A STUDY OF THE INHERITANCE OF SOME PRODUCTIVE TRAITS IN PERENDALE SHEEP

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A B S T R A C T

Genetic parameters were estimated using 3,313 half-sib records from 62 sires and 1720 daughter-dam pairs. The data used were obtained over the period 1957 to 1972.

The estimates of heritability by paternal half-sib and daughter-dam regression analysis were respectively:- weaning weight (0.20 and 0.16); hogget body weight (0.27 and 0.44); fleece weight (0.32 and 0.30); quality number (0.26 and 0.31); fibre diameter (0.54 and 0.47); staple length (0.49 and 0.35); character (0.23 and 0.23). An estimate of 0.03 was obtained for lambs weaned/ewe lambing (LW/EL) by the daughter-dam regression analysis from 665 daughter-dam pairs.

Estimates of genetic correlations were in the following ranges:-

Medium negative (-0.4 to -0.6)	..	Hogget body weight with character. Quality number with staple length.
Low negative (-02. to -0.4)	..	Weaning weight with quality number, fibre diameter and character. Quality number with fleece weight and fibre diameter.
Low positive (0.2 to 0.4)	..	Hogget body weight with weaning weight and quality number. Staple length with character.
Medium positive (0.4 to 0.6)	..	Fleece weight with fibre diameter and character.
High positive (0.6 and over)	..	Fleece weight with staple length.

Phenotypic and environmental correlations were also estimated. Phenotypic correlations generally agreed with the genetic correlations. Important exceptions were hogget body weight with fleece weight, staple length and fibre diameter.

Among the environmental factors studied, age of dam and rearing rank effects for the wool traits were generally small. These effects had a marked influence on weaning weight and hogget body weight. At weaning, singles were 4.2 kg heavier than twins, while at 14 months this difference had been reduced to 2.1 kg. When comparing a two-year-old and mature age of dam effects, a 1.44 kg difference at weaning in favour of the mature age of dam reared animals, was reduced to a 1.11 kg difference at 14 months.

The estimated parameters and environmental effects were discussed with reference to their implications in selection programmes.

Relationships between hogget traits and the ewes life-time production (four consecutive years) were analysed. Records from 458 sheep were used.

Correlation coefficients indicated that hogget fleece weight, quality number, fibre diameter and staple length were good indicators of lifetime ewe performance for these traits. The results indicated that a poor relation exists between hogget body weight and number of lambs weaned by the ewe over four lambings.

A regression analysis of hogget traits on life-time economic value of the ewe indicated that fleece weight and hogget body weight were the most important variables influencing life-time economic value.

Implications of the results were discussed with reference to selection and culling programmes at the hogget age in ram breeding and non-ram breeding flocks.

TABLE OF CONTENTS

L I S T O F T A B L E S

LIST OF FIGURES

I. INTRODUCTION

A study of the inheritance of productive traits is desirable for breed or flock improvements. Information on the heritability of productive traits, and the genetic correlations between them, is essential for the formulation of breeding plans.

To predict changes, the proportion of the differences between sheep which are of genetic origin needs to be known. Sources of genetic variation in production measures fall into two main classes :

(1) differences between groups of animals which have been genetically distinct for some time (breeds, strains and studs); and

(2) differences between individual animals within a flock.

Genetic improvement in production may be achieved by exploiting one or both of these sources of differences. Use of the first often involves crossbreeding, which may change production simply through more complex interactions between genes ("heterosis"), while use of the second involves selection of parents and the subsequent decisions as to which of these selected parents are to be mated together. This selective breeding, changes the "mean", which is a function of the genotypic values and the frequency of desirable or undesirable genes in the population. Crossbreeding the Romney and Cheviot breeds and selection within the crossbred progeny has resulted in the present-day Perendale.

The breeder is confronted with the problem of choosing between alternative breeding methods. When practising selection he may use either tandem selection, independent culling levels, a selection index or a combination of these. To guide him in predicting the responses due to a particular breeding policy, knowledge of various phenotypic and genetic parameters are required.

Knowledge of genetic and phenotypic parameters in sheep breeding has increased considerably in the last 25 years. The work has been done in different countries and over a wide range of flocks. Information has accumulated for different sets of "typical" conditions. Genetic parameter estimates may vary from flock to flock, and also change with selection, so further data are of value. In New Zealand, information is available from only a few Romney flocks. As yet no published work is available on genetic parameters for the Perendale breed.

Rae (1964) wrote "the geneticists' immediate contribution to animal improvement is in the clear definition of objectives and the most effective use of selection". This still applies today. For any livestock breeding programme to be well founded, it is necessary to have knowledge of the inheritance of the various characters and their relative economic importance in a given set of circumstances, and then use this information to devise systems of selection which will be most effective in increasing production within animal husbandry practice.

The Perendale is an easy-care breed producing both meat and wool. Both factors must be considered with the objective of an optimum balance between them.

Selection may lead to two avenues of improvement:

(1) in the lifetime performance of the selected animals by selecting superior animals which will maintain superiority for the remainder of their lifetime;

(2) in the progeny by selecting superior animals whose offspring will demonstrate a high proportion of their parents' superiority.

Sheep farmers who buy all their rams are concerned more with the current flock improvement. The usual practice is to carry out the major proportion of selection on ewe hoggets. Consequently it is of interest as to what proportion of the variation in ewe hogget performance will be related to lifetime production. These farmers generally rely on the purchase of young rams genetically superior to their ewes, to improve the next generation.

Ram breeders must put emphasis on both the current flock and the progeny, for it is their responsibility to ensure that a regular supply of young rams genetically superior to the ewes to which they are mated are available to the industry as well as for their own flock. They need to make progressive genetic improvement in changing economic circumstances. As a consequence, ram breeders need to be well informed of the objectives of selection and the most efficient breeding plans in relation to genetic and phenotypic parameters, costs of evaluation of their sheep and applicability to their farming system.

The purpose of this thesis is to make some of this information available for the improvement of Perendales. Its aim is to estimate genetic parameters for the following traits:- fleece weight, fibre diameter, quality number, character, staple length, hogget body weight, weaning weight and number of lambs weaned per ewe lambing. Also it aims to examine the relationships between the observed characteristics of the hogget and their subsequent lifetime performance.

The records available for this analysis cover 20 years. They come from a foundation flock for the Perendale Breed, a flock managed in "typical Perendale country".

The thesis is timely because, with sheep breeding, many facts have been accumulating which may improve selection. A study of the inheritance of some productive characters in Perendales is needed to confirm the general applicability of recommendations arising from the findings already published and to guide breeders in the clarification of the objects of selection.

II. REVIEW OF LITERATURE

A. PERENDALES

The development of the Perendale has its origin with an investigation of the productive traits of Cheviot-Romney cross sheep, started at Massey Agricultural College in 1939 by Professor G.S. Peren.* The foundation breeders were concerned with the low lambing percentages achieved from the Romney breed and a high percentage of ewes failing to develop sufficiently to be mated, when farmed under hill country conditions.

Crossbreeding was used in an attempt to produce a type of sheep which was more closely adapted to the particular complex of environmental and economic conditions of hard hill country. Hewitt (1947) presented some of the earliest data. Details of the establishment work and how from 1938-43 it was decided to directly compare the Cheviot x Romney half-bred with the Romney was reported by Peren, Hewitt, Ballard and Phillips (1951). From the outset, the Cheviot x Romney half-bred showed an increase in fertility and other productive traits.

The objectives in establishing the Cheviot x Romney half-bred as a breed were outlined by Rae (1957).

Published papers on Perendale sheep have been reviewed by Dalton (1971). The majority of papers have drawn conclusions based on the comparison of Cheviot x Romney half-breds and the Romney when farmed on hill country. Features have been, increased number and weight of lambs weaned, improved growth rate of lambs and hoggets, and the general ability of this breed to thrive under harder conditions.

The Perendale is a sheep intended for use on hill country and thus must be bred as a self-replacing flock. The advantages of the Perendale in terms of low labour requirement and suitability for management as an easy-care sheep have been reported (Peren, 1972).

* Sir Geoffrey Peren, K.B.E., C.B.E.

A description of 'desirable' Perendale wool was given by Regnault (1972). Barton (1972) and Dalton and Kirton (1973) have discussed the Perendale's suitability as a producer of lamb.

B. ENVIRONMENTAL EFFECTS

The effectiveness of selection in producing genetic improvement depends on the degree to which the phenotype on which selection is based reflects the underlying genotype. The hogget's phenotype is a measure of both genetic and environmental effects. Thus, total variations, with certain qualifications, is the sum of the components:-

$$\sigma_P^2 = \sigma_A^2 + \sigma_D^2 + \sigma_I^2 + \sigma_{GE}^2 + \sigma_E^2$$

where,

σ_P^2 is the phenotypic variance

σ_A^2 is the additive variance component

σ_D^2 is the dominance variance component

σ_I^2 is the interaction variance component

σ_{GE}^2 is the genotype-environment interaction variance component

and σ_E^2 is the environmental variance component.

The effect of the environment is complex. An animal is subjected to environmental effects from the time of its conception to the time when it is measured. A hogget has had contributions to the environmental variance component from the pre-natal, pre-weaning and post-weaning environment.

When records for different groups of individuals are to be used jointly for purposes such as the estimation of population parameters, it is essential to know the effect of various environmental factors influencing the manifestation of that character. In sheep breeding studies, it is possible to estimate the effects of some environmental factors and to use these estimates to correct the production records. Both the accuracy of estimated genetic differences and selection for genetic merit is thus greatly increased.

Numerous studies are available showing the effect of such factors as year, rearing rank, age of dam, age and sex of individuals. The New Zealand data applicable to this study are those of Ch'ang and Rae (1961 and 1970); Tripathy (1966); Lundie (1971); Baker, Clarke and Carter (1974) for the Romney and Hight and Jury (1971) for the Romney and Border Leicester x Romney breed. Results for relevant traits are summarised in Tables 1 and 2.

The effect of year-to-year variation can be appreciable. This emphasises the necessity of either expressing corrected measurements as a deviation from the flock-year average or carrying out a within-year analysis. The "year" effect is a measure of the influence of many factors which are difficult to isolate and measure separately. These include the level of nutrition, climatic conditions and management peculiar to the records made in each year.

The effect of year may also contain a genetic component (Ch'ang and Rae, 1970). This occurs with genetic changes in the average merit of the animals where the sires and ewes have been selected for any productive traits, or when the level of inbreeding changes. The possibility of confounding of genetic differences between groups of ewes born in different years or from different sources, with the true environmental differences between age of dam groups was pointed out by Baker *et al.* (1974).

Age and rearing rank have usually been the major sources of variation in weaning weight (Hazel and Terrill, 1945a, 1946a; Ch'ang and Rae, 1961, 1970; Clarke, 1967; Fahmy, Galal, Ghanem and Khishin, 1969; Hight and Jury, 1971; Baker *et al.*, 1974) but have less influence on hogget body weight (Ch'ang and Rae, 1970; Baker *et al.*, 1974). Age of dam moderately influences weaning weight, though this effect tends to persist undiminished well beyond weaning and by hogget age the extent of its influence on live weight may be comparable to that of rearing rank (Ch'ang and Rae, 1970).

TABLE 1
ESTIMATES OF ENVIRONMENTAL EFFECTS

Weaning Weight (kg)

Reference	(1)	(2)	(3)	(4)	(5)	(6)
Mean	24.1	25.26	25.53	19.32	19.73	20.4
S.D.	3.5	3.5	-	2.9	2.9	3.2
Year (range)	-	8.4	7.4	-	-	4.0
Age of Dam						
3-yr - 2-yr	-	0.4	1.4	1.1	1.2	-
4-yr - 2-yr	-	2.0	2.0	1.5	1.8	-
Mature - 2-yr	-	-	2.3	1.6	1.8	1.3
Rearing rank						
* S - T	4.6	4.2	4.4	3.4	4.7	4.2
S - TRS	3.0	2.9	1.6	1.6	2.7	2.5
Reg. on age	0.13	0.12	0.17	0.12	0.12	0.12

Hogget body weight (kg)

Reference	(2)	(4)	(5)	(6)	(7)
Mean	39.1	35.1	37.1	43.2	38.9
S.D.	5.0	3.7	4.2	4.7	-
Year (range)	6.1	-	-	11.1	6.1
Age of dam					
3-yr - 2-yr	0.95	-0.54	0.48	0.9	-
4-yr - 2-yr	2.4	-0.14	0.02	1.3	1.2
Mature - 2-yr	-	-0.14	1.3	-	-
Rearing rank					
S - T	2.2	0.09	2.0	2.10	0.77
S - TRS	0.4	-	-	1.5	0.45
Reg. on age	0.08	0.06	0.11	0.05	0.02

* S, single; T, twin; TRS, twin raised as single.
References: (1) Ch'ang and Rae (1961); (2) Ch'ang and Rae (1970); (3) Lundie (1971); (4) Hight and Jury (1971) - Romney data; (5) Hight and Jury (1971) - R x BL F_3 data; (6) Baker et. al. (1974); (7) Tripathy (1966).

TABLE 2
ESTIMATES OF ENVIRONMENTAL EFFECTS

Fleece Weight (kg) - hoggets

Reference	(1)	(2)	(3)	(4)	(5)
Mean	3.6	3.3	3.1	3.3	3.9
S.D.	-	-	0.48	0.46	0.5
Year (range)	1.49	1.36	-	-	1.2
Age of dam					
3-yr - 2-yr	0.15	0.18	-0.06[†]	-0.04	0.0
4-yr - 2-yr	0.23	0.23	-0.04[†]	0.13	0.0
Mature - 2-yr	-	0.30	-0.07[†]	0.15	-
Rearing rank					
S - T	0.12	0.24	0.14	0.23	0.1
S - TRS	0.06	0.21	-	-	0.0
Reg. on age	- 0.01	0.01	0.01	0.01	0.01

From Tripathy (1966) - hogget traits

	Mean fibre diameter (m)	Staple length (cm)	Crimps per inch	Medullation
Mean	35.81	14.14	3.25	7.89
Year (range)	6.69	2.22	0.78	5.40
Age of dam				
3-yr - 2-yr	0.50	0.11	0.02	0.26
4-yr - 2-yr	0.31	-0.01	0.07	0.34
Rearing rank				
S - T	0.11	0.41	-0.24	1.71
S - TRS	0.56	0.16	-0.30	1.02
Reg. on age	-0.06	-0.01	0.0	-0.04

† Large standard errors.

References: (1) Tripathy (1966); (2) Lundie (1971); (3) Hight and Jury (1971) - Romney data; (4) Hight and Jury (1971) - R x BL F_3 data; (5) Baker et. al. (1974).

Age of dam and rearing rank are thought to reflect the preweaning maternal handicap (Ch'ang and Rae, 1970). The causes of maternal handicap have been discussed by Dun and Grewal (1963), Lax and Brown (1967) and Bradford (1972). It results in part from the lower milk production of young dams (Barnicoat, Logan and Grant, 1949 ; Owen, 1957) or in the case of twins, from intra-uterine competition for nutrients and reduced milk intake per lamb (Hunter, 1956).

Both Ch'ang and Rae (1970) and Hight and Jury (1971) have reported that twin lambs grew faster than singles between weaning and hogget measurement. This is in agreement with other published work. The maternal influence on growth and absolute live weight of the progeny changes with the offspring's development (Dickinson, 1960; White, Legates and Eisen, 1968). Dickinson (1960) suggested that as a morphological character approaches maturity it becomes progressively more independent of the environment. After weaning the maternal handicap effects could progressively decline with advancing age as a result of compensatory growth (Schinckel, 1963; Dun and Grewal, 1963; Lawrence and Pearse, 1964; Young, Brown, Turner and Dolling, 1965; Drinan, 1968; Ch'ang and Rae, 1970).

The New Zealand studies of the estimates for effects of age of dam and rearing rank on live weight and fleece weight for early life are within the range of other published works (Hight and Jury, 1971).

Generally negligible effects of age of dam have been found on greasy fleece weight at weaning and hogget shearing (Vesely, Peters and Slen, 1965; Vesely, Peters, Slen and Robison, 1970; Hight and Jury, 1971; Baker et al., 1974). Both Tripathy (1966) and Lundie (1971) found that age of dam and rearing rank were significant for greasy fleece weight.

Significant effects of age of dam and rearing rank on mean fibre diameter and medullation have been found (Tripathy, 1966). Only the effect of rearing rank was significant for staple length and crimps per inch. Vesely et al. (1970) reported that these were not significant sources of variation for staple length, wool grade and yield. Price, Sidwell and Grandstaff (1953) found the effect of age of dam highly significant on staple length.

Maternal handicap lowers greasy and clean wool weight (Turner, 1961; Dun and Grewal, 1963; Lax and Brown, 1967), the effect being noticeable even in maturity, though in general diminishing with age. Lowered total follicle number has been shown to be the main contributing factor. Such a handicap might persist throughout adult life (Brown, Turner, Young and Dolling, 1966). If the young ewe were well-grown the handicap might be eliminated (Turner, 1961) for the provision of adequate post-natal nutrition may eliminate the difference (Doney and Smith, 1964; Gallagher and Hill, 1970).

Estimates of effects of age on hogget fleece weight, after animals have been shorn at weaning, range from 0.004 to 0.014 kg (Hazel and Terrill, 1946b; Tripathy, 1966; Hight and Jury, 1971; Baker et. al, 1974). In other wool traits age effects are less important. Small estimates have been reported for fibre diameter and staple length by Tripathy (1966) and Lax and Brown (1967). After a study was made with Merino, Corriedale and Polwarth sheep on eight different properties, Mullaney and Brown (1967) concluded that in general correction for differences in age was not likely to increase the precision of selection for wool traits at 18 months.

Ch'ang and Rae (1970) reported that effects of year of birth and age of dam showed no definite pattern on fertility measurements. Estimates of rearing rank indicated that twins on average were more fertile than singles whether at first lambing or over several lambings. This result was in agreement with others (Reeve and Robertson, 1953; Turner, Hayman, Triffitt and Prunster, 1962; Clarke, 1963; Dun and Grewal, 1963; Lax and Brown, 1968).

An important consideration is that partitioning the components of variance for reproductive rate results in extremely large error variance with only small amounts of variation controlled by main effects and interactions (Goot, 1952; Dunlop, 1963; Vesely and Peters, 1965; De Haas and Dunlop, 1969; Lundie, 1971). Ch'ang and Rae (1970) noted that their results implied that estimates of the effects of rearing rank on a ewe's fertility contain a genetic component in addition to the environmental difference between those born and reared as singles or twins. They suggested that adjustments should not be made for difference in type of birth if the aim is to study the genetic variation and covariation in fertility of the ewe.

In the absence of interactions, estimates of environmental effects may be used as additive correction factors. In the studies by Ch'ang and Rae (1970); Hight and Jury (1971) and Lundie (1971) first order interactions between years, age of dam and rearing rank effects, were statistically non-significant.

Use of additive correction factors is the most convenient and widely adopted procedure for reducing the amount of environmental variation in data prior to genetic analysis. Both Shelton and Campbell (1962) and Turner and Young (1969) have discussed correction factors in relation to the practical use of the estimated genetic parameters in sheep breeding.

C. REPEATABILITY

A knowledge of repeatability is useful in that it indicates the gain in accuracy to be expected from multiple measurement. It can be used for predicting the increase in lifetime production that may be achieved through early selection based on one record or the mean of several.

Repeatability expresses the proportion of the variance of a single measurement that is due to permanent differences between animals, both genetic and environmental.

Many estimates of repeatability for various traits in different breeds of sheep have been made. Much of the published information was reviewed by Morley (1951); Turner (1956, 1969) and Turner and Young (1969). When the first record is at the hogget age, these reviews give ranges for repeatability estimates of 0.4 to 0.8 (fleece weight); 0.5 to 0.8 (staple length); 0.5 to 0.7 (fibre diameter); 0.5 to 0.8 (body weight). Repeatability estimates of 0.46 to 0.51 and 0.60 to 0.78 have been reported respectively for character and quality number.

Estimates greater than 0.6 are considered to be high, and those from 0.3 to 0.6 medium levels of repeatability (Turner and Young, 1969).

After comparing the relative efficiency of single record selection with that based on the mean of two records, Turner and Young (1969) concluded that in Merinos, production traits such as greasy and clean wool weight, percent clean yield, fibre diameter, staple length and body weight are highly repeatable or nearly so, for adult animals. It was considered that selection for production based on the earliest adult record at 15-16 months would be almost as efficient as selection based on the mean of two records. A slightly lower efficiency of a single record would be compensated by a higher gain per year from earlier selection and the early disposal of surplus stock.

Although estimates for traits in breeds other than Merino and allied breeds are scanty, they suggest that levels for the same trait do not differ widely (Turner and Young, 1969).

It has been widely recommended that hogget wool production records be used as reflections of genetic worth for they will have been produced during a common growing period without having been subjected to age, pregnancy or lactation effects.

The repeatability for lambing rate and its components has either been estimated by the usual intra-class correlation, or by the regression of subsequent on early performance. Full details of analyses reported was given by Turner (1968). Generally subsequent lambing rate is positively related to early performance, however the relationship is not linear. Methods of estimating repeatability by intra-class correlation assume linearity, so that the estimates, and the prediction of selection gains based on them, will only be approximate.

Estimates of repeatability for lambs weaned per ewe joined have usually been low. Values between 0.01 to 0.17 have been reported (Young et al., 1963; Purser, 1965; Kennedy, 1967; Inskeep, Barr and Cunningham, 1967; Lundie, 1971). The estimates based on ewes lambing rather than ewes mated are generally higher. Turner (1969) considered that, among the components of lambs weaned per ewe joined, lambs born per ewe present seemed to be the most profitable criterion of selection for gain in the current flock.

D. RELATIONSHIP BETWEEN HOGGET CHARACTERS AND LIFE-TIME PERFORMANCE.

The breeder who buys all his rams from an outside source is limited in what he can do to initiate genetic gains. Such a high percentage of ewes have to be retained that the selection differential is low and consequently gains (independent of any genetic gain or loss from the rams used) will only be modest. Emphasis is put on the gain in production which will remain throughout the life-time of the flock as a result of picking better ewe replacements.

The degree to which lifetime gains will be made depends on the repeatability of the character in question. However, the usefulness of this parameter is limited.

A review of literature shows few studies of the relationship of hogget characters to life-time production over a number of generations.

Two early studies were those of Gartner and von Ungern-Stenberg (1938) and Wolf (1951) with, respectively, Mutton Merino and Bavarian Land-Merino sheep breeds. Correlation coefficients between yearling and lifetime wool production of 0.61 and 0.63 were reported.

Both concluded that yearling fleece weight formed a practical basis for the determination of the average lifetime wool production.

More extensive studies are those of Terrill (1939) with 18 years of Rambouillet ewe data, and Wright and Stevens (1953) with 16 years of data from Romney and Corriedale ewe records. Reported correlation coefficients between hogget measure and mature lifetime wool average (i.e. second to fifth year) for fleece weight were 0.59 (Rambouillet), 0.44 (Romney) and 0.72 (Corriedales). Wright and Stevens (1953) had adjusted their data for lambing performance. Coefficients calculated within-year of birth were roughly 0.05 higher.

When hogget data are included in the total lifetime fleece weight, the correlation involves a part-whole relationship. For this measure correlation coefficients of 0.62 (Romney's) and 0.84 (Corriedale's) were reported by Wright and Stevens (1953).

Terrill (1939) also reported a correlation coefficient of 0.69 for staple length and regression coefficients for hogget measurements on lifetime mature averages of 0.50 (fleece weight) and 0.61 (staple length). The correlation coefficients were highly significant and Terrill (1939) considered that yearling measurements appeared to have a useful predictive value for lifetime wool merit.

More literature has been reported where the interest has been on the extent that the performance of ewes could be affected by culling ewe hoggets on body weight records. Studies by Terrill and Stoehr (1942) with 15 years of records on ewes of the Columbia, Corriedale and Rambouillet breeds; Purser and Roberts (1959) with Scottish Blackface records; Shelton and Menzies (1968) with Rambouillet data and Basuthakur, Burfening, van Horn and Blackwell (1973) involving Targhee and Columbia sheep, have been reported.

Shelton and Menzies (1968) results came from 36 years of records. Some of their results are reproduced in <u>Table 3</u> along with those of Basuthakur et al. (1973) because of the similarity of findings. These studies showed that yearling body weight was positively related to all measures of lamb and wool production. In general the relationships were significant but of low magnitude.

TABLE 3
RANGE OF SIMPLE CORRELATIONS AMONG TRAITS
From Shelton and Menzies (1968) and Basuthakur et al. (1970).

	Yearling Weight	Number of lambs born	Number of lambs raised	Number multiple births	Mean fleece weight	Total wool product -ion	Total lamb product -ion
Weaning weight	0.58 to 0.66	0.10 –	0.08 to 0.09	0.09 to 0.13	0.06 to 0.27	0.10 to 0.15	0.06 to 0.10
Yearling weight		0.06 to 0.13	0.08 to 0.12	0.11 to 0.15	0.10 to 0.30	0.07 to 0.15	0.08 to 0.11

All analyses were made on a within year-of-birth basis with no adjustments of data. Mean fleece weight, as used by Shelton and Menzies (1968) represented the mean of a minimum of 3 annual weights taken between the ages of 3 and 7 years. Lifetime production came from sheep aged 2 to 10 years; removal from the flock being a result of death or from normal culling. Approximately 85% of the sheep records were from sheep less than 7 years of age and 45% were greater than 3 years. Basathakur et al. (1973) made their study with ewes born over a 12 year period; however they made no mention of age distribution or when ewes were finally culled.

Higher, significant correlation coefficients between hogget body weight and the average weight of lambs weaned per ewe year for the first 4 lambings were reported by Terrill and Stoehr (1942), with Columbias (0.25), Corriedales (0.31) and Rambouillets (0.29). It was concluded that ewes which were heavier as hoggets, on average wean more pounds of lamb per ewe year during their lifetime. This advantage was due more to a higher percent of lambs weaned, than to heavier weaning weights. A slight advantage in the lifetime average fleece weight in favour of ewes which had been heavier as hoggets was also shown, but there was practically no difference for fleece lengths.

Corresponding regression coefficients have been reported. Both Purser and Roberts (1959) and Shelton and Menzies (1968) results indicate that for 1 kg increase in hogget body weight there was 0.02 kg increase for mean fleece weight. Shelton and Menzies (1968) indicate that for a 1 kg increase in hogget body weight there was a 2.34 kg increase in total lamb production which compares with the previously reported 0.25 kg to 0.31 kg (Terrill and Stoehr, 1942) and 0.17 kg (Purser and Roberts, 1959) yearly average increase in weight of lamb weaned.

Further points of interest arise from these studies. Purser and Roberts (1959) noted that regression coefficients, in general, decreased with increasing age of ewe, so that the relationships were greatest in the first year or two of production. Terrill (1939) and Shelton and Menzies (1969) respectively showed correlation coefficients of 0.68 and 0.67 and regression coefficients of 0.72 and 0.59 between hogget and mature body weights.

General conclusions are that small changes in subsequent lifetime production can be brought about by increasing hogget body weight through selection. The effect of increasing the weight by feeding may be quite different.

E. ESTIMATES OF HERITABILITY

Estimates of heritability for different traits of sheep have been reported by a large number of workers. In their review of published estimates, Turner and Young (1969) drew attention to the extremely large range of values for each trait. Since estimates of heritability depend on both the genetic and environmental variances, it is not surprising to have different values for the same trait in different flocks, particularly when the flocks are situated in different environments and have different selection histories. At least part of the large variation in values of published estimates is due to the inclusion of estimates with large sampling errors. With early sheep breeding experiments, poor estimates based on a small amount of data were unavoidable. Because of this, only estimates pertinent to this study will be reviewed here.

Excellent reviews of earlier works are those of Morley (1951), Rae (1956) and Turner (1956). A summary of heritability estimates appear in Tables 4, 5 and 6.

Values of 0.3 or more may be regarded as high levels of heritability, those between 0.1 and 0.3 intermediate, and those below 0.1 as low (Turner and Young, 1969).

1. Estimates for Wool Traits.

In general, wool traits are regarded as highly heritable. From Table 4, the following ranges exist:- fleece weight (0.11 to 0.84); quality number (0.10 to 0.47); fibre diameter (0.17 to 0.57); staple length (0.22 to 0.56) and character (0.12 to 0.39).

Estimates by Schinckel (1958) came from strong-woolled Australian Merinos while Morley (1951, 1955a, 1955b); Young, Turner and Dolling (1960b); Beattie (1962) and Brown and Turner (1968) made their estimates with various strains of medium to strong-wool Merinos.

Rae (1964) summarized the available estimates of heritability for the Romney breed. He concluded that the fleece characteristics other than fleece weight had heritabilities of a similar order to those found for other breeds in other countries. The main discrepancy was in fleece weight where early estimates were substantially lower than those obtained for other breeds, particularly the Merino. Later estimates, Tripathy (1966); Lundie (1971) and Rae (1958) were higher. These were in line with a fleece weight selection experiment, where preliminary assessment of the progress suggested that heritability was higher and that useful progress could be made (Rae, 1964).

Fibre diameter has been neglected in most studies. The Australian work shows it to be highly heritable. It

TABLE 4
SOME ESTIMATES OF HERITABILITY FOR WOOL TRAITS

Breed	Fl.Wt	Qu.No.	F.D.	St.L.	Ch.	Refer -ence	Method of Estimat-ion
Romney	0.10 - 0.15	0.35-0.40	-	-	0.14	(1)	
	0.17	0.27	-	0.35	0.24	(2)	
	0.31	0.34	-	0.50	0.16	(3)	D.D.Reg.
	0.32	0.47	-	0.48	0.12	(3)	Pat.½-sib.
	0.43	-	0.17	0.46	-	(4)	D.D.Reg.
	0.23	-	-	-	-	(5)	Pat.½-sib.
Merino	0.39	-	-	0.22	-	(6)	D.D.Reg.
	0.67	-	0.26	0.24	-	(6)	Pat.½-sib.
	0.40	-	-	0.56	-	(7)	D.D.Reg.
	0.44	-	-	0.52	0.38	(7)	Pat.½-sib.
	0.45	-	0.45	0.37	-	(8)	D.D.Reg.
	0.35	-	0.57	0.50	-	(9)	D.D.Reg.
	0.42	-	0.47	0.43	-	(10)	D.D.Reg.
	0.30	0.32	0.49	0.31	0.32	(11)	D.D.Reg.
Corriedale	0.22	0.37	0.44	0.44	0.37	(11)	D.D.Reg.
Polwarth	0.14	0.36	0.30	0.53	0.39	(11)	D.D.Reg.
Navajo	0.34	-	0.35	0.23	-	(12)	D.D.Reg.
Rambouillet	0.59	-	-	0.49	-	(13)	Pat.½-sib.
	0.11	-	-	0.46	-	(13)	Pat.½-sib.
	0.31	0.10	-	0.25	-	(14)	Pat.½-sib.
Romnelet	0.48	-	-	-	-	(15)	D.D.Reg.
	0.29	0.45	-	0.39	-	(14)	Pat.½-sib.
Welsh Mountain	0.61	-	-	0.73	-	(16)	D.D.Reg.
Others	0.12	-	0.39	0.44	-	(17)	Pat.½-sib.
Average	0.36	0.34	0.40	0.40	0.39		

Source: (1) McMahon (1943); (2) Rae (1946); (3) Rae (1958); (4) Tripathy (1966); (5) Lundie (1971); (6) Morley (1951); (7) Morley (1955a, 1955b); (8) Young et al.(1960b); (9) Beattie (1962); (10) Brown and Turner (1968); (11) Mullaney et al. (1970); (12) Hall et al. (1964); (13) Basset et al. (1967); (14) Vesely et al. (1970); (15) Vesely and Slen (1961); (16) Doney (1958); (17) Gjedrem (1969).

would appear from Table 4 that the heritability of staple length is fairly high for all breeds of sheep reported. The heritabilities were determined under widely different environmental conditions; hence considerable reliance can be placed on the conclusion that staple length is highly heritable.

It is of interest to know heritabilities of characters concerned with "quality" of wool. Estimates for, number of crimps per inch and degree of definition of staple crimp (character), colour and handle, usually range from 0.3 to 0.6 in Merinos (Morley, 1955b; Schinckel, 1958; Beattie, 1962; Young et al. 1960b). In Romneys, colour and character appear to have a low heritability (Rae, 1958). Very high heritabilities have been found for expressions of medullation:- 0.34 to 0.87 (Rae, 1958; Tripathy, 1966), 0.45 to 0.57 (Purser, 1963, 1966); and 0.67 to 0.74 (Gjedrem, 1969).

2. Estimates for Weaning and Hogget Body Weight.

From the estimates given in Table 5 it can be seen that the average heritability estimate for weaning weight is about 0.25 to 0.30 with a range 0.10 to 0.59; and for hogget body weight 0.45 to 0.50 with a range 0.36 to 0.82. The situation found by Ch'ang and Rae (1970) is typical:- there is a tendency for the value of heritability to rise with increasing age of the individual from weaning to about 14 months old. They suggested that this trend may have resulted from a greater opportunity for the individuals own genetic constitution to express itself independently of the maternal effects, with increasing intervals of time from weaning. Ercanbrack and Price's (1972) paper is concerned with the change in expression of genotype with maturity and showed that distinct trends were evident in magnitude of heritabilities and correlations involving body weights.

A difference in heritability estimates for weaning weight between singles and twins was reported by Gjedrem (1967) with estimates 0.04 ± 0.03 for twins and 0.26 ± 0.14 for singles. He suggested an environmental difference may

TABLE 5

SOME ESTIMATES OF HERITABILITIES FOR WEANING WEIGHT AND HOGGET BODY WEIGHT

Breed	W.Wt	H.B.Wt	Method of Estimation	Reference
Romney	0.35	-		Ch'ang & Rae (1961)
	0.30	0.51	Pat. ½-sib	Ch'ang & Rae (1970)
	0.23	0.46	D.D. Reg.	Ch'ang & Rae (1970)
	0.35	-	Pat. ½-sib	Lundie (1971)
Merino	0.45	-	D.D. Corr.	Young <u>et al</u>. (1965)
	0.10	-	Pat. ½-sib	Young <u>et al</u>. (1965)
	0.18	0.40	Pat. ½-sib	Pattie (1965a, b)
	0.28	0.47	D.D. Corr.	Pattie (1965a, b)
	-	0.65	D.D. Reg.	Brown & Turner (1968)
	-	0.36	D.D. Reg.	Morley (1955a)
	-	0.09	Pat. ½-sib	Morley (1955a)
	-	0.54	D.D. Reg.	Beattie (1962)
Rambouillet	0.27	-	Pat. ½-sib	Hazel & Terrill (1945b)
	0.34	-	D.D. Reg.	Hazel & Terrill (1945b)
	0.38	0.82	Pat. ½-sib	Basset <u>et al</u>. (1967)
	0.45	0.62	Pat. ½-sib	Ercanbrack & Price (1972)
	0.18	-	D.D. Reg.	Blackwell & Henderson (1955)
	0.14	0.45	Pat. ½-sib	Burfening <u>et al</u>. (1971)
	0.13	-	Pat. ½-sib	Veseley <u>et al</u>. (1970)
Romnelet	0.28	0.37	D.D. Reg.	Veseley & Slen (1961)
Corriedale	0.59	-	Full sib corr.	Botkin (1964)
Welsh Mountain	0.68	0.59	D.D. Reg.	Doney (1958)
	0.48	0.16	D.D. Reg. (corrected)	Doney (1958)

be the most important reason for the difference.

It is generally concluded that once the environmental factors have been corrected for, then the heritability of weaning weight indicates that reasonable gains from selection can be expected. It appears that hogget body weight is a highly heritable character.

3. Estimates for Number of Lambs Weaned.

As a measure of a flock's productivity in relation to reproduction rate, the number of lambs weaned per ewe joined per year, is the most practical. When using "number of lambs weaned" as a measure of fertility, it must be realised that this measure has been confounded with effects associated with the viability of the young and with other factors which are not associated with an animal's potential reproductive capacity.

A summary of estimates of heritability for number of lambs weaned can be seen in Table 6. Where both estimates are available for the same flock, the heritability of lambs born per ewe joined is usually higher than for lambs weaned, e.g. Young, Turner and Dolling (1963). For lambs born per ewe lambing the estimate is in general higher again, though estimates are not on the same flock (Turner, 1969).

For number of lambs born, Young et al. (1963) and Purser (1965) have shown that the age of the ewe affected the value of heritability. In both cases the heritability estimate was low for the first lambing but for later lambings it was sufficiently high to predict that there would be a response to selection. With Australian Merinos, Young et al. (1963) found the heritability estimate rose from 0.03 at 2 years of age to 0.35 at 3 years of age. Purser (1965) working with Scottish Blackface and Welsh Mountain sheep found an increase in heritability of litter size with age, though this was significant ($P < 0.01$) only in the case of the Welsh flock. The highest heritability estimates were at the third lambing for the Welsh ewes (0.32) and at the fourth lambing for the Blackface (0.31).

TABLE 6

HERITABILITY ESTIMATES FOR

NUMBER OF LAMBS WEANED/EWE JOINED.

Breed	Estimate		S.E.	Age of Ewes (years)	Reference	Method of Estimation
Merino	0.03	±	0.06	2	Young *et.al.* (1963)	Pat. ½-sib.
Merino	0.15	±	0.10	3	Young *et.al.* (1963)	Pat. ½-sib
Merino	0.09	±	0.10	2 & 3	Young *et.al.* (1963)	Pat. ½-sib
Merino	0.06	±	0.08	2	Kennedy (1967)	Pat. ½sib
Welsh Mountain	0.03	±	0.04	2 - 4	Purser (1965)	Pat. ½-sib
S. Blackface	0.00	±	0.03	2 - 6	Purser (1965)	Pat. ½-sib
Rambouillet	0.22	±	-	Lifetime	Shelton & Menzies (1968)	Pat. ½-sib
Rambouillet	0.27	±	-	Lifetime	Shelton & Menzies (1968)	Intrasire regression.

Similarly Johansson and Hanson (1943; cited Ryder and Stephenson, 1968) reported a figure for one lambing in Cheviot ewes at 0.04, while if three lambings were considered, heritability for this breed increased to 0.18.

Ch'ang and Rae (1970) found that the estimates of heritability, if calculated by daughter-dam regression, rose when they considered the first three lambings (0.045, 0.111 and 0.205). However, this was not the case if the heritability was calculated by paternal half-sib correlation (0.053, 0.121 and 0.032 respectively). Young et al. (1963) also found that the heritability of the sum of the first two lambings was higher than the first alone (0.19 versus 0.03) but was not as high as for the second lambing alone (0.35); corresponding figures for lambs weaned are 0.09 versus 0.03, with second lambing, lambs weaned heritability estimate being 0.15.

For the Romney, estimates for number of lambs born or weaned (0 to 0.17) indicate it to be a lowly heritable character (Rae and Ch'ang, 1955; Ch'ang and Rae, 1970; Clarke, 1963; and Lundie, 1971).

F. ASSOCIATION BETWEEN PRODUCTIVE TRAITS.

In studies on the breeding of farm animals, considerable emphasis has been placed on the investigation of covariance between traits. Hazel (1943) pointed out that a phenotypic correlation may occur for two reasons. First some of the genes affecting one character may also affect the other character. Secondly, the two traits may be correlated because some of the external and internal environmental influences affecting one may also affect the other.

The phenotypic correlation can be partitioned into genetic and environmental correlations. Unless the phenotypic correlation is separated into these two parts it is impossible to forecast the genetic effects which selection will have on a population (Rae, 1952). If the environmental effects are large they may either mask or enhance the genetic effects, but only the latter will be demonstrated in the next generation (Turner and Young, 1969).

A phenotypic correlation between two traits therefore does not necessarily mean that they have a common genetic basis; i.e. selection for one character does not always bring about an increase in other characters positively correlated with it phenotypically. In fact the opposite may occur if the genetic correlation is negative even though the phenotypic correlation is positive. For this to be the case, the environmental covariance between the two traits would have to be positive and larger in absolute value than the negative genetic covariance between the traits.

Estimates of phenotypic and genetic correlations between wool and body characteristics in Merinos and their crosses have been given by Morley (1955a, 1955b), Schinckel (1958), Beattie (1962), Turner (1964), Young et al. (1965), Brown and Turner (1968), Mullaney, Brown, Young and Hyland (1970) in Australia and Bosman (1958) in South Africa.

Estimates of the genetic correlations for wool traits have been generally similar in sign and magnitude to the phenotypic correlations for the same characteristics (Mullaney et al., 1970).

Phenotypic and genetic correlations between reproduction rate and other traits in Australian Merinos have been reported by Young et al. (1963) and Kennedy (1967).

The range of these correlation estimates have been summarized by Turner and Young (1969) and Turner (1972) and those pertinent to this thesis appear in Table 7.

Turner and Young (1969) point out that the two sets of estimates available for correlations between numbers of lambs born and weaned and some wool and body characteristics in Australian Merinos, are not in agreement.

TABLE 7

ESTIMATES OF GENETIC (above diagonal) AND PHENOTYPIC (below diagonal) CORRELATIONS BETWEEN CHARACTERISTICS *1 IN MERINO SHEEP

	Body wt.	Fl. wt.	F.D.	St. L.	LB/EJ *2	LW/EJ
Body wt.	.....	-0.11 to 0.26	-0.21 to 0.12	-0.26 to 0.04	0.23 (0.20)	0.47 (0.06)
Fl. Wt.	0.24 to 0.36	.....	0.13 to 0.47	-0.02 to 0.70	0.34 (-0.52)	0.34 (-0.85)
F.D.	0.13	0.13 to 0.36	.....	-0.11 to 0.44	-0.38	-0.33
St. L.	0.00 to 0.10	0.23 to 0.30	-0.16 to 0.11	.....	0.11 (-0.42)	0.21 (-1.18)
LB/EJ	0.12 (0.07)	0.09 (-0.09)	0.10	0.09 (-0.03)	......	-
LW/EJ	0.15 (0.06)	0.03 (-0.12	0.09	0.06 (0.03)	-	.....

*1 Wool and body characteristics measured at 15-16 months.

*2 Lambing data, estimates from performance at first three lambings (2-4 years of age) or for figures in brackets, at 2 years of ago.

Sources:- Morley (1955a, 1955b); Schinckel (1958); Bosman (1958); Beattie (1962); Young et.al. (1963); Young et.al. (1965); Kennedy (1967); Brown and Turner (1968) Mullaney et. al. (1970).

Young et al. (1963) report positive phenotypic and genetic correlations between greasy fleece weight and reproductive traits, the latter being the average for ewes aged 2-4 years. Kennedy (1967) found negative correlations in all cases, with lambing data on ewes aged 2 years. They suggest that this discrepancy could be due to the difference in age, or to difference between the two flocks.

Shelton and Menzies (1968) noted a consistent negative relationship between fleece weight and all measures of fertility and lamb production in an analysis of the association in mature sheep over a lifetime performance. Turner (1972) discussed the association between wool weight and reproduction rate and drew attention to the fact that sometimes the wool weight used in a correlation has been from a shearing before the ewes have been mated; sometimes it has been from shearings at older ages, after the ewes have entered the breeding flock. The number of lambs born or weaned has a marked influence on the ewe's fleece weight (for a review see Turner and Young, 1969) and unless a correction is applied to the ewe's wool weight, a negative estimate of genetic correlation will be obtained through this environmental effect. Shelton and Menzies (1968) reported that no adjustments to their data were made. Their ewe records were from ewes in a breeding flock aged from 2 to 10 years, consequently some error may exist in their result.

More pertinent to this thesis is Table 8 summarizing the results of Rae (1958), Tripathy (1966), Sumner (1969), Ch'ang and Rae (1970) with Romney data.

G. SELECTION FLOCK RESULTS

Given the necessary estimates of genetic parameters, population genetic theory allow certain inferences to be made concerning the rate of genetic improvement possible under specified selection procedure. Heritability, combined with the selection differeential provides an estimate of the permanent genetic improvement to be

TABLE 8

ESTIMATES OF GENETIC (above diagonal) AND PHENOTYPIC (below diagonal) CORRELATIONS IN ROMNEY SHEEP

	W. Wt.	H.B. Wt.	F. Wt.	Qu. No.	F. D.	S.L.	No. L. W.
Weaning Wt.	.....	0.74 to 0.90					0.32 to 0.40
Hogget body wt.		.....	0.54		0.16	0.21	0.56 to 0.81
Fleece wt.		0.47 to 0.61	...	0.47	0.58	0.25 to 0.40	
Quality No.		0.08 to 0.22	-0.03 to -0.33	.....		-0.73	
Fibre diameter		0.29	0.53	-0.63	....		0.68
Staple length		0.01 to 0.24	0.22 to 0.51	-0.46 to -0.69	0.41 to 0.48	....	
Character		0.05 to 0.26	-0.09 to 0.27	0.06 to 0.38		-0.27 to 0.20	......
No. lambs born	0.13 to 0.15	0.23					...

Source :- Rae (1958); Tripathy (1966); Sumner (1969); Ch'ang and Rae (1972); Wickham, Ross and Cockrem (unpublished).

expected among the progeny. Conversely heritability estimates can be checked by examining the actual changes induced in a population, following the application of a measured selection intensity. This may be considered as a dynamic application of population genetic theory, and heritability estimated in this way has been termed the realized heritability by Falconer (1960). This method is perhaps the most effective way of estimating the proportionate amount of additive genetic variance, and in addition is no doubt the best way of assessing the practical utility of proposed breeding schemes. However, when one or more generations of selection have been made, the precise measurement of the genetic response actually obtained introduces several problems. These are matters of procedure rather than principle and have been discussed in detail by Falconer (1953, 1960), Henderson et al. (1958), Smith (1962) and Hill (1971, 1972a, 1972b, 1972c).

It is of interest to note indications of the rate that responses to selection in sheep breeding accumulate with time; also the reconciliation between "realized heritabilities" and correlated responses, to the predictions from estimated heritabilities and genetic correlations. Selection experiments are also of value, in indicating the biological components of the responses achieved, and in providing material for an experimental analysis of the physiological processes that have contributed to any genetic changes produced. This has been extensively covered by Turner, Brooker and Dolling (1970). Aspects of it will not be discussed here, nor will any attempt be made in discussion of results. This will be covered later.

Peters, Slen and Hargrave (1961) wrote "reports on the effectiveness of selection for economic traits in farm animals have generally indicated less response than expected on the basis of estimated heritability of those traits". To some degree this could be due to the accuracy of early parameter estimates.

In emphasizing the importance of environmental effects such as age of dam, type of birth, year of birth, sex and age of the animal, Hazel and Terrill (1945a) pointed out that the selection effectiveness was reduced to one-half when the records for weaning weight were not adjusted for these effects. Shelton and Campbell (1962) found heritability estimates for weaning weight by the intrasire regression method ranged from 0.138 to 0.251 depending on methods of adjusting parent and offspring records, and 0.264 to 0.422 by half-sib correlation. The better understanding and improvement in correcting for environmental effects has meant more accurate heritability estimes.

Whilst estimates of phenotypic and genetic parameters are mainly based on ewes and wethers, comparisons of these parameters between sexes has failed to show any marked differences between rams and ewes (Young, Turner and Dolling, 1960b; Beattie, 1962; Pattie, 1965a; Gjedrem, 1969; and the same estimates are used for predictions of gains in either sex. It is to be noted that Kyle and Terrill (1953) found lower heritability estimates in yearling rams than in yearling ewes for wool weight and some of its components; though differences were not significant. If lowered heritability estimates for rams were confirmed, predictions of genetic progress based on ewe estimates would require modifications.

In a review of selection theory and experimental results, Chapman (1973) emphasised the importance of a control population when estimating the genetic shift in upward or downward selection lines. He states that realized heritabilities tended to be smaller than the half-sib correlation and offspring-parent regression estimates of heritability; that there was a tendency for fitness traits to decline with selection in either direction and that genetic maternal effects have played a prominant role in some experiments. With regard to domestic animals, an explanation for the fact that many populations do not actually change as rapidly as heritability estimates and selection differentials indicate they should, may be due to the heritability not being as high, and selection rarely being as intense as thought to be.

Single trait selection in sheep has, as a rule, given results that seem to be consistent with expectation based on heritability and genetic correlations (Chapman, 1973). Preliminary results have been reported (Rae, 1956; Turner, 1958; Terrill, 1958; Purser, 1963; Pattie and Williams, 1966, 1967). Longer-term selection response for wool and body traits have been analysed and reported in detail in only a few cases. These have been trials with Australian Merinos:-

(1) Pattie (1965a, 1965b) analysed results for direct response to selection for weaning weight and correlated responses in the productive traits after four generations had elapsed;

(2) Robards and Pattie (1967) reported on changes in crimp frequency during five generations of direct selection for high and low crimp frequency;

(3) Pattie and Barlow (1974) have reported the results of direct response for high and low clean fleece weight after 14 years (approximately 5 generations); while

(4) Barlow (1974) reported the correlated responses.

(5) Turner, Dolling and Kennedy (1968) have discussed selection for high clean wool weight with a ceiling on fibre diameter and degree of skin wrinkle from 18 years of records;

(6) Mayo, Potter, Brady and Hooper (1969) report response to partial selection on fleece weight after 14 years of selection;

(7) Turner, Brooker and Dolling (1970) have given a very detailed analysis of response to single character selection for high and low values of wool weight and its components. Both direct and correlated responses have been reported in 10 traits and 8 pairs of lines for hogget characters.

Patterns of response:-

Although Pattie (1965a) had found no significant sex differences in the estimates of heritability, both the actual weights and responses were more erratic for rams and they showed little response to selection for high corrected weaning weight in the last two (i.e. third and fourth) generations. In contrast, the ewes responded steadily and consequently showed a significant greater realized heritability for corrected weaning weight; (0.31 for ewes compared to 0.19 for rams). Estimated heritabilities had been for ewes 0.28 and 0.18, and for rams 0.32 and 0.19, by respectively dam offspring and paternal half-sib methods of estimation. No significant asymmetry of response occurred. After 10 years, percentage deviation from the random flock for ewes was + 18% for high and -8% for low weaning weight selection with cumulated selection differentials of + 50% and -25% respectively.

A significant initial direct selection response in the expected directions for hogget body weight was reported by Turner et al. (1970). This occurred in both sexes and symmetry was shown. However, continuing downward response was greater than upward response.

With eight pairs of lines (clean wool weight per head, clean wool weight per unit skin area, body weight, wrinkle score, fibre diameter, fibre number per unit skin area, staple length and percentage clean yield), Turner et al. (1970) observed significant initial direct selection response in the expected direction for both sexes in all lines. There were two exceptions; clean wool weight per head Minus and percentage clean yield Plus in ewes. There was a considerable variation in the symmetry of initial response. Continuing response varied considerably.

Of interest, is that Turner et al. (1970), observed symmetry for fibre diameter and a high positive response for wool weight per head and fibre number. Two lines (staple length Plus and fibre number Minus) showed no continuing response at all, although the initial response had been marked (+ 12.8% and -14.4% respectively). Ewes in the staple length Minus and percent clean yield Plus, which had little initial response, showed marked continuing response. The symmetry of continuing response varied; wool weight per head, fibre diameter and staple length, continuing downward response was greater than upward, while upward response trend in fibre number was variable and downward negligible.

Both Robards and Pattie (1967) and Pattie and Barlow (1974) showed that the pattern of response could not be predicted before selection commenced.

Response to selection was markedly different in the crimp Plus and crimp Minus flocks (Robards and Pattie, 1967). In the former, steady response followed selection and the overall realized heritabilities agreed well with estimates for a base flock. In contrast the crimp Minus flock showed a marked initial response in the first generation, with realized heritabilities of 0.96 and 0.89 for ewes and rams respectively, but in the following four generations there was a much slower rate of change, particularly with rams, realized heritabilities were 0.30 and 0.12 respectively. Previous estimates had shown crimp frequency to be highly heritable, heritability being 0.4 to 0.6 (Morley, 1955a).

A marked non-linearity of response to selection for greater fleece weight was shown in the results of Pattie and Barlow (1974). This necessitated separate estimates for realized heritability for the two periods, generation 1 and 2 and generations 3 to 5. Good agreement between realized and theoretical heritabilities predicted from a combination of selection differentials existed for the fleece Minus flock and for the first two generations of the fleece Plus flock. Realized heritabilities respectively were 0.41 and 0.59. Estimated heritability was 0.47 (Morley, 1955a). However, the realized heritabilities after the second generation, were considerably lower in the fleece Plus flock (0.07) and response practically ceased despite continued selection pressure.

The results of Mayo et al. (1969) emphasized the importance of identifying genotypically superior animals and consequently applying the desired selection pressure. They compared the efficiency of two bases of selection for increased wool production. Selection on the basis of an index of net merit computed from measured characters of economic importance, viz. fleece weight, body style, staple length, quality, yield, and absence of undesirable economic faults (malformed jaws, faulty hocks, excessive skin development) resulted in a realized heritability of 0.43. This was in agreement with heritability estimate (Morley, 1955a). However, the visual appraisal selection method, as used by normal commercial methods and on similar standards, only realized a heritability of 0.23.

Correlated responses:-

Where a genetic correlation existed (i.e. at a level of 0.2 or higher) and where direct response occurred, there was in general a correlated response in the expected direction (Turner et al., 1970; Barlow, 1974). Similarly, reasonable agreement in reciprocal selections for all wool weight components were found (Turner et al., 1970). One exception to the previously reported correlations, was that the negative correlation between fibre number and staple length was not exhibited under selection in either character.

In only one case, in the study by Turner et al. (1970), was a correlated response greater than a direct one and that was in the line selected for fibre diameter Minus. Here an increase in fibre number per unit skin area was slightly greater than under direct selection. It was significant that the negative fibre number x fibre diameter genetic correlation is the strongest among those relevant in their study.

Turner et al. (1968); Mayo et al. (1969) and Barlow (1974) found that when clean fleece weight was increased by selection, the largest correlated responses were in staple length and fibre number per unit area. This was as expected from reported genetic correlations.

Realized genetic correlations between weaning weights and other traits were reported as having values between estimated dam-offspring and paternal half-sib correlations, but closer to the dam-offspring figures (Pattie, 1965b). Their results, as summarized in Table 9, indicate some inheritance of maternal effects.

TABLE 9

SOME PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN CORRECTED WEANING WEIGHT AND OTHER CHARACTERISTICS FOR MERINO EWES (Pattie, 1965b).

Characteristic	Phenotypic Correlation	Genetic Correlation		
		Dam-Offspring	Paternal half-sib	Realized
Greasy wool wgt	0.17 **	0.06	0.48	0.08
Clean wool wgt	0.18 **	0.12	0.55	0.24
Staple length	0.09 **	-0.15	0.46	0.17
Crimps/inch	0.01	-0.7	-1.32	-0.17
17 mth body wgt	0.65 **	0.93	0.50	0.72

Fleece weight selection:-

A significant initial direct selection response was shown by Turner, et al. (1970). With restrictions imposed, Turner et al. (1968) showed a fluctuating response about a steadily rising line, indicating increasing average fleece weight of 2.6% per annum. Further, Mayo et al. (1969) confirmed that clean fleece weight can be increased by selection with a 0.23 kg per head advantage with 'index selection', compared to 'visual appraisal'. So did Pattie and Barlow (1974) where both ewe and ram result patterns were similar. After 5 generations, response for fleece Plus were approximately 1.0 kg and fleece Minus - 2.0 kg with accumulated response (ΔG) equal to approximately 1.0 for fleece Plus and -2.0σ for fleece Minus, and accumulated selection differentials of approximately 5σ.

Fertility selection:-

Long term response to selection for number of lambs born and weaned have been reported by Turner, Hayman, Triffitt and Prunster (1962); Turner (1962, 1966 and 1968) with the Australian Merino; and by Wallace (1958, 1964) and Clarke (1972) with the New Zealand Romney. From studies on barrenness and lamb survival rate, it has been concluded that the most profitable criterion of selection to raise reproduction rate is through selection for high incidence of multiple births, Turner (1968, 1969) and Ch'ang (1973). Young et al. (1963) and Clark (1963) results indicate that twinning and barrenness did not seem to represent a similar underlying genetic phenomena. Turner (1973) wrote "more recent information (Ch'ang, personal communication) has provided higher estimates for the heritability of survival rate". She suggested the conclusion that selection should be directed to raising number of lambs born rather than number weaned because of the low heritability of survival rate, may need revision.

Success in selection for twinning was first reported by Wallace (1958). Clarke (1972) reported that in this same flock, from 1948-1970, a gradual but erratic increase for a line selected for high incidence of twinning occurred with an annual rate of response at 1.75 lambs born per 100 ewes lambing. Every indication that the response was continuing over the last few years was reported. Response was not quite so good for number of lambs docked; however a cumulative response with 1.5 lambs per 100 ewes lambing resulted.

Similar success has been reported in Merinos, 2.3 lambs born per 100 ewes lambing has been the annual rate of response reported by Turner (1968). Selection for multiple births has lead to faster results than had generally been thought possible from earlier low estimates of heritability. Even more remarkable was a response reported by Turner (1973). The annual increase was 10 lambs born per 100 ewes joined for a line selected for high multiple births, i.e. triplets or more, when compared to a line where selection is for twins, while the difference between twin selection and single selection showed an annual rate of 1.2 lambs born per 100 ewes joined.

Selection and changes in genetic parameters:-

The long-term value of breeding plans depends on the constance of the genetic parameters used in their construction. One important consideration is the possible effect of selection on estimated heritability of a character under selection. Since heritability is a ratio of additive genetic variance and phenotypic variance, changes in heritability may arise from changes in either of these variances. Brown and Turner (1968) found no evidence of any appreciable change of heritability after 12 years of selection for clean fleece weight. They also concluded that selection can be considered to have had a negligible effect in so far as phenotypic relationships are concerned. This is supported by Turner et al. (1968) and Pattie and Barlow (1974), the latter writing that mean variances for average clean fleece weight fluctuated with changes in seasonal conditions but did not show any consistent trend. The variances tended to change in the same direction as the means.

However, Brown and Turner (1968) did find significant changes in the estimated genetic correlations between traits from selected and unselected sheep. The genetic correlations between

(1) clean wool weight and body weight increased from 0.2 to 0.5

(2) clean wool weight and fibre number per unit skin area decreased from 0.4 to 0.0

(3) fibre number and fibre volume increased from -0.5 to -0.9, and

(4) fibre number and fibre diameter increased from -0.6 to -0.8.

Such changes in genetic correlations have an important bearing on breeding plans and so in any selection programme re-estimates should be made at intervals of a few years (Turner and Young, 1969).

Conclusion:-

The above selection responses give support to estimates of heritability and genetic correlations as parameters which are of value for prediction of selection response in sheep breeding. However, variances can occur. These would emphasize the importance of the need for large numbers of animals to decrease standard errors; also the need for accurate correction of data for environmental effects. Then follows the need for accurate recognition of genotype so that an effective selection differential can be obtained.

III. SOURCE OF DATA

The data studied in the present investigation have been obtained from a flock of Perendales established at the Massey University hill country property "Tuapaka", in 1953.

The "Tuapaka" farm has been described by Peren et al. (1951). It is 1,050 acres, of which 800 acres is hill country; 270 acres being poor, hard, steep hill country. The remaining hill country has an easy nature with an altitude of up to 700 feet and is regarded as second class hill country.

Initial establishment of the flock consisted of 300 first-cross ewes selected from several different sources. These were mated to first-cross rams. On attaining a balanced age composition of second generation sheep, some selection was directed towards prolificacy and on eliminating sheep showing excessive hairiness and lack of "character" in wool. Selection procedures used within the flock have varied from time to time.

In 1961, at the time the Perendale Sheep Society was founded, this flock was split, one group being chosen to form the basis of a Perendale Stud. The data from 1961 to 1972 are from sheep within the Perendale stud.

From time to time there has been introduction of ewes, mainly first-cross sheep. Some rams have been introduced from outside studs. On average, rams are used for two seasons. In earlier years, good rams have been used for up to five seasons, but in later years a more frequent turnover has been practised. These features favour the assumption that inbreeding has not been an important source of variation in this data. Since the flock has been established for a longer period it is probably more interbred than most Perendale stud flocks.

The flock is run essentially as a commercial enterprise. Normal culling practices were carried out : sheep with visible defects were eliminated from the flock.

Few ewes are culled prior to 16 months of age.

Lambs were born in August and September and remained with their dams until weaning took place in December. Hogget shearing occurred in October while ewe shearing occurred approximately one month later. Lambs were shorn in January, consequently the measurements of hogget fleece production represent only nine months wool growth.

In this analysis the wool traits, FLEECE WEIGHT, QUALITY NUMBER, FIBRE DIAMETER, STAPLE LENGTH and CHARACTER were studied along with LAMB WEANING WEIGHT, HOGGET BODY WEIGHT and either NUMBER OF LAMBS WEANED or LAMBS WEANED PER EWE LAMBING.

Fleece weight is a measure of greasy-fleece weight measured immediately after the fleece was removed from the sheep; belly wool was included in this weight.

Staple length, mean fibre diameter and quality number were measured from a midside sample of wool (Turner, 1956) obtained from the fleece after shearing.

Staple length was measured with a rule. Since the tip of the staple in Perendale wool tapers toward a point, the measurement was made from the base of the staple to a position midway between the point where the staple starts to taper and the tip, care being taken to not stretch the staple unduly.

Quality number is a visual appraisal of the spinability and hence fineness of wool. It is based mainly on staple crimp frequency and lustre (Henderson, 1965; Wickham, 1971).

Character, graded in a range from 1 to 9, was assessed mainly on the clarity and evenness of staple crimp, absence of tapering tip and medullation.

Mean fibre diameter was determined by airflow method (Anderson, 1954). The relationship between airflow and fibre diameter is not perfect. These estimates of diameter will be affected by other characteristics such as medullation and crimp. There are considerable discrepancies between projection microscope and airflow determined mean diameters of Cheviots (Wickham, 1971), and data for Romney sheep have shown the airflow technique to be unsuitable for the measurement of individual animals on account of bias (Sumner and Revfeim, 1973).

Weaning weight is the weight of lambs at about 14 to 16 weeks of age.

The hogget body weight is the post-shearing weight, usually obtained within two weeks of shearing; therefore the measurement is at 14 to 15 months of age.

This study makes use of data collected over 16 consecutive years from 1957. For the estimation of genetic parameters, hogget records were used plus the weaning weight record. These included 3313 records of half-sibs from 62 sires, 1720 and 665 daughter-dam pairs. In the latter daughter-dam regression analysis the two-tooth lamb weaning record was also used. Records from 458 sheep, each having one hogget and four consecutive adult ewe records, were used for the hogget-lifetime performance study.

All F_1 animals were excluded from the analysis since their performance is likely to be affected to a greater degree by non-additive genetic effects than is the case with the interbreds. Wickham (unpublished) found that the first cross animals in this flock were substantially higher in hogget live weight, fleece weight and number of lambs weaned than were the interbreds. The effect of these non-additive effects on estimates of genetic parameters cannot be predicted with any accuracy without some knowledge of the nature of the gene interactions.

IV. ESTIMATION OF HERITABILITY AND GENETIC CORRELATIONS

A. INTRODUCTION

Where differences between animals are quantitative in nature and characters are measured in a continuous scale there is interest in the mean value of a metric character and in the variance about that mean. The partitioning of phenotypic variance into separate components (as shown in II B) serves to explain the derivation of variation between animals, for a trait, in a population.

Genetic parameters may be estimated by an analysis of the variance and covariance that exists in a population. Use is made of the fact that variation from additive genetic effects, arising from the summed effects of individual genes, contributes directly to the resemblance between parents and offspring.

The sets of relatives most commonly used for estimating heritability and genetic correlations are those used in this study -

(a) Analysis of variance and covariance methods for half-sibs.

(b) Parent-offspring analysis using regression and correlation techniques.

The rationale underlying each method of estimation is that genetically related individuals tend to be more alike than individuals chosen at random from the same population.

B. PATERNAL HALF-SIB ANALYSIS OF VARIANCE AND COVARIANCE.

(Method 1): All currently available methods for estimating variance components from unbalanced data use in one way or another, quadratic forms of the observation

$$Y = X\beta + e$$

where Y is a vector of observations

X is a matrix of known values

β is a vector of parameters (including both fixed and random effects) and

e is a vector of customary error terms (Searle, 1971).

The covariance components required in estimating genetic correlations can be obtained from an analysis of covariance by an extension of the procedures used in the analysis of variance.

The technique used in this thesis was to define a model including the effects under study and to estimate the elements in this model by the method of least-squares. For each trait, the model was

$$y_{ijklm} = \mu + a_i + s_{ij} + c_k + d_l + e_{ijklm}$$

where :-

$i = 1 \ldots\ldots p, \quad j = 1 \ldots\ldots q, \quad k = 1 \ldots\ldots r$

$l = 1 \ldots\ldots s, \quad m = n_{ijkl}$

n_{ijkl} denotes the number of observations in the subclass,

y_{ijklm} is the record of the m^{th} individual, born in the i^{th} year, sired by the j^{th} sire within that year with the k^{th} age of dam, and reared in the l^{th} rearing rank group.

μ = the population mean; an effect common to all records of a trait.

a = the effect of the i^{th} "year" class. The a_i is an effect common to all records of a trait measured on individuals born in the i^{th} year.

s_{ij} = the effect of the j^{th} sire within the i^{th} year.

c_k = the effect of the k^{th} "age of dam" class.

The age of dam subclasses were a_1 = 2-year olds (two-tooths), a_2 = 3-year olds (four-tooths), a_3 = 4-year olds (six-tooths) and a_4 = 5-year old and older ewes (mature ewes).

d_l = effect of the l^{th} "rearing rank" class. There were 2 classes; d_1 = hoggets reared as single lambs and d_2 = twin lambs. Any triplets were included in the d_2 subclass because of their very small number.

e_{ijklm} = random error term peculiar to each datum. It represents the discrepancy between the actual value of a datum and its expected value based on sum of the effects stated in the model. This discrepancy is caused by the effects of many factors not included in this study.

The s_{ij} and e_{ijklm} were assumed to be random variables distributed normally with zero mean and constant variances. The a_i, c_k and d_l are fixed effects in the model. Consequently, the model can be described as a "mixed model" (Searle, 1971).

The model could be improved if an age correction had been included, but the early data did not include birth dates. Age in days at measurement is particularly important for estimates involving weaning weight for age contributes towards total variance. The incorporation of age correction factors are unlikely to make any major change in the estimated genetic parameters.

Interactions between main effects were not included. These would have considerably increased the complexity of computation. For most purposes little error will result from assuming interactions to be insignificant (Yalcin and Bichard, 1964).

The efficiency with which the variance components are estimated depends on the assumption that interactions are negligible. Also, non-normality of error terms is likely to be accompanied by the loss of efficiency in the estimation of treatment effects for a linear model. More serious though is the possible correlation between mean and the variance in the data. No information for this data about these points is available.

The problem is to obtain unbiassed estimates of variance and covariance components for this mixed model with unequal subclass frequencies.

Disproportionate subclass numbers always cause the different classes of effects to be non-orthogonal. This means that the different effects -(year, sire-within-year, age of dam and rearing rank) cannot be separated directly without entanglement (Harvey, 1960). In order to free these effects from the entanglement or confounding, it is necessary to resort to simultaneous consideration of all effects. Statistical methods have been developed to do this and one of importance is the "least squares method" of analysis originally put forward by Yates (1934).

The general theory involved with using least-squares procedures in the mixed model with unequal subclass numbers, has been discussed by Henderson (1953); King and Henderson (1954); Searle and Henderson (1961); Searle (1968); Grossman and Gall (1968) and Searle (1971). Computational techniques techniques with worked examples are given by Harvey (1960 and 1970).

For this analysis, a computer programme was written following Harvey (1960, 1970) to compute the variance and covariance components by Method 3 (Henderson, 1953). Method 3 is the most satisfactory for mixed models when it is computationally feasible because it yields unbiassed estimates. This technique is based on the method of fitting constants traditionally used in fixed effects models. All random effects in the mixed model other than the random errors, are temporarily regarded as fixed. After using the method of fitting constants to compute the reductions in sums of squares desired, due to fitting different subgroups of factors in the model, these effects are again regarded as random and the expected values of the computed reductions in sums of squares are determined. These will be linear functions of the variance components. The computed values are equated to the expected values and the resulting equations are solved to obtain estimates of the variance components. Similar reasoning is followed in the estimation of the variance components.

The expectations of sire and error mean squares are :

Sire Mean Square = $\sigma_e^2 + K\sigma_s^2$

Error Mean Square = σ_e^2

Sire Mean Cross-products = $\text{cov}\ ee' + K\ \text{cov}\ ss'$

Error Mean Cross-products = $\text{cov}\ ee'$

where the prime (′) denotes the corresponding trait in the cross-product.

For both heritability and genetic correlation estimation, the following must be calculated from the data, for each trait.

(1) The coefficient of the variance component K.

(2) The sum of all the squared observations

$$\sum_{ijk\ell m} y^2_{ijk\ell m}$$

(3) The reduction in Sums of Squares due to fitting all effects.

$$R(\mu, a_i, s_{ij}, c_k, d_\ell)$$

(4) The reduction in Sums of Squares due to fitting all except effects for sires within year.

$$R(\mu, a_i, c_k, d_\ell)$$

The sums of squares associated with s_{ij} was computed as a difference between reduction in sums of squares due to fitting all constants $R(\mu, a_i, s_{ij}, c_k, d_\ell)$ and that due to fitting all except the s_{ij} effect - $R(\mu, a_i, c_k, d_\ell)$.

For the computation of covariance components required in the genetic correlation estimation, the following additional figures must be claculated from the data.

(1) The sum of cross-products

$$\sum_{ijk\ell m} x_{ijk\ell m} \; y_{ijk\ell m} \quad .$$

where $x_{ijk\ell m}$ and $y_{ijk\ell m}$ are the 2 traits involved.

(2) The reduction in cross-products for fitting all constants except the sire effects.

$$C(\mu, a_i, c_k, d_\ell)$$

(3) The reduction in cross-products for fitting all constants $C(\mu, a_i, s_{ij}, c_k, d_\ell)$

For this model the

ERROR DEGREES OF FREEDOM = $n_{....} - t - r - s + 2$.

where $n_{....}$ is the total number of records.

The degrees of freedom for the "sire-within-year" class = $t - p$ = DEGREES of FREEDOM S.

Estimation of heritabilities and genetic correlations follows from these calculated quantities -

1. ERROR SUMS of SQUARES $= \sum_{ijklm} x_{ijklm}^2 - R(\mu, a_i, s_{ij}, c_k, d_l)$

2. ERROR MEAN SQUARE [M.S(E)] $= \dfrac{\text{ERROR SUMS of SQUARES}}{\text{ERROR DEGREES of FREEDOM}}$

3. ERROR COVARIANCE $= \dfrac{\sum_{ijklm} x_{ijklm}\, y_{ijklm} - C(\mu, a_i, s_{ij}, c_k, d_l)}{\text{ERROR DEGREES of FREEDOM}}$

4. SUMS of SQUARES for S (i.e. sires-within-years) $= R(\mu, a_i, s_{ij}, c_k, d_l) - R(\mu, a_i, c_k, d_l)$

5. MEAN SQUARE S [M.S(E)] $= \dfrac{\text{SUMS of SQUARES for S}}{\text{DEGREES of FREEDOM S}}$

6. COVARIANCE SIRES $= \dfrac{C(\mu, a_i, s_{ij}, c_k, d_l) - C(\mu, a_i, c_k, d_l)}{\text{DEGREES of FREEDOM S}}$

The sire-within-year variance component

$$= \frac{\text{M.S.(S)} - \text{M.S.(E)}}{K}$$

The sire covariance component Cov $s_x s_y$

$$= \frac{\text{COVARIANCE SIRES} - \text{ERROR COVARIANCE}}{K}$$

Error variance component equals mean square error,

i.e. = M.S.(E).

$$\text{Heritability} = 4\left[\frac{\text{sire-within-year variance component}}{\text{sire-within-year variance component} + \text{error variance component}}\right]$$

Consequently

$$\hat{h}^2 = 4\left(\frac{\sigma_s^2}{\sigma_s^2 + \sigma_e^2}\right)$$

and the genetic correlation

$$\hat{r}_G = \frac{\text{Cov}\ s_x s_y}{\sqrt{\sigma_{x s}^2 \cdot \sigma_{y s}^2}}$$

The steps involved in the computation of $R(\mu, a_i, s_{ij}, c_k, d_l)$ $R(\mu, a_i, c_k, d_l)$, $C(\mu, a_i, s_{ij}, c_k, d_l)$ and $C(\mu, a_i, c_k, d_l)$ appear in more detail in Appendix I. Appendix II shows the calculation of the coefficient K.

The approximate sampling error of $\hat{h}^2$ was derived from the corresponding intra-class correlation based on the formula given by Falconer (1960). The sampling error of $\hat{r}_G$ was computed using the method described by Tallis (1959).

C. DAUGHTER-DAM REGRESSION

(Method 2)

Several methods of estimating heritability and genetic correlations are based on parent-offspring covariance. The method used in this thesis is similar to that used by Ch'ang and Rae (1970, 1972). The regression of daughter on dam ignoring sires was used.

This method required the assumption that sires used constitute a random sample of the population of sires, matings are at random, and all sire groups are run together. With these assumptions, between sire components in the covariance analysis have zero expectation and the analysis is simplified by ignoring sires and calculating the regression coefficient directly (Turner and Young, 1969).

To calculate the regression of daughter on dam, the records were initially sorted into groups according to the daughter's year of birth. Within each formed year of birth group, the records were further subdivided depending on the dam's birth year, the dam's record being repeated for each additional daughter. If any subgroup contained less than three pairs, the subgroup was excluded.

In a subgroup so formed, the dams were all comparable for year of birth, and the daughters for year of birth and age of dam. In addition, the data of the daughter, being already comparable for age of dam, were corrected for rearing rank, whereas those of the dam were corrected for age of dam and rearing rank. No adjustments were made for "number of lambs weaned". The correction factors applied to the data were those estimated in the paternal half-sib analysis.

Because each female is mated several times in her life, she usually has a number of offspring even when multiple births are uncommon. Consequently some bias to the estimates may result. Turner and Young (1969) discussed three ways of estimating heritability in such cases. In this analysis, the regression of individual offspring on parent, repeating the parent value as many times as there were offspring, was used. Kempthorne and Tandon (1953) pointed out that this would be valid only if the correlation among the offspring of a parent were zero. This is not quite the case, consequently this procedure may not be optimal in the sense of minimum variance. From the studies by Bohren, McKean and Yamada (1961) and McKean and Bohren (1961) it is suggested that a serious loss of efficiency in estimates of heritability based on the effective range in number of offspring per dam expected in the present data, is unlikely to occur. The values of heritability found using the relationship between daughter and dam therefore, were not verified by the weighted regression method proposed by Kempthorne and Tandon (1953). A similar approach was followed by Ch'ang and Rae (1970) and Brown and Turner (1968).

Like in the paternal half-sib analysis, only weaning weight, hogget body weight and hogget wool traits were analysed. Because of the requirement of equal numbers for the computation of covariances between traits, the only records used were those where all traits in the study were present. As a consequence of culling or failure of some hoggets to lamb as a 2-year old, the number of records available was greatly reduced by adding the trait number of lambs weaned per ewe lambing (LW/EL). Consequently two runs were made. The first ignored using LW/EL so enabling the degrees of freedom of the sample to be much greater than when LW/EL was included.

The term LW/EL differentiates the difference between one or two lambs only. Because the data from ewes having zero lambs weaned were ignored, this term has a different meaning to the normally used definition of "number of lambs weaned" which differentiates between 0, 1 and 2 lambs. This latter term is used in the hogget-lifetime ewe performance study (section V).

A computer programme was written to carry out the analysis. The sums of squares for the daughters and dams, the cross-products between them and the degrees of freedom were computed within subgroups and then pooled to find the heritabilities and genetic correlations.

The formula used for the estimation of heritability of the i^{th} trait was

$$\hat{h}_i^2 = 2\left(\frac{\widehat{cov(x_i\, y_i)}}{\hat{\sigma}_{x_i}^2}\right)$$

where $cov(x_i\, y_i)$ = covariance between dam and daughters record for the i^{th} trait;

and, $\sigma_{x_i}^2$ = variance of the dams record.

The formula used for the estimation of genetic correlations for all combinations of the i^{th} and j^{th} traits was

$$\hat{r}_{G_{ij}} = \frac{\frac{cov(x_i\, y_j) + cov(x_j\, y_i)}{2}}{\sqrt{cov(x_i\, y_i)\cdot cov(x_j\, y_j)}}$$

where x = dam's record;

y = daughter's record;

and, i and j refer to the i^{th} and j^{th} trait.

The standard error for $\hat{h}_i^2$ was computed from a formula given by Falconer (1960) while the approximate standard error for $\hat{r}_{G_{ij}}$ was computed by a formula developed by Reeve (1955) for a large sample.

Phenotypic correlations were also estimated using the covariances and variances estimated by this programme. The formula used was

$$\hat{r}_{P_{ij}} = \frac{cov\ y_i\, y_j}{\sqrt{\sigma_{y_i}^2 \cdot \sigma_{y_j}^2}}$$

In an attempt to gain some knowledge into possible reasons for the discrepancies between the genetic and phenotypic correlations, environmental correlations were claculated using the formula given by Searle (1961):

$$r' = (R - r\sqrt{hH} \,/\, \sqrt{(1-h)(1-H)})$$

where r' is the environmental correlation between two traits;

R is the phenotypic correlation calculated by the daughter-dam regression method;

r is the genotypic correlation, calculated from the same data and method as ; and

h and H represent the heritability estimates in the narrow sense of the two traits.

This relationship between the three correlations, phenotypic, genetic and environmental, was derived in Lerner (1950) using the method of path coefficients. Genetic-environmental interations are assumed zero.

D. RESULTS AND DISCUSSION

1. Environmental Effects

The estimates of environmental effects expressed as deviations from the overall mean, together with their standard deviations derived from the error mean square, for each trait, are presented in Table 10.

The results are in general agreement with other published estimates.

Age of dam and rearing rank effects:-

The estimates for wool traits show that the influence, age of dam and rearing rank are low compared to the year effects. This agrees with Tripathy (1966) where year accounted for 47% of the total variation in greasy fleece weight, 35% in fibre diameter and 19% for staple length; unknown sources of variation were responsible for a large proportion of the total variation, particularly for staple length. Tripathy (1966) reported the effects age of dam and rearing rank were negligible for these traits.

For the wool traits, the present estimates of age of dam and rearing rank are lower than those reported by Tripathy (1966), particularly for fibre diameter. In general, the maternal handicap of litter size is greater than that of age of dam (Turner and Young, 1969) as in the present data.

The magnitude and sign of the rearing rank effect on hogget fleece weight, are consistent with those for Romney data reported by Tripathy (1966); Hight and Jury (1971) and Baker et al. (1974) but lower than Lundie (1971) and the Romney x Border Leicester F_3 data of Hight and Jury (1971); and are within the range reviewed by Turner and Young (1969).

The difference between the mature and 2-year old age

TABLE 10

ESTIMATES OF ENVIRONMENTAL EFFECTS

	W. Wt (kg)	Hgt B.Wt (kg)	F. Wt (kg)	Qu. No.	F. D. (μ)	S. L. (cm)	Char.
Mean	22.8	37.3	2.4	52.24	30.98	11.75	5.03
S.D.	3.0	3.9	0.4	1.9	2.22	1.43	1.12
Year of Birth							
1957	-0.21	-0.16	-0.02	1.23	0.29	0.27	0.42
1958	-3.43	-4.30	-0.47	1.70	-2.32	-0.45	0.88
1959	1.85	1.24	-0.20	0.78	-0.76	-1.39	-0.35
1960	1.92	1.32	-0.11	1.11	-1.04	-1.57	0.46
1961	1.33	-2.39	0.25	0.70	-0.93	0.36	0.92
1962	-1.16	0.35	-0.20	1.64	-1.48	-0.57	0.18
1963	-1.90	-0.42	0.28	0.86	-0.06	0.97	0.03
1964	-2.21	-3.08	0.15	-1.26	0.13	1.11	0.28
1965	-2.67	-4.38	-0.03	-0.67	-0.44	0.57	0.40
1966	-0.83	-2.44	-0.15	-0.65	0.62	0.17	-0.53
1967	2.10	-2.46	0.38	-0.46	1.54	1.87	-1.37
1968	0.88	4.87	0.46	0.48	2.38	0.07	-1.10
1969	1.71	2.87	-0.25	-0.66	-0.51	-0.76	-0.32
1970	0.44	2.58	-0.25	-1.72	0.29	-0.58	1.25
1971	-0.53	1.48	-0.13	-1.15	-0.35	-0.39	0.36
Age of dam							
2-yr	-0.95	-0.68	-0.04	-0.07	-0.10	0.01	-0.03
3-yr	-0.04	-0.05	0.00	0.00	-0.02	-0.01	0.00
4-yr	0.49	0.30	0.03	0.02	0.20	0.01	-0.02
Mature	0.49	0.43	0.01	0.04	-0.07	-0.01	0.05
Rearing rank							
Single	2.10	1.06	0.06	0.10	-0.03	-0.10	0.07
Twin	-2.10	-1.06	-0.06	-0.10	0.03	0.10	-0.07

of dam effect on their offspring hogget fleece weight is less than half the size of that given by Turner and Young (1969) and those of other published New Zealand works with two exceptions. No effect was reported by Baker et al. (1974) and a negative result with a large standard error was reported with the Romney data by Hight and Jury (1971).

In Merinos the lowered clean fleece weight in twins and the progeny of two-year old ewes was due mainly to a lowered total follicle number (Turner, 1961; Dun and Grewal, 1963). This difference arose from a deficiency in secondary follicles. The remaining difference in wool weight may be attributable to lower body size or other factors lowering the output per follicle (Ryder and Stephenson, 1968). In a study of wool follicle development with Romneys, Sumner and Wickham (1970) observed no noticeable effects of age of dam at weaning or hogget shearing. A significant birth rank effect on the secondary/primary follicle ratio was recorded at weaning. Their results indicated a delaying of secondary follicle maturation among the twin animals, but this delay was only transient for by one year of age a similar secondary/primary ratio was observed.

Results from this data indicate that the nature of the effects of rearing rank and age of dam on fleece weight for Perendales compared to Merinos and Romneys, may be intermediate for those in these two later breeds.

It is of interest that in this study singles have heavier fleece weights, improved character, shorter staple length and finer wool (based on both mean fibre diameter and quality number). Similar results occurred in hogget-lifetime performance relationships, except that no difference occurred for wool fineness.

The rearing rank effects on fibre diameter and staple length are opposite to Tripathy (1966) but are in agreement with ewe hogget results of Lax and Brown (1967). The lowered total follicle number of twins could perhaps explain these results. Lax and Brown (1967) observed an increased ($p < 0.01$) number of fibres per mm^2 for singles.

Their conclusion, that output per follicle, as estimated from fibre diameter and staple length, is slightly higher in the twins but not high enough to compensate for the decreased number of follicles, may apply to sheep in this study. But for any conclusion it must be appreciated that rearing rank effects on staple length and fibre diameter are negligible. Also, staple length is not an accurate indicator of average fibre length (Whan, 1972). The wool bearing area for twins is expected to be less than singles and this is supported by the rearing rank effects on hogget body weight where a 2.1 kg difference favouring the singles occurred.

The estimates of age of dam and rearing rank on weaning and hogget body weights show that twins and the progeny of younger ewes are lighter. These are thought to reflect the preweaning maternal handicap (Ch'ang and Rae, 1970). Their sign and magnitude are in general agreement with those found in other breeds (Turner and Young, 1969) and with those studied under New Zealand conditions (Ch'ang and Rae, 1961, 1970; Lundie, 1971; Hight and Jury, 1971; Baker et al. (1974), but age of dam effects are smaller than in previous New Zealand studies.

In the present data a difference of 4.2 kg in body weight between singles and twins at weaning was reduced to 2.1 kg at the hogget age. When comparing 2 year-old and mature age of dam effects, a 1.44 kg difference at weaning was reduced to a 1.11 kg difference at hogget age. These indicate that after weaning some compensatory growth occurs with animals maternally handicapped by both effects. This is at variance with the findings of Ch'ang and Rae (1970) who showed age of dam effects tended to remain undiminished well beyond weaning. Ch'ang and Rae (1970) presumed that the age of dam effect on weaning weight was insufficiently severe, compared with type of birth and rearing effect to trigger post-weaning compensatory growth. This statement has some support when age of dam effect for two-year and three-year ewes are compared. The small three-year ewe handicap remained while the larger handicap with the two-year dam has been reduced.

If selection was practised for weaning weight and/or weight of lambs weaned, correction factors would need to be applied (Shelton and Campbell, 1962; Young et al., 1965; Pattie, 1965a). This is an accepted practice. For example, the National Flock Recording Scheme adds 4.5 kg for a twin lamb reared as a twin, 2.3 kg for a lamb born to a two-year old and 0.9 kg for a lamb born to a three-year old ewe. Results from this thesis show a 4.2 kg difference between singles and twins which agrees quite well with the National Flock Recording Scheme's correction factors. However, the National Flock Recording Scheme's correction factors for age of dam effects would over-correct the data in this study. The difference between mature ewes and two-year and three-year ewe dams was 1.4 kg and 0.5 kg respectively.

At the hogget age, the rearing rank and age of dam effects are of varying practical significance. Turner (1961) calculated the influence on genetic progress and current production in wool weight. It was found to be negligible with the magnitude found in Merinos, but selection on wool weight alone could result in differential culling of twin lambs. When selection is practised at the hogget age, corrections for rearing rank and the progeny of two-year old dams on hogget body weight and fleece weight data are the only corrections that should generally deserve attention. Without these corrections, gains from selection for shorn fleece weight and/or hogget body weight may be affected because :

(1) a lowering in genetic selection differential would occur if genetically superior animals were culled because of their lowered phenotypic value for either body weight or fleece weight due to the handicap of being reared as a twin or by a 2-year old ewe.

(2) these rejections would in effect be selection against twinning if these animals happened to be twins.

(3) rejection of the progeny of two-year old ewes will tend to increase the generation interval and decrease genetic merit since these animals would have a higher

generation number than the progeny of older ewes.

The maternal effects considered are also environmental complications in estimating genetic parameters and a point for consideration is, should estimates of genetic parameters be made on data adjusted for these environmental influences. Adjustments for maternal handicap lowers the environmental fraction of the variance and so increases the heritability estimate. Genetic gain predicted from such adjusted heritability values would be over-estimated in flocks where birth data are not available and corrections for the handicap cannot be made. Because it is the relative size of the parameters and the sign of the genetic relationship which are of importance, their use for correction is generally justified.

In this analysis no distinction is made between twin born lambs reared as singles and those reared as twins. Nor were adjustments made for age. Heritability estimates should be made with the end use in mind and under extensive hill country conditions where Perendales are usually grazed and an easy-care management policy followed, the date of birth and any twin deaths may not be known.

Year effects:-

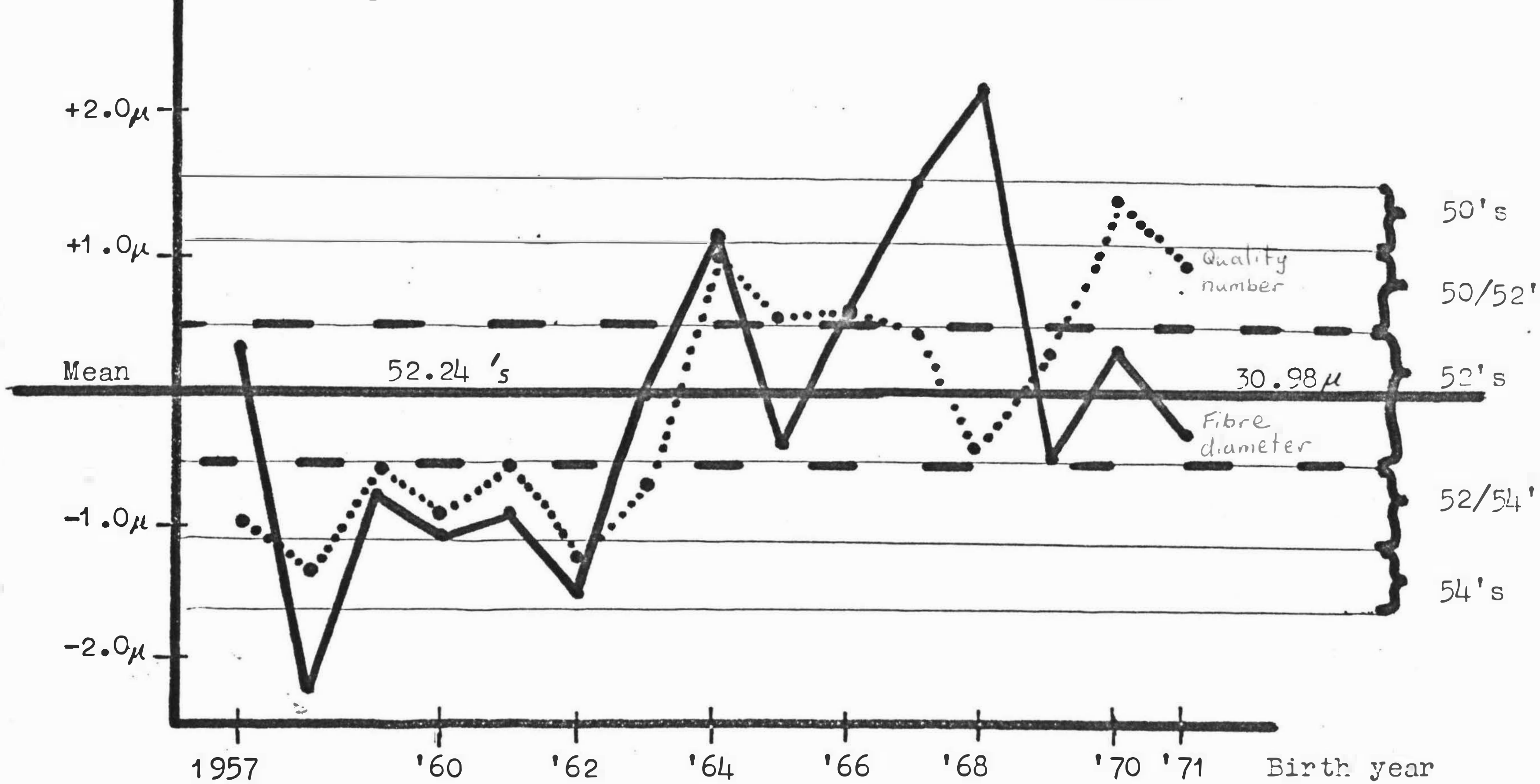
The results are as expected. However, a point of practical value arising is that quality number shows a coarsening trend from 52/54's to 50/52's over the data collection period but fibre diameter remained about the same over the 15-year period. These estimates appear in <u>Fig. 1</u>. In earlier years the fibre diameter trends are closely in line with quality number but are inconsistent after 1964.

This may indicate a response to selection. The influence that selection procedures have on changing the fibre diameter/quality number relationship with a Romney flock was reported by Wickham (1971). For three sub-flocks (selection of sheep entirely (1) at random; (2) for heavier fleeces; and (3) towards open faces)

Fig. 1.

YEARLY VARIATION IN QUALITY NUMBER
AND FIBRE DIAMETER

The points on the graph are least-squares estimates expressed as deviations about zero i.e. the mean.



reported quality number did not relate to similar changes in fibre diameter.

It is evident from Fig. 1 that wide divergence can exist between fibre diameter and quality number. The relationship between quality number and mean fibre diameter of individual fleeces within a clip is not strong (Wickham, 1971). Whan and Paynter (1967) reported that 48% of the variation in fibre diameter within flocks is associated with differences in appraised quality number.

The average fibre diameter within flocks varies with season and level of nutrition. Roberts (1970) reported how the sensitivity of diameter to lower nutrition resulted in a diameter much less than would have been expected from the visual quality number appraisal. Previous results reported by Sumner and Wickham (1969) had suggested that a change in stocking rate may have affected the relationship between quality number and fibre diameter. They considered that this effect was apparently due to the wool being more lustrous at the higher stocking level.

The 1969 season's measurements indicate a favourable season nutritionally, for hogget body weight was 4.87 kg above the mean, and hogget fleece weight 0.46 kg above (Table 10). The reverse trend is evident in the 1958 and 1965 year of birth records (Fig. 1) where hogget body weight and fleece weight are below the mean.

The results of the 1968 year of birth (Fig. 1) may support the findings that "nutritional effects cause a greater change in fibre thickness than in staple crimp" (Roberts and Dunlop, 1957). But any such effect with the present data would infer a strong relationship between staple crimp and quality number. Quality number in greasy wool is defined in terms of several wool attributes (Ryder and Stephenson, 1968). Trade estimates of quality number are mainly influenced by the frequency of crimping in greasy-wool staples (Lang, 1947; Dunlop and Young, 1960; Hopkins and Whiteley, 1973); with reliance also on lustre (Wickham, 1971). Consequently this inference does not seem unreasonable.

A genetic point of interest is how diameter can be so responsive to environmental changes and yet quality number so insensitive to them. Roberts and Dunlop (1957) consider that normal selection procedures practised on Merinos aim in each flock at an ideal crimp frequency (quality number) which has an intermediate value. Selection toward this in seasons of varying nutrition would, to some extent be effective family selection for small response to environmental variation. If there is little genetic correlation between responses to environment in the two traits, the present environmental stability of crimp and lability of diameter may have resulted. A similar selection practise could have applied over a long period in the parent Romneys and the present Perendale flock as quality number has probably always been a selection criterion.

This result indicates that if fibre fineness is an objective of selection, then for accurate evaluation, measured fibre diameter is essential. It further highlights the difficulty for accurate identification of genotype from phenotypic expresssion and the need to consider environmental correction factors.

2. Heritability Estimates.

The estimates of heritability calculated by both paternal half-sib (Method 1) and daughter-dam regression (Method 2) analysis, along with their standard errors and degrees of freedom appear in Table 11.

Accumulated heritability estimates were estimated for various intervals over the total years of the daughter-dam regression analysis. These results appear in two sets of graphs (Fig. 2). Estimates in Fig. 2A come from ewe hogget records before hogget selection has occurred. The 1971 estimates are those accumulated over the full time period as presented in Table 11. Results in Fig. 2B include the trait LW/EL from the two-year old ewe performance and consequently does not include data from ewes that were either culled or failed to lamb as a two-tooth.

It can be seen that :

(1) these heritability estimates are in close agreement to the average of the heritability estimates reviewed in Tables 5, 6 and 7;

(2) the standard errors are low compared with their corresponding heritability estimates; and

(3) differences in the heritability estimates exist between the two methods of estimation.

The standard errors may be considered low in comparison to the heritability estimates and the standard errors for other studies. This was to be expected because of the large number of observations and the closeness to optimum family size for experimental evaluation of genetic parameters (Robertson, 1959). Consequently errors due to sampling may be considered small and reliance may be placed on these estimates.

The accumulated estimates from the daughter-dam regression analysis shown in Fig. 2A and 2 B would indicate that at least 500 degrees of freedom were required before estimates become consistent. The consistency of

TABLE 11

HERITABILITY ESTIMATES

Trait	Method 1		Method 2	
	Paternal half-sib		Daughter-dam regression	
		± S.E.		± S.E.
Weaning wt	0.20	0.008	0.16	0.045
Hgt body wt	0.27	0.010	0.44	0.028
Fleece wt	0.32	0.010	0.30	0.034
Quality No.	0.26	0.009	0.31	0.035
Fibre diameter	0.54	0.014	0.47	0.016
Staple length	0.49	0.013	0.35	0.038
Character	0.23	0.009	0.23	0.032
LW/EL*			0.03	

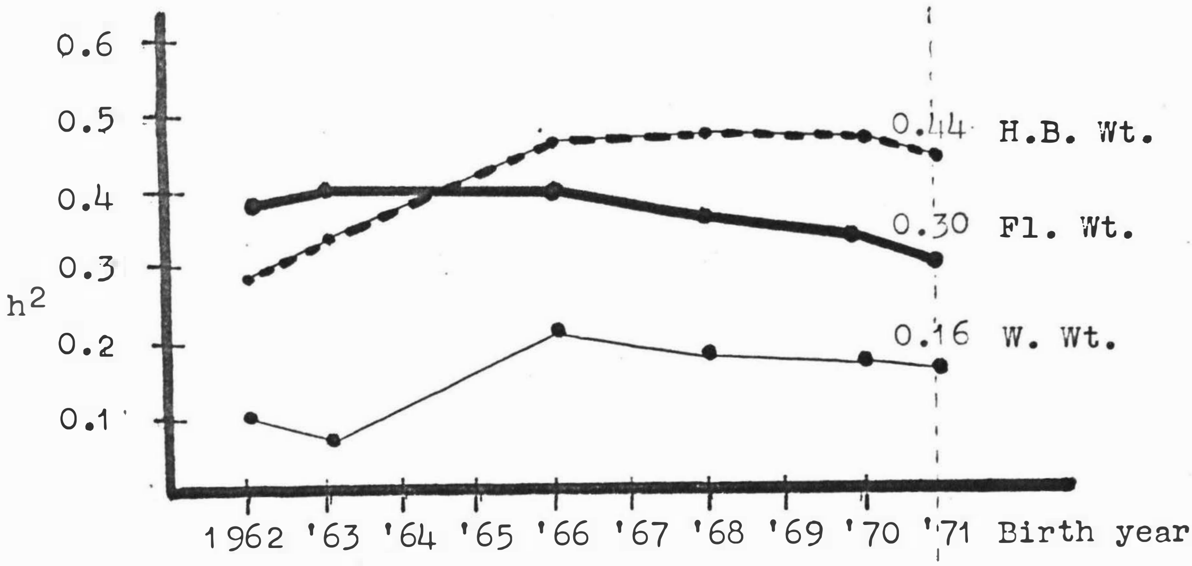
	No. of records	d.f.
Paternal half-sib	3313	3194
Daughter-dam regression	1720 pairs	1651
D-D regression LW/EL	665 pairs	604

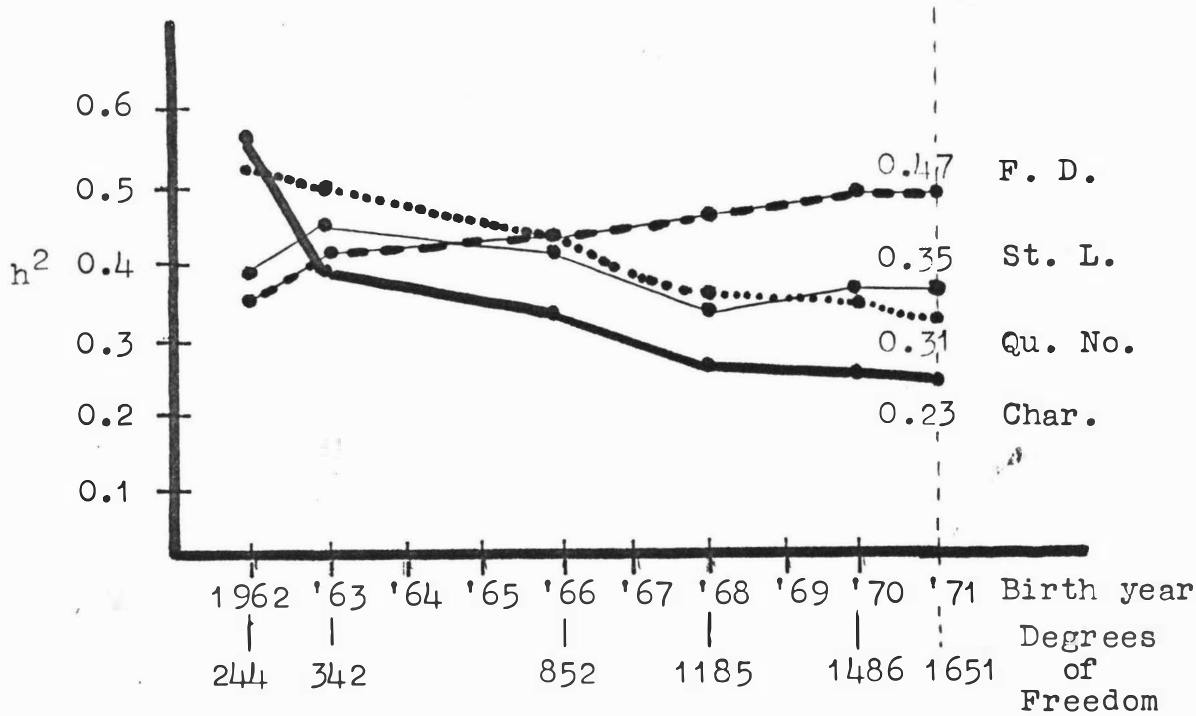
* Represents number lambs weaned from those ewes weaning lambs.

Fig. 2A

HERITABILITY ESTIMATES

(Daughter-dam regression study)

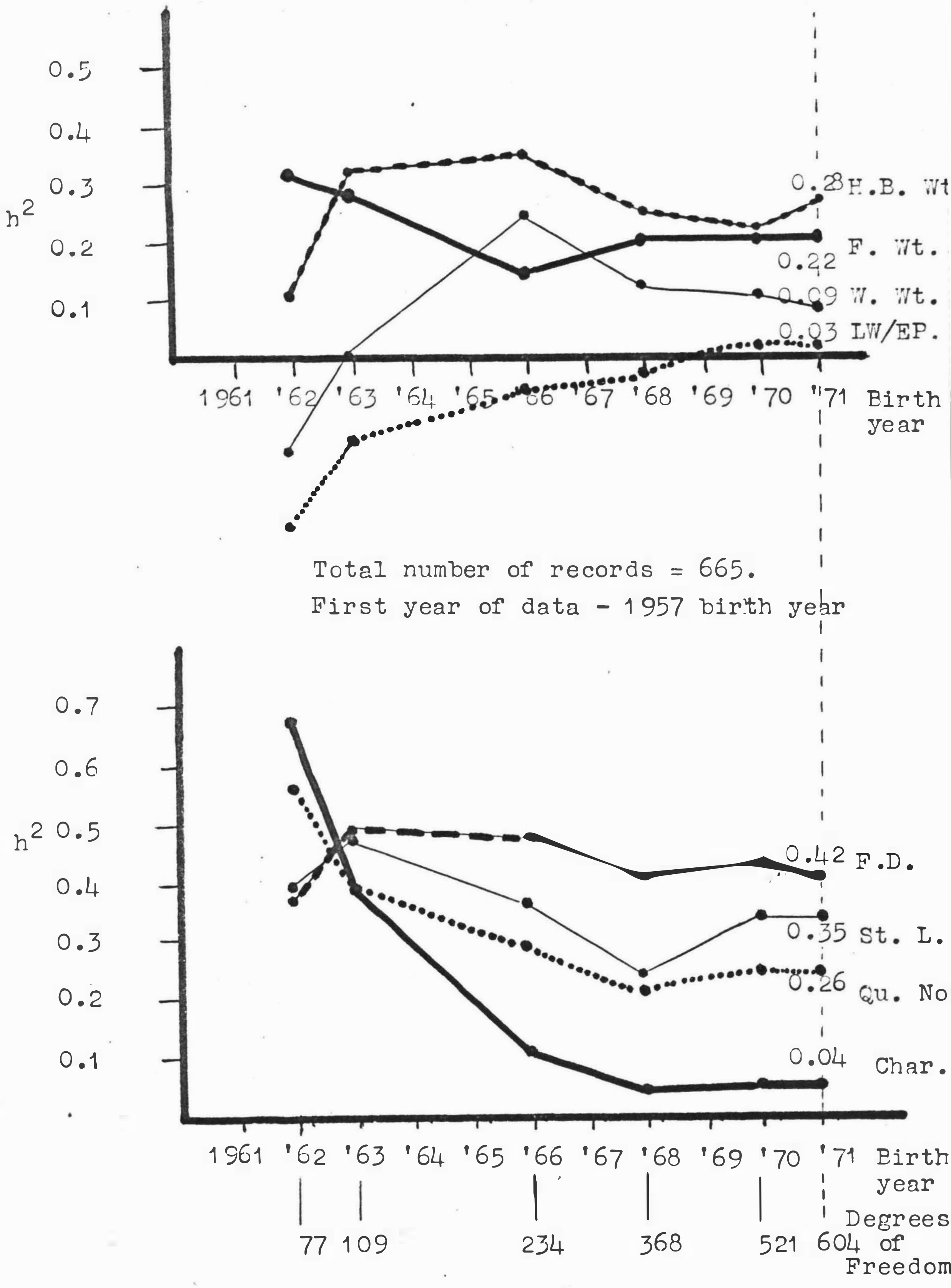




Total number of records = 1720.

First year of data - 1957 birth year.

Fig. 2B
HERITABILITY ESTIMATES
(Daughter-dam regression study).



results in Fig. 2A from 1968 on (1185 d.f) add weight to the accuracy of these heritability estimates.

An examination of the differences between the heritability estimates obtained by the two methods of estimation in relation to their standard errors, suggests that the differences for weaning weight, fleece weight and quality number are not significant. A real difference exists with hogget body weight, staple length and fibre diameter.

A recognised difference between the daughter-dam regression method and the paternal half-sib method is that maternal effects may contribute to the former whereas the latter does not contain variance due to maternal effects.

Maternal effects:-

The influence of a dam on her offspring is due to both genes transmitted and by the maternal environment provided during the suckling period; the latter may in itself be partly heritable. Consequently, there will be one genetic and one environmental influence. The environmental influence of some of the maternal effects such as rearing rank and age of dam have been corrected for in this analysis but other maternal effects may be present and included in the heritability estimate. These may cause additional resemblance between daughter and dam, particularly for weaning age measurements.

Post-weaning measurements may also be affected by the presence of carryover maternal effects. Ch'ang and Rae (1972) showed that carryover maternal effect had made a small and in most cases negligible contribution to the estimates of heritability of post-weaning liveweight measurements. A similar or smaller contribution may therefore be expected on other hogget trait heritability estimates.

The magnitude of the variance due to maternal effects included in the heritability estimate will depend on the correlation between "maternal ability" and the expression of the particular trait in the dam (Doney, 1958). The role of this correlation is quite independent of the heritability of that trait.

The presence of maternal effects, if genetically controlled will cause further bias. Koch and Clark (1955) showed the assumption that environmental variance is uncorrelated to genetic variance may not be appropriate if the trait is subject to an influence of maternal environment which is itself heritable. Owen (1957) obtained an estimate of 0.50 ± 0.07 for the heritability of milk production in ewes which would support the theory that maternal ability is inherited. A heritability estimate for maternal effect at weaning of 0.12 ± 0.06 was found by Gjedrem (1967). Additional evidence for genetic variation in maternal performance comes from crossbreeding experiments (Holtmann and Bernard, 1969).

As a consequence, a complicated situation with several coefficient components of the daughter-dam covariance exists when direct and maternal effects are considered, with even more existing when direct, maternal and grand maternal effects are considered (Willham, 1972). These will affect both heritability estimates and the fraction of the selection differential realized (Willham, 1963; Ch'ang, and Rae, 1972).

In theory it is possible to estimate the maternal contribution to parent-offspring correlation as the difference between the estimated additive genetic variance by the two different methods. In practice sampling errors may confuse the comparison. However theoretical considerations would suggest that if maternal effects are present then daughter-dam regression estimates would be biased upwards in relation to those by paternal half-sib analysis.

The heritability estimates for weaning weight by the daughter-dam method have been greater than those by the paternal half-sib method when estimates by both methods have been reported (Hazel and Terrill, 1946b; Pattie, 1965a, 1965b; and Young et al.,1965). In this study and that of Ch'ang and Rae (1970), weaning weight heritability estimates are smaller for daughter-dam regression analysis (see Table 12). Although standard errors do not permit making an accurate interpretation of the result, the consistency between these two results may confirm this apparent difference.

TABLE 12

COMPARISON OF RESULTS OF CH'ANG AND RAE (1970) AND OF THIS THESIS FOR WEANING WEIGHT AND HOGGET BODY WEIGHT HERITABILITY ESTIMATES.

	Method 1 Paternal half-sib		Method 2 Daughter-dam regression	
	Weaning wt	Hogget body wt	Weaning wt	Hogget body wt
Results	0.20 ± 0.01	0.27 ± 0.01	0.16 ± 0.05	0.44 ± 0.03
Ch'ang and Rae (1970)	0.30 ± 0.12	0.51 ± 0.12	0.23 ± 0.11	0.46 ± 0.11

This result may suggest the possibility of a negative genetic correlation between the direct and maternal effect on weaning weight for Perendales. Many studies in domestic mammals have suggested a negative genetic correlation between direct and maternal effect (Willham, 1972). Ch'ang and Rae (1972) reported a negative genetic correlation between maternal effect and weaning weight of the order -0.76 for Romney sheep. If a negative genetic correlation exists it would not be possible to state in detail the consequences of selection for weaning weight.

The largest difference (0.17) that exists between the heritabilities estimated by the two methods is for hogget body weight. Carryover maternal effects may have made a small contribution to the daughter-dam regression estimate (Ch'ang and Rae, 1972). A further possibility is that the paternal half-sib correlation is biased due to selection.

Selection effects:-

Selection of sires is considered a possible reason for estimates by the paternal half-sib correlation method being lower than those found by the daughter-dam regression method (Gjedrem, 1969). This downward bias increases with increasing heritability and intensity of selection (Ronningen, 1972a). Following Ronningen (1972a), if direct selection was for hogget body weight, then at the observed heritability estimate of 0.27 and with 5% of rams being selected, a negative bias of -0.10 to -0.20 is not unreasonable. However, for any bias to have been present due to this cause, it would have to be assumed that the choice of rams was in effect selection for hogget body weight. As there was no intended selection for hogget body weight, any bias present can be regarded as small.

It has previously been mentioned that little selection had taken place prior to the age of collection of this data. Natural deaths and the little culling of lambs that may have occurred would cause a small negative bias according to the degree that these causes may be considered as selection of progeny on body weight. However, this bias would be about the same size for both methods of estimation (based on deductions from data presented in Ronningen 1972a, 1972b). Also, any bias to the daughter-dam regression estimate due to selection of dams would be minimal for a heritability estimate of this size and expected degree of selection intensity applied.

The effects of selection in biasing heritabilities estimated by the daughter-dam regression analysis has been reported by Ronningen (1972b). Some support for this bias may be indicated from comparison of the final heritabilities shown in Fig. 2A and Fig. 2B. The difference between the two figures is due to records being excluded from the data for Fig. 2B of those ewes that had hogget records but were either culled before entering the breeding flock or failed to rear a lamb to weaning as a 2-year old. Consequently, a portion of the differences in heritabilities may be due to selection. Caution in drawing conclusions though arises for the second sample is a subgroup of the daughter-dam sample used previously.

Of interest is the unexplained trend present in Fig. 2A and Fig. 2B for character and also the difference in final heritability estimates for weaning weight (0.16 and 0.09), hogget body weight (0.44 and 0.28) and character (0.23 and 0.045). Further, if estimates in Fig. 2B are biased downward, then similarly it may imply the possibility of the estimate for LW/EL is biased downward.

Estimate values:-

If individual selection is to be of value, phenotypic differences among individuals must be highly heritable, and heritability will need to be greater than 0.2 before it can be considered as having a high value, (Turner and Young, 1969). They considered that high levels of heritability were those greater than 0.3, intermediate levels of heritability were those in the range of 0.1 to 0.3, and low values were those less than 0.1.

Using these values to express the magnitude of the heritabilities calculated in this thesis, the following applies:

(1) hogget body weight, fleece weight, fibre diameter and staple length have high levels of heritability;

(2) weaning weight, quality number and character may be regarded as having medium to low heritability; and

(3) LW/EL has a negligible heritability.

Comparing these estimates with those estimated from Romney data (Rae, 1958; Tripathy, 1966; Lundie, 1971; and Ch'ang and Rae, 1961 and 1970), these estimates are very similar for fleece weight and staple length, lower for weaning weight, hogget body weight and quality number, while that for fibre diameter is higher.

Because no corrections for age at weighings were made, this would contribute to an error (Blackwell and Henderson, 1955) and could account for the lower heritabilities for weaning and perhaps hogget body weight found in this study compared to those of Ch'ang and Rae (1970) where age corrections were applied (see Table 12).

Results here, like those of Ch'ang and Rae (1970) and others (see review) show a higher heritability for hogget body weight when compared with the heritability of weaning weight. This difference is considered to arise from the greater opportunity for the individual's own genetic constitution to express itself independently from the maternal effects (Ch'ang and Rae, 1970).

It has previously been mentioned that fibre diameter data was obtained by the air flow method which has associated errors compared to the projection microscope method from which other estimates have been computed. However the estimate in this study compares with fibre diameter heritabilities estimated from Merino and other fine wool breeds. The only estimate for Romneys (0.17) by Tripathy (1966) is very much lower than any other estimates and gives doubt to its accuracy.

No other reported heritabilities exist for the trait LW/EL for 2-year old ewes. A standard error could not be calculated for the computed information and as it is expected to be relatively large compared with the corresponding heritability estimate, only tentative conclusions can be made about the statistic. However, the value is similar to other estimates for number of lambs weaned for 2-year old performance. Like the Romney, it can be expected that with the Perendale, fertility is a character of low heritability and that direct selection for genetic improvement can be expected to be relatively slow.

In conclusion, there may be some differences between the heritability estimates in this thesis and those of previous Romney estimates. But in all cases the standard errors will also vary. It is difficult in practice to estimate the difference between heritability in a synthetic breed (like the Perendale) and those of its parental breeds (Romney and Cheviots in this case) with acceptable precision in order to predict future performance and compare merits of the breeds concerned. When heritabilities have been estimated in new breeds, their values were not found to differ from those in their parental breeds (Lopez-Fanjul, 1974).

3. Association Between Traits.

The genetic, phenotypic and environmental correlations obtained in the analyses are presented in Table 13. The genetic correlations estimated by the two methods (paternal half-sib correlation and daughter-dam regression) are presented separately with their standard errors.

The results from this analysis will be discussed bearing in mind that it is the genetic correlations that are of primary interest. The phenotypic and environmental correlations have been calculated to provide supporting information.

It can be seen that :

(1) the standard errors are relatively high;

(2) differences in the genetic correlation estimates exist between the two methods of estimation;

(3) some phenotypic correlations are not in agreement with the range of genetic correlations; some negative environmental correlations exist.

The results will be discussed with reference to these points.

Standard errors.

The standard errors of the genetic correlations (excluding those for associations involving LW/EL are all relatively large compared with the corresponding estimate.

Where magnitude and signs of the estimated genetic correlations by the two methods are in agreement, then conclusions may be considered with more confidence.

The large standard errors may account for differences in many of the associations. With some other factors must be considered.

The standard errors of the genetic correlations involving LW/EL are high. Consequently, no reliance may be placed on their value.

TABLE 13

ASSOCIATION BETWEEN TRAITS

Traits	Genetic Correlation				Correlations	
	Pat. ½-sib.	± S.E.	D-D. Reg.	± S.E.	Pheno-typic	Environ-mental
Hgt B. Wt x						
W. Wt	0.13	0.14	0.66	0.10	0.44	0.08
Char.	-0.47	0.20	-0.31	0.11	0.00	0.14
S. L.	-0.06	0.15	0.22	0.08	0.13	0.06
F. D.	-0.02	0.14	0.00	0.08	0.15	0.12
Qu No.	0.37	0.15	-0.10	0.09	-0.03	-0.04
F. Wt	-0.07	0.15	0.18	0.09	0.39	0.12
Fleece Wt x						
W. Wt	0.01	0.16	0.27	0.15	0.21	0.03
Char.	0.52	0.17	0.32	0.12	0.23	0.03
S. L.	0.76	0.17	0.44	0.06	0.44	0.00
Qu No.	-0.48	0.16	0.09	0.12	-0.16	-0.11
F. D.	0.43	0.14	0.44	0.07	0.50	0.04
Fibre D. x						
W. Wt	-0.32	0.15	0.15	0.13	0.04	-0.04
Char.	0.09	0.14	0.10	0.10	0.12	0.01
S. L.	0.53	0.14	0.31	0.08	0.34	0.02
Qu No.	-0.46	0.15	-0.27	0.11	-0.26	0.03
Quality No. x						
W. Wt	-0.40	0.17	-0.17	0.16	0.01	0.05
Char.	-0.13	0.16	0.44	0.13	0.13	0.11
S. L.	-0.63	0.16	-0.41	0.15	-0.45	0.01
Staple L. x						
W. Wt	-0.19	0.15	0.30	0.15	0.00	0.10
Char.	0.47	0.19	0.03	0.12	0.10	0.03
Character x W. Wt	-0.24	0.17	-0.21	0.19	0.04	0.06
No. Lambs Weaned x						
W. Wt			-0.47	1.11	0.10	0.04
Hgt B. Wt			+0.80	1.41	0.08	0.11
F. Wt			0.47	0.87	0.04	-0.05
F. D.			0.40	0.63	0.02	-0.06
Qu No.			-0.86	1.23	0.02	0.11
S. L.			0.23	0.62	0.00	0.03
Char.			-0.88	1.97	0.03	0.08

The large standard errors are expected because of the low parent offspring covariance for LW/EL. With a heritability estimate of 0.03 for LW/EL, large numbers of parent-offspring pairs would be required to narrow the confidence intervals that can be placed on the estimate.

Because no reliance may be placed on the gentic correlation estimates involving LW/EL, no further discussion will be entered into.

Phenotypic correlations.

Many of the phenotypic correlations fall into the negligible range defined by Brown and Turner (1968) as -0.2 to 0.2. Following Brown and Turner (1968), those outside this range may be summarized as follows:

High negative (-0.6 and over)	..	None
Medium negative (-0.4 to -0.6)	..	Quality number with staple length
Low negative (-0.2 to -0.4)	..	Quality number with fibre diameter
Low positive (0.2 to 0.4)	..	Fleece weight with weaning weight, hogget body weight and character. Fibre diameter with staple length.
Medium positive (0.4 to 0.6)	..	Hogget body weight with weaning weight. Fleece weight with fibre diameter and staple length.
High positive (0.6 and over)	..	None.

The sign of these phenotypic correlations and in general the sizes, are similar to those reported in Tables 7 and 8.

It is of interest that the phenotypic correlations between hogget body weight and other traits are lower than the reported Romney figures but are closely in line with those for the Merino breed. Significant among these are the medium-sized positive phenotypic correlations for hogget body weight with weaning weight and fleece weight.

Of particular interest to selection programmes are the negative associations of fleece weight with quality number and the associations of fibre diameter with staple length and fleece weight.

The phenotypic correlation (-0.16) for fleece weight with quality number is lower than the range of -0.34 to -0.45 reported for Merino, Corriedale and Polwaorth (Mullaney et al., 1970), but within the range of -0.03 to -0.33 reported for Romneys (Rae, 1958; Wickham, Ross, Cockrem, unpublished; Sumner, 1969). A higher phenotypic correlation than the range of 0.13 to 0.36 reported from Merino data occurs though for fleece weight with fibre diameter. The figure of 0.50 is in agreement to the Romney figure of 0.53 (Tripathy, 1966).

The phenotypic correlation between fibre diameter and staple length (0.34) is lower than those for Romneys with the range of 0.41 to 0.48 (Ross, 1964; Tripathy, 1966) but higher than most for Merinos where the range of reported estimates is -0.11 to 0.44.

It would appear that phenotypic correlations for the Perendales may be considered intermediate between Romney and Merino breeds.

The following points are of practical significance :

(1) The low phenotypic correlation between quality number and fibre diameter further supports the conclusion that for accurate assessment of wool fineness, fibre diameter should be measured.

(2) Hogget body weight has only a low (0.10) phenotypic correlation with LW/EL.

(3) The very low positive phenotypic correlation of 0.04 for LW/EL with fleece weight.

Environmental correlations

Positive environmental correlations greater than 0.09 are :

Hogget body weight	x fleece weight	(0.12)
Hogget body weight	x fibre diameter	(0.13)
Hogget body weight	x character	(0.15)
Weaning weight	x staple length	(0.10)
Quality number	x character	(0.11)

Negative environmental correlations exist for :

Weaning weight	x fibre diameter	(-0.05)
Hogget body weight	x quality number	(-0.08)
Fleece weight	x quality number	(-0.03)

The environmental correlations between weaning weight and staple length or fibre diameter may be due to an age effect while that between quality number and character may be due to an observer effect.

Apart from quality number, the environment can be considered to be acting with a similar masking or enhancing of wool traits and hogget body weight in allowing the expression of the genotype.

Some significance could be attached to the fact that environmental correlations involving weaning weight are mainly smaller than those with hogget body weight. This is shown in Table 14. The difference in age is considered to be the most important reason for this difference in magnitude of environmental correlations.

TABLE 14

ENVIRONMENTAL CORRELATIONS BETWEEN THE TRAITS WEANING WEIGHT AND HOGGET BODY WEIGHT WITH OTHER TRAITS

Trait	W. Wt	H.B.Wt
Fl.Wt	0.02	0.12
Qu.No.	0.05	-0.08
F.D.	-0.05	0.13
S.L.	0.10	0.06
Char.	0.04	0.15

The environmental component of the phenotypic correlation results from a developmental environment shared by the two traits; individual sheep reared on poor nutrition for example, are likely to have both a low body weight and a low wool weight (Falconer, 1960). Consequently it can be expected that part of this above difference is a result of the removal of the maternal contribution at weaning. These Perendale hoggets have had to develop under hill-country conditions. After weaning it is solely this environment that will determine the expression of genotype and consequently the resulting phenotype.

Comparison of phenotypic and genetic correlations.

Differences occur between genetic and phenotypic correlations. Those considered of most practical importance are -

Hogget body weight and fleece weight	0.39	-0.07
Hogget body weight and staple length	0.13	-0.06
Hogget body weight and fibre diameter	0.15	-0.02
* * * * *		
Weaning weight and quality number	0.01	-0.40
Weaning weight and character	0.04	-0.24

Once again an age effect may be responsible for the differences where weaning weight is concerned.

The closeness between phenotypic and genetic correlations involving fleece weight with staple length and fibre diameter, and fibre diameter with staple length, is of practical significance.

The genetic and environmental correlation relationship.

Bearing in mind the standard errors, it can be said that a difference in sign between genetic and environmental correlations occurs with the following associations

Weaning weight with chracter and quality number
Hogget body weight with character and probable with quality number.
Quality number with staple length and fibre diameter.

A difference in sign between the two correlations shows that genetic and environmental sources of variation effect the traits through different physiological mechanisms.

Paternal half-sib v. Daughter-dam Regression analysis estimates:

At least 9 associations exist where standard errors can not explain the discrepancies between genetic correlations estimated by paternal half-sib and daughter-dam regression. Factors causing bias must be considered.

The same conclusions drawn for the heritability estimates may be applied to the genetic correlations. It is considered that results obtained using the paternal half-sib analysis are not complicated by the presence of maternal sources of variation.

Theoretical considerations suggest that maternal contribution is a source of complication in using the relationship between daughter and dam. This effect causes the values found to be higher than paternal half-sib estimates (Ch'ang and Rae, 1972). This is evident for all traits involved with weaning weight. For the genetic correlation of hogget body weight with fleece weight and staple length, discrepancies between the two methods may be due to carry-over maternal effects.

It is noted that a negative environmental correlation exists where there is both a change in sign for the genetic correlations and large differences existing between the two methods of estimation. For the other associations where a change in sign exists, there tends to be large environmental correlations present. This can be seen in the following Table 15.

Although the standard errors would indicate that the accuracy of several genetic correlations is less than satisfactory, where there is general agreement between the two methods, some prediction of the magnitude of genetic correlations is permissible.

TABLE 15

ENVIRONMENTAL CORRELATIONS WITH THOSE ASSOCIATIONS WHERE GENETIC CORRELATION ESTIMATES DIFFER IN SIGN

Association	Pat. ½-sib r_G	D.D. Reg. r_G	r_E
H.B.Wt x Qu.No.	+ 0.37	- 0.10	- 0.05
F.Wt x Qu. No.	- 0.48	+ 0.09	- 0.03
W.Wt x F.D.	- 0.32	+ 0.15	- 0.05
H.B.Wt x St.L.	- 0.06	+ 0.22	+ 0.06
Qu.No. x Char.	- 0.13	+ 0.44	+ 0.11
W.Wt x St.L.	- 0.19	+ 0.30	+ 0.10

<u>The Estimates of Genetic Correlations</u>: These may be summarized in the following ranges :-

High negative (-0.6 and over)	..	None
Medium negative (-0.4 to -0.6)	..	Hogget body weight with character. Quality number with staple length.
Low negative (-0.2 to -0.4)	..	Weaning weight with quality number, fibre diameter and character. Quality number with fleece weight and fibre diameter.
Low positive (0.2 to 0.4)	..	Hogget body weight with weaning weight and quality number. Staple length with character.
Medium positive (0.4 to 0.6)	..	Fleece weight with fibre diameter and character. Fibre diameter with staple length.
High positive (0.6 and over)	..	Fleece weight with staple length.

With the genetic correlations estimated here, no associations are at any appreciable variance with previous reported estimates (<u>Tables 7</u> and <u>8</u>).

A difference of practical importance is that Ch'ang and Rae (1972) reported higher genetic correlations in their Romney data for weaning weight with hogget body weight, 0.74 (paternal half-sib method) and 0.90 (Daughter-dam regression method) compared to 0.13 ± 0.14 and 0.66 ± 0.10 for the respective methods in this analysis.

An important association not mentioned in the summary above, is the low genetic correlation found for hogget body weight with fleece weight (0.07 ± 0.15 and 0.18 ± 0.02 by paternal half-sib and daughter-dam regression methods respectively). The only Romney estimate is much higher at 0.54 ± 0.17 estimated by a daughter-dam regression analysis (Tripathy, 1966), while Vesely et al. (1970) reported 0.54 ± 0.20 for the Rambouillet. The range reported in the review for Merinos is -0.11 to 0.26, which is more in agreement. Contributions were +0.26 and -0.11 by paternal half-sib and daughter-dam regression anlaysis (Morley, 1955a), 0.20 ± 0.24 by dam-offspring correlation (Beattie, 1962), and 0.26 ± 0.07 by daughter-dam regression analysis (Brown and Turner, 1968). These tend to indicate a positive association in Merinos.

Slight positive responses in body weight during selection for fleece weight have been reported which would confirm a positive genetic correlation between fleece weight and hogget body weight (Dun, 1958; Brown et al. 1966; and Turner et al. 1968).

Turner (1958) found that selection for clean fleece weight was associated initially with a slight decrease in body size. She presented evidence which suggested that, while the genetic correlation between clean fleece weight and body weight appeared to be negative, there was a positive environmental correlation between these two characters. Subsequent selection for clean fleece weight in this flock produced the correlated increase in body weight reported by Brown et al. (1966)

However, no consistent association between hogget body weight and fleece weight was observed by Barlow (1974) during a fleece weight selection trial. There was evidence of a small negative association in the flock with downward selection imposed for fleece weight.

It may be concluded that the association hogget body weight x fleece weight in Perendales must be considered to have a low genetic correlation which is possibly negative, with a strong positive environmental correlation favouring the association and so causing the higher positive phenotypic correlation. The environmental association is to be expected and Morley (1955a) drew attention to examination of its value in selecting for fleece weight.

Support for this conclusion comes from the negligible genetic correlation of hogget body weight with fibre diameter (-0.02 ± 0.14 and 0.00 ± 0.08) and the similar genetic correlations between hogget body weight and staple length (-0.06 ± 0.15 and 0.22 ± 0.08), for the genetic correlations between fleece weight with staple length and fibre diameter are consistently strongly positive.

For the hogget body weight x staple length association Tripathy (1966) reported a genetic correlation of 0.26 ± 0.16 (by daughter-dam regression method) for Romneys which is similar to the estimate for this analysis. But Merino estimates range from -0.25 to 0.04. Morley (1955a) reported estimates at -0.25 (paternal ½-sib) and -0.12 (daughter-dam regression); Beattie (1962) 0.01 ± 0.17; while -0.06 ± 0.07 (daughter-dam regression) was reported by Brown and Turner (1968). Once again a conclusion must be one of a negligible association.

The most significant practical finding with the wool traits is the high positive genetic correlation of fleece weight with staple length (0.76 and 0.44). This is higher than the range reported for the Romney (0.25 to 0.40). With Merinos, Morley (1955a) found a low association of 0.17 and -0.02 while Brown and Turner (1968) reported 0.29 ± 0.08 and Mullaney _et al_. (1970) 0.13 ± 0.14 (Merino), 0.20 ± 0.16 (Corriedale) and 0.47 ± 0.28 (Polwarth). Beattie (1962) found a high genetic correlation estimate of 0.70 ± 0.17 which gives support for a possible high correlation.

Of importance with regard to wool fineness is the consistent medium-sized positive genetic correlations for fleece weight with fibre diameter. This is supported by a negative fleece weight x quality number genetic correlation; a negative genetic correlation exists for quality number with fibre diameter.

A medium-sized positive genetic correlation exists for staple length with fibre diameter which is in agreement with the Romney estimates; Tripathy (1966). This estimate does not support an independent inheritance of fibre diameter and staple length.

Merino estimates show a wide variance from positive to negative values for the genetic correlation staple length with fibre diameter. Turner (1956) stipulated that if further information supported her finding of a lack of genetic correlation between staple length and fibre diameter, and between staple length and fibre number per unit area, it should be possible to select for any desired combination of fineness, length and number. Support had come from Turner et al. (1970) who concluded that an absence of genetic correlations between fibre diameter x staple length and fibre number per unit area x staple length indicated that selection could be for high fibre number/unit area with high staple length and low fibre diameter - in other words, a desirable fleece - with no impeding genetic correlations. Unfortunately the former part of the statement (Turner, 1956) cannot be supported by these Perendale estimates.

Genetic correlations for Perendales, reported here, show antagonism to the attainment of the desirable combination of heavier fleece weight and longer staple length with finer wool.

The positive genetic correlations of fleece weight and staple length with character signifies that any selection for fleece weight and/or staple length will be complimented by an improvement in character. This receives some support from an observed slight improvement in wool character as a correlated response to selection for clean fleece weight with Merinos (Barlow, 1974).

V. RELATIONSHIP OF HOGGET CHARACTERISTICS TO LIFETIME PERFORMANCE

A. INTRODUCTION

In breeding flocks, the number of ewe hoggets available in each year usually exceeds the number required for replacements. This surplus provides the breeder with some opportunity for culling, a practice generally regarded as a means of maintaining or improving performance within the current flock.

A part of the available selection potential will be devoted, both before and at the hogget stage, to eliminating the obviously deformed or unthrifty sheep. Following this, selection attention by farmers is usually on body size with some attention devoted to wool. Ram breeders follow similar culling practices, though varying amounts of emphasis may be put on records of hogget production and pedigree.

Clearly, the value of culling at the hogget stage for phenotypic response, will depend greatly on the phenotypic relationship between hogget characters and the subsequent performance of ewes.

Examination of the relationship has been approached by two methods :

(1) by a study of the correlation between individual hogget traits and lifetime ewe traits; and

(2) by a multiple regression analysis of lifetime economic value and hogget characteristics.

In both studies, only those sheep that had a hogget record and four succeeding records were used. Eleven years of hogget records were analysed.

This involved 458 sheep.

Records were available on the following traits :- hogget body weight, fleece weight, quality number, fibre diameter, staple length, character, and in addition for ewes, number of lambs weaned (either 0, 1 or 2).

B. Methods.

1. CORRELATION BETWEEN HOGGET AND LIFETIME EWE PERFORMANCE

A Fortran computer programme was written for a Burroughs B6700 computer to analyse the data. The programme calculated

(1) The mean of each hogget trait within each year.
(2) Mean lifetime ewe performance for the traits studied, within each birth-year.
(3) Correlation coefficients; by calculating corrected sums of squares and cross products on a within year basis and then combining to obtain the correlation coefficients over all years.
(4) Degrees of freedom associated with the correlation coefficient.

No corrections of any kind were made on the data. To avoid spurious correlations, the hogget record was not included in the lifetime performance record.

2. MULTIPLE REGRESSION ANALYSIS OF LIFETIME ECONOMIC VALUE ON HOGGET CHARACTERISTICS.

Using the same records as in the previous study, a number of multiple regression analyses were run using available BASIS (Burroughs Advanced Statistical Inquiry System) computer programmes.

The multiple regression equation had the following form

$$y = a + b_1 X_1 + b_2 X_2 + \ldots\ldots\ldots\ldots + b_n X_n + e$$

where

y = lifetime economic value for a ewe

a = constant

X_1, X_2 ...... X_n refer to independent variates. In this case X_1 = hogget liveweight, X_2, X_3, X_4, X_5, and X_6 being hogget wool traits, respectively, fleece weight, quality number, staple length, character and fibre diameter.

b_1, b_2...... b_n denotes the partial regression coefficient of y on variable X_n.

e= error term; assumed to be normally and independently distributed with a mean of zero and constant variance.

The lifetime economic value was derived from the equation

$$\text{Lifetime economic value} = \text{Total wool value} + \text{Total lamb value}$$

Four different multiple linear regression analyses were carried out, each with different economic values.

These were called :

(1) 1972/73 values;
(2) 1970/71 values;
(3) average values; and
(4) estimated values.

Lamb values were derived after a review of data contained in the Annual Reports of the New Zealand Meat Producers Board, and in the "Annual Review of the Sheep Industry" published by the New Zealand Meat and Wool Economic Service. Seasonal lamb prices were

1968/69	..	$5.50
1969/70	..	6.00
1970/71	..	5.75
1971/72	..	4.50
1972/73	..	8.50

The average value used the mean of these five seasons. The estimate value is an approximation of the value of all lambs at weaning using 1972/73 season's value.

The value for twin lambs was obtained by subtracting 20% of a single lamb value and then doubling the resulting value. The subtraction was an approximation to correct for the rearing rank effect on liveweight and fleece weight at weaning age.

The total wool values were calculated from the equation

wool value = fleece weight x price/kilo.

The estimates of price/kilo were derived from average prices quoted annually in the statistical analysis of NZ wool production and disposal (Anonymous 1969, 1970, 1971, 1972, 1973)

For the five seasons in which lamb values were quoted, average prices of greasy wool sold at auction in New Zealand were

		cents/kilo
1968/69	..	62.0
1969/70	..	56.5
1970/71	..	53.5
1971/72	..	66.5
1972/73	..	114.0

Average = 76.5 cents/kilo.

The four values were similar to those lamb values used. They were the 1972/73 and 1970/71 wool values, with average value being the mean of the last five years figures available (i.e. 1968/69 to 1972/73). The estimate values were those of 1972/73 multiplied by 1.2. This was an approximation to attain a value for Perendale wool.

To obtain price/kilo for the four values, tables titled "Types of Fleece Wool in the New Zealand Clip" were consulted.

Prices of greasy wool in cents/kilo for the range of quality number groupings was obtained from the following fleece wool groups :-

(1) Carding and Preparing
(2) Carding
(3) Short Carding
(4) Second Shear Good Length
(5) Second Shear Average Length
(6) Second Shear Short Length

By the use of the table titled "Quality and Length Brackets", in which staple length is graduated in ½ to 2 inch units for various quality numbers, values were plotted on a graph to allow estimates of price increment per staple length increment for each quality number groupings.

This technique was repeated for the four wool values used. The information obtained from this graph is presented in Table 16. These data were incorporated into the computer programme for transformation purposes.

Using the equation

$$\text{Price/kilo} = Aq + Bq \; L$$

where : -

Aq represents the zero length value for each quality number,
Bq the regression coefficient of price increment/staple length, and
L the staple length record,

The price/kilo was calculated for each ewe record on entering the constants appropriate to the quality number.

As a consequence wool value was determined from fleece weight, staple length and quality number; the influence of fibre diameter in effecting price/kilo could only be represented by substituting average fibre diameter for the corresponding coded quality number values.

TABLE 16

ZERO LENGTH VALUES AND PRICE INCREMENT PER STAPLE LENGTH INCREMENT COEFFICIENTS FOR CORRESPONDING QUALITY NUMBER RECORDS.

Quality Number Code	1972/73 values		1970/71 values		Average values		Estimate values	
44	149.00	0.050	50.00	0.025	76.00	0.010	178.8	0.050
45	146.00	0.150	55.20	0.130	76.20	0.020	175.2	0.150
46	142.00	0.300	53.50	0.250	76.48	0.027	170.4	0.300
47	137.00	0.800	52.25	0.355	76.80	0.050	164.4	0.800
48	130.50	1.350	52.40	0.475	76.90	0.067	156.6	1.350
49	122.20	2.330	52.55	0.575	73.60	0.840	146.6	2.330
50	108.50	4.800	54.30	0.730	72.50	1.250	130.2	4.800
51	90.00	7.800	55.30	0.775	69.50	2.200	108.0	7.800
52	71.30	10.670	55.80	0.800	64.85	2.890	85.5	10.670
53	75.00	11.400	55.50	1.100	64.00	3.180	90.0	11.400
54	78.00	12.000	54.70	1.300	63.75	3.350	93.6	12.000
55	68.00	13.000	53.50	1.650	64.60	3.550	81.6	13.000
56	66.50	14.000	51.40	2.010	66.25	3.750	79.8	14.000
57	64.00	15.000	50.50	2.300	68.00	4.000	76.8	15.000
58	61.50	16.000	49.60	2.600	69.40	4.200	73.8	16.000

Wool character does not enter into determining price/kilo. Data were not available for estimating the contribution of character to wool value for New Zealand fleeces.

Two further analyses were carried out to check the accuracy of this method. They were;

(1) two multiple regressions were repeated on a within-year-basis for comparison with the overall analysis; and

(2) two stepwise multiple regression analyses were carried out using, separately, quality number and fibre diameter as the basis of wool valuation.

Throughout this study, coded wool quality numbers correspond to the quality numbers and average fibre diameters shown in Appendix III.

C. RESULTS AND DISCUSSION

1. Correlation study.

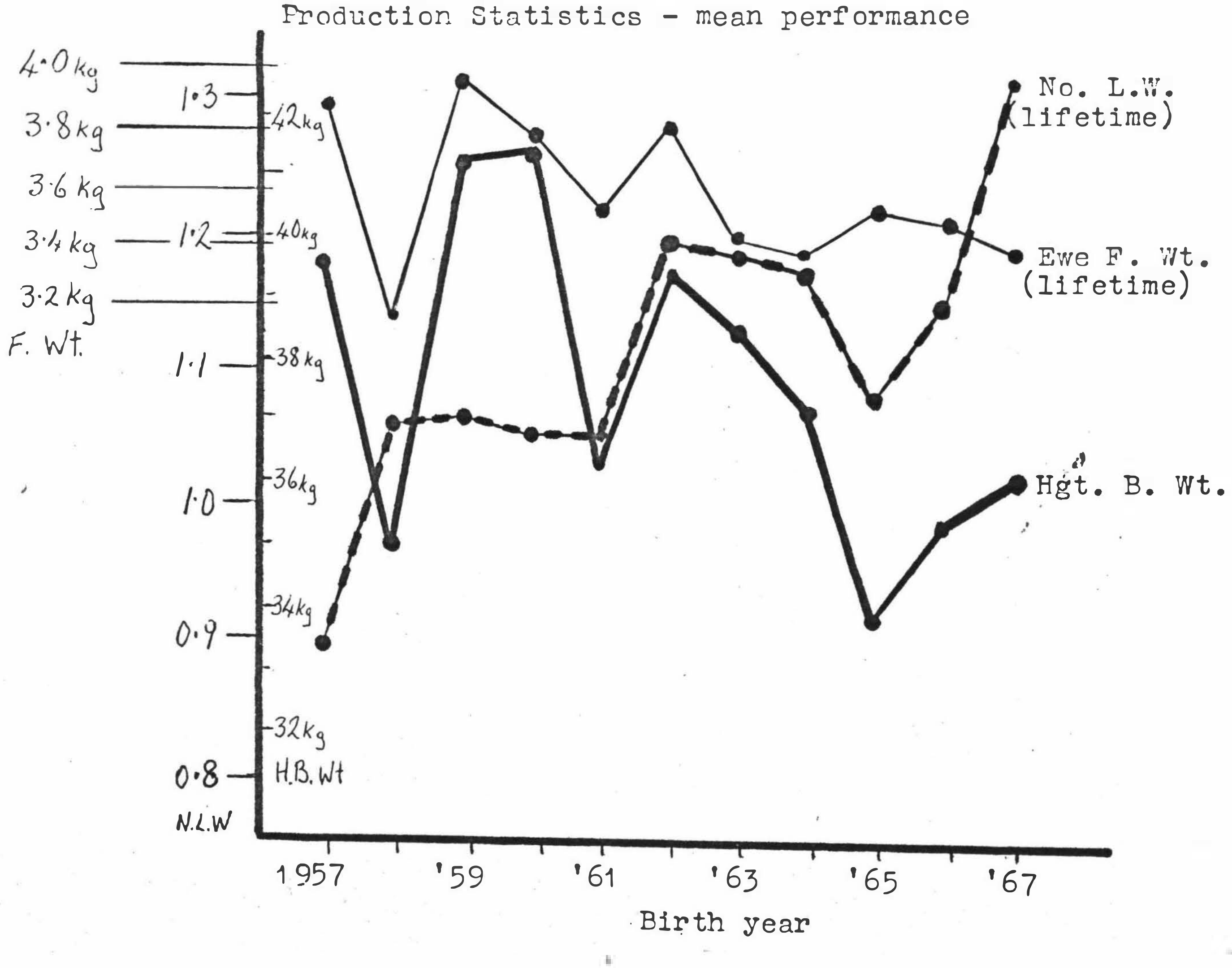
The mean hogget body weights and the mean lifetime ewe performance for the traits number of lambs weaned and ewe fleece weight for each year of birth are shown in Fig 3. Points about the data that may be deduced from this graph are

(1) Number of lambs weaned increased from 0.9 to 1·3 during the period of the analysis;

(2) Mean lifetime ewe fleece weights were erratic; and

(3) Hogget body weights, which may be considerd as an indication of nutrition, varied quite considerably between seasons.

Fig. 3
Production Statistics - mean performance



Correlation coefficients between hogget traits and the lifetime performance of the ewe appear in Table 17, along with the degrees of freedom associated with the correlations.

They may be considered under two headings.

A. Direct correlations.

These correlation coefficients indicate that the hogget traits in this study, with the exception of character, would be of useful predictive value for lifetime merit. Correlation coefficients for fleece weight, quality number, staple length and fibre diameter, are between 0.49 and 0.60. This indicates that around 24% to 36% of the variation in lifetime production can be predicted from hogget performance.

The value obtained for fleece weight (0.56) is within the range of 0.44 to 0.72 previously reported (Gartner and von Ungern - Stenberg, 1938; Terrill, 1939; Wolf, 1951; Wright and Stevens, 1953). The correlation coefficient for staple length at 0.49 is lower than the previously reported figure of 0.69 (Terrill, 1939). No literature can be found to compare the other results.

The low value for character reflects the sensitivity of this trait to enviromental influences and inconsistency associated with the technique of appraisal.

B. Indirect correlations.

The correlations between different traits are all of a relatively low value compared to the direct correlations. They indicate that there would be no advantage gained by indirect selection as opposed to directly selecting for a trait at the hogget age, for gain in lifetime ewe performance.

TABLE 17

CORRELATION COEFFICIENTS BETWEEN HOGGET TRAITS AND LIFETIME† EWE PERFORMANCE

Hogget Traits	Ewe Traits					
	No. of lambs weaned	Fleece weight	Quality Number	Fibre Diameter	Staple Length	Character
Hgt. b. wt.	0.07	0.12	-0.03	0.02	0.00	-0.03
Fl. wt.	-0.01	0.56	-0.22	0.25	0.26	0.19
Qu. No.	-0.01	-0.14	0.52	-0.29	-0.32	0.01
F.D.	0.04	0.11	-0.26	0.59	0.11	-0.07
St. L.	0.03	0.23	-0.33	0.16	0.49	0.06
Char.	-0.02	0.15	0.08	-0.02	0.01	0.28

† Lifetime = Four consecutive records from 2-yr old ewe to 5-yr old ewe (inclusive)

Degrees of freedom for the correlation coefficients = 445

"Direct correlations" are those coefficients on the diagonal; "indirect correlations" are the off-diagonal coefficients.

The sign and size of the correlations are of interest. The largest are the inter-relationship between fleece weight, staple length and fibre diameter. These correlations are of similar sign and proportionally of similar size (though lower in value) to the genetic and phenotypic correlations. It may indicate that similar genetic and environmental factors which give rise to the hogget phenotypic correlations remain responsible in later life.

The correlation coefficient shows that the relationship between hogget fleece weight and number of lambs weaned by the ewe, can be considered negligible.

No other literature is available for comparative purposes with these indirect correlations involving wool traits.

Emphasis is often placed on liveweight during hogget selection. Relationship between this trait and ewe lifetime performance for other traits are low. The highest is that between hogget body weight and lifetime ewe fleece weight. The value of 0.12 would indicate that any indirect gain in fleece weight would be minimal compared to the gain attained when attention is directly placed on fleece weight. This value is similar to the results found in other breeds (Terrill and Stoehr, 1942; Shelton and Menzies, 1968; Basuthakur et. al., 1970) where in general positive relationships were found that were significant but of low magnitude. Only a slight advantage in lifetime ewe fleece weight may be expected from heavier hoggets.

Of practical importance is the low correlation between hogget bodyweight and number of lambs weaned. Once again this figure is within the range reported by Shelton and Menzies (1968) and Basuthakur et. al. (1970).

It is lower than the phenotypic correlations reported between hogget body weight and the total number of lambs born over the ewe's first three lambings;- Young etal.(1963) reported an $\hat{r}_p$ = 0.12 for Merinos, while Ch'ang and Rae(1972) reported an $\hat{r}_p$ = 0.23 in the Romney breed.

2. Multiple Regression Study.

The results obtained for mean ewe lifetime economic values with the four multiple linear regression analyses appear in Table 18 along with the contributions made by total lamb and total wool production. A ratio of lamb to wool value is also presented.

TABLE 18
MEAN LIFETIME VALUES

Regression analyses		Economic value	Lamb value	Wool value	Ratio Lamb	:	Wool
Estimate	values	$60.85	$27.85	$33.00	1	:	1.18
1972/73	values	62.30	34.85	27.45	1	:	0.79
Average	values	38.25	24.60	13.65	1	:	0.55
1970/71	values	32.90	23.60	9.30	1	:	0.39

The ratios show that the wool values in proportion to lamb ranged from approximately 40% to 120%. This range covers the likely future proportions under New Zealand production.

The results for the multiple linear regresseion analyses are presented in Table 19.

Before drawing conclusions from this study, it must be realised that the coefficients of determination (Table19) indicate that the hogget variables used in the multiple linear regression, contribute to only a small proportion of the possible factors contributing to the determination of the ewe's lifetime economic value. Also, not all partial regression coefficients are statistically significant.

The partial regression coefficients measure the average or expected change in the lifetime economic value when a hogget variable increases by one unit and other hogget variables in the equation remain unchanged.

TABLE 19

MULTIPLE REGRESSION ANALYSIS RESULTS

Variable	Values: Estimated	1972/73	Average	1970/71
A. Partial Regression Coefficients				
Body Weight	8.65*	8.60*	5.30*	4.76*
Fleece Weight	187.83*	150.15*	73.58*	49.28*
Quality Number	39.75*	38.80*	16.41	10.15
Fibre Diameter	-14.22	-4.69	4.13	7.20
Staple length	-21.86	2.98	12.97	20.60
Character	-7.13	-32.34*	-36.92*	-44.11*
Constant	2969.94	2927.91	2033.56	1859.27
Economic Value	6084.56	6232.16	3824.60	3287.88
B. Beta Coefficients - Standard Partial Regression Coefficients.				
Body Weight	0.11	0.10	0.09	0.09
Fleece Weight	0.22	0.17	0.11	0.08
Quality Number	0.10	0.09	0.05	0.03
Fibre Diameter	-0.04	-0.01	0.02	0.03
Staple length	-0.05	0.01	0.04	0.06
Character	-0.01	-0.05	-0,08	-0.10
Standard Error of Estimate	782.28	898.64	610.54	580.61
Coefficient of determination	0.07	0.04	0.03	0.03
Coefficient of determination (adj)	0.05	0.03	0.02	0.02
Multiple correlation coefficient	0.26	0.20	0.18	0.18
Multiple correlation coef. (adj.)	0.23	0.17	0.14	0.13

* Statistically significant (t - test 5% level of t)

These indicate that, an increase in hogget fleece weight by one pound would result in an increase in lifetime economic value of approximately 50 cents (1970/71 values), 74cents (average values), \$1.50 (1972/73 values) and \$1.90 (estimated values). Similar but negative values would apply if hogget values were one pound lighter in weight.

Similar deductions can be made concerning the other traits. Hoggets that were one pound heavier in body weight show an increase in ewe lifetime economic value of 4.76 to 8.65 cents. In all cases, improvement in hogget wool character shows a decrease in ewe lifetime economic value ranging from 7 to 44 cents per character grade. Raising quality number of hogget wool will increase ewe lifetime economic values.

The partial regression coefficients are not statistically significant for deductions to be made about staple length and fibre diameter; and similarly quality number at the average and 1970/71 values (i.e. those values where wool is relatively of low value in relation to lamb values).

In this study, interest lies in the relative importance of the hogget variables in determing the lifetime economic value of a ewe. The standard partial regression coefficients are the partial regression coefficients when each variable is in standard measure; i.e. when expressed as a deviation from the mean in units of its standard deviation. Since each standard partial regression coefficient is independent of the original units of measurement, a comparison of any two indicates the relative importance of the hogget variables involved. This ranking of the hogget traits may be seen in <u>Fig 4</u>.

Fig. 4
A graph of standard partial regression coefficients V ratio wool : lamb value from four multiple linear regression analyses.

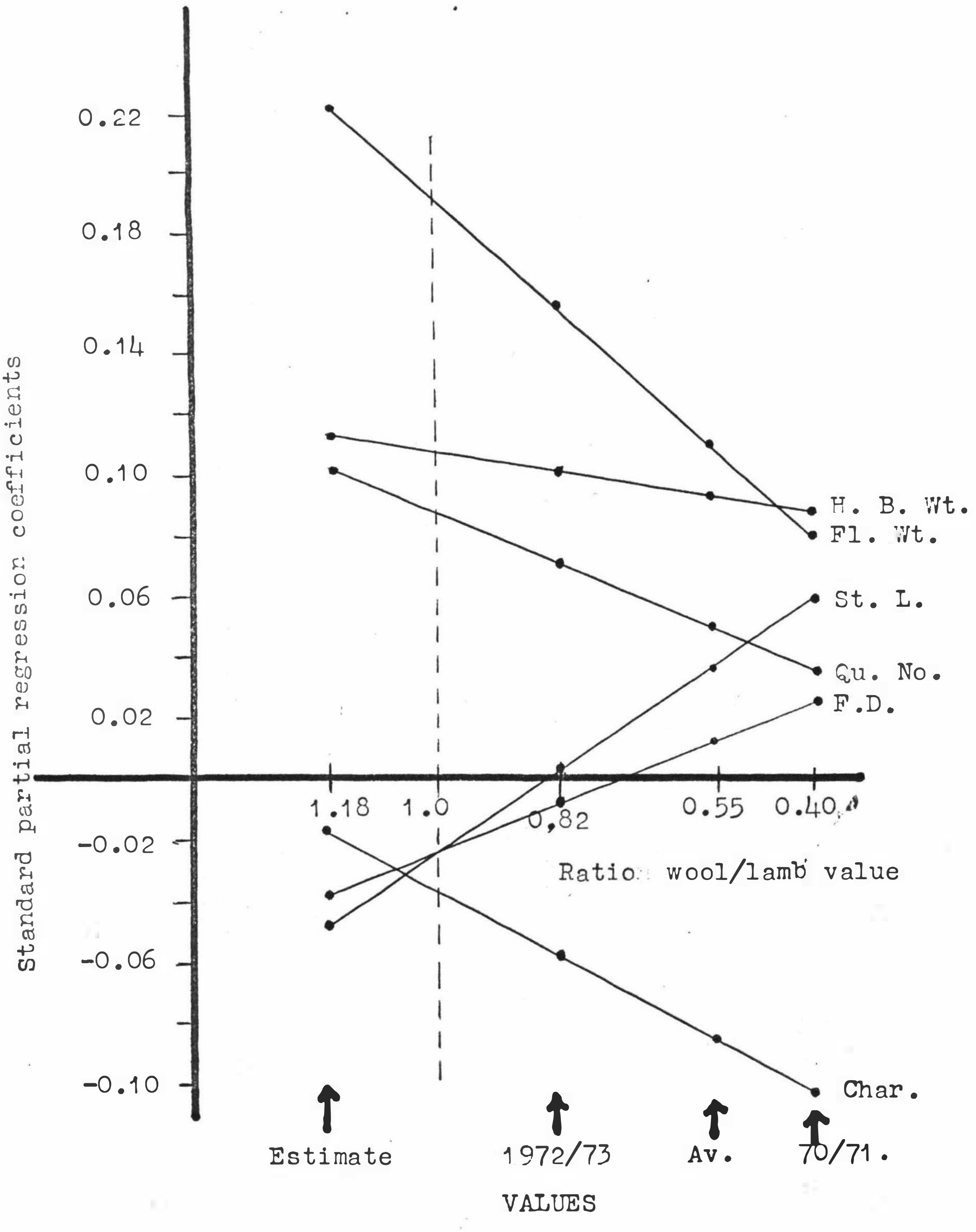


Fig. 4 shows the standard partial regression coefficients from the four multiple regression analyses plotted on a graph. These are spaced apart on the horizontal axis in accordance with the value of the ratio wool/lamb, from each multiple regresseion analysis. A wide range of contributory wool and lamb values are represented from which can be deduced the relative importance of the hogget traits.

From observation of Fig. 4, indications are that :-

(1) When wool values are low in comparison to lamb values, hogget body weight is of slightly greater importance than the hogget fleece weight.

(2) With increasing importance of wool values in relation to lamb value, fleece weight becomes markedly greater in importance than body weight.

(3) At low wool values relative to lamb values, the standard partial regression coefficients for the hogget wool traits, staple length, quality number and fibre diameter are all positive and compared to fleece weight are relatively important. But with increasing wool/lamb value they have decreasing relative importance when compared with fleece weight. The standard partial regression coefficients actually become negative for fibre diameter and staple length. Fleece weight which always has the highest ranking, becomes the dominant trait in importance. This result is in agreement with Dunlop and Young (1960) who analysed the control of price for wool by the wool variables, fibre diameter, crimps per inch, staple length, quality number, character, colour, soundness and handle. They reported that in a highly competitive season when wool prices are high, there was a much less reference than usual to the normal standards of wool quality.

(4) In all cases, the standard partial regression coefficients for hogget wool character has a negative value.

The resulting standard partial regression coefficients from the multiple linear regression carried out on a within year-basis, were very similar to the previous coefficients with one exception. With character, the negative standard partial regression coefficient of -0.08 was decreased in value to -0.003, indicating it to be of negligible importance. The change in value for this coefficient may reflect variation by appraisers from year to year in their evaluation of character.

The standard partial regression coefficients from the stepwise multiple regression analysis were relatively consistent with the results from the multiple linear regression analyses. This indicates that discussion based on the multiple linear regression analysis will be acceptable as accurate rankings of the hogget variables in importance.

When fibre diameter was substituted for quality number as the basis of wool valuation, increased standard partial regression coefficients were observed for staple length (the coefficients are now all positive and of some importance). It also resulted in decreased standard partial regression coefficients for quality number and fibre diameter.

For comparison the standardised partial regression coefficients resulting from both analyses are presented in <u>Table 20</u> for the average and estimate values.

It can be concluded that when wool fineness is valued using quality number, then fleece weight, hogget body weight and staple length are important hogget variables in determining lifetime economic ewe value at the lower wool values in relation to lamb values. At higher wool values relative to lamb values, fleece weight is the most influencing trait. Hogget body weight, is also important. Quality number enters into consideration with a relative importance similar to hogget body weight. Staple length is no longer of relative importance. All other hogget variables may be considered of negligible importance.

If fibre diameter instead of quality number is the basis of wool valuation, the variable staple length is also important at the higher wool values relative to lamb values. Fibre diameter is then significantly negative to warrant its consideration as such.

TABLE 20

STANDARD PARTIAL REGRESSION COEFFICIENTS USING QUALITY NUMBER AND FIBRE DIAMETER AS THE BASIS OF WOOL VALUATION.

Trait	Average Values		Estimated Values	
	Qu. No.	Fib.Diam.	Qu. No.	Fib. Diam.
Body weight	0.09	0.10	0.11	0.08
Fleece weight	0.11	0.09	0.22	0.22
Quality Number	0.05	0.01	0.10	-0.02
Staple length	0.04	0.06	-0.06	0.07
Fibre Diameter	0.02	-0.04	-0.04	-0.13
Character	-0.08	-0.10	-0.01	0.00

DISCUSSION

In considering improvement within the Perendale breed, the usefulness of the present results depend on the extent to which they can be applied. An aim of this discussion will be to consider breeding policy in light of the results presented.

Estimates of genetic parameters apply to a particular population from which the data were drawn. In theory, these may vary from one population to another because of factors which may cause differences in either the genetic or environmental variances. Application of the results in this study to other flocks of Perendale sheep thus involves the assumption that the phenotypic and genetic relationships are similar to those found in the present flock.

The accuracy of the estimated phenotypic and genetic parameters can be considered satisfactory with the exception of those involving LW/EL. Because of this, and the fact that the results generally agree with other extimates, applied policy based on them may be accepted with confidence.

It must be realised that in addition to the parameters that have been estimated, vital statistics such as lambing percentage, death rates in all classes of stock and the annual replacement rate of the 2-yr-old ewes are needed to compute expected gains and to compare the efficiency of various selection plans within a flock.

The attributes needed for efficient sheep production will vary in relative importance according to the farming system. Desirable characteristics include fertility, wool production and the ability to survive and reproduce with the minimum of shepherding.

Genetic Selection for Wool Traits.

The heritability of fleece weight, staple length and fibre diameter are high and consequently these traits will respond to selection. Because they can be observed in both sexes, improvement for each trait individually would most simply be achieved by mass selection followed by random mating.

Quality number and character have a medium to low heritability. Response to selection will consequently be slower than with the previous traits. Selection procedures will need to be more complicated than mass selection based on performance records, if satisfactory response is desired. The low heritabilities partly reflect the inaccuracy associated with a visual appraisal system. Consequently, if it is thought desirable to select for either of these traits, then some form of family selection would aid in a more accurate identification of animals with superior genotypes. This should be followed by random mating or some form of like to like mating.

Fleece weight selection is considered the most satisfactory, proven way of influencing the profitability of wool production by sheep breeding (Wickham, 1973)

Information from this thesis and that of other literature indicates that :

(1) Fleece weight is clearly of primary economic importance.

(2) It is a trait which is not difficult to measure, requiring only simple scales and some temporary method of identifying sheep.

(3) Fleece weight is highly repeatable and gains in the current flock are possible from selection / culling procedures based on the hogget record. Information from the correlation between hogget and lifetime ewe performance, support the latter part of this statement.

(4) The results of, for example, Turner etal. (1968), Mayo etal. (1970) and Pattie and Barlow (1974), outlined in the review of literature, have shown worthwhile selection response. The heritability estimate indicates that similar results are likely to occur.

(5) Sheep with high fleece weights also have a high efficiency of conversion of food to wool and it has been shown that selection for increased wool weight has in fact lead to increased efficiency (Dolling and Moore, 1960; Dolling and Piper 1968; Ahmed, Dun and Winston, 1963; Williams and Winston, 1965; Williams, 1966; Saville and Robards, 1972).

This information indicates that selection should be directed for fleece weight improvement. Correlated changes in other wool traits and the means of improving fleece weight selection by indirect selection and / or selection on one of its components needs to be considered.

The genetic correlations among the wool traits estimated in this thesis, indicate that with improvement in fleece weight associated changes will be increases in fibre diameter, staple length and character, with a decrease in quality number.

Australian work has indicated that with Merinos, the genetic correlation between fleece weight and fibre diameter is low. Also their work has indicated independent inheritance of fibre diameter and staple length. This is not the case with these Perendale estimates. They indicate antagonisms between fleece weight and wool fineness, which with fleece weight improvement may bring about correlated changes detrimental to Perendale wool as a product. The phenotypic correlation (0.50) between fleece weight and fibre diameter is also similar to the genetic correlation (0.43).

The extent to which this antagonism will interfere with improvement, depends on the heritabilities, genetic and phenotypic correlations, and the relative economic importance of related traits.

Consideration needs to be given to the effects of indirect selection.

The relative efficiency of two methods of selection in terms of genetic gain can be simply compared by the ratio (Q) of the two gains. Therefore

$$Q = \frac{\text{gain by indirect selection}}{\text{gain by direct selection}}$$

$$= \frac{\Delta G_{2.1}}{\Delta G_2} = \frac{h_1 h_2 r_{G_{1.2}} \sigma_2 i_1}{h_2^2 \sigma_2 i_2} = r_{G_{1.2}} \frac{h_1}{h_2}$$

where : h_1^2 and h_2^2 are the heritabilities of the two traits;

$r_{G_{1.2}}$ is the genetic correlation between them;

i is the standardized selection differential;

σ is the phenotypic standard deviation;

$\Delta G_{2.1}$ = predicted genetic gain in trait 2 under selection for trait 1 ; and

ΔG_2 = predicted genetic gain in trait 2 under selection for trait 2.

Turner and Young (1969)

Estimation of the relative efficiencies of indirect selection as opposed to direct selection, shows that with the wool traits considered in this thesis, there is no case where indirect selection will lead to a greater response then will be achieved by direct selection.

Of interest though is that if staple length is used to indirectly select for fleece weight, relative efficiency in terms of genetic gain is 0.94 (paternal half-sib estimates) or 0.47 (daughter - dam regression estimates). This has two practical implications for ram breeding flocks :-

(a) where it is considered uneconomic to record fleece weight, the loss in efficiency in terms of genetic gain will be between 6% and 53%, if a staple length record is used as a substitute.

(b) Improved staple length is a desirable component contributing toward improved fleece weight. Where rams are identical in ranking, after consideration of any index including fleece weight, a measure of staple length would be useful as a base for a final selection criteria. It would indicate the ram(s) with the longer staple as opposed to a less important component making up fleece weight.

A study of selection indices (Appendix V) using the genetic and phenotypic parameters estimated, along with assumed relative economic values, indicated that greater genetic gain for fleece weight will be attained by including fleece weight, staple length and either quality number or fibre diameter, in a selection index, than would be attained by direct selection for fleece weight.

However, by using these selection indices, some genetic change towards coarser wool occurs. The index study (Appendix V (1))indicates that a "restricted index" which includes fleece weight, staple length and fibre diameter (restricted variate) will:

(a) attain slightly less genetic gain for fleece weight compared to an "unrestricted index" containing these traits;

(b) be of equal efficiency as the "unrestricted index"; and

(c) attain slightly more gentic gain for fleece weight than will direct selection for fleece weight .

A "restricted index" which includes fleece weight, staple length and quality number (restricted variate) will :-

(a) attain much less genetic gain for fleece weight compared to an "unrestricted index" containing these traits;

(b) be much lower in efficiency than the "unrestricted index"

(c) attain less genetic gain for fleece weight than direct selection for fleece weight.

Genetic Selection for Hogget Body Weight Weaning Weight.

The heritability estimates of hogget body weight are of medium value. This indicates that reasonable gains from selection can be expected if attention is placed on it.

Weaning weight was found to have a heritability in the medium to low level. However, the results indicate that a negative genetic correlation between direct and maternal effect on weaning weight may occur. If this is the case, it would not be possible to state in detail the consequences of selection.

Indirect selection for weaning weight based on hogget body weight is expected to cause a faster rate of genetic change in weaning weight than would direct selection (Ch'ang and Rae, 1972; Young et.al; (1965). This has been suggested because of the higher heritability of hogget body weight compared to weaning weight combined with the high estimates of the genetic correlation between the two traits.

However, the present estimates of the genetic correlation are lower than those reported by previous authors. If the daughter - dam regression analysis estimates (which contain some bias due to maternal effects) is more correct, indirect selection will be relatively more efficient than direct selection.

If the paternal half-sib estimates is near the true value, the indirect means is very much less effecient in terms of genetic gain.

The genetic correlations between hogget body weight and the wool traits, fleece weight, staple length and fibre diameter are of negligible size. The estimates show that there are differences between phenotypic and genetic correlations for these associations. Generally, the genetic correlations are lower than those previously reported (see Table 7 and Table 8).

Direct selection for hogget body weight is not expected to cause important changes in wool production. The results indicate that there would be no antagonism to improving fleece weight and hogget body weight simultaneously.

Selection Index

In sheep breeding, the problem is to decide which combination of traits gives the greatest improvement in profitability, while keeping the cost of carrying out the selection within certain economic limits. One aspect of this is consideration of the type of selection scheme to employ.

It has previously been mentioned that genetic parameters are required to guide a breeder in the choice of breeding methods. The relative efficiency of using independent culling, tandem selection,* importance have been compared by Young (1961). He concluded that the index was superior to the other methods, its superiority increasing with the number of traits under selection. The index was never less efficient than independent culling but in some cases it was no more so. This depended on the relative importance of the traits in the index and the various associations between the traits.

In practice it is common to include only the most important economic traits in the selection index.

* or a selection index when traits are correlated and of varying

Fertility and fleece weight must be among them. However, in some instances it may be worth including a trait of negligable economic value that is correlated to important characteristics. (Gjedrem 1967 a, 1967b.)

Selection indices usually do not include other wool traits apart from fleece weight. This has partly, arisen because of the cost of measuring these additional traits on large numbers of animals. Also it has been due in part to a lack of both relative economic weights to apply, and good estimates of genetic correlations between the traits. Using the genetic parameters calculated in this study and some assumptions on fertility parameters, based on results from other breeds, possible selection indices have been calculated (Appendix V.(2)). By including hogget body weight, the efficiency of a selection index comprising number of lambs weaned and fleece weight, was increased by nearly 11% when:— the assumed genetic correlation between hogget body weight and number of lambs used was 0.4; the assumed relative economic values of hogget body weight was 0.0; and relative economic values weighted according to lamb values being high relative to wool values. With these values, little would be gained by the addition of staple length, quality number or fibre diameter to the index.

However, when:- the genetic correlation between hogget body weight and number of lambs weaned was reduced to 0.2; the relative economic value for hogget body weight given a negative value of - 2.0 cents; the relative economic values weighted so that lamb values were lessened relative to wool value; plus the fleece weight components staple length and fibre diameter given more importance;— then the efficiency of a selection index comprising number of lambs weaned and fleece weight would be little increased on adding hogget body weight, and staple length. However, the study indicated that the addition of fibre diameter would improve the index, especially if it were constructed with a restriction so that no genetic change would occur for fibre diameter.

Final conclusions as to what selection index will be the most efficient, awaits accurate estimation of the genetic correlations between fertility and hogget body weight, and fertility and the wool traits, along with the clarification of the correct relative economic values to be used.

Improvement of Ram Breeding Flocks.

Where the aim is to improve future generations of sheep, the most desirable method of selection for 18 -month-old rams and ewes, will include consideration of a selection index involving number of lambs weaned based on the dams record, the hoggets own fleece weight record and possible hogget body weight after correcting for rearing rank and rearing by a two-year-old dam. The index will give a ranking based on these traits with the object of providing information on which to base selection.

Final selection may be influenced by other wool traits such as fibre fineness, colour, staple length and handle, and also criteria involved in current flock improvement (especially those associated with fertility e.g. hogget oestrus activity).

Fleece weight has a relative economic value which is much greater than either fibre diameter or quality number. In practice the above policy may imply that some small decrease in fibre fineness may be justifiable in order to gain greater efficiency in selection for the more remunerative traits.

It may be desirable to use an independent culling level to maintain fibre fineness and so limit increases in fibre diameter or decreases in quality number. Because of its simplicity and relatively low cost, an independent culling level for fibre fineness based on quality number appraisal is likely to be used for the selection of females, and in the less important studs, the rams as well.

The accuracy of quality number appraisal as an indicator of fibre fineness is questionable. Agar and Thompson (1974) reported that with sale lots of halfbred, merino and crossbred wools, quality number classing within clips clearly showed that a registered classer was able to divide a single farmer's clip into lots with an average differnce in mean fibre diameter of 1.3 microns. Mean fibre diameter of the wool ranged from 20 to 38 microns. This indicates that reasonable accuracy could be attained in keeping fibre fineness from changing.

This thesis presents information though, which suggests that if fibre fineness is an objective of selection, then for accurate evaluation, measured fibre fineness is essential. Also, if selection for fibre diameter is done indirectly by selecting on quality number performance, the relative efficiency in terms of genetic gain is only 22 to 32%. Further, the inclusion of fibre diameter in a selection index will improve the efficiency of an index to a greater extent than will quality number. Also, the cost in terms of total genetic gain of providing a restriction to change in wool fineness is much less when fibre diameter is the trait under attention.

Consequently, in ram breeding flocks, particularly nucleus flocks associated with large scale breeding programmes (Hight and Rae, 1970) measured fibre diameter performance of ram hoggets should be used as supporting information on which to base selection.

Current Flock Improvement

Among the traits studied, fleece weight and hogget body weight are the two of most importance on which culling should be directed where the aim is for improvement in lifetime ewe performance. The difference in the relative importance of these traits will depend on the ratio of wool to lamb values attained from a particular flock.

The two most important ewe traits (number of lambs weaned and fleece weight) appear in Table 21 to show the relative importance of the relationship of the hogget traits to the lifetime ewe performance for these two traits.

TABLE 21

CORRELATION COEFFICIENTS FOR HOGGET TRAITS WITH LIFETIME EWE PERFORMANCE.

Hogget trait	Lifetime Ewe Performance	
	No. lambs weaned	Fleece wt.
Body wt.	0.07	0.12
Fl. wt.	-0.01	0.56
St. L	0.03	0.23
Qu. No.	-0.01	-0.14
F.D.	0.04	0.11
Char.	0.02	0.15

Important points are :-

(1) the correlation coefficient between hogget fleece weight and lifetime ewe fleece weight (0.56) when compared to the range of repeatability estimates (0.5 to 0.8) is at the low end of the range;

(2) only a low correlation exists between hogget body weight and lifetime ewe performance for number of lambs weaned;

(3) the results indicate that where an attempt is made to improve the lifetime ewe performance for number of lambs weaned by basing culling on any of the hogget traits included in the study, negligible improvement can be expected; and

(4) culling hoggets on fleece weight is expected to result in an improvement of lifetime ewe performance for fleece weight and a negligible change in number of lambs weaned.

These points may reflect characteristics of hill country sheep production not present in data from sheep producing on better class land.

In this thesis, relationships were not recorded between hogget traits and successive ages of ewes. However, it can be expected that they decrease with age (Purser and Roberts, 1959). Classical methods of estimating repeatability by intra-class correlation assume linearity. Though subsequent performance is positively related to early performance the relationship may not be linear and so repeatability estimates will only be approximate.

Carryover effects from a previous seasons production may effect a current seasons production.

Shelton and Menzies (1970) report on results from ewes in a poor environment. They suggested that apparently the process of successful reproduction, such as raising one or more offspring, can have an adverse effect on the dam resulting in a lowering of repeatability, especially in the case where some element of nutritional stress is involved.

The results of Hight and Jury (1973) indicated the need in hill country flocks to offset the effect of the previous years lambing on the more fertile ewes by substantially increasing their weight from weaning lambs until the next mating.

Coop and Hayman (1962) considered it would be unusual if complex relationships did not exist between size of animal and production such as fertility, milk and wool production.

Further, the known limits to achievement of potential under hill country conditions are largely nutritional and are inherent in the low quality and cyclical nature of utilizable food supply. Annual interactions apply not only within the annual animal cycle but also over an animal's lifetime (Gunn, 1975).

These points highlight the requirements of a knowledge of genetical, physiological and environmental factors influencing production and consequently management factors influencing lifetime production.

The low correlation between hogget body weight and the lifetime ewe performance for number of lambs weaned, questions the using of hogget body weight as a criteria for culling. The regression study shows that if culling low liveweight animals results in an increase (independent of change in other traits) to the mean ewe hogget body weights by one kg, only about an additional 10 to 20 cents/ewe is gained over her lifetime.

This is in agreement with Purser and Roberts (1959) who considered culling on the basis of hogget weight at six months of age in a Scottish Blackface flock. They showed that increasing culling levels from 25 to 33%, increased the mean hogget body weight by 1 lb, but the nett effect on flock production was very small. It was considered that the practice was only justified from accumulated genetic gains over several generations.

Several hogget wintering studies have shown that residual greater liveweight and therefore body condition at 18 months in better wintered groups resulted in a higher incidence of multiple births in the first productive year. But over five years, as a whole, there was virtually no difference (Gunn, 1968; Bradford et. al. 1961; Purser and Roberts, 1961). Gunn(1968) concluded that feeding sheep at a high level during their first winter to face hard hill country conditions, was quite unprofitable in terms of their subsequent performance as breeding ewes. Everything pointed to the low level of nutrition in spring, summer and autumn as being the greatest drawback to improved performance.

Ch'ang and Rae (1972) using Romney data looked at the phenotypic relationships between, weaning weight, March liveweight, June liveweight, hogget liveweight

(14 months), number of hogget oestruses, the various liveweight gains between weaning and hogget measurement, and the ewes fertility (number of lambs born) over three lambings. The data had been adjusted for environmental differences. The phenotypic correlation estimate at 0.23 for the hogget liveweight showed that the absolute predictive value of potential fertility of the ewe was low at this age. All correlations between liveweight characters and measurements of fertility used, exhibited an age trend. The values tended to rise with increasing age of the individual from weaning to the hogget liveweight.

The above information leads to the suggestion, that with this Perendale data, there may exist considerable growth differences between individuals from hogget weighing until first mating. As a consequence of this, combined with the possibility of carryover effects from the previous years production, repeatability for the hogget liveweight with later pre-mating liveweights may not be high. Also, age corrections, rearing rank and age of dam correction factors have not been applied to the hogget records. It seems reasonable to suggest that these factors have contributed to the low correlation recorded between hogget body weight and number of lambs weaned by a ewe over her lifetime.

Thus, in commercial flocks, which do not have a sophisticated recording scheme, at the hogget age, culling should be directed against low fleece weight animals only. Other literature suggest that one or more overt oestruses at the hogget stage is associated with above-average lifetime lamb production (Hulet, Wiggans and Ercanbrack, 1969; Ch'ang and Rae, 1972). As this would only require temporary individual identification (sire-sign crayon), this is another hogget character that may be considered in a culling programme at the hogget age.

Fertility

The ram breeder cannot relax selection for fertility.

The review of literature indicated that it has a low heritability but worthwhile improvement can be made. Evidence suggests that a ewes lifetime fertility is positively genetically correlated with hogget body weight (Young et al., 1963; Shelton and Menzies, 1968; Ch'ang and Rae, 1972) and number of hogget oestruses (Ch'ang and Rae, 1972). Consequently, when it comes to selection decisions at the hogget age a combination of records of her dams fertility, hogget body weight and oestrus activity can be expected to produce improved fertility.

The small effects at normal culling levels on phenotypic liveweight performance does not necessarily predict the genetic effects from this type of culling (Hight and Jury, 1973). They suggest that at high culling rates the selection of the heaviest young ewes could assist in the formation of a flock with a high incidence of multiple births for recording in large-scale breeding schemes (Hight and Rae, 1970).

Twins v Singles

Finally, the acceptability of any plan for increased fertility will partly depend on the extent to which maternal handicap reduces the productive quality of sheep born in multiple births. The relative production and economic values of single and multiple born animals have been discussed by various authors including Turner (1961), Dun and Grewal (1963), Lax and Brown (1967), Purser (1969) and van Westhuysen (1973). The general conclusion is that twins are better producers.

Appendix IV indicates support for this conclusion. The difference in lifetime wool weight is negligible while twins weaned 3% more lambs over their lifetime. Consequently, it is considered that it would be undesirable to select in a way that would prejudice the retention of twins.

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APPENDICES

APPENDIX I: COMPUTATION OF $R(\mu, a_i, s_{ij}, c_k, d_l)$, $R(\mu, a_i, c_k, d_l)$ $C(\mu, a_i, s_{ij}, c_k, d_l)$ & $C(\mu, a_i, c_k, d_l)$

Using the model outlined in the thesis, a computer programme was written which carried out the computations as follows. As the data were read in, the matrices for the least-squares equations were accumulated. These comprised two components.

(1) the 'variance-covariance matrix' of coefficients. This was obtained by counting the number of times each parameter occurs in the subclass totals for each subclass in the model.

(2) the 'right hand members' (RHM) column vectors, one for each trait. The value in this RHM is the sum value for each trait over all the data belonging to the subclass.

Only those hogget records were used when observations for all 7 traits in the study were present. Consequently, the variance-covariance matrix was the same, and was used, for both variance and covariance component analysis.

Computation of $R(\mu, a_i, s_{ij}, c_k, d_l)$

The following steps were followed.

(a) Absorption.

Because the number of a_i (15) and s_{ij} (115) subclasses were large, an indirect approach had to be used to solve the least-quares equations; the key feature of which, when applied to the model under consideration is the sweeping out or absorption of the equations for the $\mu + a_i + s_{ij}$ The working model was partitioned as

$$Y = X\beta_1 + Z\beta_2 + e$$

Constants to be fitted were arbitrarily divided into two sets. The β_1 set included only those constants that could be conveniently absorbed, and the β_2 set of constants included all constants to be fitted other than those absorbed. The least-squares equations for this model can be represented in matrix notation as

$$\begin{bmatrix} D & N \\ N' & S \end{bmatrix} \begin{bmatrix} \hat{\beta}_1 \\ \hat{\beta}_2 \end{bmatrix} = \begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix}$$

where for the present example -

D is a diagonal matrix whose diagonal elements comprised the number of records for each sire-within-year subclass and was of the order t x t (i.e. 115 x 115);

N is a matrix of coefficients for $\hat{c}_k$ & $\hat{d}_\ell$ in the μ + a + b equations of the order t x (r + s) i.e. 115 x (4 + 2);

N' is the transpose of N :

Y_1 is the matrix of RHM's for the $\mu + a_i + s_{ij}$ equations of the order t (i.e. 115 x 1 vectors); and

Y_2 is the matrix of RHM's for the other equations i.e. $\hat{c}_k$ and $\hat{d}_\ell$ subclass value totals, of the order r + (i.e. 6 x 1 vectors).

The absorption process follows from the following matrix operations.

(i) Calculation of "new coefficients" - a 6 x 6 matrix

$$S - N' D^{-1} N$$

(ii) Calculations of "new RHM" a set of 6 x 1 vectors.

$$Y_2 - N' D^{-1} Y_1$$

(b) Imposing Restrictions.

Before a unique solution of the equations can be obtained, it is necessary to impose certain restrictions. The restrictions imposed were that $\sum_k \hat{c}_k = \sum_\ell \hat{d}_\ell = 0$ where the $\wedge$ denotes "the estimate of". For this restriction to be imposed, the coefficient of one equation in the

c_k and one equation in the d_ℓ had to be subtracted from other coefficients by columns and rows of the variance-covariance matrix. The last coefficients, $\hat{c}_4$ and $\hat{d}_2$ were subtracted by column and row, only within the c_k and d_ℓ coefficients, respectively. The last member for c_k and d_ℓ classes for the RHM's was then subtracted from the other c_k and d_ℓ members, respectively.

(c) Estimation of Constants.

The method of solving the simultaneous equations was as follows. The estimates of constants included in the set were obtained from

$$\underset{[4\times 4]}{\hat{\beta}_2} = \underset{[4\times 4]}{\left[S - N'D^{-1}N\right]^{-1}} \underset{[4\times 1]}{\left[Y_2 - N'D^{-1} - Y_1\right]}$$

Because $\sum_k \hat{c}_k = \sum_\ell \hat{d}_\ell = 0$, the remaining constants were computed from

$$\hat{c}_4 = -(\hat{c}_1 + \hat{c}_2 + \hat{c}_3)$$

and

$$\hat{d}_2 = -\hat{d}_1$$

Estimates of the constants included in the β_1 set were then computed from

$$\underset{[115\times 1]}{\hat{\beta}_1} = \underset{[115\times 1]}{D^{-1}(Y_1 - N\hat{\beta}_2)}$$

The $\hat{\beta}_1$ consists of least-squares subclass means. In order to obtain separation of the constants, the restriction $\sum \hat{a}_i = \sum \hat{s}_{ij} = 0$ was imposed, and the averages of the $\hat{\mu} + \hat{a}_i + \hat{s}_{ij}$ were computed

from
$$\hat{\mu} + \hat{a}_i = \sum_j \frac{(\hat{\mu} + \hat{a}_i + \hat{s}_{ij})}{q_i}$$

$$\hat{\mu} = \sum_i \sum_j \frac{(\hat{\mu} + \hat{a}_i + \hat{s}_{ij})}{\sum q_i}$$

Then

$$\hat{a}_i = \hat{\mu} + \hat{a}_i - \hat{\mu} \quad \text{and}$$

$$\hat{s}_{ij} = \hat{\mu} + \hat{a}_i + \hat{s}_{ij} - \hat{\mu} + \hat{a}_i \, .$$

(d) Calculation of Reduction in Sums of Squares.

The R $(\mu, a_i, s_{ij}, c_k, d_l)$ was calculated by the summation of the constant estimates multiplied by the original RHM values.

$$\left[\hat{\mu}, \hat{a}_i \ldots \hat{a}_p, \hat{s}_{ij} \ldots \hat{s}_{pq}, \hat{c}_k \ldots \hat{c}_r, \hat{d}_l \ldots \hat{d}_s\right] \times \overset{RHM.}{\begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix}} = R(\mu, a_i, s_{ij}, c_k, d_l)$$

$$\text{i.e.} \quad \hat{\beta}' \times Y = R(\mu, a_i, s_{ij}, c_k, d_l)$$

Computation of R(μ, a_i, c_k, d_l)

The steps of absorption, restriction and estimation of constants were used again, similar to that used in the computation of R $(\mu, a_i, s_{ij}, c_k, d_l)$ except that now the model had been reduced by the exclusion of the sire-within-year effects. Consequently, after carrying out these steps, the final matrix multiplication gives R (μ, a_i, c_k, d_l) - the reduction in sums of squares-

$$\left[\mu, \hat{a}_i \ldots a_p, \hat{c}_k \ldots \hat{c}_r, \hat{d}_l \ldots d_s\right] \times \overset{R.H.M}{\begin{bmatrix} \\ \\ \end{bmatrix}} = R(\mu, a_i, c_k, d_l)$$

Computation of $c(\mu, a_i, s_{ij}, c_k, d_l)$ and $c(\mu, a_i, c_k, d_l)$

These were computed by the transposed vector of constant estimates for one trait being multiplied by the RHM vector for another trait with each model, respectively.

APPENDIX II: CALCULATION OF THE COEFFICIENT, K.

The indirect method was used in computing K for the sire-within-year component.

$$K = \frac{n_{\cdots\cdot\cdot} - \sum_i \sum_j R^{ij} N_{ij}}{\text{Degrees of Freedom S}}$$

where,

n.....is the total number of records used ;

Degrees of Freedom S is equal to t - p = 115 - 15 = 100.

$\sum_i \sum_j R^{ij} N_{ij}$ is computed from the sum of the diagonals in the matrix resulting from the multiplication $N' R^{-1} N$ where,

N is the segment of the original complete set of least-squares equations which contained the coefficients associating the effects under consideration with all others in the model; and

R^{-1} is the inverse of the variance-covariance matric where all effects except the set for which the variance component coefficient is to be computed (i.e. the s_{ij}'s) are excluded from the model. i.e. the inversed variance-covariance matrix derived in the process of computation of $R(\mu, a_i, c_k, d_\ell)$. If the matrix inverse of the variance-covariance matrix under the reduced model is partitioned as follows -

$$\begin{bmatrix} D & N \\ N' & S \end{bmatrix}^{-1} = \begin{bmatrix} A & G \\ G' & C \end{bmatrix}$$

then C is the inversed restricted matrix after the absorption process for the reduced model. This matrix had to be first built up from a 4 x 4 to a 6 x 6 by setting $\sum_k C_k = \sum_\ell d_\ell = 0$, (the original restriction imposed).

Then

$$G = -D^{-1} N C \quad \text{and}$$

$$A = D^{-1}(I - NG')$$ where I is an identity matrix.

APPENDIX III: CODED WOOL QUALITY NUMBERS

The coded wool quality numbers and their corresponding quality number as well as the average micron value and range, that were used throughout the analysis of the data, appear in the following Table.

TABLE III (1)
CODED WOOL QUALITY NUMBERS
AND
MICRON VALUES

Code	Quality Number	Fibre Diameter (microns) Average	Range
44	44's	38.3	37.8 - 38.8
45	44/46's	37.2	36.7 - 37.7
46	46's	36.2	35.8 - 36.6
47	46/48's	35.3	34.9 - 35.7
48	48's	34.4	34.0 - 34.8
49	48/50's	33.5	33.1 - 33.9
50	50's	32.6	32.3 - 33.0
51	50/52's	31.7	31.3 - 32.1
52	52's	30.8	30.5 - 31.2
53	52/54's	30.1	29.8 - 30.4
54	54's	29.4	29.1 - 29.7
55	54/56's	28.7	28.4 - 29.0
56	56's	28.0	27.7 - 28.3
57	56/58's	27.3	27.0 - 27.6
58	58's	26.6	26.3 - 26.9

APPENDIX IV: PERFORMANCE OF TWINS v SINGLES

Data from the correlation study involving the relationship between hogget and lifetime ewe performance does allow some points to be noted on the comparison of twins and singles.

Mean values of hogget and lifetime ewe records for singles and twins are presented in Table IV (1).

TABLE IV (1)

MEAN VALUES FOR RECORDS FROM TWINS AND SINGLES

Trait	Mean Values				
	Singles	± S.E.	Twins	± S.E.	Differences
Hogget traits					
Body Wt. (kg)	37.89	0.62	36.30	0.80	1.59
Fl. wt. (kg)	2.53	0.05	2.38	0.07	0.15
Qu. No.	52.94	0.12	52.91	0.15	0.03
F.D.	30.75	0.13	30.28	0.16	0.47
St. L.	11.81	0.10	12.03	0.13	0.22
Char.	5.52	0.08	5.16	0.11	0.36
Ewe traits					
Fl. wt. (kg)	3.56		3.47		0.09
Qu. No.	50.90		50.86		0.04
F.D.	34.93		34.96		0.03
St. L.	13.96		14.10		0.14
Char.	5.52		4.88		0.64
No. lambs weaned	1.10		1.13		0.03

For the hogget traits, it can be seen that rearing rank differences occur. Twins are lighter in both body weight and fleece weight. Also they have finer wool, longer staple length and a lower wool character grade.

These rearing rank differences are in agreement to the earlier reported rearing rank effects calculated in estimates of environmental effects (Table 11).

A small difference is evident in the mean lifetime ewe performance values for fleece weight, staple length and character. Standard deviations were not available for the lifetime ewe performance. Consequently standard errors could not be computed. It is expected that only character would be significantly different.

Dun and Grewal (1963) wrote that generally twin-born ewes show a reduced productivity at maturity of the order of two to eight percent of clean fleece weight, principally due to a reduction in the total number of wool fibres possessed by the animal. They point out that the magnitude of this production deficit is largely governed by season and environment to the extent that these affect the pre-natal and post-natal nutrition of the lamb. Consequently, the twin and single born mean lifetime ewe fleece weights for each year-of-birth group are presented in Fig. IV (1).

Fig. IV (1)
Life-time Ewe Fleece Weight.

It can be seen from Fig. IV (1) that values are very similar except for 1959, 1961 and 1964. The similarity in production over most years would support Turner's postulation that if the young ewe were well grown the effect of maternal handicap might be eliminated, (Turner, 1961). Evidence of compensatory growth in fibre volume has been observed in several experiments where density has been reduced by nutritional stress (Henderson, 1953; Short, 1955).

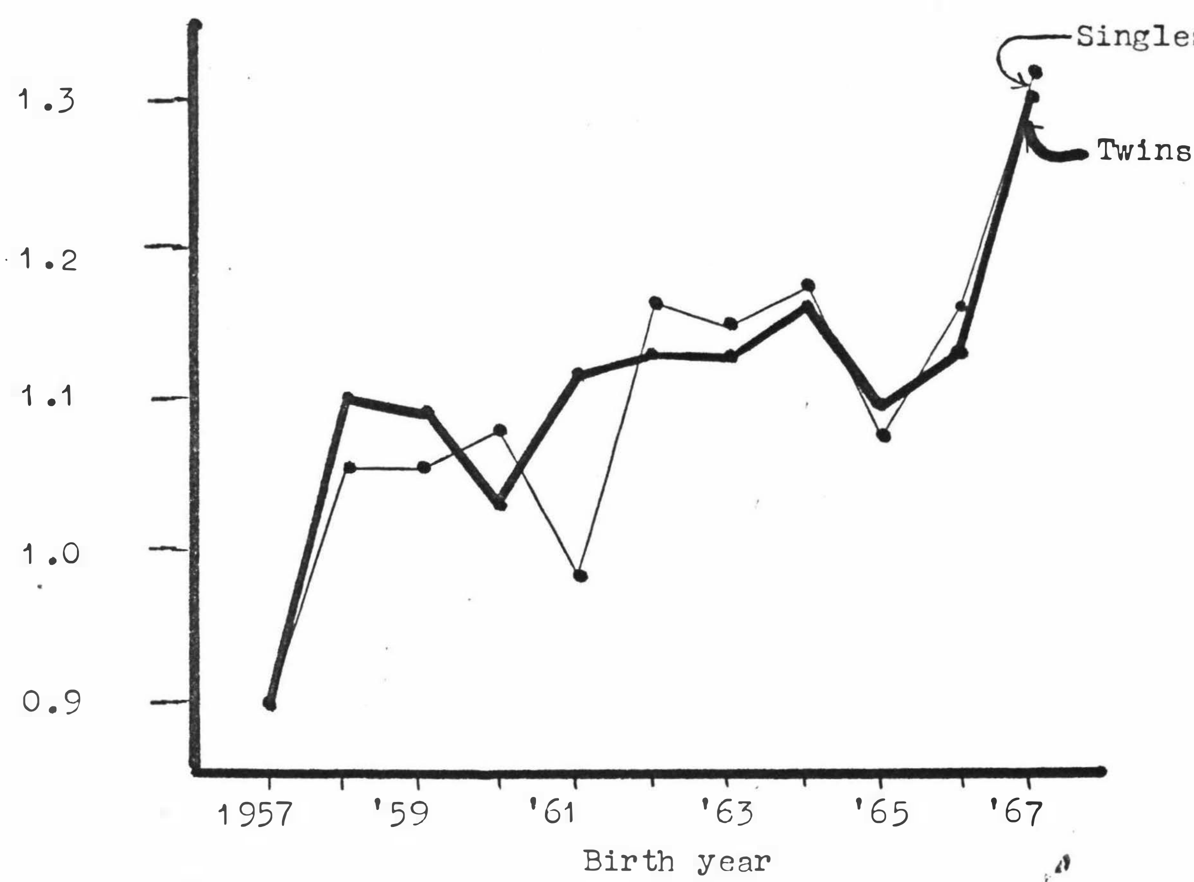
No information on components of fleece weight is available from the data to explain the differences. When discussing fleece weight recovery from handicap situations, Dun and Grewal (1963) suppose discrepancy between results from field and laboratory can be explained on the basis of differential alteration of density and surface area. This situation may exist here to explain the rearing rank differences in 1961 and 1964. Wool production has been reduced permanently by a nutritionally induced reduction in follicle density (Schinckel and Short, 1961). Turner's (1961) results suggest that reduced density could become increasingly important in less favoured sheep country where larger productive difference between twins and singles can be expected.

However the results of Sumner and Wickham (1970) led them to conclude that a situation in which permanent changes in the follicle population could be induced, would be extremely rare for Romney sheep under New Zealand grazing conditions.

It may be supposed that the ewes born as twins in 1961 and 1964 either did not show sufficient compensatory growth in fibre volume to compensate for any permanent reduction in follicle density or that in these years they did not recover from their rearing rank handicap of reduced wool producing surface area.

Mean lifetime values (Table IV (1)) show that twin ewes weaned 3% more lambs over their lifetime. The differences between singles and twins for ewes from each year of birth appear in Fig. IV (2). In most years differences were negligible. It may be seen that in some year-of-birth groupings, singles weaned slightly more lambs over their lifetime than did twins. In only four cases (1958, 1959 1961 and 1965 birth years) did twins wean more lambs than singles. The largest difference (12%), an advantage for the twins, occurred in 1961.

Fig. V (2)
Life-time Ewe Lambing Performance
(Lambs weaned)



It must be appreciated that the statistical significance of the results shown in Fig. IV (1) and Fig. IV (2) could not be calculated from the information computed.

Some differences were also evident in the correlation coefficients for the relationships between hogget and lifetime ewe performance. Some of interest are :-

Hogget trait	- Ewe trait	Correlation Coefficients		
		Overall	Singles	Twins
Body weight	No. lambs weaned	0.07	0,06	0.11
Fleece weight	No. lambs weaned	-0.01	0.04	-0.03
Body weight	Fleece weight	0.12	0.16	-0.06
Fleece weight	Fleece weight	0.56	0.62	0.41
Fibre diameter	Fleece weight	0.11	0.15	-0.02
Body weight	Fibre diameter	0.02	0.16	-0.16
Fleece weight	Fibre diameter	0.25	0.37	-0.03

APPENDIX V: SELECTION INDEX STUDY

(1) A study of genetic progress from a selection index involving fleece weight, staple length and quality number with one involving fleece weight, staple length and fibre diameter and their comparison with direct gain from mass selection for fleece weight only.

In consideration of programmes designed for sheep improvement, fleece weight is one trait to which attention is usually directed. With Perendales, it is regarded that an increase in fleece weight while maintaining or improving wool fineness is desirable. The genetic parameters that have been calculated suggest that with fleece weight improvement, continued correlated changes in quality number and fibre diameter may be detrimental to the whole product.

In this study, interest lies in the relative efficiency of selection for fleece weight using an index with either, (1) fleece weight, staple length and quality number or (2) fleece weight, staple length and fibre diameter in it, with and without restrictions* on quality number and fibre diameter for (1) and (2) respectively, compared to mass selection for fleece weight.

The following two indices with the parameters as listed below, were computed using a computer programme following Cunningham (1969).

* A selection index may be restricted by requiring that the genetic changes it produces in one or more traits equal zero or some predetermined value, or are of specified sign (Cunningham, Moen and Gjedrem, 1970). In this selection index study, an "index with restriction" will be one where 100% restriction on the trait concerned has been applied. It implies zero change (i.e. no genetic gain) in the trait on which the restriction has been placed.

Selection Index one

Fleece weight, staple length, quality number.

Trait	R.E.V.	Phen. S.D.	h^2	Correlations Phenotypic		Correlations Genetic
1. Fleece wt (kg)	100.0	0.89	0.32	(1)x(2)	0.44	0.76
2. Staple length (cm)	3.0	1.54	0.49	(1)x(3)	-0.16	-0.48
3. Quality No.	5.0	1.95	0.26	(2)x(3)	-0.45	-0.63

Selection Index two

Fleece weight, staple,length, fibre diameter.

Trait	R.E.V.	Phen. S.D.	h^2	Correlations Phenotypic		Correlations Genetic
1. Fleece wt (kg)	100.0	0.89	0.32	(1)x(2)	0.44	0.76
2. Staple length (cm)	5.0	1.54	0.49	(1)x(3)	0.50	0.43
3. Fibre diameter (u)	-10.0	2.30	0.54	(2)x(3)	0.34	0.53

This was followed by the construction of restricted indices which kept respectively, quality number or fibre diameter unchanged for selection index one and two.

The results are shown in Table V(1).

TABLE V (1).

Results for the four selection indices under study.

Variate	Unrestricted Index			Restricted Index		
	β Value	Value of Variate	% of Gain	β Value	Value of Variate	% of Gain
Selection index one:						
Fl. wt.	23.3	17.7	99.7	18.01	22.78	95.04
St. Lt.	11.7	10.6	6.5	6.11	6.24	4.96
Qu. No.	0.3	0.0	-6.2	8.55	43.06	0.00
Dummy: Qu. No.				-40.8	-42.03	
Selection index two:						
Fl. Wt.	28.7	23.9	95.5	30.10	59.54	91.35
St. Lt.	11.4	12.5	9.5	10.67	11.78	8.64
F.D.	-5.7	6.3	-5.0	-7.46	63.47	0.00
Dummy: F.D.				3.04	-0.76	

where:

β value is the weighting factor for the index.

Value of variate is the contribution which each variate makes to genetic gain, or percent reduction of overall genetic gain if that variate is omitted.

% of gain is the percentage of total economic gain accounted for by the gain in each trait.

Dummy: indicates the trait on which the restriction has been placed. To impose the restriction that the index shall produce no change in Y_i (the additive genotype of the trait concerned) the index equations are solved subject to

$$Cov(Y_i, I) = 0$$

Part of the procedure to augment the basic unrestricted equations is to add a dummy variable to the index (Cunningham et.al. (1970).

The results indicate that fleece weight has considerable greater relative importance in terms of the percentage of total economic gain and for the value that each variate makes to genetic gain.

Staple length makes a valuable contribution to genetic gain, though the total economic gain that it accounts for is small.

It is of interest that with selection index one (unrestricted) the value of the variate quality number was 0.01. This indicates that it makes a negligible contribution towards genetic gain for the aggregate genotype.

In both cases a negative value of variate exists for the Dummy variate. This indicates the percentage increase in genetic gain in aggregate genotype if that particular restriction is lifted. In effect it indicates the genetic cost of the restriction. Consequently, by removing the restriction on quality number in the index containing fleece weight, staple length and quality number, the expected genetic gain will increase by about 42%. In contrast, the effect of removing the restriction on fibre diameter, or conversely, the genetic cost of including the restriction, is negligible.

For selection index one, the correlation of the index (I) with the aggregate genotype (H) i.e. r_{HI}, was equal to 0.65 (unrestricted index) and 0.45 (restricted index). For selection index two, r_{HI} was equal to 0.65 for both the unrestricted and restricted index.

The efficiency of indices is represented by r_{HI}^2,

$0.65^2 = 0.42$ and $0.45^2 = 0.20$

Therefore, the selection index which includes fleece weight, staple length, with a restriction on quality number is less efficient than the other three indices.

The genetic gain (ΔG) from mass selection for fleece weight, is represented by

$$\Delta G = \sigma h^2 i$$

where:

σ = phenotypic variance = 0.89

h^2 = heritability of fleece weight = 0.32

i = standardized selection differential = 1.0

Therefore

$$\Delta G = 0.28$$

The genetic gain for fleece weight (trait i) in an index is represented by

$$\Delta H_i = \beta_{H_i I} \sigma_I$$

where:

$\beta_{H_i I}$ = regression of fleece weight on index

σ_I = standard deviation of index

Values for ΔH_i are :-

<u>Selection index one</u>	Unrestricted index	Restricted index
ΔH_i	0.33	0.21
<u>Selection index two</u>		
ΔH_i	0.31	0.29

These results indicate that the genetic gain/year for fleece weight will be increased, when compared with mass selection, by including staple length and either quality number (without restriction) or fibre diameter (with or without restriction) in an index with fleece weight.

(2) <u>A study comparing a selection index with its series of reduced indexes</u>.

It is desirable to know the relative contribution of each trait to genetic progress for the defined aggregate genotype. The cost of including that trait can then be measured against its effectiveness in the index.

The relative economic values of traits give some indication of the relative importance of including a trait in a selection programme. However, the combined effect of genetic and phenotypic parameters is relatively complicated. It is only by constructing a selection index that the relative efficiency of either including or excluding a trait (s) can be determined.

A. At first a selection index was constructed including all available traits. Then the extent to which the unimportant traits gave additional information of the genetic variance of the more important traits was investigated.

The traits included were number of lambs weaned, fleece weight, hogget body weight, staple length, quality number and fibre diameter. Parameters used were those estimated in the thesis plus some assumed values as shown in Table V (2).

TABLE V (2)

Parameters used in construction of the main index.
(Study 2 A)

Trait	R.E.V.	h^2	Phen. S.D.	Correlations	Phenotypic	Genetic
1. No. lambs weaned *	800.0	0.12+	0.60	1 x 2	0.04	0.00+
2. Fleece wt.	100.0	0.32	0.89	1 x 3	0.08	0.40+
3. Hogget body wt.	0.0	0.27	8.73	1 x 4	0.00	0.00+
4. Staple length	3.0	0.49	1.54	1 x 5	0.02	0.00+
5. Quality No.	5.0	0.26	1.95	1 x 6	0.02	0.00+
6. Fibre diameter	-10.0	0.54	2.30	2 x 3	0.39	-0.07
				2 x 4	0.44	0.76
				2 x 5	-0.16	-0.48
				2 x 6	0.50	0.43
				3 x 4	0.13	-0.06
				3 x 5	-0.03	0.37
				3 x 6	0.15	-0.02
				4 x 5	-0.45	-0.63
				4 x 6	0.34	0.53
				5 x 6	-0.26	-0.46

+ Assumed values.

* The index was constructed under the assumption that No. lambs weaned is the mean of three mating seasons of the dam, with repeatability 0.3.

The results for the main index are shown in Table V(3).

TABLE V (3)

Results for the main index

Variate	β Value	Value of Variate	β Hi I Regression	% of Gain
1. No. lambs weaned	87.03	27.98	0.0010	80.24
2. Fleece wt.	15.56	1.85	0.0018	18.35
3. Hogget body wt.	3.03	10.29	0.0245	0.00
4. Staple length	9.97	2.59	0.0039	1.17
5. Quality No.	-0.18	0.00	-0.0004	-0.20
6. Fibre diameter	-5.71	2.06	-0.0004	0.44
S.D. of index *	54.89			
S.D. of aggregate genotype 172.56				

* This is the value in economic units of the genetic gain in aggregate genotype achieved by one standard deviation of selection on the index.

To get an indication of the value of each trait, a series of reduced indices were produced, dropping out each time the last trait listed in Table V(3). The efficiency of the reduced index relative to the original index is the ratio of the standard deviations of the two indexes (Cunningham, 1969).

The standard deviations and relative efficiencies were -

Index	Traits	S.D.	Relative Efficiency
Main index	(1,2,3,4,5 and 6)	54.89	100%
Reduced index	(1,2,3,4 and 5)	53.76	97.9%
" "	(1,2,3 and 4)	53.74	97.9%
" "	(1,2 and 3)	52.34	95.4%
" "	(1 and 2)	46.38	84.5%

These results show that although hogget body weight has in this case no economic value, its inclusion in an index comprising number of lambs weaned and fleece weight will increase the efficiency of the index by nearly 11%. This is because of the medium heritability of hogget body weight, and the generally positive associations with number of lambs weaned and fleece weight.

The addition of staple length to an index comprising number of lambs weaned, fleece weight and hogget body weight further increases the efficiency of the index by about 3%. With an index containing these four traits (number of lambs weaned, fleece weight, hogget body weight and staple length) the addition of quality number does not increase the efficiency, while the addition of fibre diameter to this index plus quality number, will cause a further 2% increase.

The cost of including a trait in the main index of this study can be measured against its effectiveness in the index. The relative cost of recording the traits must be in proportion to the above percentages before it is worth retaining the variates in the index.

If the assumed relative economic values and genetic parameters are close to the actual values, then these results indicate that the most favourable selection index would include number of lambs weaned, fleece weight and hogget body weight.

B. The investigation was then repeated with some changes.

The relative economic values were changed to give more importance to the wool traits. The staple length and fibre diameter R.E.V's were doubled; and the R.E.V. for number of lambs weaned was reduced to 600. In addition a negative R.E.V. was placed on hogget body weight, and the assumed genetic correlation between hogget body weight and number of lambs weaned was reduced to 0.2

The values used are shown in Table V(4)

TABLE V (4)

Parameters used in construction of the main index

(Study 2b)

Trait	R.E.V.	h^2	Phen. S.D.	Correlations	Phenotypic	Genetic
1. No. lambs weaned*	600.0	0.12+	0.60	1 x 2	0.04	0.00+
2. Fleece wt.	100.0	0.32	0.89	1 x 3	0.08	0.20+
3. Hogget Body wt.	-2.0	0.27	8.73	1 x 4	0.00	0.00+
4. Staple length	6.0	0.49	1.54	1 x 5	0.02	0.00+
5. Fibre diameter	-20.0	0.54	2.30	2 x 3	0.39	-0.07
				2 x 4	0.44	0.76
				2 x 5	0.50	0.43
				3 x 4	0.13	-0.06
				3 x 5	0.15	-0.02
				4 x 5	0.34	0.53

\+ Assumed values.

* The index was constructed under the assumption that No. lambs weaned is the mean of three mating seasons of the dam with repeatability 0.3

A similar study to that of 2(a) was carried out. This was followed by constructing a restricted index, which included the same values as above with the restriction placed so that no genetic change could be made for fibre diameter.

The results for both selection indices are summarized in Table V (5).

TABLE V (5)

Results for the main and restricted indices

(Study 2b)

Variate	Unrestricted Index				Restricted Index			
	β Value	Value of Variate	$\beta_{Hi.I}$ Regr.	% of Gain	β Value	Value of Variate	$\beta_{Hi.I}$ Regr.	% of Gain
N.L.W.	66.77	24.07	0.0007	39.9	66.82	25.04	0.0007	40.77
F.W.	35.96	15.99	0.0044	44.1	33.50	14.89	0.0052	52.02
H.B.W.	-0.52	0.44	-0.0056	1.1	-0.61	0.62	-0.0069	1.39
S.L.	9.55	4.30	0.0074	4.4	10.95	6.26	0.0097	5.82
F.D.	-11.56	13.73	-0.0052	10.5	-8.03	28.67	-0.0000	0.00
Dummy:								
F.D.					-6.17	-1.65		

The standard deviations and the relative efficiencies of the main index and reduced indices (unrestricted index only) were :-

Index	Traits	S.D.	Relative efficiency
Main index	(1,2,3,4 and 5)	44.95	100.0%
Reduced index	(1,2,3 and 4)	38.78	86.3%
" "	(1,2 and 3)	37.54	83.5%
" "	(1 and 2)	37.38	83.2%

The results show that with these assumed values, the inclusion of hogget body weight to an index comprising number of lambs weaned and fleece weight has a negligible effect on increasing the efficiency of the index.

Also, the efficiency of an index containing the traits, number of lambs weaned, fleece weight, hogget body weight and staple length, would be increased by about 14% if fibre diameter is included. Of more importance, is that with a similar inclusion, but this time with a "restriction" to inhibit genetic change for fibre diameter, the efficiency of the index would be increased by about 29%.

Like in the previous study where a restriction was placed on genetic change in fibre diameter, there was a negligible difference in the efficiency of the two main indices ("restricted" and "unrestricted" indices containing number of lambs weaned, fleece weight, hogget body weight, staple length and fibre diameter).

If the assumed relative economic values and parameters used are close to the real values, then this information would indicate fibre diameter makes an important contribution and may warrent it being recorded.

The study highlights the need for accurate relative economic values and genetic parameters of traits involved in a selection index.