactions among these sources (20%). The 'wet' ewes were found to be slightly, but statistically significantly less hairy than 'dry' ewes.

Rae (1950) attributed 3 percent of the total variance in non-kemp hairiness in New Zealand Romney ewe hoggets to environmental effects. He found that twins and twins raised singly were .08 and .05 log-units more hairy than singles. His value of regression on age for this trait was negligible.

## 2. Estimates of parameters

In analyzing scores for birth-coat in a flock of Welsh mountain sheep, Rendel (1954) found a regression of offspring score on midparent score to be 0.6 showing that the character was highly heritable.

Morley (1955) found that heritability of coat score in the Australian Merino was 0.80 and 0.59. These two values were obtained by parent offspring regression and half-sib correlation respectively.

The only estimates of heritability of percentage medullation (non-kemp hairiness) reported for yearling sheep are those published by Rae (1948, 1950) for New Zealand Romney ewe hoggets. His previous figure of 0.50 - 0.70 is quite consistent with his later estimate of 0.63.

Phenotypic and genetic correlations between hairiness and other characters have not been published for any other breed except the New Zealand Romney. Rae (1958) has reported the phenotypic and

genetic correlations between hairiness and quality number, staple length, fleece quality and fleece weight. To mention the magnitude of correlations concerned with this study, Rae's values for phenotypic correlations between hairiness and greasy fleece weight and between hairiness and staple length were 0.04 and 0.11 respectively. The corresponding genetic correlations were 0.28 and 0.41 (see Table 2 and 3).

Phenotypic and genetic association of hairiness with hogget live weight, mean fibre diameter and crimps per inch has not been reported in the literature.

### 3. Summary

There is not enough information available as yet to include hairiness as a component in a selection index. The genetic correlations mentioned above have large sampling errors but they indicate that selection for increased greasy fleece weight will result in longer staple and increased hairiness. If individual selection was to be done with a view to reduce hairiness in the offspring, the heritability figures suggest strongly that individuals with high hairiness be culled.

## E. MEAN FIBRE DIAMETER

### 1. Environmental effects

Specific information on environmental influences, such as type of birth and age of dam, on mean fibre diameter do not appear to

be available in the literature. However, a substantial amount of information on the regional variations in the thickness of fibres has been reported (Turner, 1956).

With the exception of the Indian breeds, wool on the rump or thigh has generally been found to be coarser than on the shoulder (Turner, 1956).

Reimers and Swart (1930) reported that wool from 'on' a fold was more variable in diameter than wool from 'in' a fold.

Ensminger (1942) sampled 9 regions on Shropshire and Southdown sheep and found the general body region to be uniform with finer wool on the head and stronger on the rump and breech. In the Finnish sheep, the shoulder wool was finest and the thigh wool strongest (Vainikainen and Hakola, 1952).

Turner et al. (1953) recommended the midside for general use with two additional sites, one near the hipbone and the other just behind the front leg, on the edge of the belly.

In studying the aspects of heavy stocking in the Australian Merino sheep, it was observed (C.S.I.R.O., 1965) that in the Canberra environment, wool fibres tended to be finest in Summer and variable in Winter. This seasonal variation in fibre diameter was found to be too great to have been contributed by stocking rate alone and much of its cause was attributed to the low quality of the phalaris annual grass sub clover pastures in Summer.

Short et al. (1958), working with the Australian Merino, showed that the effect of falling feed level on the ratio of mean

diameters of primary (P) and secondary (S) fibres was proportionately greater when the diameter ratio exceeded 1.0 than when it was less than 1.0, thus lending support to Lang's (1945) conclusion that under stress conditions producing 'tenderness' in wool staples there is a differential response of fibre diameter, particularly in those wools with a wide range of fibre diameters. Their analysis of variance of S/P ratio revealed that under considerable nutritional stress there had been no cessation of fibre formation, unless of course cessation was distributed amongst the secondary and primary fibres in the ratio S/P.

The results of Short et al. (1958) are not in agreement with those of Lockart (1956) who found no indication of primary and secondary fibres differing markedly in their responses to change in nutrition.

Schinckel (1958) reported that in the Australian Merino, coarse birthcoats were associated with increased variability of fibre diameter and decreased crimp rate, the increased variability of fibre diameter being the result of a significant increase in the diameter of primary fibres and a small, but statistically non-significant decrease in the diameter of secondary fibres. Earlier, Lockart (1956a) had found a correlation of 0.83 between birthcoat grade and primary-secondary diameter difference in the adult.

## 2. Estimates of parameters

In most studies, mean fibre diameter has been neglected in favour of other characters which give a reflection of this character,



and are also easily measured. These other characters, for example, crimps per inch, quality number and fleece quality, have a more direct bearing on the commercial value of wool.

The heritability of mean fibre diameter reported in the literature range from 0.28 to 0.57 (see Table 1). No heritability estimate of this trait has been published for the New Zealand Romneys, though this parameter is available for the related traits, quality number and fleece quality (Rae, 1958a).

Quality number or 'spinning count' is the trade assessment of fibre diameter for which grading is mainly done on number of crimps per inch. Lang (1947a) and Roberts and Dunlop (1955), however, have shown that the relationship between crimp and diameter is by no means constant, and that the assessment of diameter on the basis of crimp can be erroneous. Estimates of heritability of quality number for the New Zealand Romney are:- 0.35 - 0.40 (McMahon, 1943), 0.41 (Rae, 1948) and 0.27 (Rae, 1958a). Morley (1951) reported the heritability of this trait for the Australian Merino to be 0.28 and 0.40 as determined by paternal half-sib correlations and parent offspring regression, respectively. Bosman's (1958) figures for the South African Merino are, respectively, 0.20 and 0.19 for Studs A and B.

Fleece quality includes a number of features that are considered as important in manufacturing and is related to wool buyers concept of 'style' (Henderson and McMahon, 1947). Estimates of heritability of this trait for the New Zealand Romneys are 0.14 (McMahon, 1943), 0.14 (Rae, 1948) and 0.22 (Rae, 1958a).

The genetic and phenotypic correlations between mean fibre

diameter and greasy fleece weight, hogget live weight and hairiness have been dealt with in the previous sections of this chapter. Information on the magnitude of these parameters are non-existent for the New Zealand Romney Marsh.

The correlations between mean fibre diameter and staple length, and mean fibre diameter and crimps per inch are not numerous in the literature for any breed (see Table 2) and, again, such information is entirely lacking in the New Zealand Romney.

Davenport and Ritzman (1926), while studying crosses between various breeds of sheep, arrived at the conclusion that fibre length and fibre diameter were inherited independently. Basing her statement on her unpublished work, Turner (1956) suggested the possibility of independent inheritance of staple length and fibre number.

### 3. Summary

Apart from what has already been discussed about mean fibre diameter in relation to the other characters, there is no worthwhile addition to be made.

Turner (1956) has stipulated that if further information supported the indications of lack of genetic correlation between staple length and fibre diameter, and between staple length and fibre number, it should be possible to select without difficulty any desired combinations of length and number. As Table 2 shows, there does not seem to be such a lack of genetic correlations.

## F. STAPLE LENGTH

### 1. Environmental effects

Pohle and Keller (1943) considered the importance of staple length in wool production, and reviewed the literature. McMahon (1948) showed that staple length was important in relation to fineness, since wools which were too long for their fineness could fetch lower prices because they were abnormal and a repeat order could not be relied on.

Some estimates of environmental effects on staple length have been reported for some American breeds of sheep (Terrill et al., 1947, 1948; and Price et al., 1953).

Year differences were the most important cause of variation, accounting for 11 percent of the total variation in Columbias and 9 percent in Targhees (Terrill et al., 1947). The type of birth effect was greater for Targhees than Columbias. In both breeds, singles had longer staple than twins and twins raised singly, and twins had longer staple than twins raised singly. Age of dam, age at shearing, and inbreeding had no significant effect on staple length.

In Rambouillet rams, Terrill et al. (1948) found years and age at shearing the only two environmental factors having significant influence on staple length, years accounting for 5 percent and age at shearing 1 percent of the total variance.

Price et al. (1953) stated that in Navajo and Navajo cross-bred ewes, differences between breeding groups were the most important source of variation accounting for about 24 percent of the total

variance. As yearlings, the progeny from mature dams had 0.18 cm. longer staple than those from 2-year old ewes. Hazel and Ferrill (1946) found this difference to be 0.12 cm. in Rambouillets.

Rae (1950) found 3 percent of the total variation being caused by type of birth, age of dam and regression on age. Twins and twins raised singly had, respectively, 0.42 cm. and 0.30 cm. longer staples than singles. The difference due to age of dam was very small, the offspring of 2-year old dams having 0.04 cm. longer staple than the offspring of 3-year old dams.

## 2. Estimates of parameters

Heritability estimates of staple length, measured as a yearling trait, have been published by Hazel and Ferrill (1945, 1946a) for Rambouillets; by Morley (1951, 1955) for the Australian Merinos; by Rae (1948, 1958a) for the New Zealand Romney Marsh and by Bosman (1958) for the South African Merino sheep.

As would be clear from Table 1, the heritability of staple length is fairly high for all breeds of sheep reported in the literature. The reported heritabilities were determined under widely different environmental conditions; hence, considerable reliance can be placed on the conclusion that staple length is highly heritable.

The genetic and phenotypic correlations between staple length and other characters (greasy fleece weight, hogget live weight, hairiness and mean fibre diameter) have already been mentioned in the preceding sections.

The additional information, genetic and phenotypic correlations between staple length and crimps per inch, has been given by Morley (1955), Bosman (1958) and Beattie (1962). (See Table 2).

### 3. Summary

A strong genetic antagonism between staple length and crimps per inch suggests that these traits can not be improved simultaneously.

From the evidence published so far, there also appears to be a moderate genetic antagonism ( $r_g = -0.26$ ; Morley, 1955) between staple length and hogget live weight.

## G. CRIMPS PER INCH

### 1. Environmental effects

Variation in crimp number in different body regions has been studied by Reimers and Swart (1930), Narayan (1951), Turner et al. (1953) and Lockart (1954). Reimers and Swart (loc.cit.) gave the midside value higher than the value for shoulder or rump for the South African Merino. Narayan (loc.cit.) found considerable regional variation in wool character including crimps per inch for the Indian Pattawadi sheep. In both sets of Australian data, the latter workers observed a dorso-ventral trend and found that midside value was higher than the value for shoulder or rump area.

Lang (1947) has discussed the question of whether number of crimps is reliable guide to fineness, and has summarized the literature.

## 2. Estimates of parameters

The heritability estimates of crimps per inch for different breeds of sheep have been summarized in Table 1. The genetic and phenotypic correlations between crimps per inch and other traits under investigation have been dealt with in the preceding sections. Genetic parameters for crimps per inch have not been published for the New Zealand Romneys.

## 3. Summary

Preponderance of the negative genetic and phenotypic correlation between crimps per inch and the other characters studied indicates that fineness (as indicated by the number of crimps per inch) will decrease when other fleece characters are being improved.

## CHAPTER III

### SOURCE OF DATA

## Chapter III

S O U R C E   O F   D A T A

The investigations are based on the records collected over the years (1956 to 1964 inclusive) from College Progeny Test Ewe hoggets maintained at Massey University. This flock of Romney Marsh sheep has been described by Ch'ang (1955), Rae (1958a, 1958b) and Clarke (1963).

Management, typical of Manawatu area, was applied to all animals. Young replacement ewes were selected at random and were mated to lamb for the first time as two-tooths. Young rams were obtained from different sources of Romney Stud flocks in the Manawatu-Wairarapa area. Mature ewes were cast for age at about five-and-a-half years. No deliberate selection was practised for any character throughout the history of the flock.

The flock can therefore be considered to be a fairly representative sample of the Romney sheep of Manawatu. The chance of inbreeding in this data is very small on account of acquiring breeding rams from different Stud flocks and therefore it has been assumed that inbreeding is not a source of variation in the present study.

The records used in this investigation do not allow the estimation of a sire x year interaction as different sires were used each year.

Because of nonavailability of records for certain traits in



certain years, the estimates of environmental effects are based on different degrees of freedom. Complete records were available for the traits greasy fleece weight, hogget live-weight, hairiness and staple length from year 1958 to 1964, and therefore, environmental factors have been estimated for these traits with greatest degrees of freedom. Records on crimps per inch were not available for the year 1958 and the hoggets born in 1964 had no records for mean fibre diameter.

In Dam-Daughter regression analysis the dams born in 1956 and 1957 were included, but those born earlier were discarded because they had records for only a few characters and their use would inevitably complicate the analytical procedure without offering a great deal of increased accuracy of the analysis.

Most lambs were born in August and September. Coding the date of birth as one for 15 July, the average date of birth was 45, indicating that the majority of lambs were born between the last week of August and the first week of September.

The lambs were shorn at weaning in January. The measurements of fleece production used in this work therefore represent the growth of about 10 months between weaning and hogget shearing in October. Records for greasy fleece weight were taken immediately after shearing and recorded to the nearest tenth of a pound. Belly wool was included in the measurement.

The hogget live-weight used in this study is the post-shearing weight of the hoggets usually obtained within two weeks of shearing. The measurement was made to the nearest pound.

The amount of hair present in the fleece was determined by the use of medullameter as described by McMahon (1937). Samples obtained from position No.5 on the hind-quarter prior to shearing were used for the determination of hairiness. This position has been shown to be highly correlated (0.92) with total hairiness (Goot, 1945).

The mean fibre diameter was measured on samples from the midside position obtained from the fleece after shearing. One hundred and fifty fibres were measured for each sample in microns by using the method described by Lang (1947), and ASTM (1955).

Staple length was measured on the midside sample taken from the fleece after shearing and was recorded to the nearest half-centimeter. In actual analysis the figures for staple length were rounded off to whole numbers in order to facilitate proper organization of fields on I.B.M. data cards.

Lang (1947) has described the method of measuring the trait : crimps per inch. The measurement was done with the staple straightened, but at rest, as suggested by Lang, and the number of crimps was counted in relation to length of the staple in centimeters. This was later converted to crimps per inch by multiplying with the factor 2.54. For example, if a 10 cm long staple had 20 crimps, the crimps per inch was obtained as  $\frac{20}{10} \times 2.54 = 5.08$  crimps per inch.

CHAPTER IV

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METHOD OF ANALYSIS  
AND RESULTS

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## Chapter IV

METHOD OF ANALYSIS  
AND RESULTS

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A. ESTIMATION OF ENVIRONMENTAL EFFECTS

To make a meaningful genetic assessment of a quantitative character, it is essential to know the effect of various environmental factors influencing the manifestation of that character. In practical sheep breeding, it is possible to estimate the effects of some known environmental factors and to use these estimates to adjust the production records. These environmental effects obscuring genetic differences between sheep are thus eliminated, and accuracy of selection for genetic merit greatly increased.

In the present study, the effects of age of dam, type of birth, year of birth and regression on date of birth have been determined. The age of dam classification was divided into three classes: two-tooths, four-tooths and six-tooths or full mouths. The type of birth classification was also divided into three classes: singles, twins, and twins reared as singles.

Regression on date of birth was included as an independent variable.

### 1. Least squares model

The number of ewe hoggets in each of the classifications can be seen from Matrix A (Table 4). Matrix A was used to determine the above environmental effects for the characters greasy fleece weight ( $Y_1$ ), hogget live-weight ( $Y_2$ ), hairiness ( $Y_3$ ) and staple length ( $Y_4$ ). Because of missing records (see Chapter III) Matrices B and C (Tables 5 and 6) had to be formed to estimate the environmental effects on mean fibre diameter ( $Y_4$ ) and crimps per inch ( $Y_6$ ) respectively.

Yates (1934) put forward the method of least squares for the analysis of multiple classification tables with disproportionate subclass numbers. Hazel (1946) extended Yates' method to include independent variables.

The method used in the present study is similar to that of Hazel (1946) and Kempthorne (1952).

Similar mathematical models were used to solve the normal equations shown on Table 4, 5 and 6.

In the case of matrix A the constants fitted were 7 for years, 3 for age of dam, 3 for type of birth and one for regression on age, whereas the constants fitted for years in B and C matrices were 6 for years, the number of other constants being the same as in Matrix A.

The linear model assumed was:-

$$Y_{ijkl} = \mu + r_i + a_j + t_k + \beta(X_{ijkl} - \bar{X}) + e_{ijkl},$$

$$i = 1, 2, \dots, p$$

$$j = 1, 2, \dots, q$$

$$k = 1, 2, \dots, r$$

and  $l = 1, 2, \dots, n_{ijk}$

where,

$Y_{ijkl}$  = record of the  $l^{\text{th}}$  hogget of  $k^{\text{th}}$  type of birth, belonging to  $j^{\text{th}}$  age of dam classification and born in  $i^{\text{th}}$  year.

$\mu$  = Overall mean.

$r_i$  = Effect of year  $i$ .

$a_j$  = Effect of age of dam  $j$ .

$t_k$  = Effect of type of birth  $k$ .

$\beta (X_{ijkl} - \bar{X})$  is regression on date of birth with  $X_{ijkl}$ 's measured about their mean  $\bar{X}$ .

$e_{ijkl}$ 's are assumed to be uncorrelated random errors with mean = 0 and variance =  $\sigma^2$ .

Interactions were not included in the model because their inclusion would greatly increase the amount of computation and also because the review of literature indicated that they were not important.

Under the assumptions applied to the  $e_{ijkl}$ 's and considering that there are no interactions, Kempthorne (1952) has suggested the validity of the use of least squares.  $e_{ijkl}$ 's must further be assumed to be normally distributed for testing the differential effects amongst the classifications.

Theoretically, the least squares estimates of the population parameters  $\mu$ ,  $r_i$ ,  $a_j$ ,  $t_k$  and  $\beta$  are obtained by minimizing the sums of

squares of deviations -

$$Q = \sum_{ijkl} [y_{ijkl} - \mu - r_i - a_j - t_k - \beta(X_{ijkl} - \bar{X})]^2$$

and then setting up the normal equations by differentiating with regard to each parameter and equating to zero. For example, the normal equation for  $\mu$  is derived by differentiating the expression  $Q$  with respect to  $\mu$  and then equating the partial derivative to zero. This procedure is repeated for the remaining parameters. The normal equation for  $\mu + r_1$  in Matrix A (Table 4) reads  $18 a_1 + 38 a_2 + \dots + (-306.307)\beta = 894.6 = 9862.0 = 1093.1 = 1628.0$ .

In actual practice the matrix coefficients for various subclasses are obtained by actually counting the number of animals belonging to each subclass for each equation to form the variance - covariance matrix. In the present analysis the coefficients were obtained by punching different identifications on I.B.M. cards and sorting them on the sorter of the I.B.M. data processing unit.

In order to reduce the amount of work involved in matrix operations, use was made of the absorption method given by Henderson (1948). This method consists in combining the  $\mu$  with the various  $r_i$ . In the  $r_i$  equations, all terms except the  $\mu$  and  $r_i$  are transposed to the right hand sides of the equations and are then divided by the common coefficient of  $\mu$  and the specific  $r_i$ . These  $\mu + r_i$  values are then substituted in all the remaining equations.

#### Solution of normal equations

Examination of normal equations in Matrix A (Table 4)

TABLE 4

LEAST SQ. EQUATIONS FOR ESTIMATING THE EFFECTS OF  $\gamma_i, a_j, t_k$  AND  $\beta(x_{ijkl} - \bar{x})$  ON TRAITS  $Y_1, Y_2, Y_3$  AND  $Y_5^*$

MODEL:  $-Y_{ijk} = \mu + T_i + a_j + t_k + \beta(x_{ijkl} - \bar{x}) + e_{ijkl}$

MATRIX A

TOTAL NO. 801

MATRIX A								TOTAL NO. 801											
MODEL :- $y_{ijkl} = \mu + \tau_i + \alpha_j + \beta(x_{ijkl} - \bar{x})$																			



TABLE 5

LEAST SQ. EQUATIONS TO ESTIMATE THE EFFECTS OF  $\tau_i, a_j, t_k$  &  $\beta(x_{ijkl} - \bar{x})$  ON M.F.DIA. ( $Y_4$ ) \*

MATRIX B

MODEL :-  $Y_{ijkl} = \mu + \tau_i + a_j + t_k + \beta(x_{ijkl} - \bar{x}) + e_{ijkl}$ 

TOTAL NO. 686

	$\mu + \tau_1$ (1958)	$\mu + \tau_2$ (1959)	$\mu + \tau_3$ (1960)	$\mu + \tau_4$ (1961)	$\mu + \tau_5$ (1962)	$\mu + \tau_6$ (1963)	$a_1$	$a_2$	$a_3$	$t_1$	$t_2$	$t_3$	$\beta(x_{ijkl} - \bar{x})$	$\sum Y_{ijkl}$
(1) $\mu + \tau_1$	112						18	38	56	37	71	4	-326.061	3936.70
(2) $\mu + \tau_2$		102					25	22	55	47	54	1	-79.038	3270.97
(3) $\mu + \tau_3$			121				33	34	54	76	37	8	-1152.682	4253.66
(4) $\mu + \tau_4$				136			33	35	68	44	85	7	+170.283	4840.80
(5) $\mu + \tau_5$					109		33	38	38	42	64	3	+1416.146	4138.47
(6) $\mu + \tau_6$						106	25	27	54	41	60	5	-28.648	4046.78
(7) $a_1$	18	25	33	33	33	25	167	0	0	99	62	6	+328.810	5910.38
(8) $a_2$	38	22	34	35	38	27	0	194	0	85	100	9	+100.947	6995.35
(9) $a_3$	56	55	54	68	38	54	0	0	325	103	209	13	-429.757	11581.65
(10) $t_1$	37	47	76	44	42	41	99	85	103	287	0	0	-219.469	10170.85
(11) $t_2$	71	54	37	85	64	60	62	100	209	0	371	0	+269.734	13294.44
(12) $t_3$	4	1	8	7	3	5	6	9	13	0	0	28	-50.265	1022.09
(13) $\beta(x_{ijkl} - \bar{x})$	-326.061	-79.038	-1152.682	170.283	1416.146	28.648	328.810	100.947	-429.757	-219.469	269.734	-50.265	+101871.000	-73.80

\* Numbers on the upper left and right corners of the elements are to facilitate the computation by the use of IBM Computer (See the text)

TABLE 6

LEAST SQ. EQUA<sup>NS</sup> TO ESTIMATE THE EFFECTS OF  $\gamma_i, a_j, t_k$  &  $\theta(x_{ijkl} - \bar{x})$  ON CRIMPS/INCH ( $y_6$ )\*

MATRIX C		MODEL:- $y_{ijkl} = \mu + r_i + a_j + t_k + \theta(x_{ijkl} - \bar{x}) + \epsilon_{ijkl}$										TOTAL NO.689									
		$\mu+r_1$ (1959)	$\mu+r_2$ (1960)	$\mu+r_3$ (1961)	$\mu+r_4$ (1962)	$\mu+r_5$ (1963)	$\mu+r_6$ (1964)	$a_1$	$a_2$	$a_3$	$t_1$	$t_2$	$t_3$	$\theta(x_{ijkl} - \bar{x})$	$\sum y_{ijkl}$						
(1)	$\mu + r_1$	102						1	15	29	3	43	4	57	5	71	6	85	7	8	
(2)	$\mu + r_2$		121					2	9	16	10	30	11	44	12	58	13	72	14	16	
(3)	$\mu + r_3$			136				3	17	17	18	31	19	45	20	59	21	73	22	24	
(4)	$\mu + r_4$				109			4	25	18	26	32	27	46	28	60	29	74	30	32	
(5)	$\mu + r_5$					106		5	33	19	34	33	35	47	36	61	37	75	38	40	
(6)	$\mu + r_6$						115	6	41	20	42	34	43	48	44	62	45	76	46	48	
(7)	$a_1$							7	49	8	50	9	51	10	52	11	53	12	54	56	
(8)	$a_2$							8	57	22	58	23	59	24	60	25	61	26	62	64	
(9)	$a_3$							9	65	36	66	37	67	38	68	39	69	40	70	72	
(10)	$t_1$							10	73	50	74	51	75	52	76	53	77	54	78	80	
(11)	$t_2$							11	81	64	82	65	83	66	84	67	85	68	86	88	
(12)	$t_3$							12	89	78	90	79	91	80	92	81	93	82	94	96	
(13)	$\theta(x_{ijkl} - \bar{x})$							13	97	92	98	93	99	94	100	95	101	96	102	104	
								14	103	100	101	102	103	104	105	106	107	108	109	110	
								15	111	108	109	110	111	112	113	114	115	116	117	118	
								16	119	116	117	118	119	120	121	122	123	124	125	126	
								17	127	124	125	126	127	128	129	130	131	132	133	134	
								18	135	132	133	134	135	136	137	138	139	140	141	142	
								19	143	140	141	142	143	144	145	146	147	148	149	150	
								20	151	148	149	150	151	152	153	154	155	156	157	158	
								21	159	156	157	158	159	160	161	162	163	164	165	166	
								22	167	164	165	166	167	168	169	170	171	172	173	174	
								23	175	172	173	174	175	176	177	178	179	180	181	182	
								24	183	180	181	182	183	184	185	186	187	188	189	190	
								25	191	188	189	190	191	192	193	194	195	196	197	198	
								26	199	196	197	198	199	200	201	202	203	204	205	206	
								27	207	204	205	206	207	208	209	210	211	212	213	214	
								28	215	212	213	214	215	216	217	218	219	220	221	222	
								29	223	220	221	222	223	224	225	226	227	228	229	230	
								30	231	228	229	230	231	232	233	234	235	236	237	238	
								31	239	236	237	238	239	240	241	242	243	244	245	246	
								32	247	244	245	246	247	248	249	250	251	252	253	254	
								33	255	252	253	254	255	256	257	258	259	260	261	262	
								34	263	260	261	262	263	264	265	266	267	268	269	270	
								35	271	268	269	270	271	272	273	274	275	276	277	278	
								36	279	276	277	278	279	280	281	282	283	284	285	286	
								37	287	284	285	286	287	288	289	290	291	292	293	294	
								38	295	292	293	294	295	296	297	298	299	300	301	302	
								39	303	300	301	302	303	304	305	306	307	308	309	310	
								40	311	308	309	310	311	312	313	314	315	316	317	318	
								41	319	316	317	318	319	320	321	322	323	324	325	326	
								42	327	324	325	326	327	328	329	330	331	332	333	334	
								43	335	332	333	334	335	336	337	338	339	340	341	342	
								44	343	340	341	342	343	344	345	346	347	348	349	350	
								45	351	348	349	350	351	352	353	354	355	356	357	358	
								46	359	356	357	358	359	360	361	362	363	364	365	366	
								47	367	364	365	366	367	368	369	370	371	372	373	374	
								48	375	372	373	374	375	376	377	378	379	380	381	382	
								49	383	380	381	382	383	384	385	386	387	388	389	390	
								50	391	388	389	390	391	392	393	394	395	396	397	398	
								51	399	396	397	398	399	400	401	402	403	404	405	406	
								52	407	404	405	406	407	408	409	410	411	412	413	414	
								53	415	412	413	414	415	416	417	418	419	420	421	422	
								54	423	420	421	422	423	424	425	426	427	428	429	430	
								55	431	428	429	430	431	432	433	434	435	436	437	438	
								56	439	436	437	438	439	440	441	442	443	444	445	446	
								57	447	444	445	446	447	448	449	450	451	452	453	454	
								58	455	452	453	454	455	456	457	458	459	460	461	462	
								59	463	460	461	462	463	464	465	466	467	468	469	470	
								60	471	468	469	470	471	472	473	474	475	476	477	478	
								61	479	476	477	478	479	480	481	482	483	484	485	486	
								62	487	484	485	486	487	488	489	490	491	492	493	494	
								63	495	492	493	494	495	496	497	498	499	500	501	502	
								64	503	500	501	502	503	504	505	506	507	508	509	510	
								65	511	508	509	510	511	512	513	514	515	516	517	518	
								66	519	516	517	518	519	520	521	522	523	524	525	526	
								67	527	524	525	526	527	528	529	530	531	532	533	534	
								68	535	532	533	534	535	536	537	538	539	540	541	542	
								69	543	540	541	542	543	544	545	546	547	548	549	550	
								70	551	548	549	550	551	552	553	554	555	556	557	558	
								71	559	556	557	558	559	560	561	562	563	564	565	566	
								72	567	564	565	566	567	568	569	570	571	572	573	574	
								73	575	572	573	574	575	576	577	578	579	580	581	582	
								74	583	580	581	582	583	584	585	586	587	588	589	590	
								75	591	588	589	590	591	592	593	594	595	596	597	598	
								76	599	596	597	598	599	600	601	602	603	604	605	606	
								77	607	604	605	606	607	608	609	610	611	612	613	614	
								78	615	612	613	614	615	616	617	618	619	620	621	622	
								79	623	620	621	622	623	624	625	626	627	628	629	630	
								80	631	628	629	630	631	632	633	634	635	636	637	638	
								81	639	636	637	638	639	640	641	642	643	644	645	646	
								82	647	644	645	646	647	648	649	650	651	652	653	654	
								83	655	652	653	654	655	656	657	658	659	660	661	662	
								84	663	660	661	662	663	664	665	666	667	668	669	670	
								85	671	668	669	670	671	672	673	674	675	676	677	678	
								86	679	676	677	678	679	680	681	682	683	684	685	686	
								87	687	684	685	686	687	688	689	690	691				

\* Numbers on the upper left and right corners of the elements are to make use of IBM 1620 II Computer at Massey University.

reveals the fact that they have no unique solution as such because the coefficient matrix is not of full-rank. For example, out of six  $a_j$  and  $t_k$  equations, there are at most four linearly independent equations because the sum of  $a_j$  equations is equal to that of  $t_k$  equations.

Therefore, independent equations which are estimable must be found.

The most common way to obtain these equations is to establish an auxiliary relationship such as  $\sum a_j = \sum t_k = 0$  which is more commonly known as 'imposition of a restriction'. Under this assumption

$$- a_3 = a_1 + a_2 \quad \text{and}$$

$$- t_3 = t_1 + t_2.$$

Now, instead of 6 equations for  $a_j$  and  $t_k$  classifications, there are only four ( $a_1, a_2, t_1$  and  $t_2$ ) equations which easily yield a solution by the ordinary methods of solving simultaneous equations. The value of  $a_3$  and  $t_3$  are obtained by proper substitution of the values of  $a_1, a_2$  and  $t_1, t_2$  in  $- a_3$  and  $- t_3$  equations.

Having obtained the estimates for  $a_j, t_k$ , and  $\beta$  equations the estimates for  $\mu + r_i$  are easily derived by substituting the estimates of  $a_j, t_k$ , and  $\beta$  in the absorption equations.

The individual year effect is calculated by subtracting the value of  $\mu$  from each  $\mu + r_i$  estimate. Supposing  $X$  to be the total value of  $\mu + r_i$ , the estimate of  $\mu$  is obtained by the formula:

$$\sum (\mu + r_i) = X$$

$$\text{or } n\mu + \sum r_i = X$$

since  $\sum r_i = 0$  as explained earlier,

$$n\mu = X \quad \therefore \mu = \frac{X}{n}, \quad \text{where } n = \text{number of years.}$$

The various environmental effects mentioned above were obtained by the extensive use of I.B.M. 1620 II computer. Each matrix coefficient was punched on separate cards and the identification numbers (as shown on Tables 4, 5 and 6) were punched on the last few columns in order to sort the cards row-wise and column-wise in proper sequence for estimating the effects, testing the accuracy of estimates, and for the testing of significance.

The accuracy of the estimates was tested by substituting the values of the estimates back into the equations. The difference between the sum of values obtained after the substitution and the right hand side of each equation gives the accuracy for the respective estimates. The differences in most cases were in the vicinity of 0.001 confirming a high degree of accuracy of these estimates.

To solve the simultaneous equations after applying the restriction, the iterative method was used. This method consists in repeating the process of calculation until eventually the entire set of values is duplicated exactly. These are then accepted as the correct values of the unknown.

The reduction in sums of squares due to fitting all constants,  $R(\mu, r_i, a_j, t_k, \beta)$ , was obtained from the estimates of the effects. The various sums of squares (ssq.) for the test of significance of the effects were obtained in the following way.

$$\text{Error ssq: } \sum_{ijkl} Y_{ijkl}^2 - R(\mu, r_i, a_j, t_k, \beta)$$

'Year' ssq:  $R(\mu, r_i, a_j, t_k, \beta) - R(\mu, a_j, t_k, \beta)$

'Age of Dam' ssq:  $R(\mu, r_i, a_j, t_k, \beta) - R(\mu, r_i, t_k, \beta)$

'Type of Birth' ssq:  $R(\mu, r_i, a_j, t_k, \beta) - R(\mu, r_i, a_j, \beta)$

'Regression' ssq:  $R(\mu, r_i, a_j, t_k, \beta) - R(\mu, r_i, a_j, t_k)$

The quantity  $R(\mu, r_i, a_j, t_k, \beta) = \sum_{ijk} \frac{y_{ijk}^2}{n_{ijk}} + R(\beta)$

The test of significance is presented in Table 8.

## 2. Results and discussion

The least squares estimates of the various effects have been presented in Table 7 and their tests of significance have been summarized in Table 8. It is apparent from the tables that most of the effects have highly significant ( $P < .01$ ) influences on all characters studied. Type of birth and significant effects ( $P < .05$ ) on mean fibre diameter and crimps per inch. The effects of age of dam on staple length and crimps per inch, and the effect of regression-on-date-of-birth on crimps per inch were non-significant.

The comparison within the classes, regarding the magnitude of the effects, can be represented by the following Table (Table 9).

The values of regression in this Table are the same as in Table 7 but their signs have been reversed because of the fact that the estimates of regression values in Table 7 are based on the coded values of date of birth in which the earlier born animals have higher values than the late born ones.

The estimates and their tests of significance show that in the

New Zealand Romney sheep, like in other breeds of sheep, the accurate genetic assessment can only be possible if the observable sources of environmental variation are eliminated. The regression on date of birth has most significant effects on hogget live-weight and greasy fleece weight. Its effects on other traits are very small to be of much importance, although they are statistically significant.

After estimating environmental effects it was considered desirable to carry out a variance component analysis to estimate the relative importance of each effect on the various traits. Henderson's (1953) Method 1 was used to estimate the components:  $\sigma_r^2$ ,  $\sigma_g^2$  and  $\sigma_t^2$ . The regression component  $\sigma_c^2$  was calculated by the method suggested by Rae (Pers. Comm.).

The results expressed for each effect as the percentage of the total variation have been summarised in Table 9a.

Year accounted for 47.22 percent of the total variation in greasy fleece weight, most of the remaining variation being caused by other effects not included in this study. In terms of the percentage of the total variation, the variance component of type of birth was negligible for greasy fleece weight.

Type of birth was a major component of variation (49.85%) in hogget live weight, year and regression components being only of the magnitude of 6.01 percent and 2.54 percent respectively. The magnitude of the variation not accounted for is less for hogget live-weight (41.61%) than for any other traits under study.

Only about 9 percent of the total variation in hairiness was due to the effects studied, the rest being due to unknown sources

of variation. Out of 9 percent of the variation accounted for, the year component was of the highest magnitude (5.96%). The other components had low values.

Year was the major component in the variation of mean fibre diameter (34.62%) while the regression accounted for 3.14 percent of the total variation. The values for age of dam and type of birth were negligible.

Almost all variations in staple length accounted for in the present study were due to year (19.26%). Unknown sources of variation were responsible for a large portion of the total variation (81.34%).

A large portion of the total variation (82.54%) in crimps per inch was also due to unidentified sources. Of about 16 percent of the total variation attributable to the different sources, year, type of birth and regression components were 11.1 percent, 3.17 percent and 1.58 percent respectively.

TABLE 7

Least square estimates of various effects

Category	Sub-class	Greasy Fleece wt $Y_1$ lb	Hogget Live wt $Y_2$ lb	Hairiness $Y_3$ %	Mean Fibre Diameter $Y_4$ $\mu$	Staple length $Y_5$ cm	Crimps per inch $Y_6$ No.
Year	1958	-0.124	2.322	1.696	-0.756	0.291	-
	1959	-1.892	4.152	3.348	-3.635	-1.712	0.500
	1960	-1.567	-5.557	-1.427	-1.078	-0.003	-0.114
	1961	0.055	-3.823	-1.538	-0.032	0.198	0.145
	1962	1.178	6.972	-2.147	3.053	0.512	-0.094
	1963	1.357	3.244	-1.149	2.468	0.364	-0.157
	1964	0.992	-7.306	1.217	-	0.380	-0.281
Age of Dam	2-tooth	-0.28	-1.91	-0.20	-0.27	-0.03	-0.03
	4-tooth	0.06	0.06	0.06	0.23	0.08	-0.01
	6-tooth & Full mouth	0.22	1.85	0.14	0.04	-0.04	0.04
Birth Rank	Single	0.17	1.89	-0.91	-0.22	-0.19	0.18
	Twin	-0.20	-3.00	0.80	-0.11	0.22	-0.06
	Twins reared as Singles	0.03	1.11	0.11	0.34	-0.03	-0.12
$\beta$	Regr. on Date of Birth	- 0.02	-0.23	0.04	-0.06	-0.01	-0.001
$\mu$	Mean	8.035	85.707	7.893	35.812	14.142	3.248
No. of Animals used in the Estimation of Effects	-	801	801	801	686	801	689



TABLE 8

Summary of analysis of variance for the least square estimates of various effects  
(Mean squares only)

Source of Variation	Greasy Fleece wt		Hogget Live wt		Hairiness		Mean Fibre Diameter		Staple length		Crimps per inch	
	D.F.	Mean Squares	D.F.	Mean Squares	D.F.	Mean Squares	D.F.	Mean Squares	D.F.	Mean Squares	D.F.	Mean Squares
Total	800	2.65	800	134.32	800	59.25	685	195.65	800	3.16	688	2.11
Years	6	167.52**	6	3070.10**	6	460.49**	5	567.33**	6	60.45**	5	8.47**
Age of Dam	2	14.46**	2	850.50**	2	6.88**	2	11.07**	2	1.11 NS	2	0.32 NS
Type of birth	2	12.27**	2	2086.95**	2	247.61**	2	4.24*	2	14.10**	2	4.56*
θ	1	45.91**	1	4478.30**	1	112.15**	1	246.33**	1	8.85**	1	0.15 NS
Error	789	1.37	789	105.59	789	55.64	675	8.31	789	2.68	678	0.5271

\* Probability of chance occurrence  $< .05$

\*\* Probability of chance occurrence  $< .01$

NS Not significant

TABLE 9

Comparison of various effects on different traits between subclasses within classes

	Greasy Fleece wt	Hogget Live wt	Hairiness	Mean Fibre Diameter	Staple length	Crimps per inch
Single minus twin	0.37	4.89	-1.71	-0.11	-0.41	0.24
Single minus twin raised singly	0.14	0.78	-1.02	-0.56	-0.16	0.30
6-tooth and F.M. minus 2-tooth	0.50	3.76	0.34	0.31	-0.01	0.07
6-tooth and F.M. minus 4-tooth	0.16	1.79	0.08	-0.19	-0.12	0.05
Linear regression on date of birth	0.02	0.23	-0.04	0.06	0.01	0.001

TABLE 9a

Percentage of total variance attributable to different sources of variation\*

Source of Variation	Greasy Fleece wt	Hogget Live wt	Hairiness	Mean Fibre Diameter	Staple length	Crimps per inch
Year	47.22	6.01	5.96	34.62	19.26	11.11
Age of Dam	1.39	(-)	(-)	0.75	(-)	(-)
Type of Birth	(-)	49.85	2.15	(-)	(-)	3.17
Regression on Age	2.43	2.54	0.21	3.14	(-)	1.58
Remainder	48.96	41.61	91.67	61.46	81.34	82.54

\* The cells marked (-) indicate that the effect in terms of the percentage of the total variation is negligible.

## B. CORRECTION FACTORS

### 1. Introduction

The principle of the least squares model has already been explained in the previous section.

The data of this study could be arranged to form a number of dam-daughter groups in such a way that the dams were comparable with respect to year and age. This grouping obviates the necessity of having to correct the dam's records for the year effects and the daughter's records for the year and age of dam effects.

The estimates presented in Table 7 were obtained by the use of least squares models in which the year components ( $r_i$ ) were included. But since the data are analysed, as mentioned earlier, in within-group basis, the correction for year is not required; and the estimates of the other effects obtained with the inclusion of year effect in the model are invalid for obtaining correction factors for adjusting dam's as well as daughter's records. As mentioned before, while the dam's records need adjustment for the age of dam and type of birth effects, the daughter's records do not have to be adjusted for the age of dam effects. This difference necessitates the use of different models for obtaining correction factors for dams and daughters. Both dam's and daughter's records need to be corrected for regression on date of birth. The regression values are obtained from the appropriate models.

## 2. Correction factors for adjusting dam's records

### (a) Least squares model

The following mathematical model was assumed:-

$$Y_{jkl} = \mu + a_j + t_k + \beta(X_{jkl} - \bar{X}) + e_{jkl}$$

The various terms have still the same meaning as in the previous model. The obvious difference between the previous and this model is that in this case the year component ( $r_i$ ) is missing and therefore  $\mu$  and  $a_j$  are absorbed instead of  $\mu$  and  $r_i$ . The procedure of solving the normal equations for this model is exactly the same as in the model described in the preceding section.

The sum of  $\mu + a_j$ , now, has to be divided by 3 (because  $j = 1, 2, 3$ ), after making the usual assumption that  $\sum a_j = 0$ , to derive the value of  $\mu$ . The individual  $a_j$ 's are obtained by substituting the value of  $\mu$  into the  $\mu + a_j$  equations.

### (b) Results and discussion

The estimates derived by using the new model are presented in Table 10.

Instead of correcting the records separately for  $a_j$  and  $t_k$  classifications, these two were combined to form the following classes:-

21 = Age of Dam - 2-tooth;	Birth rank - single.
22 = Age of Dam - 2-tooth;	Birth rank - single.
23 = Age of Dam - 2-tooth;	Birth rank - twin raised singly.
41 = Age of Dam - 4-tooth;	Birth rank - single.
42 = Age of Dam - 4-tooth;	Birth rank - twin.

TABLE 10

Least squares estimates of  $a_j$ ,  $t_k$  and  $\beta(X_{jkl} - \bar{X})$  effects for obtaining  
correction factors to adjust dams' records

Category	Sub-class	Greasy Fleece wt $Y_1$ lb	Hogget Live wt $Y_2$ lb	Hairiness $Y_3$ %	Mean Fibre Diameter $Y_4$ $\mu$	Staple length $Y_5$ cm	Crimps per inch $Y_6$ No.
Age of Dam	2-tooth	-0.31	-1.99	-0.31	-0.24	-0.05	-0.03
	4-tooth	0.14	0.19	0.03	0.35	0.14	-0.03
	6-tooth & Full mouth	0.17	1.80	0.28	-0.11	-0.09	0.06
Birth Rank	Single	-0.00	1.94	-0.75	-0.47	-0.29	0.19
	Twin	-0.10	-2.29	1.01	-0.08	0.20	-0.03
	Twins reared as Singles	0.10	0.36	-0.26	0.56	0.09	-0.16
-	Regr. on Date of Birth	0.006	-0.099	0.014	-0.001	-0.004	0.002

43 = Age of Dam - 4-tooth;	Birth rank - twins raised singly.
61 = Age of Dam - 6-tooth and F.M;	Birth rank - single.
62 = Age of Dam - 6-tooth and F.M;	Birth rank - twin.
63 = Age of Dam - 6-tooth and F.M;	Birth rank - twins raised singly.

After combining the estimates in the manner shown above, the factors were expressed as deviations from the 61-class. In other words, the records were adjusted to the mature-dam and single birth classifications. In ordinary machine calculations, this would mean that the individuals belonging to the 61-class, which are usually most frequent in the data, would not have to be corrected.

The correction factors, shown in Table 11, are the deviations of the various effects from the 61-class with their signs changed, and the figures rounded off. In actual calculation, the actual computer print-outs with eight places after the decimal point were used.

The correction for the regression on date of birth was applied to those individuals which differed from the mean age (the mean age was 45 for A matrix and 46 for matrices B and C). The regression value was multiplied by this difference and records adjusted accordingly. The writer is grateful to his supervisor Mr Ch'ang (1966) for suggesting this method which made it very convenient to apply some modifications in his computer programme to include regression as a correction factor.

TABLE 11

Correction factors for adjusting the dams' records to 'Single' type  
of birth and '6-tooth or F.M.' age of dam classifications

$$\text{Model:- } Y_{jkl} = \mu + a_j + t_k + \beta(X_{jkl} - \bar{X}) + e_{jkl}$$

$a_j$ and $t_k$ classifications Characters	21	22	23	41	42	43	61	62	63	Regression on Date of Birth
Greasy fleece wt	+0.480	+0.588	+0.370	+0.027	+0.134	-0.084	0	+0.108	-0.111	-0.006
Hogget live-wt	+3.792	+8.021	+5.370	+1.604	+5.834	+3.183	0	+4.230	+1.578	+0.099
Hairiness	+0.588	-1.166	+0.104	+0.252	-1.502	-0.232	0	-1.754	-0.484	-0.014
Mean fib. dia.	+0.131	-0.256	-0.904	-0.468	-0.318	-1.502	0	-0.387	-1.034	+0.001
Staple length	-0.047	-0.531	-0.426	-0.235	-0.719	-0.614	0	-0.483	-0.378	+0.004
Crimps per inch	+0.086	+0.315	+0.440	+0.088	+0.317	-0.442	0	+0.214	+0.327	-0.002



### C. CORRECTION FACTORS FOR ADJUSTING DAUGHTER'S RECORDS

#### 1. Least squares model

Since the records of the daughters need adjustment for the type of birth and regression on date of birth only, the estimates obtained by using the models which include year ( $r_i$ ) and/or age of dam ( $a_j$ ) components are no longer valid.

The mathematical model used for this purpose was,

$$Y_{kl} = \mu + t_k + \beta(X_{kl} - \bar{X}) + e_{kl}, \text{ with the usual definitions of the terms.}$$

The absorption equations, in this case were formed by absorbing  $\mu$  and  $t_k$ . The  $\Sigma(\mu + t_k)$  was, after assuming  $\Sigma t_k = 0$ , divided by 3 (because  $k = 1, 2, 3$ ) to obtain  $\mu$ . The  $t_k$  were calculated by substituting the value of  $\mu$  into the  $\mu + t_k$  equations.

#### 2. Results and discussion

The estimates based on the model,  $Y_{kl} = \mu + t_k + \beta(X_{kl} - \bar{X}) + e_{kl}$  have been presented in Table 12.

All the daughter's records were adjusted to the 'single' type of birth classification by expressing the correction factors as deviations from this sub-class. The correction factors are shown in Table 13, after reversing the signs of the deviations mentioned above.

The correction for regression on date of birth was performed in the same way as in correcting the dam's records.

TABLE 12

Least squares estimates of  $t_k$  and  $\beta(X_{kl} - \bar{X})$  effects for obtaining  
correction factors to adjust daughters' records

Category	Sub-class	Greasy Fleece wt $Y_1$ lb	Hogget Live wt $Y_2$ lb	Hairiness $Y_3$ %	Mean Fibre Diameter $Y_4$ $\mu$	Staple length $Y_5$ cm	Crimps per inch $Y_6$ No.
Type of Birth	Single	-0.06	1.45	-0.82	-0.49	-0.27	0.18
	Twin	-0.07	-1.98	1.06	-0.09	0.19	-0.03
	Twins reared as Singles	0.13	0.53	-0.24	0.58	0.09	-0.15
	Regr. on Date of Birth	0.004	-0.115	0.012	-0.001	-0.004	0.001

TABLE 13

Correction factors for correcting the Daughters' records by adjusting  
to 'Single' type of birth classification

$$\text{Model:- } Y_{kl} = \mu + t_k + \beta(x_{kl} - \bar{X}) + e_{kl}$$

$t_k$ classification Characters	Singles	Twins	Twins reared singly	Regression on Date of Birth
Greasy fleece wt	0	+0.015	-0.187	-0.004
Hogget live-wt	0	+3.430	+0.919	+0.115
Hairiness	0	-1.878	-0.586	-0.012
Mean fibre diameter	0	-0.397	-1.063	+0.001
Staple length	0	-0.463	-0.362	+0.004
Crimps per inch	0	+0.208	+0.336	-0.001

## D. HERITABILITY ESTIMATES

### 1. Introduction

The practical animal breeder is mainly concerned with heritability defined, in the narrow sense, as the ratio of the additive genetic variance to the total or phenotypic variance. The consequences of gene action which differs from the additive scheme have been discussed by Lush (1937, 1949) and Lerner (1950).

The additive genetic variance is the component of total variance thought of as arising from the average effects of the genes. It reflects the variation that is transmitted from parent to offspring and is therefore considered responsible for the resemblance between relatives. The estimation of the amount of additive genetic variance depends on the measurement of the degree of resemblance between relatives. The most common relationships are between offspring and their parents, and between full or half-sibs.

It can be theoretically shown that the degree of resemblance between relatives, measured as a regression or correlation coefficient, is related to the heritability ( $h^2$ ) as follows:-

Regression of:

$$\begin{aligned}\text{Offspring on one parent} &= \frac{1}{2} h^2 \\ \text{Offspring on mean of 2 parents} &= h^2\end{aligned}$$

Intraclass correlation of:

$$\begin{aligned}\text{half sibs} &= \frac{1}{4} h^2 \\ \text{full sibs} &= > \frac{1}{2} h^2\end{aligned}$$

The intraclass correlation of full sibs is not confined to the additive variance, and therefore the correlation is augmented by part of the non-additive variance if any is present.

The most serious complication in estimating additive genetic variance arises from the fact that there are often non-genetic causes for the resemblance between certain relatives, which may increase the regression or correlation and lead to an overestimation of the heritability. It is mainly in the full-sibs that resemblance tends most often to be augmented by nongenetic causes, as they always have the same mother and are generally subjected to similar environmental conditions.

The absence of non-genetic causes of resemblance in a relationship is the most important criterion in choosing a method for estimating the heritability.

## 2. Method of analysis

Lush (1944, 1949) has described various methods of estimating heritability.

Several dam-daughter pairs had observations on all characters under study and therefore, it was possible to obtain covariance between the records of dam and daughter to estimate one half the additive genetic variance by regressing the daughter's records on dam's. This regression coefficient was then doubled to give the heritability estimates.

Prior to obtaining the regression value, the measurable non-genetic differences were eliminated from the records by applying appropriate correction factors (Tables 11 and 13) and by performing analysis on a

within-group basis to remove year effects from all records and age of dam effects from the daughter's records.

The general formula used in the estimation of heritability was:-

$$h_i^2 = 2 \times \frac{\text{cov}(X_i, Y_i)}{\sigma X_i^2}$$

$$i = 1, 2, \dots, 6.$$

where,  $\text{cov}(X_i, Y_i)$  = covariance between dam's and daughter's records and  $\sigma X_i^2$  = variance of dam's records.

The covariances used as the numerator in the formula are the same as those used as the denominator in the formula for calculating genetic correlations and are represented by the diagonal elements in Table 18. The square root of the denominator, i.e., the standard deviations of dams' records, are represented by the diagonal elements of Table 19 (upper figures).

The following example illustrates the use of the formula for estimating the heritabilities.

The heritability of greasy fleece weight (say, 1) is obtained as follows:-

$$\begin{aligned} h_1^2 &= 2 \times \frac{\text{cov}(X_1, Y_1)}{\sigma X_1^2} \\ &= 2 \times \frac{0.27}{(1.12)^2} = 0.43 \end{aligned}$$

The covariance 0.27 and the standard deviation 1.12 were extracted from

Tables 18 and 19 respectively.

The standard errors of the heritabilities were obtained by doubling the standard errors of regression coefficients. The latter were calculated by the method given by Snedecor (1956).

### 3. Results and discussion

The estimates of heritabilities obtained by doubling the regression of daughter on dam have been presented in Table 20.

In the analysis, the records of the dams having twin daughters have been repeated over the daughters' records. The method generally used in a situation where there is a difference in family size is to combine the sums of squares and products from families of different size according to a weighting factor appropriate to the family size. The derivation of the weighting factors is explained by Kempthorne and Pandon (1953) and Reeve (1955). The present data has a very low proportion of dams which had twin daughters. Kempthorne and Pandon did not find any significant difference between the estimates of heritability obtained from linear regression analysis by repeating dam's records with each of her daughter's and by applying weighting factors, when major proportion of dams, like in the present data, had only one offspring. Rae's (1958) data contained 15 percent of dams which had twin ewe offspring. He considered that such a low proportion of dams with twin offspring were unlikely to make the heritability estimates obtained from regression analysis by repeating dam's records much different from those derived from the method of Kempthorne and Tandon, i.e., by using weighting factor.

Heritability estimates from regression of offspring on parent are usually considered more reliable than those based on half-sib method. When the environment is random for all individuals in a population, the variance among dam-daughter pairs contains one-half of the additive genetic variance whereas the variance among half-sibs contains only one-fourth. This is why the regression of offspring on parent is doubled to obtain the heritability estimate but the correlation among half-sibs is multiplied by 4. Sampling and non-random errors are thus inflated by only a factor of 2 in the former, but by 4 in the case of the latter estimates.

The parent offspring method excludes the effects of environment more effectively than those based on full or half-sibs, as the parent and offspring are not contemporary and are thus not subjected to the same environment as may be the case with sibs. In the data obtained from a population where selection is practised among the parents, the regression method has an additional advantage of yielding unbiased estimates of heritability.

Theoretically heritability may be estimated using the regression of the offspring on either parent but, in most animal breeding data, dams far outnumber the sires, and therefore, the estimate is usually obtained from the regression of offspring on dam. In sheep breeding data, regression of daughter on dam is more commonly applied because of the availability of dam-daughter pairs in substantial numbers and also because the method of dam-daughter regression does not require the estimation of effects of sex, and hence there is no necessity of correcting the records for sex differences.



The heritability estimates of various traits obtained from the present data by dam-daughter regression analysis are, in general, consistent with those published in the literature (compare Tables 1 and 20).

The outstanding feature of the estimates is the high heritability (0.43) of greasy fleece weight which is higher than any other estimates reported so far for the New Zealand Romney Marsh. However, the present estimate appears to be more in line with the preliminary results of a selection experiment for fleece weight being carried out at Massey University which has been commented on by Rae (1964).

The heritability of mean fibre diameter (0.17) is the lowest of all the traits studied but is comparable with 0.28 for the Australian Merino (Young et al., 1960) and 0.29 for the South African Merino (Bosman, 1958).

The heritability of crimps per inch (0.72) appears to be higher in the New Zealand Romney than any other estimates reported for other breeds of sheep.

The present estimate of heritability of hairiness (0.87) confirms the previous study made by Rae (1958a) in which he noted that hairiness was a highly heritable trait in the New Zealand Romneys, capable of responding rapidly to selection.

It is evident from Table 20 that individual productive traits of the New Zealand Romneys are strongly inherited and will respond rapidly to mass selection. The main limitation to progress is the genetic antagonism existing between some characters. The discussion

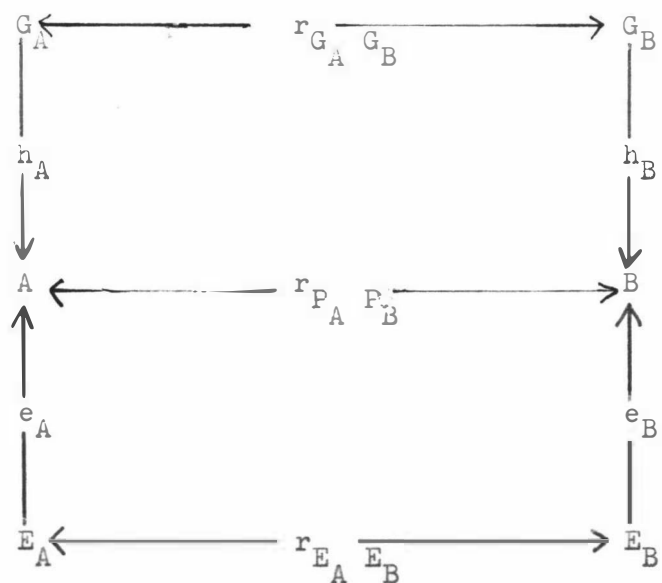
pertaining to this aspect of selection will be presented in the following section.

## E. PHENOTYPIC AND GENETIC CORRELATIONS

### 1. Introduction

A phenotypic correlation is the correlation between records of two traits on the same animal.

The following diagrammatic representation (Lerner, 1958) shows the basis of phenotypic correlation between two traits A and B.



In the diagram, it has been shown that the phenotype for a given trait (A) is determined by its genotype ( $G_A$ ) and its environment ( $E_A$ ), respectively connected to A by paths  $h_A$  and  $e_A$ . Trait B has

similar genotypic and environmental components.  $h_A$  and  $h_B$  are the square root of the heritabilities of traits A and B, respectively; and  $e_A$  and  $e_B$  are their respective environmental components.

A phenotypic correlation between two traits in a given individual may be in part the result of their genetic association resulting from common sources of genetic variation, such as pleiotropy, linkage, and the association of loci and blocks located on different chromosomes. It can also be in part the result of common environment.

The following example will further illustrate this point.

Supposing each of the traits A and B as being the sum of a genetic term and an environment (including error) term, and neglecting the general means,

$$\begin{aligned} A &= g + e \\ &\dots\dots\dots (1) \\ B &= G + E \end{aligned}$$

The genetic correlation  $r$  is the correlation between  $g$  and  $G$ ; the phenotypic correlation  $R$  is the correlation between  $A$  and  $B$ , and that between  $e$  and  $E$  is the environmental correlation, say  $r'$ .

Since a correlation, whatever its nature, is the ratio of the appropriate covariance to the product of the two standard deviations, we have,

$$r = \frac{\text{cov}(g, G)}{\sigma_g \cdot \sigma_G}$$

$$R = \frac{\text{cov}(A, B)}{\sigma_A \cdot \sigma_B}$$

and 
$$r' = \frac{\text{cov}(e, E)}{\sigma_e \cdot \sigma_E} \quad \text{where, cov}(g, G) \text{ is the}$$

covariance between  $g$  and  $G$  and  $\sigma_g$  and  $\sigma_G$  are their respective standard deviations. The other terms have similar notations.

The phenotypic correlation  $R$  is that between  $A$  and  $B$  and can be directly obtained from (1) as -

$$R = \frac{\text{cov}(g, G) + \text{cov}(g, E) + \text{cov}(G, e) + \text{cov}(e, E)}{\sqrt{[\sigma_g^2 + 2 \text{cov}(g, e) + \sigma_e^2]} [\sigma_G^2 + 2 \text{cov}(G, E) + \sigma_E^2]}$$

Assuming  $h$  and  $H$  to be the heritability estimates in the narrow sense, of the two traits  $A$  and  $B$ , defined as  $\sigma_g^2 / (\sigma_g^2 + \sigma_e^2)$  and  $\sigma_G^2 / (\sigma_G^2 + \sigma_E^2)$  respectively, Lerner (1950) established the following relationship between phenotypic, genetic and environmental correlations, by using the method of path-coefficients.

$$R = r \sqrt{h H} + r' \sqrt{(1-h)(1-H)}$$

Searle (1961) has further shown that:

- (1) the environmental correlation is negative when  $R$  and  $r$  have the same sign only if  $R/r$  is less than  $\sqrt{h H}$ ; it is negative when  $R$  and  $r$  are of opposite sign and  $R$  is negative;
- (2) equality of the heritabilities implies that when any two of the correlations are equal there is equality of all three, and;
- (3) the phenotypic correlation exceeds (or is less than) the genetic correlation according as the ratio  $r'/r$  exceeds (or is less than)

the value of  $(1 - \sqrt{hH}) / \sqrt{(1-h)(1-H)}$

## 2. Method of analysis

It is clear from the foregoing discussion that the confounding of genetic and environmental covariation in the estimation of phenotypic correlation does not allow for any approximation as to the magnitude or even the sign of genetic correlation. For this reason, a separate analysis was carried out to obtain genetic correlations between traits after calculating the phenotypic correlations by the usual product-moment method. The use of different sets of data, owing to missing records, follows the similar pattern as in obtaining genetic correlations. The phenotypic variances and covariances have been presented in Table 16.

The estimation of the genetic correlation between traits by the reciprocal correlation of one trait in the dam with another trait in the offspring has been described by Hazel (1943). His formula was -

$$r_{G_i G_j} = \sqrt{\frac{r_{X_i X_{j'}} \cdot r_{X_{i'} X_j}}{r_{X_i X_{i'}} \cdot r_{X_j X_{j'}}}} \quad \text{where, } X_i, X_j \text{ are the}$$

corresponding traits in the offspring and  $X_{i'}$ ,  $X_{j'}$  are the corresponding traits in the dam.

Koch and Clark (1955) have shown this formula as invalid where the situation is complicated by maternal environment in which case the expectation of the formula given above is not  $r_{G_i G_j}$ .

The method of estimating the genetic correlation and the importance of this parameter especially in designing selection indexes

have been discussed by Hazel (1943), Hazel et al. (1943), Reeve (1953), Jerome et al. (1956), Falconer (1960), Searle (1961) and Van Vleck and Henderson (1961).

Considering the situation described by the following table for two traits A and B,

Trait	Dam	Daughter
A	$X_1$	$Y_1$
B	$X_2$	$Y_2$

Van Vleck and Henderson (1961) showed that the genetic correlation between the traits can be estimated by the following four methods.

$$1. \quad r_{G_A G_B} = \frac{\text{cov}(X_2, Y_1)}{\sqrt{\text{cov}(X_1, Y_1) \cdot \text{cov}(X_2, Y_2)}}$$

$$2. \quad r_{G_A G_B} = \frac{\text{cov}(X_1, Y_2)}{\sqrt{\text{cov}(X_1, Y_1) \cdot \text{cov}(X_2, Y_2)}}$$

$$3. \quad r_{G_A G_B} = \sqrt{\frac{\text{cov}(X_1, Y_2) \cdot \text{cov}(X_2, Y_1)}{\text{cov}(X_1, Y_1) \cdot \text{cov}(X_2, Y_2)}}$$

$$4. \quad r_{G_A G_B} = \frac{\text{cov}(X_1, Y_2) + \text{cov}(X_2, Y_1)}{2\sqrt{\text{cov}(X_1, Y_1) \cdot \text{cov}(X_2, Y_2)}}$$

Van Vleck and Henderson (loc.cit) noted that all four methods of

estimation provided unbiased estimates of the genetic correlation when the sample size was large. For small size ( $N = 100$ ) and low heritability (0.20) of at least one trait, however, the estimates appeared to have been biased upwards, especially in the case of the estimate obtained by using the third method.

In the present analysis the fourth method has been used to estimate all genetic correlations.

The records of dams and daughters were corrected in the way mentioned earlier, before obtaining various covariances which have been presented in Table 18. These covariances are based on different number of dam-daughter pairs because of the missing data mentioned in Chapter III. Four different sets of data had to be analysed separately to obtain covariances as follows:-

- (1) All combination of covariances between greasy fleece weight, hogget live-weight, hairiness and staple length.
- (2) All combination of covariances between mean fibre diameter and other traits mentioned in (1).
- (3) All combination of covariances between crimps per inch and other traits mentioned in (1).
- (4) Covariance between crimps per inch and mean fibre diameter.

All covariances obtained from (1) were utilized in calculating genetic correlations between the traits greasy fleece weight, hogget live weight, hairiness, and staple length. These are based on maximum number of dam-daughter pairs (508) in the data. In the case of (2) and (3), only covariances containing mean fibre diameter and crimps per inch, respectively, were used, although other covariances between additional

right hand sides (see Table 14) were available. The genetic correlations associated with mean fibre diameter are based on 401 dam-daughter pairs while those associated with crimps per inch are based on 292. Because of small number of dam-daughter pairs (185) available to obtain covariance between crimps per inch and mean fibre diameter, the only covariances used from (4) were the ones forming the numerator of the formula, the appropriate terms of denominator being obtained from (2) and (3). The covariance in the numerator was obtained by forming a new matrix D (Table 15).

All covariances required for calculating genetic correlations between the traits under study, have been presented in Table 18.

Representing dam and daughter by X and Y respectively, the general formula for calculating genetic correlations can be written as follows:-

$$r_{G_i G_j} = \frac{\text{cov}(X_i, Y_j) + \text{cov}(X_j, Y_i)}{2\sqrt{\text{cov}(X_i, Y_i) \cdot \text{cov}(X_j, Y_j)}}$$

As an example, genetic correlation between greasy fleece weight (say, 1) and hogget live weight (say, 2), 0.54 (Table 19), is derived as,

$$r_{G_1 G_2} = \frac{\text{cov}(X_1, Y_2) + \text{cov}(X_2, Y_1)}{2\sqrt{\text{cov}(X_1, Y_1) \cdot \text{cov}(X_2, Y_2)}}$$

Using the covariances from Table 18,

$$r_{G_1 G_2} = \frac{1.40 + 1.30}{2\sqrt{0.27 \times 23.28}} = 0.54$$



TABLE 14

Additional right hand sides included in Matrices B and C to obtain phenotypic covariance of  $Y_4$  and  $Y_6$  with other characters

Equation No.	R.H.S.'s added to Matrix B				R.H.S.'s added to Matrix C			
	$Y_1$	$Y_2$	$Y_3$	$Y_5$	$Y_1$	$Y_2$	$Y_3$	$Y_5$
1	894.60	9682.0	1093.10	1628.0	631.50	9163.0	1148.90	1270.0
2	631.50	9163.0	1148.90	1270.0	819.20	10036.0	706.00	1715.0
3	819.20	10036.0	706.00	1715.0	1093.90	10993.0	905.00	1953.0
4	1093.90	10993.0	905.00	1953.0	966.90	9676.0	692.30	1589.0
5	966.90	9676.0	692.30	1589.0	997.20	9388.0	729.90	1542.0
6	997.20	9388.0	729.90	1542.0	1044.00	9012.0	1054.70	1675.0
7	1265.80	14044.0	1210.00	2338.0	1336.90	14375.0	1219.50	2433.0
8	1542.40	16654.0	1537.10	2771.0	1552.70	16037.0	1412.50	2710.0
9	2595.10	28420.0	2528.10	4588.0	2663.10	27856.0	2604.80	4601.0
10	2262.90	25360.0	1922.20	3984.0	2400.10	25829.0	1997.80	4142.0
11	2913.40	31318.0	3184.50	5310.0	2914.40	29964.0	3015.40	5192.0
12	227.00	2440.0	168.50	403.0	238.20	2475.0	223.60	410.0
13	1207.59	-9952.0	2212.12	-308.41	474.22	-12652.90	3176.93	1066.11

TABLE 15

Least squares equations for obtaining covariance between  
mean fibre diameter ( $Y_4$ ) and crimps per inch ( $Y_6$ )

Total No. 574

$$\text{Model:- } Y_{ijkl} = \mu + r_i + a_j + t_k + \beta(X_{ijkl} - \bar{X}) + e_{ijkl}$$

MATRIX D

( $\mu + r_i$ )

								$Y_4$	$Y_6$
	$a_1$	$a_2$	$a_3$	$t_1$	$t_2$	$t_3$	$\beta(X_{ijkl} - \bar{X})$	$\Sigma Y_{ijkl}$	$\Sigma Y_{ijkl}$
102	25	22	55	47	54	1	-136.99	3270.97	388.44
121	33	34	54	76	37	8	-1221.41	4253.66	388.77
136	33	35	68	44	85	7	+93.04	4840.80	464.91
109	33	38	38	42	64	3	+1354.20	4138.47	349.08
106	25	27	54	41	60	5	-88.84	4046.78	331.85
$a_1$	149	0	0	86	58	5	+250.37	5277.29	498.19
$a_2$	0	156	0	75	73	8	+102.67	5642.39	515.70
$a_3$	0	0	269	89	169	11	-353.04	9631.00	909.16
$t_1$	86	75	89	250	0	0	-226.51	8876.59	863.68
$t_2$	58	73	169	0	300	0	+307.89	10789.61	983.89
$t_3$	5	8	11	0	0	24	-81.38	875.48	75.48
$\beta(X_{ijkl} - \bar{X})$	+250.37	+102.67	-353.04	-226.51	+307.89	-81.38	93730.50	-126.83	154.15

TABLE 16

Phenotypic standard deviations, variances and covariances  
(upper and lower figures on diagonal elements are variances  
and standard deviations respectively and figures above the  
diagonal are covariances)

Characters	Greasy Fleece Weight	Hogget Live Weight	Hairiness	Mean Fibre Diameter	Staple Length	Crimps Per inch
Greasy Fleece wt	1.37 1.17	7.29	0.45	1.79	0.91	-0.14
Hogget Live wt		105.59 10.27	-0.80	8.79	4.08	-0.68
Hairiness			55.64 7.46	2.14	0.89	-0.52
Mean Fibre Diameter				8.31 2.88	2.32	-0.79
Staple Length					2.68 1.64	-0.74
Crimps per inch						0.53 0.73

The genetic correlations between other pairs of traits have been similarly derived.

The Standard Error (S.E.) of the genetic correlations were obtained by the method given by Rae (1950). The first bracket of his formula, which takes the following form under the present notation, contributes most to the variance:  $\text{var}(r_{G_i G_j})$ .

$$\begin{aligned} \text{var}(r_{G_i G_j}) = & \frac{(r_{G_i G_j})^2}{n} \left[ \frac{\sigma_{X_i}^2 \cdot \sigma_{Y_j}^2 + \sigma_{X_j}^2 \cdot \sigma_{Y_i}^2 + \{\text{cov}(X_i, Y_j)\}^2 + \{\text{cov}(X_j, Y_i)\}^2}{\{\text{cov}(X_i, Y_j) + \text{cov}(X_j, Y_i)\}^2} \right. \\ & + \frac{\sigma_{X_i}^2 \cdot \sigma_{Y_i}^2}{4\{\text{cov}(X_i, Y_i)\}^2} + \frac{\sigma_{X_j}^2 \cdot \sigma_{Y_j}^2}{4\{\text{cov}(X_j, Y_j)\}^2} + \frac{1}{2} \left. \right] \end{aligned}$$

where  $n$  = degrees of freedom associated with the genetic correlations.

Rae (loc.cit.) has shown that the second bracket of the formula, containing the terms arising from the covariances, could be neglected without seriously altering the results.

The standard errors obtained by the use of the first bracket of Rae's formula are presented in Table 19 (below diagonal). These values are derived by taking the square root of the value for  $\text{var}(r_{G_i G_j})$ .

### 3. Results and discussions

The estimates of phenotypic and genetic correlations obtained in this study are shown in Tables 17 and 19 respectively.

If only the phenotypic correlation is known, it can become a misleading statistic. For instance, a highly positive phenotypic correlation may mask behind it a negative genetic correlation or vice versa. For a time it may make a trait appear static or beyond improvement when actually genetic improvement is being made. However, if it is accompanied by either the genetic or the environmental correlations, it becomes helpful in making at least a fair guess as to the missing correlation. Thus, if the phenotypic correlation was zero and the environmental correlation highly positive, we would expect the genetic correlation to be highly negative unless dominance accounted for a large part of the genetic covariance.

The present phenotypic correlations between the characters are quite consistent with those reported for the same flock of sheep by Rae (1958a) and those reported for other breeds. All phenotypic correlations between crimps per inch and the other characters under study are negative. This is, again, in good agreement with the results reported in the literature (Table 2). The only positive value (0.05) of phenotypic correlation between crimps per inch and hogget live weight was reported by Morley (1955) for the Australian Merino sheep.

The low correlation between fleece weight and hairiness (0.05) is similar to those reported by Goot (1945) and Rae (1958a).

At the phenotypic level, there is some additional information

TABLE 17

Phenotypic correlations among the various characters

Characters	Greasy Fleece Weight	Hogget Live Weight	Hairiness	Mean Fibre Diameter	Staple Length	Crimps Per inch
Greasy Fleece wt		0.61 <sup>1**</sup>	0.05 <sup>1</sup>	0.53 <sup>2**</sup>	0.48 <sup>1**</sup>	-0.17 <sup>3**</sup>
Hogget Live wt			-0.01 <sup>1</sup>	0.29 <sup>2**</sup>	0.24 <sup>1**</sup>	-0.09 <sup>3*</sup>
Hairiness				0.11 <sup>2**</sup>	0.07 <sup>1*</sup>	-0.10 <sup>3**</sup>
Mean Fibre Diameter					0.48 <sup>2**</sup>	-0.37 <sup>4**</sup>
Staple Length						-0.63 <sup>3**</sup>
Crimps per inch						

1 Based on 789 degrees of freedom

2 Based on 675 degrees of freedom

3 Based on 678 degrees of freedom

4 Based on 564 degrees of freedom

\* and \*\* indicate that the correlation is different from zero at  $P < .05$  and  $P < .01$  respectively.

TABLE 18

Daughter

Genetic Covariances\*

$Y_j - j = 2, 3, \dots, 6$ $Y_i - i = 1, 2, \dots, 6$ $X_i - i = 1, 2, \dots, 6$ $X_j - j = 2, 3, \dots, 6$	Greasy Fleece wt	Hogget Live wt	Hairiness	Mean Fibre Diameter	Staple length	Crimps per inch
Greasy fleece weight	<u>0.27</u>	1.40	-0.28	0.37	0.10	-0.02
Hogget live weight	1.30	<u>23.28</u>	-5.79	1.26	0.74	-0.26
Hairiness	-0.41	-12.16	<u>14.08</u>	0.32	-0.01	-0.33
Mean fibre diameter	0.10	0.03	0.95	<u>0.60</u>	0.17	-0.08
Staple length	0.23	0.86	-0.34	0.65	<u>0.65</u>	-0.28
Crimps per inch	-0.04	0.06	-0.09	-0.34	-0.26	<u>0.18</u>

\*(1) The diagonal elements are:

 $\text{cov}(X_i, Y_i)$ ; where  $i = \text{character } 1, 2, \dots, 6$  and  
 $\text{cov}(X_j, Y_j)$ ; where  $j = 2, 3, \dots, 6$ .

(2) The elements above the diagonal are:

 $\text{cov}(X_i, Y_j)$ ; where  $i = \text{character } 1, 2, \dots, 5$ , and  
 $j = \text{character } 2, 3, \dots, 6$ .

(3) The elements below the diagonal are:

 $\text{cov}(X_j, Y_i)$ ; where  $i = \text{character } 1, 2, \dots, 5$  and  
 $j = \text{character } 2, 3, \dots, 6$ .

TABLE 19

Genetic standard deviations, genetic correlations and standard errors\*

$r_{G_i G_j}$ S.E.	Greasy Fleece wt	Hogget Live wt	Hairiness	Mean Fibre Diameter	Staple length	Crimps per inch
Greasy Fleece wt	1.12 1.23	+0.54 ✓	-0.18	+0.58	+0.40	-0.13 ✓
Hogget Live wt	0.17	10.05 11.57	-0.49	+0.16 ✓	+0.21 ✓	-0.05 ✓
Hairiness	0.14	0.14	5.67 7.24	+0.24	-0.06	-0.12
Mean Fibre Diameter	0.36	0.26	0.22	2.66 3.14	+0.68	-0.63
Staple Length	0.15	0.16	0.41	0.34	1.68 1.67	-0.76 ✓
Crimps per inch	0.15	0.16	0.10	0.34	0.18	0.71 0.69

\* Diagonal elements - Upper figures, std. deviations of dams; lower figures, standard deviations of daughters.

Above diagonal elements - Genetic correlations.

Below diagonal elements - Standard errors of the genetic correlations.



TABLE 20

Heritabilities estimated from the regression of  
daughter on dam

Characters	Heritability	Remarks
Greasy fleece weight	$0.43 \pm 0.10$	Based on 508 dam-dtr. pairs
Hogget live-weight	$0.46 \pm 0.10$	Based on 508 dam-dtr. pairs
Hairiness	$0.87 \pm 0.12$	Based on 508 dam-dtr. pairs
Mean fibre diameter	$0.17 \pm 0.10$	Based on 401 dam-dtr. pairs
Staple length	$0.46 \pm 0.02$	Based on 508 dam-dtr. pairs
Crimps per inch	$0.72 \pm 0.06$	Based on 292 dam-dtr. pairs

reported for the New Zealand Romney sheep. Barton (1954), Coop (1956), Cockrem et al. (1956) and Inkster (1956) reported positive phenotypic association between face cover, fertility, growth and fleece weight. They found that open-faced ewes produced more lambs than closed-faced ewes. Wallace (1961) and Coop (1962) have reported positive phenotypic association between live weight at mating and fertility in the same season.

As stated earlier, though the association between the characters at the phenotypic level may be important from the point of view of flock nutrition, it does not provide a clue as to the nature of genetic relationship between them.

The genetic correlations presented in Table 19 suggest that if several characters are to be selected, progress may be restricted because of genetic antagonism between certain traits. Though there is no unanimity on the desirable qualities of the New Zealand Romneys, Rae (1964), in stressing the need of defining objectives in sheep breeding, has outlined the ranking of productive traits based on the relative economic importance of the various characters. The importance of ranking of production traits according to their commercial profitability, and some of the difficulties involved in this approach have been discussed by Rae (1954, 1958c, 1962). He noted that lamb production ranked first, followed by fleece weight within the range of suitable quality numbers and fleece grade. On the basis of relative economic value, he suggested that comparatively minor significance should be attached to body conformation or other characters except in so far as they are correlated to the characters of major importance.

The picture emerging from the present genetic correlations

(Table 19) is that, if selection was entirely concentrated on greasy fleece weight, the hogget live weight and staple length would increase, the medullation in the hogget fleece would decrease and the fineness (as indicated by more number of crimps per inch and less fibre thickness) would decrease.

The genetic correlation between greasy fleece weight and hairiness ( $-0.18$ ) in this work is different from the estimate of Rae (1958a) which was  $0.28$  as determined by dam-daughter regression. His estimate based on paternal half-sib correlation was, however,  $-0.28$ . This inconsistency in the magnitude and sign of this statistic may well be due to sampling errors which can be expected to be large in the analyses in which the genetic correlations are based on four different covariances, each having its own sampling error. Another inconsistent estimate, is the present genetic correlation of  $-0.06$  between staple length and hairiness in comparison with Rae's (1958a)  $0.41$ . No other estimates have been reported in the literature to provide comparison to these figures.

## CHAPTER V

## DISCUSSION

## Chapter V

DISCUSSION

An estimate of heritability, in conjunction with the known selection differential, in uniform environment, gives the expected gain per generation; but it does not indicate the effect which selection pressure applied for the improvement of one trait may have on the improvement or decline of another trait. A number of investigators have studied this aspect of animal breeding. Recently, Young et al. (1965) suggested that, in the Australian Merino, with high genetic correlations between traits measured at weaning and at hogget age (fleece weight and live weight), together with high heritabilities for both traits at hogget age, due consideration be given to the relative efficiency of selection in terms of genetic gain at the two ages.

Turner (1959) and Searle (1963) have discussed the relative gains under indirect and direct selection. If two characters A and B with heritabilities  $h_A^2$  and  $h_B^2$  have the genetic correlation between them,  $r_{AB}$ , then we can write -

$$R = \frac{\Delta_{A.B}}{\Delta_{A.A}} = \frac{h_B}{h_A} r_{AB},$$

where,  $\Delta_{A.B}$  = predicted genetic gain in A under selection for B and  $\Delta_{A.A}$  = predicted genetic gain in A under selection for A. If A represents a character measured at one age and B the same character

measured at another age, the above formula can be used to estimate the efficiency of selection at two different ages.

Rae (1964a) has recently suggested the usefulness of body weights other than at weaning. The hogget weight after shearing would be of special interest because of its phenotypic and genetic association with fleece weight, fertility and other productive traits.

Using heritability estimates of 0.35 (Ch'ang and Rae, 1961) and 0.46 (this study) for weaning and hogget weights respectively, and assuming a high genetic correlation between these weights, say, 0.9 (Young et al., 1965), we have,

$$R = \frac{\sqrt{.46}}{\sqrt{.35}} \times .9 = 1.02, \text{ so that an indirect selection for}$$

weaning weight is slightly more efficient than direct selection. A great amount of accuracy can not be guaranteed in predictions based on genetic correlations unless they have been derived by using a large amount of data to reduce the sampling variations to the minimum. Young et al. (1965), however, have made some empirical observations that selection for greasy fleece weight and body weight at weaning was unlikely to be rewarding, at least in the Australian Merino, and that selection should be based on measurements at 15 - 16 months of age, even when it is desired to have high body weight at weaning.

As mentioned before, lamb production ranks first in regard to its economic importance, but this trait is lowly heritable in the New Zealand Romney (Rae, 1964) as it is in other breeds (Reeve and Robertson, 1953; Young et al., 1963) and also shows a negative genetic correlation

with fleece weight (Ch'ang, 1955). However, Cockrem's (1959) experiment with mice in which he obtained substantial progress by selecting against the direction of genetic correlation, presumably by utilizing the genetic variation not controlled by the correlation, serves to avoid undue pessimism among the breeders when they find genetic antagonism between the traits. Cockrem's results with mice, however, will have to be substantiated by experiments with larger animals before they can be of practical value in commercial animal production.

As reported in the discussion of the appropriate sections, various genetic antagonisms between traits have been found in this study. The advantages of using a selection index, in such a situation, to improve the over-all production of New Zealand Romney, have been discussed by Rae (1954).

While index selection takes into account the various genetic and phenotypic parameters and the economic aspects of animal breeding, it does not include the aspect of efficiency in the animals, a factor which is of considerable importance in a grassland system of farming. It is possible, for instance, that the highest producers may not in fact be the most efficient. The concept of animal efficiency has a considerable economic importance but unfortunately this attribute in an animal does not lend itself to an easy definition and measurement. Measures of efficiency have been suggested by Wallace (1956) for butterfat production and by Ferguson (1956) for wool production.

Ferguson defined efficiency of wool growth as the percentage of the food crude protein which is converted into wool. Since food intake was proportional to body weight, it was shown that in fact wool weight per

unit body weight was a better measure of efficiency than wool weight per head. Ferguson has discussed efficiency of wool production from two points of view. Firstly, from the point of view of selection of more efficient sheep and, secondly, from the point of view of the grazing management of improved pasture.

Schinckel (1956) suggested using wool per unit of surface area, estimated by (body weight)<sup>.6</sup>, as an alternative to wool per pound of body weight.

Turner (1958) gave formulae for the heritability of a compound character ( $X = \sum x_i$ ) and the correlation between  $X$  and  $x_i$  in terms of the variances and covariances of the components. The method of estimating corresponding heritability and correlations when  $X$  is considered as the ratio of two characters was also developed (Turner, 1959). She examined the consequences of the use of the ratio of wool weight ( $W$ ) and body weight ( $B$ ) as measure of efficiency of wool production. It was shown that the genetic correlation between  $W$  and  $W/B$  was consistently positive for a wide range of values of the parameters of  $W$  and  $B$ , so that selection for high wool weight would also increase efficiency as measured by the ratio  $W/B$ . Consistently negative and sometimes very strongly negative genetic correlations were found between  $B$  and  $W/B$  which shows that selection for high values of  $W/B$  would decrease body weight. The following results obtained from the present data exhibit a similar pattern of relationship of the ratio  $W/B$  with  $W$  and  $B$ . The procedure followed is outlined below:-

Suppose

$$x_1 = \log W$$

and  $x_2 = \log B$ , so that the ratio (say,  $X$ ) =  $\log \frac{W}{B}$



$$\text{or } X = \log W - \log B = x_1 - x_2.$$

Turner (1959) has shown that if,

$P_{11}$  = Phenotypic Variance of  $x_1$ ,

$P_{22}$  = Phenotypic Variance of  $x_2$ ,

$P_{12}$  = Phenotypic Covariance of  $x_1$  and  $x_2$ ,

$G_{12}$  = Genetic Covariance of  $x_1$  and  $x_2$ ,

$h_1^2$  = Heritability of  $x_1$ ,

$h_2^2$  = Heritability of  $x_2$ ,

$r_G$  = Genetic Correlation between  $x_1$  and  $x_2$ ,

and  $r_P$  = Phenotypic Correlation between  $x_1$  and  $x_2$ ,

the heritability of the ratio  $X$ ,

$$h_x^2 = \frac{[h_1^2 (1 + k_h^2 k^2 - 2 r_G k_h k)]}{1 + k^2 - 2 r_P k},$$

the genetic correlation between the ratio  $x$  and greasy fleece weight  $x_1$ ,

$$r_{G(X.x_1)} = \frac{1 - r_G k_h k}{\sqrt{1 + k_h^2 k^2 - 2 r_G k_h k}},$$

the genetic correlation between the ratio  $X$  and hogget live weight  $x_2$ ,

$$r_{G(X.x_2)} = \frac{r_G - k_h k}{\sqrt{1 + k_h^2 k^2 - 2 r_G k_h k}},$$

and the phenotypic correlation between the ratio X and greasy fleece weight  $x_1$ ,

$$r_{P(X.x_1)} = \frac{1 - r_P k}{1 + k^2 - 2 r_P k}, \quad \text{where,}$$

$$k_h^2 = \frac{h_2^2}{h_1^2} \quad \text{and} \quad k_2 = \frac{\text{Coefficient of variation of B}}{\text{Coefficient of variation of W.}}$$

The values of the present parameters are as follows:-

$$P_{11} = 1.37, \quad P_{22} = 105.59$$

$$P_{12} = 7.29, \quad G_{12} = 1.40$$

$$h_1^2 = 0.43, \quad h_2^2 = 0.46$$

$$r_G = 0.54, \quad r_P = 0.61$$

$$k_h^2 = 1.07, \quad \text{and} \quad k^2 = 0.82$$

The substitution of these values in appropriate formulae gave the following results:-

$$h_X^2 = 0.52$$

$$r_{G(X.x_1)} = 0.53$$

$$r_{G(X.x_2)} = -0.43$$

$$\text{and} \quad r_{P(X.x_1)} = 0.53.$$

These results, as mentioned earlier, are quite consistent with the findings of Turner (1959).

Though it is decidedly more important to base selection of livestock on simple additive theory, the other factors such as dominance, epistasis, and maternal effects etc. would eventually have to be included in the genetic studies of livestock to give a fuller genetic description of the animals.

Performance recording for use on stud and commercial farms has a great need of development in New Zealand. Rae (1964) has analysed the problems of recording, especially as applied to ram breeding flocks.

A substantial amount of work has been devoted to the problems of raising production when response to selection ceases. One approach assumes that selection operates on additively genetic variance and response ends when no more variation of this kind is readily available. However, it may be possible to expose some concealed variation by various forms of physical disturbances or by introducing and later removing single genes with major effects (Turner, 1966). Another approach is to increase genetic variability by inducing gene changes by radiation. A tremendous amount of research is also directed to finding the exact nature of gene transmission. These techniques are still in their experimental stages but it is obvious that opportunities arising from such techniques are indeed great.

## CHAPTER VI

### SUMMARY

## Chapter VI

S U M M A R Y

A study was made to determine the genetic and phenotypic parameters of greasy fleece weight, hogget live weight, hairiness, mean fibre diameter, staple length and crimps per inch in the New Zealand Romney Marsh sheep. The least squares method described by Yates (1934), Hazel (1946) and Kempthorne (1952) was used in estimating the effects of year of birth, age of dam, type of birth and regression on date of birth (Table 7). Most of these effects had a significant influence on all characters studied (Table 8). The only nonsignificant effects were those of age of dam on staple length and crimps per inch and the effect of regression on crimps per inch.

The correction factors for adjusting dam's (Table 11) were based on the linear regression model with no component for year effects, because the design of experiment was such that no adjustment for year effects was necessary in dam's records. The daughter's records did not require any adjustment for the year and age of dam effects, so that the correction factors for daughter's records (Table 13) had to be derived from the estimates based on a different linear regression model with no components for year and age of dam effects.

Heritability estimates of all the traits under study (Table 20) and the phenotypic and genetic correlations between them (Tables 17 and 19)

were computed. The method of analysis for obtaining each of these parameters has been given and the results discussed.

In general, the results of this work confirm the conclusions of the review papers that the level of heritability is high for characters associated with wool production. The heritability estimate of hogget live weight (0.46) for the New Zealand Romney, obtained in the present study, is in good agreement with the estimates published for different breeds.

The consistent estimates of heritability of traits under study, for widely different breeds of sheep raised under dissimilar environmental conditions, indicate that these are strongly inherited traits which will show a rapid response to selection for individual traits. But, even with selection for one character, however, and still more with selection for more than one, the genetic correlations between the characters would have to be taken into consideration.

A genetic antagonism has been found between crimps per inch and all other traits under investigation. Negative genetic correlations have also been found between hogget live weight and hairiness, greasy fleece weight and hairiness and staple length and hairiness.

The genetic correlations obtained in this study (Table 19) show that the genetic improvement of one productive trait by selection is liable to alter several others, some favourably, others unfavourably, e.g. the effect of selecting for higher greasy fleece weight would produce unfavourable side effects in terms of increased fibre thickness and smaller number of crimps per inch. Selection for increased hogget live weight would also have similar but less drastic effects on mean fibre diameter and crimps per inch.

The present data are not adequate for deriving accurate estimates of the genetic parameters, but this work serves to point out certain obstacles to progress from selection in the New Zealand Romney Marsh sheep and to indicate the need for further investigations.

## REFERENCES



AMERICAN SOCIETY FOR TESTING MATERIALS (1955). ASTM Designation :  
D419-55T.

BARTON, R.A. (1954). Sheepfmg. Ann., Massey Agr. Coll., p.60.

BEATTIE, A.N. (1962). Queensland J. Agr. Sc. 19 : 17.

BLACKWELL, R.L. and HENDERSON, C.R. (1955). J. Anim. Sc. 14 : 831.

BOSMAN, S.W. (1958). Proc. I. Congr. S. Afr. Genet. Soc., p.38.

BROWN, G.H., TURNER, H.N., YOUNG, S.S.Y. and DOLLING, C.H.S. (1966).  
Aust. J. Agr. Res. 17 : 557.

CASSARD, D.W., GREGORY, P.W., WILSON, J.F., ROLLINS, W.C. and WEIR, W.C.  
(1953). J. Anim. Sc. 12 : 140.

CH'ANG, T.S. (1955). Unpublished M.Agr.Sc. Thesis, Massey Agr. Coll.

\_\_\_\_\_, (1966). Personal communication.

CH'ANG, T.S. and RAE, A.L. (1961). N.Z. J. Agr. Res. 4 : 578.

CLARKE, J.N. (1963). Unpublished M.Agr.Sc. Thesis, Massey University.

COCKREM, F.R. (1959). Nature, 183 : 342.

COCKREM, F.R., BARTON, R.A. and RAE, A.L. (1956). Proc. N.Z. Soc. Anim.  
Prod. 16 : 59.

COOP, I.E. (1956). N.Z. J. Sc. Tech. A37 : 542.

\_\_\_\_\_, (1962). N.Z. J. Sc. Tech. 5 : 249.

C.S.I.R.O., (1965). Rural Research in C.S.I.R.O. 52, p.2.

DAVENPORT, C.B. and RITZMAN, E.G. (1926). Bull. N.H. Agr. Exp. Sta., No.31.

- DONEY, J.M. (1955). Proc. Br. Soc. Anim. Prod., p.3.
- DRY, F.W. (1933). N.Z. J. Agr. 46 : 10, 47 : 289.
- \_\_\_\_\_, (1934). N.Z. J. Agr. 48 : 331.
- \_\_\_\_\_, (1940). N.Z. J. Sc. Technol. A22 : 209.
- DUERDEN, J.E. (1927). S.Afr. J. Sc. 24 : 388.
- ENSMINGER, M.E. (1942). J. Anim. Sc. 1 : 355.
- FALCONER, D.S. (1960). "Introd. to Quant. Genet." Oliver and Boyd.
- FERGUSON, K.A. (1956). Proc. Aus. Soc. Anim. Prod. 1 : 58.
- FREEMAN, A.E. and HENDERSON, C.R. (1959). J. Dairy Sc. 42 : 621.
- FRENEY, M.R. and TURNER, H.N. (1938). J. Text. Inst. 29 : T132.
- GOOT, H. (1945). N.Z. J. Sc. Technol. A27 : 45.
- GOOT, H. (1945a). N.Z. J. Sc. Technol. A27 : 173.
- GRANDSTAFF, J.O. and BLUNN, C.T. (1944). J. Anim. Sc. 3 : 194.
- GRANDSTAFF, J.O. and WOLF. (1947). J. Anim. Sc. 6 : 133.
- GROENEWOLD, H.H. (1963). Proc. S.Afr. Soc. Anim. Prod. 2 : 82.
- HAZEL, L.N. (1943). Genetics 28 : 476.
- \_\_\_\_\_, (1946). Biom. Bull. 2 : 21.
- HAZEL, L.N., BAKER, M.L. and REINMILLER, C.F. (1943). J. Anim. Sc. 2 : 118.

HAZEL, L.N. and TERRILL, C.E. (1945). J. Anim. Sc. 4 : 347.

\_\_\_\_\_, (1946). J. Anim. Sc. 5 : 282.

\_\_\_\_\_, (1946a). J. Anim. Sc. 5 : 371.

HENDERSON, A.E., and McMAHON, P.R. (1947). N.Z. J. Sc. Technol.  
A29 : 22.

HENDERSON, C.R. (1948). Quoted by Landblom (1955).

\_\_\_\_\_, (1953). Biometrics 9 : 226.

HOLMAN, H.H. (1962). Biological Research Method; Oliver and Boyd.

INKSTER, I.J. (1956). Proc. N.Z. Soc. Anim. Prod. 16 : 66.

JEROME, F.N., HENDERSON, C.R. and KING, S.C. (1956). Poultry Sc.  
35 : 995.

KARAM, H.A., CHAPMAN, A.B. and POPE, A.L. (1953). J. Anim. Sc.  
12 : 148.

KEMPTHORNE, O. (1952). Design and Analy. of Expts., Wiley.

KEMPTHORNE, O. and TANDON, O.B. (1953). Biometrics 9 : 90.

KOCH, R.M. and CLARK, R.T. (1955). J. Anim. Sc. 14 : 979.

LANDBLOM, N. (1955). Copybook for Beginners in Res., Colorado.

LANG, W.R. (1945). J. Text. Inst. 36 : T243.

\_\_\_\_\_, (1947). J. Text. Inst. 38 : T241.

\_\_\_\_\_, (1947a). J. Text. Inst. 38 : T257.

- LERNER, I.M. (1950). Population Genet. and Anim. Impr., Camb. Univ. Press.
- \_\_\_\_\_, (1958). The Genetic Basis of Selection, Wiley.
- LOCKART, L.W. (1954). Aust. J. Agr. Res. 5 : 555.
- \_\_\_\_\_, (1956). Aust. J. Agr. Res. 7 : 147.
- \_\_\_\_\_, (1956a). Aust. J. Agr. Res. 7 : 152.
- LUSH, J.L. (1937). Animal Breeding Plans, Iowa St. Coll. Press.
- \_\_\_\_\_, (1941). Proc. Amer. Soc. Anim. Prod. p.293.
- \_\_\_\_\_, (1945). Animal Breeding Plans, Third Ed. Iowa St. Coll. Press.
- \_\_\_\_\_, (1949). Proc. 8th Int. Congr. of Genetics (Hereditas Supp.), p.356.
- McBRIDE, G. (1954). Proc. Aust. Soc. Anim. Prod. 1 : 155.
- McMAHON, P.R. (1937). J. Text. Inst. 28 : T349.
- \_\_\_\_\_, (1943). Proc. N.Z. Soc. Anim. Prod., p.70.
- \_\_\_\_\_, (1948). Quoted by Morley (1951).
- MORLEY, F.H.W. (1951). N.S.W. Dept. Agr. Sci. Bull. No.73.
- \_\_\_\_\_, (1955). Aust. J. Agr. Res. 6 : 77.
- NARAYAN, S. (1951). Indian J. Vet. Sc. 21 : 43.
- O'FERRALL, G.J.M. and VIAL, V.E. (1962). Irish J. Agr. Res. 1 : 157.

PHILLIPS, R.W. and DAWSON, W.M. (1940). U.S.D.A. Circ. No.538, p.17.

PHILLIPS, R.W., STOEHR, J.A. and BRIER, G.W. (1940). Proc. Am. Soc. Anim. Prod., p.173.

POHLE, E.M., KELLER H.R. and HAZEL, L.N. (1943). J. Anim. Sc. 2 : 33.

\_\_\_\_\_, (1945). J. Anim. Sc. 4 : 37.

PRICE, D.A., SIDWELL, G.M. and GRANDSTAFF, J.O. (1953). J. Anim. Sc. 12 : 697.

RAE, A.L. (1948). Proc. N.Z. Soc. Anim. Prod., p.97.

\_\_\_\_\_, (1950). Unpublished Ph.D. Thesis, Iowa St. Coll.

\_\_\_\_\_, (1954). Sheepfmg. Ann., Massey Agr. Coll., p.155.

\_\_\_\_\_, (1956). Advance in Genetics. 8 : 189.

\_\_\_\_\_, (1958a). N.Z. J. Agr. Res. 1 : 104.

\_\_\_\_\_, (1958b). Sheepfmg. Ann., Massey Agr. Coll., p.11.

\_\_\_\_\_, (1958c). Proc. N.Z. Soc. Anim. Prod. 18 : 5.

\_\_\_\_\_, (1962). Proc. N.Z. Soc. Anim. Prod. 22 : 35.

\_\_\_\_\_, (1964). Proc. N.Z. Soc. Anim. Prod. 24 : 111.

\_\_\_\_\_, (1964a). Sheepfmg. Ann., Massey Univ., p.73.

RASMUSSEN, K. (1942). Sc. Agr. 23 : 104.

- REEVE, E.C.R. (1953). J. Genetics 51 : 520.
- \_\_\_\_\_, (1955). Biometrics 11 : 357.
- REEVE, E.C.R. and ROBERTSON, F.W. (1963). Anim. Br. Abs. 21 : 211.
- REIMERS, J.H.W.T. and SWART, J.C. (1930). Fmg. S.Afr. 5 : 90.
- RENDEL, J.M. (1954). Aust. J. Agr. Res. 5 : 297.
- ROBERTS, N.F. and DUNLOP, A.A. (1955). Quoted by Turner (1956).
- SCHINCKEL, P.G. (1956). Aust. J. Agr. Res. 7 : 57.
- \_\_\_\_\_, (1958). Aust. J. Agr. Res. 9 : 567.
- SEARLE, S.R. (1961). Biometrics 17 : 474.
- \_\_\_\_\_, (1963). Pap. Biometric Soc. Conf., Cambridge.
- SHELTON, M., MILLER, J.C., MAGEE, W.T. and HARDY, W.T. (1954). J. Anim. Sc. 13 : 215.
- SHORT, B.F., FRASER, A.S. and CARTER, H.B. (1958). Aust. J. Agr. Res. 9 : 229.
- SIDWELL, G.M. and GRANDSTAFF, J.O. (1949). J. Anim. Sc. 8 : 373.
- SNEDECOR, G.W. (1956). Statistical Methods, Iowa St. Univ. Press.
- TERRILL, C.E. (1958). J. Anim. Sc. 17 : 944.
- TERRILL, C.E. and HAZEL, L.N. (1943). J. Anim. Sc. 2 : 358.
- \_\_\_\_\_, (1953). Quoted by Turner (1956).

TERRILL, C.E., SIDWELL, G.M. and HAZEL, L.N. (1947). J. Anim. Sc.  
6 : 115.

\_\_\_\_\_, (1948). J. Anim. Sc. 7 : 181.

TURNER, H.N. (1956). Anim. Br. Abs. 24 : 87.

\_\_\_\_\_, (1958). Aust. J. Agr. Res. 9 : 521.

\_\_\_\_\_, (1959). Aust. J. Agr. Res. 10 : 565.

\_\_\_\_\_, (1964). Proc. Aust. Soc. Anim. Prod. 5 : 21.

TURNER, H.N., HAYMAN, R.H., RICHES, J.H., ROBERTS, N.F. and WILSON, L.T.  
(1953). Anim. Br. Abs. 22 : 323.

VAINIKAINEN, V. and HAKOLA, R. (1952). Anim. Br. Abs. 22 : 50.

VAN VLECK, L.D. and HENDERSON, C.R. (1961). Biometrics 17 : 359.

WALLACE, L.R. (1956). N.Z. Dairy Exporter 32 : 12.

\_\_\_\_\_, (1961). Proc. Ruakura Fmrs'. Conf., p.14.

WILSON, L.O., ERCANBRACK, S.K., PRICE, D.A. and TERRILL, C.E. (1959).  
J. Anim. Sc. 18 : 1165.

WRIGHT, G.M. and STEVENS, P.G. (1953). N.Z. J. Sc. Technol. A34 : 430.

YATES, F. (1934). J. Am. Stat. Ass. 29 : 51.

YOUNG, S.S.Y. and CHAPMAN, R.E. (1958). Aust. J. Agr. Res. 9 : 363.

YOUNG, S.S.Y., TURNER, H.N. and DOLLING, C.H.S. (1960). Aust. J. Agr.  
Res. 11 : 257.

\_\_\_\_\_, (1963). Aust. J. Agr. Res. 14 : 460.

YOUNG, S.S.Y., BROWN, G.H., TURNER, H.N. and DOLLING, C.H.S. (1965).  
Aust. J. Agr. Res. 16 : 997.