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**THE GENETIC BASIS OF GROWTH,
OESTROUS BEHAVIOUR AND FERTILITY IN
ROMNEY MARSH EWES**

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fulfilment of the requirements for the degree
of Doctor of Philosophy in Animal Science
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I. INTRODUCTION

The rate of reproduction or fertility of the ewe in a breeding flock determines not only the number of surplus animals available for sale as a source of income but in addition, affects the scope of selection for improvement in all productive characters. The ewe's fertility therefore is a character whose economic significance is more nearly matched by its biological ramifications than other attributes of the sheep. The extensive usage of the Romney Marsh breed in New Zealand both in breeding flocks and as the basic ewe breed for meat production only adds importance to the need for higher fertility among the ewes of this breed.

Although it is known that under New Zealand conditions, Romney ewes can be mated as hoggets (between four and 14 months in age) for lamb production (Apps 1953; Lewis 1959), the common practice is to delay first mating until they are on average about 18 months old. This system of flock management has a two-fold effect on improvement of fertility by mass selection. First, selection for fertility can not take place until after the first lambing and second, being a corollary of the first, the annual rate of genetic gain in fertility is reduced by the increase in generation interval. Therefore, so long as the current system of flock management remains in practice, there is an obvious need to investigate hogget characters which may be used as criteria of potential fertility at the time of selection for replacements when the ewes are less than 18 months old.

The purpose of this study was to investigate some problems involved in using certain measurements of growth in live weight

and oestrous behaviour made during the hogget period as criteria of selection for higher fertility in the Romney ewe. Thus, the work was primarily concerned with estimating the amount of phenotypic and genetic variation and covariation in the characters under investigation. As an outline of the scope of the thesis, three major topics may be mentioned.

1. Estimation of environmental effects on each character so that appropriate adjustment of the data for differences in known environmental factors can be made prior to genetic studies.
2. Estimation of heritability, genetic and phenotypic correlations to provide a statistical summary of the genetic and phenotypic properties of the ewes in this flock.
3. To construct selection indices based on hogget characters and to describe the pattern of correlated response in fertility of the ewe predictable from properties of each index.

II. SOURCE OF DATA

The data used in this study, covering a period of 11 years from 1955 to 1965 inclusive, were obtained from a flock of Romney Marsh sheep kept at Massey University, Palmerston North. Since the origin and general management of this flock together with the kinds of data collected as a routine have been described elsewhere (Rae 1958 a and b), it is only necessary to outline certain aspects of management and data collection relevant to this study.

1. Management of experimental animals

This flock of Romney sheep since its founding in 1944, has been maintained by a system of random breeding. In practice, no selection for or against any productive characters in ewes or rams was made. Furthermore, the ewes within an age group, were assigned at random to the single sire mating groups. Both the ewe hogget and ewe flocks were grazed all year round on pastures, predominantly a ryegrass-white clover association except for the occasional supplementary feeding in the form of chou mollier which was offered to the ewe hoggets during late winter and early spring. Whether it was for the ewe hoggets or the ewes, the aim of grazing management was to provide an adequate level of nutrition and treat all sheep alike. During the mating and lambing season, the ewe flock was split into mobs, but periodic shifts of the various mobs were made to overcome, in part at least, any consistent difference in the level of nutrition at these two times of the year. In routine farm operations such as drenching and dipping against parasites, care of feet, crutching and

shearing; all sheep were treated in the same way. Apart from losses due to deaths and injured teats at shearing, all ewe lambs were taken into the hogget flock which in turn was taken in toto, into the ewe flock at the start of the mating season in March. The breeding ewes remained for four lambing seasons in the flock until casting for age as five-and-half year olds.

During the first or second week in March each year, at an average age of about six months the ewe hoggets were joined with three or four vasectomised rams. As a group, they remained together until the end of July or early in August when the males were withdrawn.

The breeding ewes were joined with entire rams in early March and the duration of the mating period varied only a little from year to year, being not less than 51 days or more than 58 days. For all practical purposes, each mating group was equal in number and similar in age composition of ewes. The lambing season was restricted to August, September, and early October while weaning took place towards the end of November or early in December. All wether lambs were disposed of after weaning, but ewe lambs as mentioned earlier were retained. In general, the calendar of farming operations and the pasture available for grazing by the hoggets and ewes in this flock were typical of those found on many Romney breeding properties in the Manawatu and surrounding areas.

2. Data and data collection

(a) Live weight characters

In each year, the ewe lambs were weighed at weaning. After weaning, the ewe hoggets were weighed at intervals between four to six weeks from March to July inclusive and again after hogget shearing in October. The weight of the individual was measured to the nearest pound. The dates of weighing at weaning, in March and after hogget shearing varied a little over the years, the range in dates being 10 to 15 days. The live weight characters used in this study were: weaning weight, live weight in March, live weight at the 'shortest-day' of the year (21st June) and body weight of the ewe hogget post-shearing in October. The last-mentioned weight measurement was considered most appropriately to be described as body weight since the record included a negligible amount of wool growth which on other occasions of weighing was an inseparable part of the live weight record. The measurement of live weight at the 'shortest-day' was obtained by linear interpolation between two adjacent weight records on either side of the 'shortest-day' in each year. An alternative way of describing live weight growth over the hogget period was to express it in terms of gain in live weight. The latter measurement was calculated as a difference between each adjacent pair of live weight records.

(b) Oestrous behaviour

It has been mentioned earlier that vasectomised rams were joined with the ewe hoggets early in March in each year. The vasectomised rams were raddled with coloured paste in the years from 1956 to 1958 inclusive. During the breeding season in 1959

and in subsequent years, the males were fitted with 'sire-sine' crayons (Radford, Watson and Wood 1960) which were found suitable for mating identification in the Manawatu (Ch'ang 1960). During the period of years when coloured paste was in use, it was replenished as required but usually daily. The colour of the paste or crayon was changed every two weeks.

Inspection of the ewe hoggets during the breeding season was made daily or at least once in every two days. The occurrence of oestrus was inferred from the freshly coloured patch visible on rump of the ewe hogget. The vasectomised rams were withdrawn towards the end of July or early in August when the observed incidence of oestrus became negligible. The duration of the breeding season was about four and a half-months to five months being similar to that described by Ch'ang and Raeside (1957) based on a preliminary study of Romney ewe hoggets in this flock.

(c) Fertility of the ewe

The record on number of lambs born, dead or alive per ewe at lambing, sex of lamb, type of birth and rearing of the lamb as well as identification of the dam and offspring were recorded as a matter of routine in this flock. Thus, no additional collection of fertility data was required for purpose of this study.

The total number of sires used in this flock was 49 over the period from 1955 to 1963 inclusive. Except on two occasions which will be mentioned later, each year a different group of rams was brought into the flock for mating. In choosing the sires no conscious selection for either high or low expression in the various characters studied in this thesis was made.

The sires were therefore regarded as a random sample of all sires which were available for sale to Romney breeding properties in the years under consideration. In 1962, one ram was apparently infertile during the mating period since every ewe in its group was subsequently found to be barren at end of the lambing season in that year. The fertility records of the ewes in this mating group for the year 1962 were excluded from analysis since they contributed no information on fertility of the ewes in question.

III. METHOD OF ANALYSIS

In the analysis of numerical data, choice of a mathematical model is the first step. A mathematical model is a definitive statement specifying the way in which the various factors are supposed to affect the datum. The model therefore is a description of the population from which the data are regarded as a sample. As part of the description, it is also desirable to establish a correspondence between assumptions made about the factors in the models and the biological and physical phenomena which are to be studied. The general consideration given to the choice of a model therefore depends on what is known a priori about biology of the character and the need to simplify the model so that statistical estimation may proceed.

The different models which can be used in studying genetic variation and covariation depend in the first instance on the various types of genetic relationship available in the data. In the present flock according to the mating system described earlier, the most common genetic relationships were those among the paternal half-sibs and between dam and daughter. While some full-sibs and maternal half-sibs were also present, they were too few in numbers for general use in the estimation of genetic parameters. The model used to represent the relationship between dam and daughter conceivably might be different from that appropriate for paternal half-sib analysis since the former could involve the effects due to maternal environment.

The estimates of genetic parameters are made more accurate if the environmental effects in the data were adequately removed.

The environmental sources of variation considered likely to be important were: year of birth, age of dam, type of birth and rearing and age of the individual. While these sources of variation are unlikely to account for all the non-genetic variation between records, they represent the known environmental factors in this flock.

The characters studied in this thesis are of two types. The first group consisted of weaning weight, live weight in March, live weight at the 'shortest-day', hogget body weight measured post-shearing and number of oestrus per ewe hogget during the first breeding season. For convenience of description these characters will be referred to as hogget characters. The second group of characters is composed of three measurements of fertility each expressed as number of lambs born per ewe. The first measurement of fertility is the number of lambs born per ewe at the two-year-old lambing. The second and the third measurements of fertility are expressed as total number of lambs born per ewe over the first two and three lambings respectively. These measurements of fertility will be collectively described as fertility of the ewe.

1. Estimation of environmental effects

It has been stated earlier that the known environmental factors considered likely to be of importance in the data were: year of birth, age of dam, type of birth and rearing and age of the individual. Since the mathematical model used to represent a record of the hogget character was more complete in the statistical sense than that considered appropriate for fertility of the ewe, it will be described in some detail first.

The data used in studying the environmental effects on hogget characters were based on the animals born over a period of seven years from 1955 to 1961 inclusive. The model used to represent a datum of each hogget character was:

$$y_{ijkl} = \mu + r_i + a_j + b_k + (ab)_{jk} + \beta(x_{ijkl} - \bar{x}) + e_{ijkl}$$

$$i = 1 \dots p, \quad j = 1 \dots q, \quad k = 1 \dots s \quad \text{and} \quad l = 1 \dots n_{ijk}$$

where n_{ijk} denotes the number of observations in the ijk^{th} sub-class.

The y_{ijkl} is the record of the l^{th} individual born in the i^{th} year and reared by the j^{th} age group of dam and belonging to the k^{th} type of birth and rearing class. As a part of the statement concerning the population described by the model, the year of birth, age of dam and type of birth and rearing are regarded as fixed effects. In addition, the sum of effects of the parameters within each of these classes are by definition equal to zero so that $\sum_i r_i = \sum_j a_j = \sum_k b_k = \sum_j (ab)_{jk} = \sum_k (ab)_{jk} = 0$. These specifications imply that all sub-class numbers are equal in the population.

The μ is the mean of all records of a character when equal frequencies exist in each sub-class.

The r_1 is an effect common to all records of a character measured on individuals born in the i^{th} year. For characters such as hogget body weight which was not made in the same year as the individual was born; the year of birth classifications which were chosen for convenience of description would refer to effect of the year in which the record was made. The 'year' effect used in either sense, is a measure of the variation in the data caused by environmental conditions peculiar to each year. For example, differences in the amount and distribution of rainfall and the mean monthly temperature which are known to exist between years may affect the characters of the animal, either directly or indirectly by their influences on feed supply, parasitic burden and other less tangible factors which make up the yearly environment. In the present data, the 'year' effect may also contain a genetic component since the average genetic differences between sires used in the last three years covered by this study were confounded with the 'year' effect.

The a_j is an effect due to age of dam. While four age-groups of dams were present in the flock, only three of these were used in the analysis. The three age-groups were:
 a_1 - two-year-old, a_2 - three-year-old, and a_3 - four and five-year old ewes. The b_k is an effect attributable to type of birth and rearing for which three sub-classes can be distinguished; b_1 - single lamb reared as single, b_2 - twin lambs reared singly and b_3 - twin lambs reared as twins.

It has been shown by Barnicoat, Logan and Grant (1949) that in the Romney breed younger ewes produce less milk than older ewes, and since milk represents the only diet in the early weeks of a lamb's life, the individuals reared by younger dams may be handicapped in their growth compared with those reared by mature dams. Lambs born and reared as twins have to share pre-natally the uterine environment and post-natally the milk supply of their dam. The twin lambs thus may also suffer from a handicap in growth compared with the lambs born and reared as singles. The a_j and b_k are therefore measures of these sources of variation on the weaning weight of the lamb. If these effects tend to persist after weaning when the lamb is no longer directly affected by age of dam and type of birth and rearing, they are included in the estimates of a_j and b_k for post-weaning characters.

The $(ab)_{jk}$ is an interaction effect associated with the j^{th} age of dam and k^{th} type of birth and rearing. An interaction of this kind may exist if, for example the extent of handicap in growth of twin lambs reared by mature dams is different from those reared by younger dams. The information provides some indication of the approximations involved in using age of dam and type of birth and rearing effects as additive correction factors.

The x_{ijkl} is the date of birth (in days) of the l^{th} individual born in the i^{th} year reared by the j^{th} age group of dam and belonging to the k^{th} type of birth and rearing class while $\bar{x}$ is the average date of birth of all individuals included in the present study. The term $(x_{ijkl} - \bar{x})$ expresses the difference in age of a particular individual from the average age of all

individuals. The β is a linear partial regression coefficient measuring the average change in value of y_{ijkl} for the difference of one day in age.

The e_{ijkl} is an error 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. The discrepancy is thus caused by the effects of many factors not included in this study. While some of these factors are known such as the sire effect, many others are unknown. In general, estimates of the effects are biased unless it can be assumed that the ignored sources of variation have their effects randomly distributed over the effects which are studied. As in the present data there was no known reason to suggest otherwise, the assumption appeared reasonable and therefore was made. For purposes of tests of significance, the e_{ijkl} was assumed to have a zero mean, constant variance and a normal distribution.

The distribution of sub-class numbers was non-orthogonal in the data. Hence, the method of fitting constants by least-squares procedure was used to estimate the various effects specified by the model. The principles of least-squares analysis and the detailed steps used in the estimation process have been described by Kempthorne (1952) and Harvey (1960). The latter has also discussed the types of restrictions which may be imposed on the estimates of the parameters in order to obtain unique solutions. The restrictions considered appropriate for the present analysis were $\sum_1 \hat{r}_1 = \sum_j \hat{a}_j = \sum_k \hat{b}_k = \sum_j (\hat{ab})_{jk} = \sum_k (\hat{ab})_{jk} = 0$ where the $\hat{}$ denotes 'the estimate of'.

Since interpretation of a_j and b_k depended on whether or not the interaction effect $(ab)_{jk}$ was real, the statistical significance of these terms in the model was tested first by using analysis of variance. In doing so, a short-cut method was used. More specifically, the model was re-defined as:

$$y_{ijkl} = d_{jk} + r_i + \beta(x_{ijkl} - \bar{x}) + e_{ijkl}$$

where $d_{jk} = \mu + a_j + b_k + (ab)_{jk}$. The sum of squares associated with $(ab)_{jk}$ was computed as a difference between reduction in sum of squares due to fitting all constants $R(\mu, r, a, b, ab, \beta)$ and that due to fitting all except the interaction effect $R(\mu, r, a, b, \beta)$. The error sum of squares was obtained as a difference between the raw sum of squares and that due to fitting all constants. The degrees of freedom for interaction was calculated as $(q - 1)(s - 1)$ since in the present data all sub-classes were filled. The error degrees of freedom were computed as $n \dots - p - qs$ where $n \dots$ denotes the total number of observations. The ratio between the interaction and the error mean squares was then compared with the tabulated F - values given by Snedecor (1950) as a basis for inferring statistical significance of the interaction effect.

If an interaction effect was found to be statistically significant, a reasonable approach to assess its practical importance in relation to the development and use of additive correction factors involves consideration based on the size of the interaction effects. The values of $\hat{d}_{jk}$ computed in the process of finding the reduction in sum of squares due to fitting all

constants are available as right-hand members (RHM) of the following set of simultaneous equations which may be used to estimate the μ , a_j , b_k and the interaction effects $(ab)_{jk}$.

	$\mu + a_j$	b_k	$(ab)_{jk}$	RHM
$\mu + a_j$	n_j	$\sum_k n_{jk}$	$\sum_k n_{jk}$	$\sum_k n_{jk} d_{jk}$
b_k	$\sum_j n_{jk}$	$n_{..k}$	$\sum_j n_{jk}$	$\sum_j n_{jk} d_{jk}$
$(ab)_{jk}$	n_{jk}	n_{jk}	n_{jk}	$n_{jk} d_{jk}$

In the equations above, the n_{jk} denotes the number of observations in the j^{th} and k^{th} sub-class, whereas the dot (.) represents summation over the subscript which it replaces.

The steps involved in solving the equations were: first, absorbing the $\mu + a_j$ equations into the remaining equations; second, imposing the restriction $\sum_k \hat{b}_k = \sum_j (\hat{ab})_{jk} = \sum_k (\hat{ab})_{jk} = 0$ and obtaining the solution of the reduced equations by iteration and third, substituting the $\hat{b}_k$ and $(\hat{ab})_{jk}$ into the $\mu + a_j$ equations to solve for $\mu + \hat{a}_j$.

The model used to represent a datum of fertility in the ewe was:

$$y_{ijkl} = \mu + r_i + a_j + b_k + e_{ijkl}$$

The meanings of the various elements shown in the model above were the same as those described for the previous model except in the case of 'year' effect r_i . The different years of birth involved in the fertility data will be specified below. It also should be noted that b_k , type of birth and rearing

classification takes on a connotation in the present context, somewhat different to that attributed to it in the earlier model. For example, the type of birth classification of the ewe itself is to a large extent determined by her dam's phenotype for fertility which is in part due to genetic causes. The type of birth effect on fertility of the ewe therefore is unlikely to be wholly attributable to environmental causes. This complication will be further discussed in presenting the results.

The fertility data used in the analysis were: for the first two measurements (number of lambs born at the first and over the first two lambings) the data were based on ewes born over the period from 1955 to 1962 inclusive and for the third measurement (total number of lambs born over the first three lambings) the data were based on ewes born over the period from 1955 to 1961 inclusive.

2. Interaction between sire and year in hogget characters

The ranking of a sire based on average performance of its offspring within a group of sires may alter from year to year. The sire-year interaction if real, tends to lower the accuracy of selection. The present investigation is concerned with the sire-year interaction in hogget characters.

It has been mentioned in II (c) that on two separate occasions, some or all of the sires used in the previous year were retained for further mating in a second year. More specifically, of the seven sires mated in 1955, four chosen at random were kept for use in 1956. In 1957 four different sires

were brought into service and these same four sires were used again in 1958. The data available for the present analysis were therefore based on those collected over two consecutive two-year periods (1955, 1956 and 1957, 1958). The data available from daughters of the three sires which were not used in 1956 have been excluded from the present study in order to lighten the computational burden. The data thus excluded could not have contributed information towards the sire-year interaction although they would have provided extra degrees of freedom for estimating the error mean squares.

The mathematical model chosen to represent the record of a character in each of the two-year periods was:

$$y_{ijklm} = \mu + s_i + r_j + (sr)_{ij} + a_k + b_l + \beta(x_{ijklm} - \bar{x}) + e_{ijklm}$$

$i = 1 \dots p, \quad j = 1 \dots q, \quad k = 1 \dots t, \quad l = 1 \dots u \quad \text{and}$

$m = 1 \dots n_{ijkl} \quad \text{where the } n_{ijkl} \text{ denotes the number of observations in the } ijkl^{\text{th}} \text{ sub-class.}$

The $\mu, r_j, a_k, b_l, x_{ijklm}$ and β are the mean, year of birth, age of dam, type of birth and rearing, date of birth and the partial linear regression coefficient on age respectively.

These elements have the same meaning as those described for the model used in studying the environmental effects. The s_i in the present model, is an effect common to records of a character of all daughters in the i^{th} sire group. The $(sr)_{ij}$ is an effect common to records of a character of the daughters in the i^{th} sire group born in the j^{th} year. The e_{ijklm} is an error or residual peculiar to each record.

The usual assumptions made about s_1 and $(sr)_{1j}$ are that they have zero means and variances σ_s^2 and σ_{sr}^2 respectively. These assumptions are pertinent if the aim of the analysis is to estimate variance components attributable to sires and sire-year interaction. The small numbers of sires and years available for the present study would render the estimates of variance components if calculated, unreliable. The objective of the analysis therefore was confined to a test for the presence of sire-year interaction in the hogget data. The s_1 and $(sr)_{1j}$ were thus regarded as fixed effects while e_{ijklm} was assumed to have a zero mean, constant variance and a normal distribution. The computational steps used in finding the sum of squares and mean squares needed for the test of significance of sire-year interaction effect were the same as those described earlier for testing the significance of age of dam-type of birth and rearing effect.

3. Preliminary analysis of annual fertility of the ewe

Since a ewe may produce zero, one, two or occasionally more lambs per year, a discrete scale based on the number of lambs produced by a ewe is clearly a meaningful measure of annual fertility in the ewe. However, the limited number of classes or coarse grouping which is a property of the annual fertility data presents certain problems in statistical analysis using the small sample techniques. The main difficulty lies in the interpretation of tests of significance and the

estimates of sampling errors derived by methods more appropriate for normally distributed variables. A satisfactory theoretical solution to overcome this and other related problems is not available. While the problem of coarse grouping may be overcome in part at least, by using the average or total number of lambs born per ewe over several lambings as a measure of fertility, it appears worthwhile in the first instance to study the more basic phenotypic relationship between a hogget character and annual fertility of the ewe using methods more appropriate for frequency data.

The phenotypic relationships between number of hogget oestrus and annual fertility of the ewe at two-, three-, four-, and five-year-old lambing were studied initially using the chi-square method, then by a method of weighted regression described by Yates (1948) and lastly, by regression analysis based on the method of least-squares (Snedecor 1950). The data used in each analysis were the same, being those collected over the period of years from 1955 to 1963 inclusive. A detailed account of each method of analysis is presented below.

(a) Chi-square analysis

The aim of this series of analysis was to provide an appropriate test for mutual independence among number of hogget oestrus, type of birth and annual fertility of the ewe. For the present purpose, the data may be arranged in a three dimensional contingency table with r -rows, c -columns and l -layers. The r -rows consist of two type-of-birth classes which refer to whether the ewe was itself born as a single or a twin or triplet.

The c-columns are represented by three mutually exclusive reproductive attributes; barrenness, single-birth and multiple-birth characterising annual fertility of the ewe. The l-layers are composed of the different numbers of hogget oestrus. Thus, the first layer corresponds to zero oestrus while the sixth and last layer refers to five or more oestrus. The observations were few in number for the six-, seven- and eight-oestrus classes, hence, these observations were combined with those in the five-oestrus class.

The observed frequency in the cell of the i^{th} row, j^{th} column and k^{th} layer may be denoted by n_{ijk} and the probability of an observation falling in the ijk^{th} cell is correspondingly designated as p_{ijk} .

The test for mutual independence among the variates is specified by the null-hypothesis; $H_0 : p_{ijk} = (p_{i..})(p_{.j.})(p_{..k})$ against the general alternative $H_A \neq H_0$. The test statistic is:

$$\chi^2 = \sum_{ijk} \left[n_{ijk} - \frac{(n_{i..})(n_{.j.})(n_{..k})}{N^2} \right]^2 / \left[\frac{(n_{i..})(n_{.j.})(n_{..k})}{N^2} \right]$$

Where the subscript is replaced by a dot, it implies the summation over the classes represented by the subscript. For example, the grand total $N = n_{...}$. The χ^2 above has $(rc - r - c - 1 + 2)$ degrees of freedom since only the grand total N has been restrained in advance with random sampling elsewhere including the sub-totals, $(n_{i..})$, $(n_{.j.})$ and $(n_{..k})$ in the contingency table.

If the null-hypothesis H_0 is rejected, it does not necessarily imply that there is association between all possible pairs of variates. The composite null-hypothesis H_0 then may be subdivided into three mutually exclusive sub-hypotheses (Lewis 1962). The sub-hypotheses tested in the present data were:

(1) $H_{01} : p_{ijk} = (p_{.j.}) (p_{..k})$ or independence between reproductive attributes and number of hogget oestrus. The test statistic χ^2 with $(c - 1) (l - 1)$ degrees of freedom was computed as squared deviations from the expectations applicable to a two-way contingency table between reproductive attributes and number of hogget oestrus.

(2) $H_{02} : p_{ijk} = (p_{1.k}) (p_{.jk}) / (p_{..k})$ or conditional independence between type of birth and reproductive attributes given the number of hogget oestrus. The test statistic is:

$$\chi^2 = \sum_{ijk} \left[n_{ijk} - \frac{(n_{1.k})(n_{.jk})}{(n_{..k})} \right]^2 / \left[\frac{(n_{1.k})(n_{.jk})}{(n_{..k})} \right]$$

with $l(r - 1) (c - 1)$ degrees of freedom.

(3) $H_{03} : p_{1.k} = (p_{1..}) (p_{..k})$ or independence between type of birth and number of hogget oestrus. The test statistic χ^2 with $(r - 1) (l - 1)$ degrees of freedom was computed as squared deviations from expectations applicable to a two-way contingency table between type of birth and number of hogget oestrus.

The validity of the sub-division of H_0 into three sub-hypotheses has been discussed by Lewis (1962). As an approximate check in a given sample, the value of χ^2 associated with H_0 should be equal or nearly equal to the sum of three separate

χ^2_8 each associated with a sub-hypothesis. This check was carried out in the present analysis.

It should be pointed out that the composite hypothesis (H_0) may be decomposed into sub-hypotheses other than those stated above. However, the sub-hypotheses (H_{01} , H_{02} and H_{03}) formed were considered to be particularly relevant to the present study. The main objective as mentioned earlier was to provide some evidence in order to establish in a general way, whether or not the reproductive attributes of the ewe at each lambing was independent of number of hogget oestrus (H_{01}). The tendency for ewes themselves born as twins or in higher ordered births to be somewhat higher in the level of fertility than those born as singles has been observed both in the present flock (Rae and Ch'ang 1955) and in other studies (see review by Reeve and Robertson 1953). Therefore, it was also of interest to test using H_{02} , the independence between type of birth and reproductive attributes of the ewe given the number of hogget oestrus. The independence between type of birth and the occurrence or absence of oestrus at the hogget stage has been reported in a preliminary study by Ch'ang and Raeside (1957). The test using H_{03} , of independence between type of birth and number of hogget oestrus based on the present data therefore provides further evidence on this aspect.

(b) Weighted regression analysis

The chi-square method described above is useful as it gives a valid test of association between variates which are based on frequency data. However, the chi-square method has several shortcomings (Cochran 1954). Particularly relevant to the

present study is that the chi-square analysis provides no means of detecting the pattern of deviations between the observed and the expected frequencies which may exist if the null-hypothesis is rejected. In order to strengthen the chi-square analysis and to obtain a quantitative measure of the specific pattern of deviations which it may suggest, a weighted regression method (Yates 1948) appropriate for frequency data was used. The weighted regression method therefore provided a further description of the phenotypic relationship between number of hogget oestrus and annual fertility of the ewe.

A scoring system was required for the weighted regression analysis (Yates 1948). In the present data; barrenness, single-birth, twin-birth and triplet-birth were scored as zero, one, two and three respectively. The scores assigned to number of hogget oestrus corresponded to the actual number of oestrus except for the last score, six, which included higher ordered oestrus as well.

The statistical significance of each regression coefficient was tested according to the criterion and method given by Yates (1948). Since the present hypothesis was confined to whether there was increased fertility with increasing number of hogget oestrus, the test was based on the probability of a normal deviate with zero mean and unit variance exceeding the value of $\sqrt{\chi^2}$ calculated from the data. It is worth noting that validity of this test does not depend on the system of scoring (Yates 1948 and Cochran 1954). The interpretation of the weighted regression coefficient based on arbitrarily chosen scores may be difficult in some instances. However, the scoring

system used in the present analysis corresponded almost exactly to the phenotypic expression of the characters in question, sensible interpretation of the coefficients was thus possible even though the underlying scale for each character was assumed to be unknown.

(c) Least-squares regression analysis

Since the weighted regression developed by Yates (1948) based on the one-tailed test of significance is a large sample technique, the results obtained according to this method of analysis may differ from those given by the least-squares regression. In using the latter method, it is necessary to assume that the dependent variable - annual fertility of the ewe has a normal distribution and the other properties of the data implied by this assumption. The main uncertainty about the normality assumption was caused by the possible correlation between the mean and the variance of annual fertility which as described earlier was measured by a discrete scale containing relatively few classes. More specifically, annual fertility may be regarded as having a multinomial rather than a normal distribution. The purpose of estimating the least-squares regression of annual fertility on number of hogget oestrus therefore was to provide some empirical evidence for assessing, by comparison of results with those obtained from the weighted regression, the approximations involved in using the more versatile least-squares method of analysis.

As a first step towards computing the least-squares regression coefficient, the data were initially sorted into

type of birth and age of ewe sub-classes. Within each subclass, sum of squares for each character, crossproducts between the characters and degrees of freedom were computed for all individuals born in the same year. These values were then pooled over the year of birth groups to compute the regression coefficient, one for each type of birth and age of ewe classification. The tests of significance for the regression coefficients were made using the method and t - table given by Snedecor (1950).

4. Estimation of phenotypic and genetic parameters

A statistical description of phenotypic and genetic properties of a sheep flock may be provided by the variance-covariance matrix of the characters under investigation. However, it is often more convenient to summarise such information by expressing it as correlations or heritabilities. For instance, estimates of phenotypic correlations between hogget characters and fertility of the ewe are immediately indicative of the relative accuracy with which the potential fertility of the ewe can be predicted by each of the several hogget characters. The heritability of each character and the genetic correlation between each pair of characters are also useful as they provide a more readily interpretable evidence for describing the pattern of response and correlated response to selection in the group of characters under study. The most common types of genetic relationships available for estimation of genetic parameters in a sheep flock are those among the paternal half-sibs and between dam and offspring. 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.

(a) Paternal half-sib analysis

In a population mating at random, four times the variance among sires is an estimate of additive genetic variance plus an unknown amount of variance due to non-additive genetic phenomena such as dominance and epistasis, if they exist as sources of variation in the character under investigation. Similarly and

with the same reservation, additive genetic covariance between each pair of characters may be estimated as four times the covariance among sires. The first step towards estimation of heritability and genetic correlation using the paternal half-sib method however is concerned with analysis of variance and covariance components attributable to the sires.

The model chosen to represent a datum of a particular hogget character was:

$$y_{ijklm} = \mu + r_i + s_{ij} + a_k + b_l + e_{ijklm}$$

and for a second character was:

$$y'_{ijklm} = \mu + r'_i + s'_{ij} + a'_k + b'_l + e'_{ijklm}$$

$i = 1 \dots r$, $j = 1 \dots s_1$, $k = 1 \dots t$, $l = 1 \dots u$ and $m = 1 \dots n_{ijkl}$ where n_{ijkl} denotes the number of observations in the $ijkl$ th sub-class. The y_{ijklm} or y'_{ijklm} is the record of the m th individual born in the i th year and j th sire group and reared by the k th age group of dam and belonging to the l th type of birth and rearing class. The μ or μ' is an effect common to all records of a character. The r_i or r'_i , a_k or a'_k and b_l or b'_l are fixed effects attributable to year of birth, age of dam and type of birth and rearing respectively. The s_{ij} or s'_{ij} is an effect due to the j th sire within the i th year and the e_{ijklm} or e'_{ijklm} is an error peculiar to each record. The s_{ij} , s'_{ij} , e_{ijklm} and e'_{ijklm} were assumed to be random variables distributed with zero means and variances σ_s^2 , $\sigma_{s'}^2$, σ_e^2 and $\sigma_{e'}^2$, respectively

and covariance among sires cov ss' and error covariance cov ee' .

In estimating the sire and error variances and covariances, the working models used were:

$$\tilde{y}_{ijklm} = \mu + r_i + s_{ij} + e_{ijklm} \quad \text{and}$$

$$\tilde{y}'_{ijklm} = \mu' + r'_i + s'_{ij} + e'_{ijklm} \quad \text{where}$$

$$\tilde{y}_{ijklm} = \hat{y}_{ijklm} + \hat{a}_k + \hat{b}_l \quad \text{and}$$

$$\tilde{y}'_{ijklm} = \hat{y}'_{ijklm} + \hat{a}'_k + \hat{b}'_l$$

The $\hat{a}_k$ or $\hat{a}'_k$ and $\hat{b}_l$ or $\hat{b}'_l$ were derived from the data used in studying the environmental effects on hogget characters according to the reduced models:

$$y_{klm} = \mu + a_k + b_l + e_{klm} \quad \text{and}$$

$$y'_{klm} = \mu' + a'_k + b'_l + e'_{klm}$$

The procedure used in adjusting the data for differences in age of dam and type of birth and rearing was less satisfactory than that proposed by Henderson (1953 Method 2). However, within the limitations imposed by the available computing facilities and knowledge of writing more sophisticated computer programmes, the present procedure of data correction was thought to be a reasonable compromise.

A similar procedure as that outlined above was used to estimate the variance components (σ_s^2 and σ_e^2) for each measurement of fertility in the ewe and the covariance components between each hogget character and fertility except that no

correction was made for differences in the fertility data due to type of birth and rearing. Some evidence which will be presented at a later stage is available from the present data in support of this procedure. The estimates of age of dam effect on fertility of the ewe used as correction factors were therefore derived using the following one-way model:

$$y_{km} = \mu + a_k + e_{km}$$

the data used for this purpose being the same as those used in the analysis of environmental effects on fertility of the ewe.

The expectations of sire and error mean squares and cross-products are:

$$\begin{aligned} \text{Sire Mean Square} &= \sigma_e^2 + k_0 \sigma_s^2 \\ \text{Sire Mean Crossproducts} &= \text{cov } ee' + k_0 \text{cov } ss' \\ \text{Error Mean Square} &= \sigma_e^2 \\ \text{Error Mean Crossproducts} &= \text{cov } ee' \end{aligned}$$

The coefficient k_0 was calculated as

$$1/\sum_1 (s_1 - 1) \left[\sum_1 n_1 - \sum_{1j} (n_{1j}^2/n_1) \right]$$

where n_{1j} is the number of offspring in the j^{th} sire group within the 1^{th} year and n_1 is the total number of individuals in the 1^{th} year.

The estimates of phenotypic correlation ($\hat{R}_p$), heritability ($\hat{H}$) and genetic correlation ($\hat{R}_g$) were calculated using the following expressions:

$$\begin{aligned} \hat{R}_p &= (\widehat{\text{cov}} ss' + \widehat{\text{cov}} ee') / (\hat{\sigma}_s^2 + \hat{\sigma}_e^2)^{\frac{1}{2}} (\hat{\sigma}_{s'}^2 + \hat{\sigma}_{e'}^2)^{\frac{1}{2}} \\ \hat{H} &= 4 \hat{\sigma}_s^2 / \hat{\sigma}_s^2 + \hat{\sigma}_e^2 \quad \text{and} \quad \hat{R}_g = \widehat{\text{cov}} ss' / \hat{\sigma}_s \hat{\sigma}_{s'} \end{aligned}$$

It should be pointed out that in computing the variance and covariance components, no allowance was made for the degrees of freedom utilised as a result of adjusting the data for differences in age of dam and where applicable for type of birth and rearing. The frequency distribution of these environmental classifications is not exactly proportional among the sires therefore, the values of variance and covariance components may be biased (Henderson 1953).

The sampling error of $\hat{H}$ was derived from that of 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). In computing the sampling errors of heritability and genetic correlation, the degrees of freedom for sires were based on the number of different sires rather than the total number of sires which had been used in the variance and covariance component analysis.

(b) Covariance analysis between dam and daughter

The regression of offspring's phenotype on that of the dam is widely used as a method for estimation of heritability (Lush 1940) and genetic correlation (Hazel 1943). For example, the heritability (H) of character P_1 or P_j and the genetic correlation ($r_{G_1G_j}$) between them may be estimated, under simplifying assumptions according to the following expressions:

$$\hat{H}_1 = 2 \hat{\beta}_{P_1 P'_1} = 2 \widehat{\text{cov}} P_1 P'_1 / \sigma_{P'_1}^2$$

$$\hat{H}_j = 2 \hat{\beta}_{P_j P'_j} = 2 \widehat{\text{cov}} P_j P'_j / \sigma_{P'_j}^2$$

$$\text{and } \hat{r}_{G_1 G_j} = \widehat{\text{cov}} P'_1 P_j / 2 (\widehat{\text{cov}} P'_1 P_1 \widehat{\text{cov}} P'_j P_j)^{\frac{1}{2}}$$

$$\text{or } \hat{r}_{G_1 G_j} = \widehat{\text{cov}} P'_j P_1 / 2 (\widehat{\text{cov}} P'_1 P_1 \widehat{\text{cov}} P'_j P_j)^{\frac{1}{2}}$$

The underlying models and the assumptions made about variables in the models are:

$$P_1 = G_1 + E_1 \quad P_j = G_j + E_j$$

$$P'_1 = G'_1 + E'_1 \quad P'_j = G'_j + E'_j$$

where the prime denotes the maternal generation. Under random mating, $E(G_1) = \frac{1}{2} G'_1$ and $E(G_j) = \frac{1}{2} G'_j$; the G being defined as the additive genetic value of the character. In addition, the E is assumed as a random environmental value which is uncorrelated with the G so that $E(\text{cov } GE) = 0$.

Expressing each variable as a deviation from its mean value;

$$E(\text{cov } P'_1 P_1) = \frac{1}{2} \sigma_{G_1}^2, \quad E(\text{cov } P'_j P_j) = \frac{1}{2} \sigma_{G_j}^2, \quad E(\text{cov } P'_1 P_j) =$$

$$E(\text{cov } P'_j P_1) = \frac{1}{2} \text{cov } G_1 G_j. \quad \text{The heritabilities and genetic}$$

correlation are then estimated by definition as:

$$\hat{H}_1 = \hat{\sigma}_{G_1}^2 / \hat{\sigma}_{P_1}^2, \quad \hat{H}_j = \hat{\sigma}_{G_j}^2 / \hat{\sigma}_{P_j}^2 \quad \text{and} \quad \hat{r}_{G_1 G_j} = \widehat{\text{cov}} G_1 G_j / \hat{\sigma}_{G_1} \hat{\sigma}_{G_j}.$$

In the models described above, E was defined as a random environmental deviation uncorrelated with the G . This assumption, as suggested by Koch and Clark (1955) may not be appropriate

if the character is subject to the influence of a maternal environment (P'_m) which is itself heritable. In other words, E_1 is now re-defined as $E_1 = P'_m + E_1$ and $E(P'_m) = G'_m + E'_m$ thus $E_1 = G'_m + E'_m + E_1$ where E'_m is the environmental deviation of maternal environment and E_1 , the non-maternal environmental deviation of P_1 . The E'_1 may be similarly re-defined as: $E'_1 = G''_m + E''_m + E'_1$ where the double prime denotes the grand dam's generation. Under the direct influence of a maternal environment, the $E(\text{cov } G'_1 E_1)$ and $E(\text{cov } G_1 E'_1)$ is not zero but contains systematic components due to genetic variation and covariation of the maternal environment.

In the present study, weaning weight of the lamb was the only character directly affected by maternal environment. The remaining characters were all expressed by the individual after weaning and therefore could be influenced by the maternal environment only if a carryover maternal effect exists. An attempt was made in the following sections to evaluate the contribution made by the maternal environment and its carryover effect to covariance between dam and daughter.

(11) Maternal environment and weaning weight

For present purpose, the maternal environment (P'_m) may be considered as an influence attributable solely to the dam on her offspring between birth and weaning. In so far as weaning weight of the lamb is concerned, a major component of maternal environment is the quality and quantity of milk produced by the dam. Studies on milk production in the Romney breed (Barnicoat, Logan and Grant 1949) showed that ewes comparable in age and

number of lambs suckled differed in composition and the amount of milk produced. However, maternal environment conceivably includes other less tangible factors of the dam as well, such as the ability to shelter and shield the lamb from hazards of life and other factors which affect viability and health of the lamb. The present view point therefore is to regard phenotype of weaning weight (P_w) as a result of several factors and definable as: $P_w = G_w + E_w + P'_m$ where

$E(G_w) = \frac{1}{2} G'_w$ and $E(P'_m) = G'_m + E'_m$. A pair of weaning weight records between the offspring and the dam each reared by its own dam may be stated as:

$$P_w = \frac{1}{2} G'_w + E_w + G'_m + E'_m$$

$$\text{and } P'_w = G'_w + E'_w + G''_m + E''_m$$

The $E(\text{cov } P'_w P_w) = \frac{1}{2} \sigma_{G_w}^2 + 1\frac{1}{4} \text{cov } G_w G_m + \frac{1}{2} \sigma_{G_m}^2$ since

$E(\text{cov } G'_w G''_m) = \frac{1}{2} \text{cov } G_w G_m$, the G''_m being the additive genetic deviation of maternal environment of the grand dam. These expectations may be verified by using a path-coefficient diagram such as that given by Koch and Clark (1955 Figure 3).

The contribution of maternal environment to covariance between dam and offspring, under the present formulation is represented by $1\frac{1}{4} \text{cov } G_w G_m + \frac{1}{2} \sigma_{G_m}^2$. Since a direct measurement of maternal environment is not available, the evaluation of $\text{cov } G_w G_m$ and $\sigma_{G_m}^2$ presents considerable difficulty. For example, Koch and Clark (1955) compared the values of correlations obtained from different kinds of relatives such as

paternal and maternal half-sibs and between dam and offspring in order to provide some information on the genetic correlation between maternal environment and a character affected by it. This approach as pointed out by Koch and Clark (1955) can not lead to a point estimate of the genetic correlation in question because a series of assumed values of heritability of maternal environment were used in calculating the genetic correlations. In the present study, an attempt was made to obtain point estimates of $\text{cov } G_w G_m$ and $\sigma_{G_m}^2$, thus enabling a point estimate of genetic correlation between weaning weight and maternal environment to be calculated.

The observed weaning weight of a lamb reared by a ewe other than its own dam may be defined as:

$$F_w = \frac{1}{2} G'_w + E_w \quad \text{and}$$

$$F'_w = G'_w + E'_w \quad \text{the } F'_w \text{ being weaning}$$

weight record of its dam which was also fostered as a lamb. The expectations of dam-offspring covariances involving both fostered and dam-reared weaning weight records are:

$$E (\text{cov } F'_w F_w) = \frac{1}{2} \sigma_{G_w}^2$$

$$E (\text{cov } F'_w P_w) = \frac{1}{2} \sigma_{G_w}^2 + \text{cov } G_w G_m$$

$$E (\text{cov } P'_w F_w) = \frac{1}{2} \sigma_{G_w}^2 + \frac{1}{4} \text{cov } G_w G_m$$

$$\text{and } E (\text{cov } P'_w P_w) = \frac{1}{2} \sigma_{G_w}^2 + 1\frac{1}{4} \text{cov } G_w G_m + \frac{1}{2} \sigma_{G_m}^2$$

as already derived. The dam-offspring relationships therefore provide a useful approach under the present formulation, for

evaluation of genetic contribution made by maternal environment if a sufficiently large number of fostered dams and offspring were available in the flock.

In the present flock, fostering was not a regular practice but had been necessary and carried out for various reasons. The major reasons for fostering were the death of dam, injury or disease of the udder of the dam. The ewe to which a lamb is fostered for practical purpose, is chosen at random except that the foster ewe would have lambed at about the same time as the fostered lamb was born. Over the years from 1951 to 1966 inclusive, weaning weight records were available for 129 fostered ewe and wether lambs. It was therefore decided to compute $\text{cov } P'_W F_W$ in order to provide a point estimate for $\text{cov } G_W G_m$, using the relationship

$$E(\text{cov } P'_W F_W) = \frac{1}{2} \sigma_{G_W}^2 + \frac{1}{4} \text{cov } G_W G_m.$$

The $\hat{\sigma}_{G_W}^2$ used for this purpose was that found from the paternal half-sib analysis which has been described earlier, the $\sigma_{G_W}^2$ was estimated as four times the between sire variance for weaning weight. More specifically, $\text{cov } G_W G_m$ was estimated as:

$$\widehat{\text{cov } G_W G_m} = 2 \hat{\sigma}_{G_W}^2 - 4 \widehat{\text{cov } P'_W F_W}$$

$$\text{hence, } \hat{\sigma}_{G_m}^2 = 2 \widehat{\text{cov } P'_W P_W} - \hat{\sigma}_{G_W}^2 - 2\frac{1}{2} \widehat{\text{cov } G_W G_m}$$

$$\text{and } \hat{r}_{G_W G_m} = \widehat{\text{cov } G_W G_m} / \hat{\sigma}_{G_W} \hat{\sigma}_{G_m}$$

The sampling errors of $\widehat{\text{cov } G_W G_m}$ and $\hat{\sigma}_{G_m}^2$ are expected to be large since the amount of data available for their

estimation was far from being satisfactory. These estimates would have been more reliable if $\text{cov } G_w G_m$ could have been estimated from the relationship between P'_w and P_w . The way in which $\widehat{\text{cov } P'_w P_w}$ and $\widehat{\text{cov } P'_w P_w}$ were computed and the adjustment for known environmental effects on weaning weight will be described at a later stage.

(11) Carryover maternal effect and post-weaning characters

Since a post-weaning live weight measurement may be expressed as the sum of weaning weight plus live weight gain over each of the specifiable periods it is convenient to examine first, the contribution of carryover maternal effect to dam-daughter covariance among the live weight characters.

Let P_t represent a live weight measured at time t post-weaning and P_k , the gain in weight during the k^{th} period defined as the interval from weaning to the time when P_t is measured. If P_k is heritable, it may be represented as $P_k = G_k + E_k$. Since the identity $P_t = P_w + P_k$ is true, P_t may be written in terms of its genetic and environmental components as:

$$P_t = G_w + G_k + G'_m + E_w + E_k + E'_m$$

or more simply, $P_t = G_t + G'_m + E_t$ by letting $G_t = G_w + G_k$ and $E_t = E_w + E_k + E'_m$. Similarly, the dam's weight measured at time t may be specified as:

$$P'_t = G'_t + G''_m + E'_t.$$

The covariance between P'_t and P_t , given that $E(G_t) = \frac{1}{2} G'_t$ and $E(G'_m) = \frac{1}{2} G''_m$ has the expectation $E(\text{cov } P'_t P_t) = \frac{1}{2} \sigma_{G_t}^2 + 1\frac{1}{4} \text{cov } G_t G_m + \frac{1}{2} \sigma_{G_m}^2$. The carryover maternal contribution to $\text{cov } P'_t P_t$ is similar to the maternal component in $\text{cov } P'_w P_w$ except $\text{cov } G_t G_m$ replaces $\text{cov } G_w G_m$. This result appeared reasonable since P_w and P_t bear the same relation as a part to the whole. In other words, $\sigma_{G_t}^2$ and $\text{cov } G_t G_m$ may be written in terms of their respective components as:

$$\sigma_{G_t}^2 = \sigma_{G_w}^2 + 2 \text{cov } G_w G_k + \sigma_{G_k}^2 \quad \text{and}$$

$$\text{cov } G_t G_m = \text{cov } G_w G_m + \text{cov } G_k G_m.$$

Using the models described above, the expected values of $\text{cov } P'_t P_w$ and $\text{cov } P'_w P_t$ are:

$$E(\text{cov } P'_t P_w) = \frac{1}{2} \text{cov } G_t G_w + \frac{1}{4} \text{cov } G_w G_m + \text{cov } G_t G_m + \frac{1}{2} \sigma_{G_m}^2$$

$$E(\text{cov } P'_w P_t) = \frac{1}{2} \text{cov } G_t G_w + \text{cov } G_w G_m + \frac{1}{4} \text{cov } G_t G_m + \frac{1}{2} \sigma_{G_m}^2$$

There are two points worth noting. First, in the absence of a maternal effect on weaning weight, $E(\text{cov } P'_t P_w) = E(\text{cov } P'_w P_t) = \frac{1}{2} \text{cov } G_t G_w$ which provides the usual method of estimating $\text{cov } G_t G_w$, as an average value of the reciprocal covariances between dam and daughter. Second, in the assumed presence of a maternal effect on weaning weight the expected value of $\text{cov } P'_t P_w$ is no longer the same as that of $\text{cov } P'_w P_t$. The inequality between the reciprocal covariances however enables $\text{cov } G_t G_m$ to be estimated as follows:

$$\widehat{\text{cov}} G_t G_m = 1\frac{1}{2} (\widehat{\text{cov}} P'_t P_w - \widehat{\text{cov}} P'_w P_t) + \widehat{\text{cov}} G_w G_m$$

Furthermore, $\sigma_{G_t}^2$ can now be calculated as:

$$\widehat{\sigma}_{G_t}^2 = 2 \widehat{\text{cov}} P'_t P_t - (2\frac{1}{2} \widehat{\text{cov}} G_t G_m + \widehat{\sigma}_{G_m}^2).$$

The estimate of $r_{G_t G_m}$ was therefore found as:

$$\widehat{r}_{G_t G_m} = \widehat{\text{cov}} G_t G_m / \widehat{\sigma}_{G_t} \widehat{\sigma}_{G_m}$$

A similar procedure to the one outlined above was used to estimate the genetic correlation between maternal environment and each of the reproductive characters (P_1) where $1 = 0, 1, 2, 3$ corresponding to number of hogget oestrus, and each of the three measurements of fertility in the ewe. The P_1 and P'_1 were assumed to be represented by the following models:

$$P_1 = \frac{1}{2} G'_1 + E_1 \quad \text{since} \quad E(G_1) = \frac{1}{2} G'_1$$

and $P'_1 = G'_1 + E'_1$ expressing the fact that maternal environment is not a direct source of variation in the reproductive characters. On the other hand, the $\text{cov } P'_1 P_t$ or $\text{cov } P'_t P_1$ contains maternal contributions. For present purpose, the subscript t may be re-defined for convenience so that $t = 1, 2, 3$ and 4. The range of t is extended to include weaning weight and each of the three post-weaning live weight measurements because P_w and P_t as shown earlier, contain the same amount of contribution from the maternal environment. The P_t and P'_t where $t = 1, 2, 3$ and 4 may be stated as:

$$P_t = \frac{1}{2} G'_t + G'_m + E_t \quad \text{and}$$

$$P'_t = G'_t + G''_m + E'_t.$$

The expectations of $\text{cov } P'_1 P_t$ and $\text{cov } P'_t P_1$ are:

$$E(\text{cov } P'_1 P_t) = \frac{1}{2} \text{cov } G_1 G_t + \text{cov } G_1 G_{mt} \text{ and}$$

$$E(\text{cov } P'_t P_1) = \frac{1}{2} \text{cov } G_1 G_t + \frac{1}{2} \text{cov } G_1 G_{mt} \text{ where}$$

the additional subscript t in $\text{cov } G_1 G_{mt}$ is inserted as a means of identifying the source of data from which a particular $\text{cov } G_1 G_m$ was estimated. For each (1^{th}) reproductive character, four separate estimates of $\text{cov } G_1 G_m$ were made according to the following relationship:

$$\widehat{\text{cov } G_1 G_{mt}} = 1\frac{1}{2} (\widehat{\text{cov } P'_1 P_t} - \widehat{\text{cov } P'_t P_1})$$

The genetic correlation between the 1^{th} reproductive character and maternal environment ($r_{G_1 G_m}$) was estimated based on the average genetic covariance ($\text{cov } G_1 G_{mt}$) and product of the appropriate genetic standard deviations, σ_{G_1} and σ_{G_m} .

More specifically, $\widehat{\text{cov } G_1 G_{mt}} = \frac{1}{4} \sum_{t=1}^4 \widehat{\text{cov } G_1 G_{mt}}$, $\widehat{\sigma}_{G_1} = (2 \widehat{\text{cov } P'_1 P_1})^{\frac{1}{2}}$ and since $\widehat{\sigma}_{G_m}$ was already available, the $r_{G_1 G_m}$ was calculated as:

$$\widehat{r}_{G_1 G_m} = \widehat{\text{cov } G_1 G_{mt}} / \widehat{\sigma}_{G_1} \widehat{\sigma}_{G_m}.$$

(111) Estimation of heritability and genetic correlation

The method used to find the amount of genetic variance in each post-weaning character has been described in (11) above. Under the assumed presence of a maternal effect, the genetic

variance and the corresponding heritability of weaning weight could not be estimated from the existing data using the relationship between dam and offspring. However, estimates of heritability for weaning weight and other live weight measurements ignoring the maternal and its carryover effects, were obtained by doubling the appropriate regression of daughter on dam. Under the assumed presence of a carryover maternal effect, the heritability (H) of each post-weaning live weight measurement was calculated as a ratio of genetic variance (σ_G^2) to the average phenotypic variance between dam and daughter in the following way:

$$\hat{H} = \hat{\sigma}_G^2 / \frac{1}{2} (\hat{\sigma}_{P_1}^2 + \hat{\sigma}_{P_2}^2).$$

The genetic correlation (R_g) between characters P_1 and P_j calculated ignoring the maternal and its carryover effects was found as:

$$\hat{R}_g = (\hat{\text{cov}} P_1'P_j + \hat{\text{cov}} P_j'P_1) / 2 (\hat{\text{cov}} P_1'P_1 \hat{\text{cov}} P_j'P_j)^{\frac{1}{2}}.$$

In order to estimate genetic correlations under the assumed presence of a carryover maternal effect on post-weaning live weight characters, the following genetic covariances are required. There are in general two kinds of covariances depending on the characters in question. Using the symbols and subscripts defined in (11) above, the genetic covariance between two successive live weight measurements where the subscripts $t = 1$ and $t = 2$, for example was calculated as:

$$\hat{\text{cov}} G_1G_2 = (\hat{\text{cov}} P_2'P_1 + \hat{\text{cov}} P_1'P_2) - 1\frac{1}{4} (\hat{\text{cov}} G_1G_m + \hat{\text{cov}} G_2G_m) - \hat{\sigma}_{Gm}^2.$$

The genetic covariance between the t^{th} live weight (P_t) and the 1^{th} reproductive character (P_1) was estimated as:

$$\widehat{\text{cov}} G_1 G_t = (\widehat{\text{cov}} P_1' P_t + \widehat{\text{cov}} P_t' P_1) - 1\frac{1}{4} \widehat{\text{cov}} G_1 G_{mt}.$$

The genetic correlation (R'_g) between each pair of these characters was then found as a ratio of genetic covariance ($\text{cov } GG''$) to the product of the respective genetic standard deviations ($\sigma_{G''}$ $\sigma_{G'}$), thus:

$$\widehat{R}'_g = \widehat{\text{cov}} GG'' / \widehat{\sigma}_{G'} \widehat{\sigma}_{G''}.$$

The genetic standard deviation of weaning weight used in this case was that obtained from the paternal half-sib analysis.

(iv) Computation of covariance between dam
and daughter

The data were initially sorted into groups according to year in which the offspring was born. Within each offspring year-of-birth group, the records were further sub-divided based on year in which the dam was born. For each sub-group, the dams were comparable in year of birth and the offspring, comparable in year of birth and age of dam. The records in each sub-group were adjusted for environmental differences as follows:

(a) The records of live weight and number of hogget oestrus of the daughter were adjusted for difference in type of birth and rearing. The weaning weight of a fostered wether lamb was made comparable with that of a ewe lamb by subtracting three pounds, being the average difference between ewe and wether

lambs in this flock (Ch'ang and Rae 1961). The records of live weight and number of hogget oestrus of the dam were adjusted for differences in age of dam and type of birth and rearing by the same correction factors as those used in the paternal half-sib analysis.

(b) The fertility records of the dam were adjusted for difference in age of dam, the correction factors being the same as those used in the paternal half-sib analysis. The fertility records of either the dam or the daughter were not adjusted for difference in type of birth. However, in a separate analysis the fertility records were adjusted for both the age of dam and type of birth and rearing effects, so that estimates of genetic variance in fertility of the ewe by these two methods of data correction could be compared.

The sum of squares for the daughter and the dam, the cross-products between daughter and dam and the degrees of freedom were computed for the data in each sub-group. These results were then pooled over the sub-groups to form the variance and covariance matrix used in the estimation of heritabilities and genetic correlations.

5. Construction of selection indices

The principles underlying the construction of a selection index for genetic improvement have been outlined by Hazel (1943). More recently, Kempthorne and Nordskog (1959) and Tallis (1962) have shown that restrictions may be built into an index so that the expected changes in additive genetic values for certain characters are equal to the amounts previously specified. For instance, an index may be constructed so that the average additive genetic value of a given character remains unchanged while the genetic improvement in other characters is allowed to proceed at the maximal rate. Whether or not restrictions are imposed on the characters under study, the statistical problem in constructing an index is to find a linear function of the observed variables which has a maximum correlation with the specified criterion of improvement.

In the present study, selection indices each based on two hogget characters were constructed using different criteria for purpose of predicting changes in either the additive genetic value or phenotype of fertility in the ewe. The relative efficiencies of the indices were evaluated by comparison both among the indices themselves and each with genetic improvement resulting from direct selection for higher fertility. The general form of an index may be stated as:

$$I_i = \sum_{1j} b_{1j} P_{1j} \quad \text{where}$$

$i = 1, 2 \text{ or } 3$ referring to the particular criterion according to which the i^{th} index is constructed and $j = 1 \text{ and } 2$ denoting number of hogget oestrus and hogget body weight respectively.

The b_{1j} therefore is the weighting factor of the j^{th} hogget character in the i^{th} index. All indices except the first were constructed so that the correlation between each index and the additive genetic value (G_{yk}) or phenotype (P_{yk}) of the k^{th} measurement of fertility in the ewe was a maximum. Since no new principles are involved, the description of index construction will be given in terms G_y or in other words, the genetic improvement of fertility in the ewe.

The first index (I_1) was constructed so that r_{I_1H} was a maximum where $H = G_1 + G_2$, the G_1 and G_2 being the additive genetic values of number of hogget oestrus and hogget body weight respectively. The present viewpoint was to regard changes in additive genetic value of either hogget character as being equally desirable. This appeared reasonable since neither character under the current system of flock management contribute directly to financial returns of the farm. The intention therefore was to produce in the first place, maximum genetic change in the aggregate genetic values of the hogget characters (H) and second, to evaluate the correlated response in fertility of the ewe based on properties of the index thus constructed. The r_{I_1H} was initially differentiated with respect to b_{1j} and then the first derivatives were equated to zero. The values of b_{11} and b_{12} were found by solving the following pair of simultaneous equations:

$$b_{11} \hat{\sigma}_{P_1}^2 + b_{12} \widehat{\text{cov}} P_1 P_2 = \hat{\sigma}_{G_1}^2 + \widehat{\text{cov}} G_1 G_2$$

$$b_{11} \widehat{\text{cov}} P_1 P_2 + b_{12} \hat{\sigma}_{P_2}^2 = \hat{\sigma}_{G_2}^2 + \widehat{\text{cov}} G_1 G_2$$

The second criterion used to construct a series of indices, denoted in general by I_2 , was the maximum correlation between I_2 and G_y or P_y . The $r_{I_2 G_y}$ (or $r_{I_2 P_y}$) was differentiated with respect to b_{2j} and the first derivatives equated to zero yielding the following equations:

$$b_{21} \hat{\sigma}_{P_1}^2 + b_{22} \widehat{\text{cov}} P_1 P_2 = \widehat{\text{cov}} G_1 G_y \text{ (or } \widehat{\text{cov}} P_1 P_y \text{)}$$

$$b_{21} \widehat{\text{cov}} P_1 P_2 + b_{22} \hat{\sigma}_{P_2}^2 = \widehat{\text{cov}} G_2 G_y \text{ (or } \widehat{\text{cov}} P_2 P_y \text{)}$$

The process described above led to two types of indices; one intended to cause phenotypic improvement (I_{2P}) and the other, genetic improvement (I_{2G}) in fertility of the ewe. Since the individuals selected according to I_{2P} and I_{2G} may or may not be the same depending on the correlation between I_{2P} and I_{2G} , it appears desirable to construct a general purpose index (I'_2) in such a way so that optimal improvement both in the same and the next generation, of fertility may be achieved. The problem then is to find the weighting factors β_{21} and β_{22} so that the correlation between I'_2 and I_{GP} is a maximum. The I'_2 and I_{GP} may be defined as follows:

$$I'_2 = \beta_{21} P_1 + \beta_{22} P_2$$

$$I_{GP} = C I_G + D I_P \text{ where } C \text{ and } D$$

are the amounts of relative emphasis to be placed on I_G and I_P respectively. Let $I_G = b_{G1} P_1 + b_{G2} P_2$ and $I_P = b_{P1} P_1 + b_{P2} P_2$, I_{GP} may then be written as:

$$I_{GP} = (C b_{G1} + D b_{P1}) P_1 + (C b_{G2} + D b_{P2}) P_2 \text{ or}$$

more simply, $I_{GP} = t_1 P_1 + t_2 P_2$ where $t_1 = (C b_{G1} + D b_{P1})$ and $t_2 = (C b_{G2} + D b_{P2})$. By differentiating $r_{I'_2 I_{GP}}$ with respect

to β_{21} and β_{22} and equating the first derivatives to zero, the following equations were obtained:

$$\beta_{21} : t_1 \hat{\sigma}_{P_1}^2 + t_2 \widehat{\text{cov}} P_1 P_2 = \beta_{21} \hat{\sigma}_{P_1}^2 + \beta_{22} \widehat{\text{cov}} P_1 P_2$$

$$\beta_{22} : t_1 \widehat{\text{cov}} P_1 P_2 + t_2 \hat{\sigma}_{P_2}^2 = \beta_{21} \widehat{\text{cov}} P_1 P_2 + \beta_{22} \hat{\sigma}_{P_2}^2$$

Since the values of C and D are unknown, the results may be more conveniently expressed in matrix notation:

$$\begin{bmatrix} B_{21} \\ B_{22} \end{bmatrix} = \begin{bmatrix} b_{G1} & b_{P1} \\ b_{G2} & b_{P2} \end{bmatrix} \cdot \begin{bmatrix} C \\ D \end{bmatrix}$$

In the event that equal emphasis is placed on genetic and phenotypic improvement of fertility, $C = D = 1$ the particular solutions are:

$$\hat{\beta}_{21} = \hat{b}_{G1} + \hat{b}_{P1} \quad \text{and} \quad \hat{\beta}_{22} = \hat{b}_{G2} + \hat{b}_{P2}.$$

The third criterion used to construct a series of indices denoted in general by I_3 , was the same as that used in constructing I_2 except a restriction was imposed so that $b_{31} \text{cov } G_1 G_m + b_{32} \text{cov } G_2 G_m = 0$ where G_m is the additive genetic value of maternal environment. A comparison between the properties of corresponding I_2 and I_3 was considered as one way to provide some information on the importance of carryover maternal effect on genetic improvement by indirect selection for fertility in the ewe. Accordingly, I_3 was constructed by maximising the expression

$$r_{I_3 G_y} \quad (\text{or } r_{I_3 P_y}) + \lambda (b_{31} \text{cov } G_1 G_m + b_{32} \text{cov } G_2 G_m)$$

in which the λ is an undetermined Lagrange's multiplier.

The normal equations resulting from partial differentiation of the above expression with respect to b_{3j} were:

$$b_{31} \hat{\sigma}_{P_1}^2 + b_{32} \widehat{\text{cov}} P_1 P_2 + \widehat{\text{cov}} G_1 G_m = \widehat{\text{cov}} G_1 G_y \text{ (or } \widehat{\text{cov}} P_1 P_y \text{)}$$

$$b_{31} \widehat{\text{cov}} P_1 P_2 + b_{32} \hat{\sigma}_{P_2}^2 + \widehat{\text{cov}} G_2 G_m = \widehat{\text{cov}} G_2 G_y \text{ (or } \widehat{\text{cov}} P_1 P_y \text{)}$$

$$b_{31} \widehat{\text{cov}} G_1 G_m + b_{32} \widehat{\text{cov}} G_2 G_m = 0$$

These equations were solved to find b_{31} and b_{32} for each set of data. Using the principles outlined earlier, a general purpose index (I'_3) was also constructed based on I_{3P} and I_{3G} . Further details of these and other selection indices will be given later in the results.

The values of variances and co-variances used in computing the selection indices described in this section were, except for $\widehat{\text{cov}} G_1 G_m$ and $\widehat{\text{cov}} G_2 G_m$ being those obtained by the paternal half-sib analysis. The genetic covariances involving the maternal environment used in constructing each I_3 were those given by the dam-daughter covariance analysis.

IV. RESULTS AND DISCUSSION

1. Estimates of environmental effects

The main purpose of estimating environmental effects was to provide correction factors for each character used in the present study. The use of additive correction factors is the most convenient and a widely adopted procedure for reducing the amount of environmental variation in the data prior to genetic analysis. Consequently, the extent to which the correction factors may depart from additivity is a part of the problem in their estimation and application. The method of analysis of variance was used to detect the presence of a first-order interaction between age of dam and type of birth and rearing in the hogget data. Since a serious departure from additivity would affect the derivation and accuracy of correction factors, the results obtained from the study of interaction effects will be presented first.

(a) Interaction between age of dam and type of birth and rearing

The hogget data used in the analysis were based on 691 individuals born over the period from 1955 to 1961 inclusive. The values of mean squares (MS) and the degrees of freedom (d. f.) used in the test for presence of an interaction effect are presented in Table 1.

Table 1. Estimates of Mean Squares

Character	Interaction MS	Error MS	Error MS
Wean. wt.	175.3*	58.2	58.9
March L. wt.	189.6*	73.7	74.4
Short. -day L. wt.	121.3	86.9	87.1
Hogg. B. wt.	212.8	122.4	123.0
No. Hogg. oestrus	3.3	2.9	2.9
d. f.	4	675	679

* denotes significance at the five per cent level.

The values shown in the last column of Table 1 were the estimates of error mean squares obtained using the reduced model in which the interaction effects were assumed to be equal to zero.

The test of significance showed that interaction between age of dam and type of birth and rearing was present in weaning weight and March live weight. The presence of an interaction implies that the sub-class means are dependent on not only the main effects but also a joint effect between the main classifications. Furthermore, a precise interpretation of the main effects in the presence of an interaction between them is not possible since an appropriate error term is not available for test of significance of the main effects.

The observed significant interactions in the present data

have raised a number of problems in relation to the development of correction factors for weaning and March live weight measurements. A major problem is concerned with assessing the practical importance of the significant interactions. For example, if one of the main classifications could be regarded as a random effect, its practical importance may be evaluated by variance component analysis. However, in so far as their effects on live weight measurements are concerned and taking into consideration the population represented by the mathematical model, it appeared more appropriate to regard age of dam and type of birth and rearing as fixed rather than random classifications (Wilk and Kempthorne 1955).

In order to provide some information on the practical significance of the observed interaction effects, two steps were taken. First, the values of error mean squares found using the 'interaction' model were compared with those calculated according to the 'reduced' model. A close agreement existed in value between the corresponding error mean squares which were presented in Table 1. The empirical evidence suggests that the extent of departure from linearity between age of dam and type of birth and rearing in the weaning and March live weight data has only a negligible practical significance. This was thought to be reasonable, considering the approximations generally involved in the use of correction factors as a method for reducing environmental variation in the data. A further step taken to assess the practical implications of the observed interactions was to estimate the values of interaction effects in the weaning weight and March

live weight data. The estimates of these and other environmental effects are presented in the next section.

(b) Estimates of environmental effects on
hogget characters.

The symbol used to represent each environmental effect has been specified previously as part of the description of the model. In brief, the symbols and the subscripts used were: year of birth effect (r_1); age of dam effect (a_j) where two-, three-year old and mature ewes were represented by a_1 , a_2 and a_3 respectively; type of birth and rearing effect (b_k) where the single, twin reared singly and twin were denoted by b_1 , b_2 and b_3 respectively. The partial regression on date of birth expressed in days, was designated as β . These symbols will be used in Table 2 in which for each character, a mean (μ), a standard deviation (σ) derived from the appropriate error mean square and the estimates of environmental effects are presented.

Table 2. Estimates of Environmental Effects on Hogget Characters

Character	Wean wt.	March L.wt.	Wean wt.	March L.wt.	Short. - day L.wt.	Hogg. B.wt.	No. Hogg. oestrus
$\hat{\mu}$	55.7	67.7	55.5	67.6	78.7	86.2	2.38
$\hat{\sigma}$	7.6	8.6	7.7	8.6	9.3	11.4	1.70
Year of Birth							
1955	2.3	- 0.3	2.2	- 0.4	- 2.0	7.3	- 0.15
1956	9.5	3.6	9.5	3.7	7.8	0.5	1.25
1957	7.3	1.4	7.2	1.3	0.2	- 1.0	- 0.56
1958	- 0.7	0.3	- 0.8	0.1	2.9	1.5	0.01
1959	- 2.3	0.4	- 2.1	0.6	- 4.2	3.0	- 0.09
1960	- 6.3	1.5	- 6.2	1.6	1.9	- 6.3	0.13
1961	- 9.9	- 6.9	- 9.8	- 6.9	- 6.6	- 5.0	- 0.60
Age of Dam							
$\hat{a}_3 - \hat{a}_1$	3.0	2.7	4.5	4.2	5.3	5.3	0.45
$\hat{a}_3 - \hat{a}_2$	0.9	1.0	0.9	1.0	2.0	2.1	0.42
Type of Birth and Rearing							
$\hat{b}_1 - \hat{b}_3$	9.5	7.2	9.3	6.9	6.0	4.9	0.07
$\hat{b}_2 - \hat{b}_3$	7.2	5.0	6.4	4.0	3.2	0.9	0.33
Partial Regression	- 0.26	- 0.22	- 0.26	- 0.22	- 0.19	- 0.18	- 0.036
Interaction							
$(\hat{ab})_{11}$	- 1.9	- 1.7					
$(\hat{ab})_{12}$	2.5	2.6					
$(\hat{ab})_{13}$	- 0.6	- 0.9					
$(\hat{ab})_{21}$	1.5	1.6					
$(\hat{ab})_{22}$	- 1.0	- 1.1					
$(\hat{ab})_{23}$	- 0.5	- 0.5					
$(\hat{ab})_{31}$	0.4	0.1					
$(\hat{ab})_{32}$	- 1.4	- 1.4					
$(\hat{ab})_{33}$	1.0	1.3					

The statistical significance of environmental effects was tested using analysis of variance. The values of the mean squares and the degrees of freedom used in the test of significance are presented in Table 3.

Table 3. Estimates of Mean Squares

Character	Error		Age of Dam	Type of Birth and rearing	Partial Regression
	d. f.	MS	d. f. = 2	d. f. = 2	d. f. = 1
Wean. wt.	675	58.2	—	—	5,496.4 **
March. L.wt.	675	73.7	—	—	4,096.2 **
Short.-day L. wt.	679	87.1	1,964.8 **	2,481.7 **	3,033.0 **
Hogg. B.wt.	679	123.0	1,988.2 **	1,699.3 **	2,708.3 **
No. Hogg. Oestrus	679	2.9	22.6 **	6.5	107.4 **

** denotes statistical significance at the one per cent level.

Although the year of birth effects were estimated and presented in Table 2, their statistical significance was not tested since a specific interpretation of the 'year' effect is seldom possible. However, it is of some interest to note that the estimates of 'year' effect on weaning weight exhibited a trend in time. Since the 'year' effect was caused by factors such as nutrition, climate and management peculiar to each year, the observed trend suggested that at least one of the factors had an adverse effect on weaning weight which became more pronounced each year over the period from 1956 to 1961 inclusive. The

alternative suggestion of a gradual deterioration in genetic merit of weaning weight in this flock was possible in view of the partial confounding between year and sire effect in the present data. However, the latter suggestion was considered unlikely to be the real cause of the observed trend since the sires were not selected either for a high or low expression in weaning weight or with respect to other characters used in this study. The known circumstances surrounding the management of the ewe flock between lambing and weaning appear to offer the most likely explanation of the observed 'year' trend. It has been described earlier that size of the ewe flock was increased each year by taking into the breeding flock all available replacements. Thus, the number of ewes rose from 180 in 1956 to 329 in 1961 at mating although the area on which the lactating ewes and their lambs were kept, had remained relatively constant in size and pastures unimproved over the years in question. The net result was presumably a gradual reduction in plane of nutrition between lambing and weaning. Since nutritional effect on the level of milk production and the relationship between milk production and growth of the lamb are well known (Wallace 1948; Barnicoat, Logan and Grant 1949), the observed trend in 'year' effect on weaning weight is likely to be nutritional in origin.

Another aspect of the data presented in Table 2 which requires some comment prior to the general discussion of results is the estimates of interaction effect $(ab)_{jk}$ on weaning weight and March live weight. The larger estimates, in absolute values tended to be associated with b_2 (twin reared singly) and with a_1 and a_2 (two- and three-year old dams respectively).

Since relatively few twins were reared singly, the values of $(\widehat{ab})_{j2}$ were much affected by sampling errors. Any interpretation based on these values would be unreliable. The less frequent occurrence of twins reared singly, also meant that correction factors constructed ignoring this source of interaction effect would be satisfactory for most practical purposes. Among the remaining estimates of interaction effects, the values of $(\widehat{ab})_{11}$ (single reared by two-year-old dam) and $(\widehat{ab})_{21}$ (single reared by three-year-old dam) were larger than those of the others. The mechanism giving rise to these interaction effects is not known although the values themselves may be a reflection of inadequacy of the model in which other and higher order interactions have been ignored. Whatever was the real reason, since the values of $(\widehat{ab})_{11}$ and $(\widehat{ab})_{21}$ were only moderate in size, they were considered unlikely to cause undue bias in the additive correction factors constructed without reference to their contribution. However, presence of the interactions in weaning weight and March live weight data did result in modification of the procedure used in testing the main effects. In other words, statistical significance of the effects due to age of dam and type of birth and rearing on weaning weight and March live weight was not tested, as an appropriate error mean square was not available.

(c) Estimates of environmental effects on
fertility of the ewe.

It is known from general knowledge that the level of fertility in the ewe varies between years. It is also clear from published information (see for example, Reeve and Robertson 1953) that the average fertility differs between ewes dependent on whether the ewes themselves were born as singles or as twins. However, no published information appears to exist on the effects due to age of dam on fertility of the ewe. The present analysis was undertaken to provide some information on variation in fertility of the ewe attributable to the various sources cited above. The data used for this purpose were based on the individuals born over a total period of eight years. More specifically, the records of number of lambs born per ewe at the first lambing (Fert. 1) and over the first two lambings (Fert. 2) were collected from the ewes born in the period from 1955 to 1962 inclusive. The records of number of lambs born per ewe over the first three lambings (Fert. 3) were based on the ewes born in the period from 1955 to 1961 inclusive.

The mean, the standard deviation derived from the error mean square and degrees of freedom for each measurement of fertility and the environmental effects are presented in Table 4.

**Table 4. Estimates of Environmental Effects
on Fertility of the Ewe**

Character	Fert. 1	Fert. 2	Fert. 3
$\hat{\mu}$	0.939	2.098	3.457
$\hat{\sigma}$	0.660	1.019	1.381
d.f.	773	729	583
Year of Birth			
1955	0.008	0.364	0.499
1956	0.207	0.066	- 0.022
1957	- 0.136	- 0.324	- 0.144
1958	0.016	0.113	- 0.238
1959	0.125	- 0.065	0.137
1960	- 0.325	- 0.237	- 0.214
1961	0.065	0.094	0.018
1962	0.040	- 0.011	—
Age of Dam			
$\hat{a}_3 - \hat{a}_1$	- 0.081	- 0.032	- 0.113
$\hat{a}_3 - \hat{a}_2$	- 0.050	0.020	0.039
Type of Birth and Rearing			
$\hat{b}_1 - \hat{b}_3$	- 0.113	- 0.242	- 0.386
$\hat{b}_2 - \hat{b}_3$	0.016	0.026	0.153

The estimates presented in Table 4 were found according to the least-square procedure and the values appeared reasonable

as measures of the magnitude of the various effects studied. The statistical significance of the estimates however is unknown because some doubt exists as to validity of a test based on analysis of variance in the type of data such as the present. However, the data presented in Table 4 are useful as a summary of background information on variation in fertility of the ewes in this flock. A brief discussion of the results will be made at a later stage.

Discussion

With few exceptions, no published information is available for comparison with the results presented above. For this reason and since the various estimates such as the mean, the standard deviation and the environmental effects are self-explanatory, a detailed discussion of each result appears unnecessary. It is proposed therefore, to discuss only a few aspects either because a comparison with the literature merits comment or a discernable pattern is suggested by the data.

(i) Weaning weight

A considerable amount of information exists in the literature in so far as environmental effects on weaning weight is concerned (Hazel and Terrill 1945 and 1946, Sidwell and Grandstaff 1949, Blackwell and Henderson 1955; Ch'ang and Rae 1961). In view of the observed interaction between age of dam and type of birth and rearing classifications in the present data, two sets of environmental effects on weaning and March live weight were presented in Table 2 for purpose of comparison. The corresponding values of the main effects showed close agreement between the two sets of estimates, thus providing further evidence in support of the earlier suggestion that the observed significant interaction did not represent a serious departure from additivity. This conclusion is in line with what is generally found in other studies (Hazel and Terrill 1945 and 1946; Ch'ang and Rae 1961) which using a similar model as the present, showed that departure from additivity was not significant in all first-order interactions.

Among the main environmental effects on weaning weight, type of birth is the most important. The present estimates, in the order of nine to 10 lb in favour of the single are typical of those within the range of values reported in most of the other studies cited earlier. The present estimates of age of dam effect and regression on age (date of birth) are also within the range of values found in the literature. In general, it appeared reasonable to conclude that additive correction factors constructed from the linear estimates of environmental effects, being simple in application, may be used with a minimum loss of accuracy.

(11) Compensatory growth in live weight

Although the interpretation of individual effects for age of dam and type of birth and rearing on live weight measurements presented in Table 2 is made difficult because the statistical significance of these effects on weaning weight and March live weight is unknown, the contrasting pattern of effects between them over the hogget period require at least a comment. Taking estimates based on the reduced model at their face value, over the period from weaning to post-hogget shearing the type of birth and rearing effects may be seen at first, rapidly and later slowly diminishing in size, whereas age of dam effects remained relatively stable. In other words, the individuals born and reared as twins, compared with the singles or twins reared singly tended to grow at a faster rate - exhibiting the phenomenon of compensatory growth (Wilson and Osbourn 1960) over the hogget period.

The individuals reared by younger dams, while on average being somewhat lower in weaning weight than those reared by mature dams, were apparently insufficiently depressed in pre-weaning growth - a pre-requisite for occurrence of compensatory growth; thus their pattern of growth was different from that of the more severely handicapped twins during the hogget stage.

(111) Number of hogget oestrus

The average number of (overt) oestrus per ewe hogget in the present data was 2.4, being similar to the value of 2.0 reported by Hafez (1952) for this character in the Kentish Romney Marsh breed at Cambridge, England.

The results presented in Tables 2 and 3 showed that number of hogget oestrus was little affected by year of birth and type of birth and rearing, but age of dam effects on this character were real and relatively large in value. In the light of the results presented by Hafez (1952) and Allen and Lamming (1961) which suggest a positive relationship between growth in live weight and occurrence of first oestrus or puberty in the ewe, the contrasting effects between age of dam and type of birth and rearing on number of hogget oestrus in the present data are interesting since they imply the contrary to what has been reported on this topic. In other words, it appears reasonable to expect a relatively large type of birth and rearing effect on a number of hogget oestrus in comparison with that due to age of dam as the former tends to be a somewhat larger effect on live weight of the individual. The contradiction may be resolved

in part at least, if the post-weaning compensatory growth of the twins discussed earlier, can be supposed as a major source of variation in number of hogget oestrus. Since the relative importance of several factors including the post-weaning live weight growth on variation in number of hogget oestrus has been studied and the results to be presented elsewhere, further discussion on this topic will be postponed until a later stage.

(iv) Fertility of the ewe

The estimates of year of birth, age of dam and type of birth and rearing effects on each of the three measurements of fertility were presented in Table 4. The year of birth effects showed no definite pattern. The type of birth and rearing effects were both more consistent among the various measurements of fertility and larger in size than most of the effects due to age of dam. However, the effects of age of dam on fertility were considered sufficiently large to justify correcting the data for this source of environmental variation prior to genetic analysis.

In the present data, the tendency for ewes themselves born as twins to be higher in level of fertility than those born as singles is in accord with existing information from the literature (Reeve and Robertson 1953, Rae and Ch'ang 1955, Turner, Hayman, Triffitt and Prunster 1962; Dunn and Grewal 1963). Since type of birth effect on fertility may contain a genetic contribution from the dam and because its statistical significance is unknown, any interpretation of the values found in terms of an environmental or genetic effect is unlikely to be correct or reliable.

2. Sire-year interaction in hogget characters

It has been noted previously that the amount of data available for studying sire-year interaction was limited, being based on two consecutive two-year periods. Within each period, the same four sires were used in both years. In period I (1956 and 1957) and period II (1958 and 1959) a complete set of records of hogget characters were available for 102 and 187 individuals respectively.

The presence of sire-year interaction in the data of each period was tested using analysis of variance as described in section III 2. The values of mean squares calculated and used for the test of significance are presented in Table 5.

Table 5. Estimates of Mean Squares
(Sire-year d.f. = 3)
(Error d.f. = 89 Period I, Error d.f. = 174 Period II)

Character	Interaction MS		Error MS	
	Period I	Period II	Period I	Period II
Wean. wt.	27.9	39.8	60.7	47.8
March L. wt.	26.7	8.2	72.1	65.1
Short.-Day L. wt.	40.8	37.3	81.0	73.0
Hogg. B. wt.	216.0	32.1	105.4	92.6
No. Hogg. oestrus	0.8	7.0*	3.3	2.6

* denotes statistical significance at the five per cent level.

Although the results presented in Table 5 would require confirmation for purpose of generalisation, absence of important heredity-environment interactions appears to be typical for many

of the characters in the sheep thus far investigated (see Dunlop 1963). The only character - number of hogget oestrus in the present data which showed a significant sire-year interaction did so, only barely in the sense that the calculated F - value exceeded its expectation only by a negligible amount. Even for this character, the sire-year interactions were inconsistent between periods I and II. Therefore, it appears reasonable to conclude that for the hogget data used here and elsewhere in the present study, sire-year interaction may be regarded as a negligible source of variation. The practical importance in terms of variance components, of the sire-year interaction was not evaluated since the result would be unreliable in view of the small number of degrees of freedom available for its estimation.

3. Preliminary results based on analysis of annual fertility of the ewe

The relationships among number of hogget oestrus, type of birth of the ewe itself and annual fertility at each of the four lambings have been studied using different methods of analysis as described in section III 3. For a particular lambing the same data were used in each method of analysis, the data being those available from the ewes born over the period between 1955 to 1961 inclusive. As an example, the data at two-year-old lambing expressed as number of ewes classified according to the reproductive attributes: barrenness, single - and twin - births, in each type of birth by number of hogget oestrus sub-class are presented in Table 6.

Table 6. Two-year-old Reproductive Performance
(1957 to 1963)

Type of Birth of the ewe	Single				Multiple			
No. Hogg-oestrus	Barren	Single	Twin	Lambing Per Cent	Barren	Single	Twin	Lambing Per Cent
0	31	31	5	61	21	49	11 *	89
1	14	31	4	80	9	34	3	87
2	19	21	13	89	18	36	15	96
3	12	24	7	88	12	38	12	100
4	15	28	12*	96	10	21	16 ^{2*}	117
5 or more	8	19	6	94	6	29	14 ^{2*}	120

* Triplet birth

The lambing per cent of the ewes, differing in number of hogget oestrus presented in Table 6, was calculated from the ratio of the number of lambs born per ewe mated, excluding the ewes which died prior to lambing.

The data shown in Table 6 may be analysed to provide information in two ways. First, using the chi-square method, the differences among the proportions of ewes classified in various ways may be tested for statistical significance. Second and the more meaningful analysis is to detect significant trends in the data with the ordering of the various classifications. For the present data and those at other lambings, a weighted and the least-squares regression analyses were used to provide some information on the linear relationship between number of hogget oestrus and annual fertility of the ewe.

(a) Test of mutual independence by
chi-square analysis

The composite hypothesis of mutual independence (H_0) among number of hogget oestrus, type of birth and reproductive attributes of the ewe at each of the four lambings has been tested using the chi-square method. The values of chi-square calculated under the composite hypothesis and where applicable for each sub-hypothesis are presented in Table 7.

Table 7. Values of Chi-square associated with
Hypotheses of Independence

H_0 : Mutual independence

H_{01} : Independence between number of hogget oestrus
and reproductive attributes at lambing

H_{02} : Conditional independence between type of
birth of the ewe and reproductive attributes
at lambing, given the number of hogget oestrus

H_{03} : Independence between type of birth of the
individual and number of hogget oestrus

Hypothesis	d. f.	Two-year- old	Three-year- old	Four-year- old	Five-year- old
H_0	27	55.2 **	49.5 **	21.9	41.1 *
H_{01}	10	30.0 **	11.2	-	17.2
H_{02}	12	16.1	29.5 **	-	20.9
H_{03}	5	6.3	8.9	-	4.3
No. of ewes		654	488	355	249

* and ** denote statistical significance at the five and one per cent levels respectively.

The values of chi-square presented in the first row of Table 7 suggest that the composite hypothesis of mutual independence (H_0) may be rejected in all cases except the third lambing at four years of age. Accordingly, for each rejected composite hypothesis three sub-hypotheses H_{01} , H_{02} and H_{03} as specified above, were formed so that the observed dependence could be studied more specifically.

The chi-square values associated with H_{01} and H_{02} shown in Table 7 have provided some but not clear cut evidence of associ-

ation between reproductive attributes and number of hogget oestrus (H_{01}) or type of birth (H_{02}) of the ewe. For example, significant differences in the proportions of ewes classified according to the reproductive attributes among the various hogget oestrus classes were found at the two-year-old but not at the other lambings. The same was true for type of birth, except the significant chi-square value was observed at the three-year-old lambing. For the final lambing at five-year-old, the chi-square values computed from the data under the sub-hypotheses did not attain, although those associated with H_{01} and H_{02} were approaching significance at the five per cent level.

In contrast to the results described above, the chi-square values calculated from the data under H_{03} showed more definite evidence of independence between type of birth of the ewe and number of hogget oestrus. This finding is consistent with the earlier conclusion based on the least-squares analysis which showed a negligible difference in average number of hogget oestrus between individuals born as singles and as twins (see Table 2).

The data have provided insufficient evidence to reject the composite hypothesis of mutual independence (H_0) at the four-year-old lambing. An explanation for this result, being different from those at the other lambings, is not available except to note that the ewes at this age are approaching or have reached the peak of their reproductive ability. The main difference in reproductive attributes between ewes, classified according to

either number of hogget oestrus or its own type of birth is therefore likely to be based on variation in the proportion of single - and twin - births because the incidence of barrenness is, in general at a much lower level at this age than previous lambings. The nature of the association under investigation as a consequence, is somewhat different. In addition, the model used may not be adequate for example, the three-way interaction among number of hogget oestrus, type of birth and age of the ewe at lambing assumed to be negligible in the data, might have also contributed to the present result.

Since neither arbitrary scales nor a priori knowledge of the underlying distribution of the data is necessary for analysis by chi-square, this method may be expected to provide information, useful as an alternative to that given by other types of analyses. However, the conservative nature of the chi-square test (Cochran 1954) and the unknown sources of variation not taken into consideration in the present analysis are factors likely to be responsible in part at least, for the complexity observed in the results.

(b) Weighted and least-squares regression of
 annual fertility of the ewe on number
 of hogget oestrus

The regression of annual fertility of the ewe at each lambing on number of hogget oestrus was estimated using two methods. Both the weighted and the least-squares regression analyses required the use of arbitrary scores but differed in respect to the assumptions, made for purpose of tests of significance as

outlined in section III, 3 (a) and (b). The assumption of a normal distribution in the fertility data by the least-squares analysis leads to an exact test of significance but the mean squares, used for this purpose, may be either under - or over - estimated depending on the extent of departure from normality. The test of significance of the weighted regression coefficient is only approximate, in the sense that it is asymptotically efficient for large samples. While neither method is completely satisfactory, each is expected to provide some useful information on the relationship between annual fertility of the ewe and number of hogget oestrus. For purpose of comparison, the weighted and the least-squares regression coefficients (b) together with the standard errors (σ_b) of the former coefficients are presented in Table 8.

Table 8. Estimates of Regression Coefficient of Annual Fertility on Number of Hogget Oestrus

Methods		Weighted Regression			Least-squares Regression	No. of Ewes
Age of Ewe	Type of Birth	$\hat{b}$	$\hat{\sigma}_b$	a. P	$\hat{b}$	
Two-year-old	Single Twin	0.064**	0.022	0.002	0.072**	300
		0.064**	0.020	0.001	0.076**	354
Three-year-old	Single Twin	0.009	0.024	0.350	0.004	244
		0.052*	0.026	0.020	0.060*	244
Four-year-old	Single Twin	-0.042	0.034	0.113	-0.026	169
		0.003	0.023	0.456	0.009	186
Five-year-old	Single Twin	0.100**	0.040	0.006	0.047	113
		0.088**	0.036	0.008	0.080*	136

a. Probability (P) based on the table of normal integral (Fisher and Yates 1953).

* and ** denote significance at the five and one per cent levels respectively.

The corresponding weighted and least-squares regression coefficients presented in Table 8 showed close agreement in value and reasonable agreement in so far as tests of significance were concerned. The pattern of relationship shown by either regression analysis is consistent with the previous observations using the chi-square method. In particular, the hypothesis of independence between fertility of the ewe and number of hogget oestrus at the four-year-old lambing is confirmed by results based on the present methods of analyses. As mentioned earlier a definite explanation for this result is not available. However, whatever is the real cause of the observed discrepancy, the net effect is less accurate prediction of life-time fertility based on oestrous performance of the ewe at the hogget stage.

In general, apart from the four-year-old lambing the present results suggest that the relationship between number of oestrus recorded at the hogget stage and subsequent fertility of the ewe is positive. The values of the significant regression coefficients presented in Table 8 showed that for each additional hogget oestrus, the average increase in fertility is in the range between 0.05 to 0.10 of a lamb or five to 10 per cent increase in lambing percentage.

In a preliminary report by Wiggins (1955), some evidence for a positive relationship between occurrence of oestrus and level of fertility in the ewe at the first lambing was found in Rambouillet and Columbia but not in the Targhee breed. These results were presented in terms of occurrence or non-

occurrence of oestrus at the hogget stage and the proportion of barren ewes, thus a detailed comparison with the present findings did not appear to be warranted. However, it was thought necessary to cite the above study since it represented the only source of published information on this subject based on the sheep, known to the writer.

Finally, the available evidence showed that the different methods used in the present analysis did not lead to any contradictions in results. The evidence suggests that provided the sample size is not unduly small, the different assumptions made about distributional properties of the fertility data have had in this case, little influence on interpretation of the results. A similar conclusion was also reached by Young, Turner and Dolling (1963) in a study of inheritance of fertility in the Merino ewe. For the remaining analyses in the present investigation involving fertility of the ewe, it was therefore decided to make the assumption of normality for purpose of tests of significance or calculation of sampling errors in order to provide an approximate guide for the interpretation of results.

4. Estimates of phenotypic correlations

The method used to estimate phenotypic correlations has been described in section III 4 (a). In brief, a phenotypic correlation coefficient was calculated as the ratio of covariance to the product of the appropriate standard deviations derived from the data used in paternal half-sib analysis. Since the amount of data used varied according to the characters in question, it is convenient to present the results separately for the hogget characters among themselves and between each hogget character and the various measurements of fertility in the ewe.

(a) Hogget characters

The data used to estimate phenotypic correlations between each pair of hogget characters were based on 851 individuals born over the period from 1955 to 1963 inclusive.

Since the hogget data used in paternal half-sib analysis were adjusted, prior to calculation of mean squares or cross-products for differences in age of dam and type of birth and rearing, the within-year estimates of phenotypic correlations to be presented in Table 9 were also freed from the differences due to these sources.

Table 9. Estimates of Phenotypic Correlations (d. f. = 841)

Character	March Lwt.	Short.-day L.wt.	Hogg. B. wt.	Gain 1	Gain 2	Gain 3	No. Hogg. oestrus
Wean. wt.	0.82**	0.74**	0.62**	-0.14**	-0.10**	-0.05	0.39**
March Lwt.		0.89**	0.74**	0.45**	-0.17**	-0.05	0.44**
Short.-day L. wt.			0.85**	0.37**	0.31**	0.03	0.47**
Hogg. B.wt.				0.33**	0.28**	0.50**	0.43**
Gain 1					-0.13**	0.03	0.16**
Gain 2						0.03	0.10**
Gain 3							0.04

** denotes statistical significance at the one per cent level.

In order to provide a more complete description of live weight growth during the hogget stage, gains in live weight were also calculated and presented in Table 9. Thus Gain 1, Gain 2 and Gain 3 refer to the increment in live weight between weaning and March, March and the 'shortest-day' of the year and from the 'shortest-day' to post-hogget shearing in October respectively. The results showed that the various measurements of live weight, being related as a part to the whole, were all highly correlated among themselves as might be expected. Each of the post-weaning live weights was positively correlated with gain in weight during the preceding period, the coefficients being moderate in size.

The data also showed that there was a tendency for the weight already attained at weaning to be related inversely with the post-weaning weight gains. The values of correlation

coefficients between weaning weight and each post-weaning weight gain presented in Table 9 were all negative and relatively small, the values between weaning weight and gain in the first two periods being different from zero. These observations are consistent with the phenomenon of post-weaning compensatory growth discussed previously. It was of some interest to note the small but real, negative correlation between weight gains made in the first and second period (Gain 1 and Gain 2) post-weaning. This and other negative correlations mentioned above suggest a fluctuating pattern of growth in the ewe hogget from weaning to the 'shortest-day' of the year, a period which covers a major portion of the breeding season in the Romney ewe hogget under New Zealand conditions (Ch'ang and Raeside 1957; Lewis 1959).

The phenotypic correlations between each live weight or gain in live weight and number of hogget oestrus with no exception, were all positive. The potential influence of live weight growth induced experimentally by nutritional treatments, on date of first oestrus in the ewe hogget has been demonstrated by Allen and Laming (1961). In addition, live weight growth and chronological age of the individual have been suggested by Hafez (1952) as being important factors in relation to occurrence of first oestrus or puberty based on studies of several breeds of sheep. Since many of the live weight measurements, in one form or another are correlated among themselves and each with age (see Table 2, regression on date of birth), the relative importance of growth and age as factors affecting variation in occurrence of oestrus of the ewe hogget can not be assessed without

taking into consideration the correlational structure between them. In order to provide some information on this topic and to aid the interpretation of phenotypic correlations between number of hogget oestrus and the various weight measurements presented in Table 9, a study was made using Path-coefficient method (Wright 1934) to evaluate the relative importance of weaning weight, weight gains in periods 1 and 2 and chronological age of the individual on variation in number of hogget oestrus. The results are presented below.

(b) Relative importance of growth and age in the
determination of number of hogget oestrus

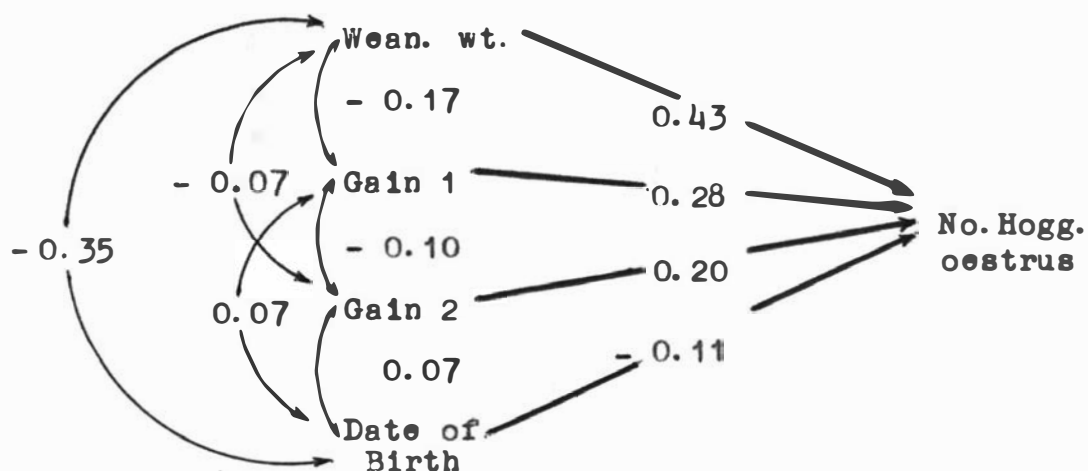
The correlations required for the Path-coefficient analysis were calculated from the same data as those used in the study of environmental effects on hogget characters since the sum of squares of age, measured by date of birth and crossproducts between it and the remaining characters were already available. Each correlation was based on 681 degrees of freedom as 10 degrees of freedom, having been utilised in adjusting the data for differences in the mean, year of birth, age of dam and type of birth and rearing, were subtracted from the total of 691 observations. The values of the correlation coefficients rounded to three places are presented in Table 10.

Table 10. Correlation Coefficients Used in the Path-coefficient Analysis (d. f. = 681)

Character	Gain 1	Gain 2	Date of Birth	No. Hogg. oestrus
Wean. wt.	-0.172	-0.072	-0.348	0.410
Gain 1		-0.100	0.074	0.074
Gain 2			0.073	0.134
Date of Birth				-0.228

The corresponding correlation coefficients presented in Table 10 above and in Table 9 based on more intensive data are similar in value.

The point of view taken in the study of relative importance of growth and age as factors determining variation in number of hogget oestrus may be more clearly represented by the Path-coefficient diagram below.



The values of the path-coefficients found have been inserted in the diagram above for ease of interpretation. Using Wright's

convention, the double-headed arrows denote the correlations while the single-headed arrows are paths of influence, from the postulated causes to the observed effect. The multiple correlation coefficient calculated according to the scheme of determination was 0.53, being statistically significant beyond the one per cent level and accounting for about a quarter of the total variation in number of hogget oestrus.

The scarcity of published information relevant to the present study has been indicated in a review on puberty in female farm animals by Joubert (1963). Since a sensible interpretation or suggestion of the underlying biological mechanism of the path-coefficients reported above depends, to a large extent on existing knowledge of this topic, the scope for discussion of the results is limited.

The present values of path-coefficients suggested that age, measured by date of birth was the least important, among the factors studied, source of variation in number of hogget oestrus; its influence being about a half and a quarter of that as post-weaning weight gains and weaning weight respectively. A slightly greater influence on number of hogget oestrus was noted for weight gain made during the first period (Gain 1) between weaning and March, than that in the second period (Gain 2) from March to the 'shortest-day' of the year. These two 'growth' periods appeared particularly relevant to the study of variation in number of hogget oestrus, since the first and the second period corresponded to growth in live weight made prior to the start and during a major portion of the breeding season in the Romney ewe hogget under New Zealand conditions (Ch'ang and Raeside 1957;

Lewis 1959). By far the most important factor, under the present formulation, affecting variation in number of hogget oestrus is weaning weight. Since much of the growth in live weight pre-weaning, is dependent among other factors, on milk supply of the dam, the carryover maternal effect may well represent an indirect source of variation in number of hogget oestrus.

(c) Hogget characters and fertility of the ewe

The amount of data used in estimating phenotypic correlations between a hogget character and each of the three measurements of fertility differed slightly depending on the particular measurement of fertility in question. Since the data available for present analysis were based on individuals born over a total period of nine years from 1955 to 1963 inclusive, the year 1965 was the terminal year for the fertility data collection. Thus, the data used for studying phenotypic correlations between each hogget character and Fert. 1 were based on those individuals born over the entire period from 1955 to 1963 inclusive; between each hogget character and Fert. 2, from 1955 to 1962 and between each hogget character and Fert. 3, from 1955 to 1961 inclusive. In view of the unavoidable selection of data for purpose of the present analysis because either the ewe had died, gone missing or lost its identification number over the years, some bias could have been introduced into the results. In order to present information on this problem, the estimates of phenotypic standard deviation of each hogget character are also presented together with the values of phenotypic correlations in Table 11.

Table 11. Estimates of Phenotypic Correlations ($\hat{R}_p$)
Between Hogget Characters (x) and
Fertility of the Ewe (y)

Hogget Character	Fert. 1		Fert. 2		Fert. 3	
	$\hat{R}_p$	$\hat{\sigma}_x$	$\hat{R}_p$	$\hat{\sigma}_x$	$\hat{R}_p$	$\hat{\sigma}_x$
Wean. wt.	0.134**	8.40	0.151**	8.20	0.152**	8.23
March L.wt.	0.191**	9.31	0.191**	8.94	0.199**	8.95
Short.-day L. wt.	0.227**	9.66	0.225**	9.45	0.223**	9.43
Hogg. B. wt.	0.232**	11.14	0.224**	10.93	0.234**	11.03
Gain 1	0.123**	5.35	0.091*	5.13	0.102*	5.22
Gain 2	0.096*	4.53	0.094*	4.47	0.069	4.53
Gain 3	0.067	5.87	0.055	5.75	0.082*	5.90
No. Hogg. oestrus	0.179**	1.70	0.198**	1.67	0.177**	1.72
$\hat{\sigma}_y$	0.672		1.025		1.384	
d. f.	841		733		587	

* and ** denote statistical significance at the five and one per cent levels respectively.

The estimates of phenotypic standard deviations of each hogget character in Table 11 showed good agreement among the three sets of data and each estimate was also similar in value to the corresponding standard deviation presented in Table 2. The empirical evidence therefore indicates that the present estimates of phenotypic correlation are little, if at all biased by the manner in which the fertility data became available for analysis.

The estimates of phenotypic correlations presented in Table 11 above were calculated according to the method

described in section III 4 (a), noting that no adjustment was made for differences due to type of birth and rearing in the fertility data. The information provided by the correlation between a hogget character and each measurement of fertility is not independent in the sense that many of the same individuals were involved in each of the three correlations. The extent of the redundancy in information is dependent in part on repeatability of annual fertility in the ewe. Previous studies using data from this flock (Ch'ang 1955; Clarke 1963) and other reports (Reeve and Robertson 1953) have suggested that repeatability measured by number of lambs born per ewe is low in the order of 0.10 to 0.15.

The most useful set of phenotypic correlations from the viewpoint of selection for phenotypic improvement in fertility during the life-time of a ewe in the breeding flock is that between each hogget character and Fert. 3. However, the results presented in Table 11 showed that the three estimates of correlation between a hogget character and each measurement of fertility were all similar in value. A trend has been noted showing that among the live weight measurements, value of the correlation tends to increase with increasing intervals from weaning. Thus, the phenotypic correlation between hogget body weight, taken when the hogget was about 14 months old and each measurement of fertility was a little larger in value than that between fertility and other weight measurements. A definite explanation for this trend is not available, since its origin by definition of a phenotypic correlation, may be either genetic or environmental in nature.

It may be concluded that for practical purposes, apart from weaning weight and the various measurements of gain in live weight, all other characters included in this study are essentially, equally useful as criteria of potential fertility in the ewe. The choice among these hogget characters as to which ones are the more useful, for purpose of early recognition of fertility in the Romney ewe, therefore has to be made in relation to other evidence to be presented in the following sections.

5. Estimates of heritability and genetic correlation

The relationship among paternal half-sibs and that between dam and daughter have been used to provide two methods for estimating the amount of genetic variation and covariation in the characters under investigation. The main results, to be presented below, however, are expressed in terms of heritabilities and genetic correlations. Since the daughter-dam analyses were made using different assumptions regarding the presence or otherwise of maternal sources of variation in the data, it was thought that the estimates of genetic variance and covariance obtained from these analyses should also be presented so that if needed, the values would be available for comparison.

The hogget data used in each analysis were based on the individuals born over the period from 1955 to 1963 inclusive, except in the case of weaning weight records of the 'fostered' lambs which covered the period from 1951 to 1966 inclusive. The fertility data were collected from ewes born in different periods of years, the various year-of-birth periods being: Fert. 1, 1955 to 1963; Fert 2, 1955 to 1962 and Fert. 3, 1955 to 1961 inclusive.

The data were adjusted for differences in a number of environmental factors prior to estimation of either heritability or genetic correlations. The year of birth effects in the data were removed since according to the methods of analysis described in section III 4 (a) and (b) the variances and covariances were calculated on a within year-of-birth basis. In addition, the hogget data were adjusted for differences in age of dam and type

of birth and rearing. These classifications were regarded as mainly environmental in effect on the individual both at weaning and during the hogget stage. The fertility data, on the other hand, were adjusted for differences in age of dam but not for those caused by type of birth and rearing. The evidence, to be presented in this section, suggested that this was an appropriate procedure for the present data.

(a) Estimates of heritability

(1) Hogget characters

For each hogget character, two different estimates and for some, three estimates of heritability were available depending on the methods of analysis and whether or not, the presence of a carryover maternal effect was assumed as a source of variation in the data. In order to make clear the various methods used, it is convenient to designate Method 1, as paternal half-sib analysis: Method 2, daughter on dam regression ignoring the maternal and the carryover maternal effects and Method 3, covariance analysis between dam and daughter assuming the presence of a carryover maternal effect. The steps involved in calculating the values of heritability by each Method have been described in section III 4. The estimates of phenotypic variance (σ_p^2), heritability (H) and its standard error (S.E.) are presented in Table 12.

Table 12. Estimates of Heritability of Hogget Characters

- Method 1. Paternal half-sib analysis
 Method 2. Regression of daughter on dam
 Method 3. Covariance between daughter and dam assuming the presence of a carryover maternal effect

Method	1		2		3	
Character	$\hat{H} \pm \text{S.E.}$	$\hat{\sigma}_p^2$	$\hat{H} \pm \text{S.E.}$	$\hat{\sigma}_p^2(\text{Dam})$	$\hat{H}$	$\hat{\sigma}_p^2$
Wean. wt.	0.30 ± 0.12	70.51	0.23 ± 0.11	67.72	—	—
March L.wt.	0.45 ± 0.15	86.75	0.35 ± 0.10	84.16	0.41	79.59
Short-day L.wt.	0.39 ± 0.14	93.24	0.42 ± 0.11	83.50	0.42	81.98
Hogg. B.wt.	0.51 ± 0.12	124.16	0.46 ± 0.11	111.20	0.44	103.31
Gain 1	0.30 ± 0.12	28.59	0.12 ± 0.10	31.97	0.13	28.13
Gain 2	0.15 ± 0.10	20.65	0.09 ± 0.12	17.98	0.09	19.15
Gain 3	0.24 ± 0.11	34.48	0.35 ± 0.12	28.46	0.33	30.53
No. Hogg-oestrus	0.32 ± 0.13	2.90	0.27 ± 0.10	2.95	—	—
d. f.	39 (Sires)		518 (Daughters)		518 (Daughters)	

$\hat{\sigma}_p^2$ is the average phenotypic variance between daughter and dam

The heritabilities estimated using Method 1 were based on 39 degrees of freedom for sires. However, eight sires had been used in each of two years, the sire degrees of freedom were accordingly reduced to 31 for calculating the standard error of heritability. The standard errors of heritabilities found by Method 2 were calculated using 339 degrees of freedom for dams, the value being based on the number of different dams present in the data. In the analysis by Method 3, the standard errors of heritabilities were not available since the method of estimation was unknown. Nor did the present data analysed by

Method 3 allow an estimate of heritability for weaning weight to be calculated.

(11) Fertility of the ewe

The heritability of fertility or number of lambs born per ewe was estimated by the paternal half-sib method (Method 1) and regression of daughter on dam. In the latter analysis, as mentioned earlier two types of adjustments were made in the data. First, the data analysed on a within year-of-birth basis, were adjusted for differences in age of dam only (Method 2a). Second, the data were identically analysed as by Method 2a, except that the differences in type of birth and rearing were also removed prior to computing the variances and covariances (Method 2b). The estimates of phenotypic variance ($\hat{\sigma}_p^2$) and heritability ($\hat{H}$) are presented in Table 13.

Table 13. Estimates of Heritability of Fertility in the Ewe

Method	1			2a			2b	
Character	Sire d.f.	$\hat{H}$	$\hat{\sigma}_p^2$	Daughter d. f.	$\hat{H}$	$\hat{\sigma}_p^2$ (Dam)	$\hat{H}$	$\hat{\sigma}_p^2$ (Dam)
Fert. 1	39	0.053	0.452	518	0.045	0.396	-0.018	0.392
Fert. 2	33	0.121	1.051	411	0.111	0.869	-0.033	0.838
Fert. 3	29	0.032	1.916	307	0.205	1.694	0.024	1.640

The standard errors of heritabilities of fertility were all relatively large, the values ranged from 0.08 to 0.10 for the estimates by Method 1 and from 0.11 to 0.15 in the regression analysis by Method 2a. These standard errors were computed using different numbers of sires and dams, in the same way as that

described for hogget characters. Since the size of standard errors suggest that specific comparisons among the estimates of heritability is not possible, the individual values of standard errors were therefore, not presented in Table 13. Although estimates of heritability of fertility in the present data were all small in value, they are in general agreement with what is known on this subject in the literature which will be discussed at a later stage.

A comparison of estimates of heritability by Methods 2a and 2b showed that an additional adjustment of the data for average differences in type of birth and rearing has reduced the size of the estimated heritability. This was caused in each case, by a lower value of genetic variance found according to Method 2b in which type of birth and rearing effects were assumed to be entirely due to environmental differences and were removed from the data prior to calculating genetic variance of fertility in the ewe. The evidence implies that at least a part of the observed difference in fertility between ewes themselves born as singles and those born as twins, is genetic in nature. It was therefore decided that for present purposes and that of estimation of genetic covariance between each hogget character and fertility of the ewe, year of birth and age of dam were the only environmental effects which may be appropriately removed from the fertility data.

Discussion (Estimates of heritability)

As a first step towards discussing the results, it is necessary to consider briefly the contribution to the estimates of heritability, from environmental correlation between relative and non-additive genetic effects which may be present in the data. An estimate of heritability is not expected to be biased by environmental correlation between relatives, if experimental randomisation has been effective in removing this source of error. Although it can never be certain that this is so in every sample of data, the knowledge of general management practiced in the present flock suggests that contribution from this source to estimates of heritability presented earlier, is negligible. Since no effort was made in the management of the flock to treat paternal half-sib groups differently or dam and daughter alike, it was thought that the tendency, caused by environmental agencies, for characters measured on related individuals to vary together would not be greater or any less than that between the un-related flock mates.

Since most of the individuals involved in the present study were reared by their own dams, maternal environment could cause additional resemblance between daughter and dam particularly with respect to weaning weight and the post-weaning weight measurements. In the analysis by Method 3, the presence of a carry-over maternal effect was assumed. The values of heritability of post-weaning weight measurements found according to Method 3 presented in Table 12, showed reasonably close agreement with those

estimated by Methods 1 and 2. Hence, the data suggest that the carryover maternal effect has made a small and in most cases negligible contribution to the estimates of heritability of post-weaning weight measurements.

The non-additive genetic phenomena such as dominance and epistasis may also affect the estimate of genetic variance used to find heritability of each character. However, genetic variance estimated using the paternal half-sib or daughter-dam relationship is free from effects due to dominance deviations but may include, to a varying extent, a part of the epistatic variance if any of that exists. The importance of epistasis in characters used in this study is unknown, although some evidence based on studies of crossbreeding (Rae 1952) between different breeds of sheep contains a suggestion that non-additive genetic effects may be responsible for many of the low values of heritability of fertility found in the sheep.

The expectation of mean square among sires obtained according to the nested linear model used in Method 1 contains a component attributable to sire-year interaction. The efficiency with which the variance component was estimated therefore depended on the assumption that sire-year interaction was a negligible source of variation in the data. The presence of sire-year interactions in the hogget characters was studied and the results, presented in Table 5, suggested that the present estimates of heritability of hogget characters would be little, if at all, biased by the sire-year interaction effects. Whether or not dam-year interaction is present in the data, is unknown since

very few dams during their life-time in this flock leave more than three daughters; in general, suitable data for studying interaction between dams and years in the sheep are difficult to obtain.

In forming the daughter-dam pairs for regression analysis, the dam's record was repeated for each additional daughter whose record was also available. This procedure, being equivalent to weighting the information on the dam by number of daughters in the hogget or breeding ewe flock may or may not be optimal, in the sense of minimum sampling variance (Kempthorne and Tandon 1953). The number of daughters per dam in the present data varied between one and up to six with an effective range from one to three which covered 96 per cent of all dams. The studies made by Bohren, McKean and Yamada (1961 a and b) suggested that a serious loss of efficiency in estimates of heritability, based on the effective range in number of offspring per dam as 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).

The corresponding estimates of heritabilities by different methods of analysis presented in Tables 12 and 13 showed, with one exception, good agreement. A fairly large discrepancy was observed between values of heritability of Fert. 3 by paternal half-sib analysis (Method 1) and regression of daughter on dam (Method 2a). A definite explanation is not available although sampling errors have no doubt contributed to the observed discrepancy. The degrees of freedom, derived from different numbers

of sires and dams, available for estimating the heritabilities of Fert.3 were relatively small being 21 and 198 respectively.

The estimates of heritability of weaning weight (0.30, Method 1; 0.23, Method 2) and hogget body weight measured on the individual at about 14 months old (0.51, Method 1; 0.46, Method 2; 0.44, Method 3) presented in Table 12 are comparable with most of the published values of heritability for these characters in the literature (Rae 1956). More recently, Young, Turner and Dolling (1960) reported a value of 0.64, being the estimate of heritability of yearling body weight (10 to 16 months old) in the Australian Merino. The evidence suggests that even at an average value of about 0.5, yearling weight of the sheep must be regarded as a highly heritable character. No published estimates appear to be available for comparison with the present values of heritability for March live weight and live weight at the 'shortest-day' of the year which are intermediate in size between those of weaning weight and hogget body weight. In each set of results, there was a tendency for the value of heritability of live weight measurement to rise with increasing age of the individual. The observed trend may be expected if, as it has often been argued, the environmental contribution of maternal effect tends to become a smaller proportion of the total variation with increasing interval of time from weaning. However, a more definite explanation of the increase in heritability values of live weight measurements over the hogget age must await further investigations.

The estimates of heritability of weight gains were also

presented in Table 12. This serves two purposes. First, they provide a more complete description of the genetic basis of growth during the hogget stage and second, they illustrate that heritability of weight gain measurements based on dam-daughter relationship is free from the carryover maternal effect. It is clear that while the live weight measurements themselves are assumed to be affected by either a maternal or its carryover effect, the expected value of covariance for gain in weight between daughter and dam contains no contribution from the maternal sources; the values of maternal terms vanish as an algebraic consequence of subtracting one measurement of live weight from the other, in the process of finding an expression for gain in weight. The corresponding estimates of heritability of weight gains by Methods 2 and 3 would have been identical in size but for the slightly different values of the denominator (σ_p^2) used in their calculation.

Although the genetic basis of age at first egg in pullets has been extensively documented (Lerner 1958), little is known of inheritance in puberal characters on a within-breed basis for other species of farm animals. No published data are available for comparison with the present estimates of heritability of number of hogget oestrus. The scarcity of published work on this topic is perhaps understandable since under the current systems of flock management, either the occurrence or number of hogget oestrus has little or no economic significance in most breeds of ewes which are not mated until the start of their second breeding season. However, as an extended breeding season in the ewe, such as that in the Merino and Dorset Horn breed,

can provide opportunities for extra lamb production, the present estimates of heritability of number of hogget oestrus point to the possibility of improvement, by selection towards a more prolonged breeding season in the Romney breed.

The estimates of heritability of fertility in the ewe presented in Table 13 suggest that it is a lowly heritable character. The present evidence is supported by previous results obtained from the same flock (Ch'ang 1955, Rae and Ch'ang 1955; Clarke 1963) and consistent with progress from selection experiments reported by Wallace (1964) based on Romney sheep under New Zealand conditions. The inheritance of fertility in the Romney breed is in general agreement with what has been known of this character, whether expressed as number of lambs born per ewe or incidence of multiple births, in other breeds of sheep (see review by Reeve and Robertson 1953, Sidwell 1956, Rendel 1956, Karam 1957, Roberts 1957; Kennedy 1959). In a more recent study of fertility (numbers of lambs born per ewe) in the ewe, Young, Turner and Dolling (1963) found some evidence which indicated that heritability of fertility in the Merino sheep might be somewhat higher than most of the known estimates for that breed or other breeds of sheep. However, this finding awaits confirmation by selection experiment which is underway (Turner, Hayman, Triffitt and Prunster 1962). The current state of knowledge therefore suggests that heritability of fertility in the ewe is low, being in the vicinity of 0.10 to 0.15. The present study showed that the heritability of fertility based on more than one lambing is not much, if at all, higher in value than previous estimates (Ch'ang

1955, Clarke 1963 and others cited above) using annual lambing records. The implication, taking all evidence into consideration, therefore is that genetic improvement in fertility of the Romney ewes by direct selection is likely to be slow.

(b) Estimates of genetic correlation

The same data and relationships used to find the heritabilities were also available for estimating genetic correlations, as described in section III 4 (a) and (b). The methods of analyses used in the present study, may be similarly designated as follows: Method 1, paternal half-sib analysis; Method 2, regression of daughter on dam ignoring the maternal sources of variation and Method 3, covariance analysis between dam and daughter assuming the presence of a carryover maternal effect. Since the tables showing the values of genetic correlations and covariances are all relatively large in size, for simplicity and convenience the results will be presented according to the Method of analysis.

(1) Paternal half-sib analysis

The estimates of genetic correlation are presented in Table 14. The corresponding genetic covariance used to find each genetic correlation is shown as the lower member in each pair of values in Table 14.

Table 14. Estimates of Genetic Correlation and Genetic Covariance (Method 1)

Character	March L.wt.	Short- day L.wt.	Hogg. B. wt.	No. Hogg. oestrus	Fert. 1	Fert. 2	Fert. 3
Wean. wt.	0.73 25.8	0.86 23.8	0.74 27.0	0.30 1.32	0.32 0.22	0.40 0.67	0.32 0.31
March L.wt.		0.96 36.2	0.86 42.8	0.35 2.10	0.45 0.44	0.41 0.85	0.38 0.49
Short-day L. wt.			0.96 45.7	0.52 3.00	0.72 0.67	0.96 2.03	0.63 0.82
Hogg. B.wt.				0.56 4.31	0.81 1.00	0.56 1.59	0.65 1.18
No. Hogg. oestrus					0.56 0.08	0.65 0.22	0.44 0.10
d.f. (Sire)	39				39	33	29

The approximate standard errors of genetic correlations among the hogget characters and between each hogget character and fertility of the ewe were calculated, the range of values being 0.20 to 0.40 and 0.40 to 0.70 respectively.

(11) Estimates of covariance between dam
and daughter

In order to make clear the values used to compute the genetic covariance by Methods 2 and 3, the estimates of cross-covariances between dam and daughter are presented on the opposite page. The 'fostered' weaning weight records were based on ewe and wether lambs. The sex effect was minimised by converting all to a ewe lamb basis. A value of three pounds, being the estimate of sex effect reported by Ch'ang and Rae (1961), were subtracted from each weaning weight record of the wether lamb.

The covariances presented in Table 15 showed two trends. First, among the hogget characters, the estimates below and to the left of the main diagonal were each larger in value than the corresponding estimate above and to the right of the main diagonal. Second, between each hogget character and fertility of the ewe, with one exception (dam's Fert. 2 and daughter's weaning weight) the estimates shown below and to the left of the main diagonal were each smaller in value than the corresponding estimate above and to the right of the main diagonal. These results therefore showed two different patterns of asymmetry, opposite in direction depending on whether it is within the group of hogget characters or between hogget characters and the various measurements of fertility in the ewe.

A definite explanation for the observed patterns described above is not available although two possibilities may be

mentioned. The first and also the more difficult one for its substantiation, is concerned with the bias which may be present in the data caused by excluding from the analysis, those dams which have left no daughters in any one year.

This is considered as the most serious deficiency in using the relationship between dam and daughter as a method of estimating genetic parameters. The second possibility is the presence of systematic variation in the data caused by maternal or carryover maternal effect. An attempt, therefore, was made to study the maternal contribution to covariance between dam and daughter. The results of this study may be compared with those obtained from regression of daughter on dam ignoring the maternal sources of variation and with those given by the paternal half-sib analysis.

(111) Regression of daughter on dam and covariance
analysis between dam and daughter

The estimates of genetic correlation together with the corresponding genetic covariance shown as a lower number of the pair, found using regression of daughter on dam (Method 2) are presented in Table 16.

Table 16. Estimates of Genetic Correlation and Genetic Covariance
(Method 2 Regression of daughter on dam)

Character	March L.wt.	Short.- day L.wt.	Hogg. B. wt.	No. Hogg. oestrus	Fert. 1	Fert. 2	Fert. 3
Wean. wt.	0.96	0.97	0.90	0.66	1.27 ⁺	0.83	-0.02
	20.6	22.8	25.6	2.32	0.67	1.10	-0.05
March L.wt.		0.98	0.86	0.60	1.16 ⁺	0.75	0.15
		31.4	33.5	2.86	0.84	1.29	0.46
Short.-day L. wt.			0.90	0.60	0.82	0.47	-0.20
			38.5	3.13	0.66	0.96	-0.62
Hogg. B.wt.				0.65	0.72	0.16	-0.24
				4.14	0.70	0.34	-0.91
No. Hogg. oestrus					0.98	0.87	0.57
					0.12	0.24	0.34

+ Value exceeds theoretical limit of a correlation coefficient.

The value of genetic variance obtained from the paternal half-sib analysis (Method 1) for weaning weight ($\hat{\sigma}_{G_w}^2 = 20.89$) was used to compute the genetic variance of maternal environment ($\hat{\sigma}_{G_m}^2 = 64.49$) and the genetic covariance between weaning weight and maternal environment ($\hat{\text{cov}} G_w G_m = -27.85$). The available estimates of genetic correlation and the corresponding genetic covariance shown as a lower member of the pair, obtained using covariance analysis between dam and daughter assuming the presence of a carryover maternal effect (Method 3) are presented in Table 17.

Table 17. Estimates of Genetic Correlation and Genetic Covariance
(Method 3 Covariance analysis between dam and daughter)

Character	Wean. wt.	March L.wt.	Short.- day L.wt.	Hogg. B. wt.	No. Hogg. oestrus	Fert. 1	Fert. 2	Fert. 3
Maternal Environment	- 0.76 -27.8	- 0.59 -27.1	- 0.54 -25.5	- 0.43 -23.3	0.11 0.77	-0.19 -0.21	-0.32 -0.80	-0.49 -2.32
Wean wt.		0.95 24.8	0.93 25.0	0.81 25.1	0.32 1.28	1.10 ⁺ 0.68	0.62 0.89	0.42 1.14
March L.wt.			0.98 32.7	0.84 32.1	0.46 2.31	1.47 ⁺ 1.12	1.19 ⁺ 2.10	0.77 2.58
Short.-day L. wt.				0.88 35.0	0.44 2.28	0.95 0.75	0.94 1.72	0.53 1.84
Hogg. B.wt.					0.46 2.73	1.25 ⁺ 1.13	0.67 1.40	0.49 1.96

+ Value exceeds theoretical limit of a correlation coefficient.

The accuracy of genetic covariances and correlations presented in Table 17, found using Method 3 is partly dependent on the amount of weaning weight data based on the 'fostered' lambs in this flock. While the number of 'fostered' lambs available for study was less than desirable, the results however, all appeared to be reasonable. In addition, the variance of weaning weight of the 'fostered' lambs ($\hat{\sigma}_{P_W}^2 = 70.7$) was found to be in close agreement with that of their own dams ($\hat{\sigma}_{P_W}^2 = 70.6$) and with other estimates of this character ($\hat{\sigma}_{P_W}^2 = 70.5$, by paternal half-sib analysis; $\hat{\sigma}_{P_W}^2 = 67.7$, by regression of daughter on dam) presented in Table 12 based on more extensive data. Since physical stress and other effects associated with the practice of 'fostering' could have affected growth, hence causing the variance of weaning weight of the 'fostered' lambs to be much different from that of the 'dam-reared' individuals, the similarity in size of variances noted above, suggests that in the present data, the effect of 'fostering' per se are not likely to be a major source of error.

It is also pertinent to point out at this stage that the present study of maternal environment in the sheep using data based on 'fostered' lambs does not represent a new approach to this problem. Two early examples may be cited. The analysis by Wright (1931) for studying the relative importance of heredity and environment in determination of human intelligence and the work by Chapman (1946) on ovarian weight response in the rat to a gonadotropic hormone treatment, have both used data obtained from 'fostered' individuals to evaluate the magnitude of

maternal (or home environment in the case of human intelligence) contribution. In the absence of any noted disturbance of the results derived using the weaning weight data based on 'fostered' lambs and in view of the general applicability of analysis employing 'fostered' individuals, a little more confidence in the values of genetic correlations, presented in Table 17, between maternal environment and other characters under investigation appears to be justified.

Discussion (Estimates of genetic correlation)

The literature contains little information on the genetic basis of covariation either among live weight measurements themselves or between a series of live weights and reproductive characters in the sheep. The genetic correlations, obtained using paternal half-sib analysis, between yearling weight (10 to 16 months old) and fertility (number of lambs born per ewe) in the Australian Merino ewe have been reported by Young, Turner and Dolling (1963), the values being 0.47 and 0.23 for the ewe at the first and over the first two lambings respectively. These genetic correlations are somewhat lower in value compared with the corresponding estimates (0.81 and 0.52, between hogget body weight and Fert. 1 and Fert. 2 respectively) from paternal half-sib analysis in the present study. However, both sets of results agree in placing the sign of the genetic correlations as being positive.

Since no other published estimates based on the sheep, are available for comparison with the present values of genetic correlations, the following discussion is mainly confined to the results found in this study, but where applicable, reference to work on other mammalian species will be made. The results obtained using the paternal half-sib analysis (Method 1) are unbiased and not complicated in their interpretation by the presence of maternal sources of variation. It appears reasonable, therefore, to use genetic correlations found according to Method 1 (Table 14) as a basis for comparison with those given

by Methods 2 (Table 16) and 3 (Table 17), being the regression of daughter on dam and covariance analysis between dam and daughter respectively.

In general, the corresponding genetic correlations showed good agreement between the different Methods of analysis. The notable exceptions were the genetic correlations between live weight measurements and total number of lambs born per ewe over the first three lambings or Fert.3 for which the values found by Method 2 were lower than those by Method 1; but more importantly, they were opposite in sign. The discrepancies noted for these characters originated in the difference of the signed values shown in Table 15 between corresponding cross-covariances computed for the dams and the daughters and presumably were caused by maternal sources of variation in the data which had been ignored in the analysis by Method 2. This suggestion was supported by results obtained from Method 3 which gave comparable values of genetic correlations, in nearly all cases, as Method 1. Some of the genetic correlations found using Method 3 presented in Table 17, exceeded the theoretical limiting value of unity; sampling errors no doubt have contributed to these results. The evidence discussed above points to maternal contribution as a source of complication in using the relationship between dam and daughter genetic correlations.

Any attempt at interpretation of a genetic correlation between maternal environment and measurements of growth or reproduction involves consideration of the biological components represented by phenotype of maternal environment. In so far

as the post-natal period is concerned, milk production of the dam is a meaningful and in terms of growth in the lamb, a major component of maternal environment. This point of view was taken in the present study and appeared to be also held by a number of workers (for example, Dickerson 1947, Koch and Clark 1955; Young, Legates and Farthing 1965). Therefore, the genetic correlations presented in Table 17 between maternal environment and other characters may be regarded essentially as a measure of the amount of genetic covariation between milk production and growth of the lamb initially up to weaning; then between the effect of milk production already present in the individual at weaning, the carryover maternal effect and post-weaning growth or oestrous performance of the hogget and finally, between it and fertility of the breeding ewe. For example, the negative genetic correlation (-0.43 , Table 17) between maternal environment and hogget body weight implies that the dams which are above the flock average in hogget body weight tend to leave daughters which are below the flock average in milk production and vice versa.

The genetic correlations between maternal environment and live weight measurements presented in Table 17 are all negative in sign. The largest value is associated with the weight at weaning (-0.76), comparable with the range of values (from -0.65 to -0.68) reported by Koch and Clark (1955) for the genetic correlation between post-natal maternal environment and weaning weight in beef cattle. The present estimates of genetic correlations between maternal environment and the live

weight measurements tended to decrease in absolute values with increasing age of the individual. Since the correlation coefficients were all negative, the results imply that the genetic covariation between maternal environment and post-weaning weight gains is positive, a point which was also observed in beef cattle and reported by Koch and Clark (1955).

The study of maternal environment in the mouse by Young, Legates and Farthing (1965) suggested that lactational performance of the dam has little direct effect upon the prolificacy or lactational performance of the young she nursed. On the other hand, Falconer (1965) showed a negative maternal effect on litter-size of the daughter. Since the methods of analysis and assumptions made about the maternal effect were different between the first and last mentioned studies, significance of these different findings is not at all clear. The present results (Table 17) suggest that in Romney ewes, the genetic correlation between post-natal maternal environment and fertility of the ewe is negative and its values ranged from -0.19 at the first lambing to -0.49 for the third measurement of fertility expressed as total number of lambs born per ewe over three lambings.

In contrast to the negative correlations discussed above, the genetic correlation between maternal environment and number of hogget oestrus in the present data was positive but smaller in value (0.11). If, in reality, inheritance of these two characters is independent of each other, this property suggests that predictions made about the response and correlated response

using number of hogget oestrus as a criterion of selection are more likely to be realised in practice than those based on the live weight measurements which are complicated by the maternal sources of variation.

Discussion

(Estimates of heritability and genetic correlation)

It has been mentioned that the accuracy of some estimates of heritabilities and several genetic correlations is less than satisfactory. The present findings require confirmation. On the other hand, there was general agreement in results obtained using different methods of analysis. The more serious discrepancies which have been noted earlier in discussing the genetic correlations are tentatively attributed to complications caused by maternal sources of variation and covariation in the relationship between a dam and her daughter. Although uncertainty about the real value of the genetic parameters does not allow definite conclusions to be drawn from the present estimates, an outline of the general pattern of response and correlated response to selection with reference to genetic improvement in fertility of the ewe, can be sketched for the characters under investigation. The results used for this purpose are those obtained by the paternal half-sib analysis, all presented in Table 14 except in the case of genetic correlations involving maternal environment which are shown in Table 17.

The heritabilities suggest that in varying degrees, each hogget character is heritable. To the extent that the genetic variance used to calculate the heritability is additive in effect, response to selection in all hogget characters is expected to continue for some time. The values of heritability indicate that hogget body weight measured on the individual at about 14 months in age, is the character most likely to show

rapid response to selection; but only a moderate rate of gain can be expected from selection based on the remaining weight measurements or for a greater number of hogget oestrus.

Since the genetic correlations between hogget characters and fertility of the ewe are all positive, selection for an increased expression in any one of the hogget characters, is expected to cause correlated change towards an enhanced level of fertility in the ewe. However, judging by the negative genetic correlation between maternal environment and fertility, the gains thus achieved, will be partly offset by poorer lactational performance of the individual as it, in turn becomes the dam of the next generation. The negative genetic correlations between live weight measurements, but weaning weight in particular, and maternal environment also imply deterioration in the latter, as the average additive genetic value of a live weight character increases in response to selection. The maternal environment, therefore, appears to be in the role of a regulatory agency with the effect of conserving what is status quo by restoring, in part at least, the change caused by selection as it may be predicted from the knowledge of heritabilities and genetic correlations. Consequently, selection for higher fertility of the ewe based on hogget live weight character, is likely to be made less effective by the homeostatic properties of maternal environment. This assessment need not imply a permanent^{an} obstacle to improvement. For example if the reduction of average weaning weight, resulting from deterioration of the maternal environment, should reach a serious magnitude of say nine to 10 lb, it may be speculated

that at this point or beyond, post-weaning compensatory growth as that described for the twins in section IV 1, could operate as a mechanism enabling the hoggets to overcome partially the severe growth handicap imposed prior to weaning. While the oscillating pattern of changes outlined above have the main effect of making response to selection short of the total and the correlated responses less predictable, the results suggest that worthwhile genetic improvement is still possible.

Finally, the results may be summarised by noting:

- (1) The hogget characters under investigation were all heritable. The values of heritabilities of hogget characters ranged from 0.23 to 0.51 (Table 12) each being larger in size than the heritabilities of fertility in the ewe (0.04 to 0.20, Table 13).
- (2) The genetic correlation between each pair of hogget characters was without exception, all positive in sign and varying in size from 0.30 to 0.98 (Tables 14, 16 and 17). The genetic correlations between hogget characters and each measurement of fertility of the ewe, with few exceptions, were all positive. The values ranged from 0.32 to 0.81, by paternal half-sib analysis (Table 14); from - 0.24 to unity, by regression of daughter on dam ignoring the maternal effects (Table 16) and from 0.42 to unity, by covariance analysis between dam and daughter assuming the presence of maternal effects (Table 17).

- (3) The genetic correlations between maternal environment and all characters except number of hogget oestrus (0.11) were negative in sign and the values ranged from - 0.19 to - 0.76 (Table 17).
- (4) The pattern of response and correlated response in the presence of maternal effects was outlined with particular reference to genetic improvement of fertility in the ewe. Despite the negative genetic correlations with maternal environment, reasonably good prospects of improving fertility in the ewe by indirect selection based on hogget characters, are indicated by the results.

6. The selection indices

The methods used to construct each of the three types of selection indices denoted by I_1 , I_2 and I_3 have been outlined in section III 5. Each index was constructed using two hogget characters: number of hogget oestrus (P_1) and hogget body weight (P_2) measured on the individual at about 14 months in age. Although the criteria used in constructing the indices were varied for purpose of making comparisons among the results, the common objective was to produce an index which in its use, may lead to maximum improvement in fertility of the ewe.

The variances and covariances used in constructing the various types of indices, except the genetic covariances between maternal environment and the hogget characters, were all obtained from the paternal half-sib analysis and their values are presented in Table 18. The genetic variance and covariance are each shown as a lower member of the pair of values.

Table 18. Estimates of Variances and Covariances used in Constructing the Selection Indices

Covariance	No. Hogg. oestrus	Hogg. B. wt.	Fert. 1	Fert. 2	Fert. 3	Maternal Environment
No. Hogg. oestrus (P_1)	— —	8.122 4.312	0.204 0.085	0.338 0.218	0.420 0.096	— 0.772
Hogg. B. wt. (P_2)	— —	— —	1.740 1.000	2.507 1.594	3.571 1.178	— -23.300
Variance	2.901 0.934	124.162 63.425	0.451 0.024	1.051 0.127	1.961 0.061	— —

$$(a) \quad I_1 = b_{11}P_1 + b_{12}P_2$$

The first index (I_1) was constructed by maximising the correlation between I_1 and H , where $H = G_1 + G_2$. The values of b_{11} and b_{12} were found to be 0.34 and 0.52 respectively. The index, therefore has the form:

$$I_1 = 0.34 P_1 + 0.52 P_2$$

The correlation between I_1 and H is 0.71 based on the values of covariance between I_1 and H ($\widehat{\text{Cov}} I_1 H = 37.24$) and the respective standard deviations ($\widehat{\sigma}_H = 8.54$, $\widehat{\sigma}_{I_1} = 6.10$). The simplest way to provide some evidence on the effectiveness of I_1 as a basis of selection for higher fertility in the ewe is to compute the correlation between I_1 and either the phenotype or the additive genetic value of fertility. By expressing each of the latter correlations as a fraction of the square root of heritability of the appropriate measurement of fertility, the relative efficiency of selection between the indirect and the direct methods of selection for fertility may be found. These results are presented in Table 19.

Table 19. Values of Correlation (R) Between I_1 and Fertility of the Ewe and the Ratio of Relative Efficiency of Selection (RES)

I_1 and	Character	$\widehat{R}$	RES
Phenotype of	Fert. 1	0.24	-
	Fert. 2	0.23	-
	Fert. 3	0.24	-
Additive Genetic Value of	Fert. 1	0.58	2.5 {2.8} ⁺
	Fert. 2	0.42	1.2 {1.3}
	Fert. 3	0.43	2.4 {1.0}

+ indicates that the value of the denominator used to calculate the ratio shown in brackets, is derived from heritability of fertility reported in Table 13 based on regression of daughter on dam (Method 2a).

$$(b) \quad I_2 = b_{21}P_1 + b_{22}P_2$$

The second series of indices denoted in general by I_2 , were constructed by maximising the correlation between each index and either the phenotype or the additive genetic value of fertility in the ewe. The values of these correlations, weighting factors and standard deviation of each index and the ratio of relative efficiency of selection are presented in Table 20.

Table 20. Values of Correlation (R) Between I_2 and Fertility of the Ewe and the Ratio of Relative Efficiency of Selection (RES)

I_2 and	Character	$\hat{b}_{21}$	$\hat{b}_{22}$	$\hat{\sigma}_I$	$\hat{R}$	RES
Phenotype of	Fert. 1	0.038	0.011	0.166	0.25	-
	Fert. 2	0.073	0.015	0.253	0.24	-
	Fert. 3	0.079	0.024	0.343	0.25	-
Additive Genetic Value of	Fert. 1	0.008	0.007	0.093	0.57	2.5(2.7)
	Fert. 2	0.048	0.010	0.159	0.45	1.3(1.4)
	Fert. 3	0.008	0.009	0.106	0.44	2.5(1.0)

For a given measurement of fertility for example, Fert. 3, two selection indices have been constructed. It is therefore of some interest, to study the extent to which a ewe within a group available for selection, is ranked the same or differently by the two indices. This tendency may be most simply assessed by computing the correlation coefficient between each pair of indices for the three measurements of fertility. The values of the correlation coefficients were: 0.95, 1.00 and 0.96 for Fert. 1, Fert. 2 and Fert. 3 respectively, indicating that virtually the same ewes would be selected as replacements

whether improvement of fertility was intended for the current or the next generation. For practical purposes, therefore, it would be convenient if each pair of the corresponding indices could be combined into a single general purpose index. The method for doing this has been described in section III 5. A general purpose index which may be used to select for improvement in fertility of the ewe over the first three lambings (Fert. 3) was constructed. To construct this index, the assumption was made that phenotypic and genetic improvement in this character would be equally desirable, as indeed a logical basis for different weightings was not available. The general purpose index (I'_2) is:

$$I'_2 = 0.087 P_1 + 0.033 P_2 \quad \text{or more simply,}$$

$$I'_2 = 2.6 P_1 + P_2.$$

$$(c) \quad I_3 = b_{31}P_1 + b_{32}P_2$$

The presence of maternal effects and the complication they may cause in predicting the response and correlated response to selection have been discussed previously. In an attempt to minimise the carryover maternal effect on the hogget characters, a restriction, $b_{31} \text{Cov } G_1 G_m + b_{32} \text{Cov } G_2 G_m = 0$ was imposed in the process of constructing the third type of indices denoted in general by I_3 . In the restriction stated above, $\text{Cov } G_1 G_m$ and $\text{Cov } G_2 G_m$ are genetic covariances between maternal environment and number of hogget oestrus and hogget body weight respectively. The relevant results are presented in Table 24.

Table 21. Values of Correlation (R) Between I_3 and Fertility of the Ewe and the Ratio of Relative Efficiency of Selection (RES)

I_3 and	Character	$\hat{b}_{31}$	$\hat{b}_{32}$	$\hat{\sigma}_I$	$\hat{R}$	RES
Phenotype of	Fert. 1	0.073	0.002	0.137	0.20	—
	Fert. 2	0.118	0.004	0.218	0.21	—
	Fert. 3	0.151	0.005	0.279	0.20	—
Additive Genetic Value of	Fert. 1	0.033	0.001	0.063	0.41	1.8 (1.9)
	Fert. 2	0.076	0.002	0.141	0.39	1.1 (1.2)
	Fert. 3	0.038	0.001	0.070	0.29	1.6 (0.6)

A general purpose index (I'_3) constructed using Fert. 3 as the criterion of improvement is:

$$I'_3 = 0.189 P_1 + 0.006 P_2 \quad \text{or more simply}$$

$$I'_3 = 31.5 P_1 + P_2.$$

(d) Properties of the selection indices

The expected change in fertility of the ewe resulting from the use of a hogget selection index may be found as a regression of this character on the index. In a similar manner, the expected genetic gain of the hogget characters may be evaluated. In both instances, the results used to find the correlations presented in Tables 19, 20 and 21 were re-cast in the form of the relevant regressions. In general terms, the expected changes in phenotype (ΔP) and in additive genetic value (ΔG) resulting from selection based solely on the index, are:

$$\Delta P = (\text{Cov PI}/\sigma_I) Z/p \quad \text{and}$$

$$\Delta G = (\text{Cov GI}/\sigma_I) Z/p.$$

The Z/p is the intensity of selection defined as the difference in standard deviation units between the mean of the truncated portion of the population and the mean of the population prior to selection, p being the proportion selected. Since Z/p is constant for all indices, it has been omitted from the calculations of ΔP and ΔG . The expected gains have not been computed for every index or all measurements of fertility. The results presented in Table 22 below are applicable to the improvement of fertility in the ewe over the first three lambings.

Table 22. The Expected Gains (in standard deviation units) from the Use of Hogget Selection Indices

Character	I_1	I_2	I_3	Nature of Improvement
No. Hogg-oestrus	0.42	0.44	0.58	Genetic
Hogg. B.wt.	5.68	5.71	3.41	Genetic
Fert. 3	0.11	0.11	0.20	Genetic
Fert. 3	0.33	0.10	0.10	Phenotypic

Discussion

Selection indices have been constructed according to three different criteria of maximisation. As a common denominator of the effectiveness of each index, its correlation with fertility of the ewe was computed. The correlations between phenotype of fertility and each index varied within a narrow range of values, from 0.20 to 0.25, regardless of which criterion was used in constructing the index and applicable to every measurement of fertility. These values are near the upper limit of the individual phenotypic correlations of the hogget characters with fertility of the ewe (0.17 to 0.23, see Table 11). The correlations between the additive genetic value of each measurement of fertility and the indices constructed using different criteria, showed a greater range of values, varying from 0.4 to 0.6 with one exception at 0.3, but all grouped around the lower limits of the individual genetic correlations between the hogget characters and the fertility of the ewe (number of hogget oestrus, from 0.4 to unity, see Tables 14 and 16; hogget body weight, from 0.6 to unity, see Tables 14 and 17). Taking all results into consideration, the reality of a positive correlation between fertility of the ewe and these two hogget characters, either taken singly or combined as an index, may be considered as established, although uncertainty exists about its actual size.

By comparing the corresponding values presented in Table 20 for I_2 with those of I_3 in Table 21, some indications may be gained of the carryover maternal effect on correlated

response in fertility of the ewe. The most noticeable effect associated with the restriction imposed on I_3 is the marked reduction in value of the weighting factor (b_{32}) for hogget body weight. This tendency is opposite to the change in value of the weighting factor (b_{31}) associated with number of hogget oestrus. The weighting factors (b_{31}) in I_3 all showed some increase in value compared with the corresponding estimates (b_{21}) in I_2 . These results imply that if the carryover maternal effect is to be minimised, less emphasis should be placed on hogget body weight in selection. This interpretation appears to be reasonable in view of the relatively strong genetic correlation (-0.43) between hogget body weight and maternal environment compared with the small value (0.11) of the genetic correlation between number of hogget oestrus and maternal environment. It is also noted that the correlation between each I_3 and fertility of the ewe presented in Table 21, are each somewhat lower in value than the corresponding estimate in Table 20, obtained using I_2 as the index. This presumably, was a consequence of the shift in relative emphasis from hogget body weight to number of hogget oestrus described above. If this is the cause, it is understandable because the genetic correlations between hogget body weight and measurements of fertility are, in general, somewhat larger in size than the corresponding estimates between number of hogget oestrus and fertility of the ewe as indicated earlier in the discussion. The present evidence, therefore, agrees with the point made previously that an effect of the carryover maternal influence is to cause the response in ewe's fertility which is correlated

with the change resulting from selection in the hogget live weight characters, to fall short of what is the predictable total. At the same time, it appears reasonable to suggest that the properties of the restricted hogget index (I_3) are more likely to be realised in practice than those of the other types of indices constructed without reference to the possible effects of maternal environment.

Finally, it is clear that in order to make more systematic use of the estimates already available for the phenotypic and genetic parameters of the characters under study, selection indices were constructed. In general, the results presented in this section are consistent with the previous findings based on heritabilities and genetic correlations which suggest that selection using hogget characters is a feasible method for improving fertility in the ewe. If the estimates of variances and covariances used in constructing the indices can be relied on, the results of relative efficiency of selection, presented in this section, would suggest that under certain circumstances, indirect selection based on properly constructed hogget indices may be preferable to direct selection, as a method for improvement of fertility in the ewe. The probable amounts of correlated response in fertility of the ewe over the first three lambings and the gains in each hogget character to be expected from the use of each type of index have been presented in Table 22. Assuming that 60 per cent ($Z/p = 0.64$) of the total number of ewe hoggets were selected as replacements according to I_3 - the restricted hogget index, and converting all to actual units of measurement used in this study, the expected gains per

generation in each character are:

Number of hogget oestrus	0.4	Oestrus
Hogget body weight	2.2	lb
Genetic improvement in fertility	0.13	Lamb
Phenotypic improvement in fertility	0.06	Lamb

While the amounts of gain to be expected from use of the index do not suggest rapid improvement in either fertility of the ewe or number of hogget oestrus, it is clear from the values presented that worthwhile progress can be made.

V. APPLICATIONS

The level of lamb production during the 'life-time' of a ewe depends on both the total number of lambs she reared and the average weaning weight of her lambs. The lamb production, thus defined, is governed to a large extent by the total number of lambs born which has been used in this study as a measure of fertility. Since lamb production represents a substantial contribution to total productivity of the sheep, the economic importance of a satisfactory level of fertility in the ewe flock can not be over-stressed. At the same time, the need for simultaneous improvement in lamb and wool production should serve as a constant reminder of the limitations of the present results, in their application to sheep production under practical conditions.

The evidence presented in this study has suggested that indirect selection, based on hogget characters can be an alternative to direct selection for higher fertility in the Romney ewe. However, in the application of results, it is above all, necessary to assume that the genetic and environmental relationships in other Romney flocks are similar to those found in the present flock. Several reasons may be put forward in support of this assumption. First, the foundation ewes and a large proportion of the sires used, were drawn from a number of ram breeding flocks located in the Manawatu and Wairarapa, an area in which many of the well-established and popular Romney stud flocks are found. Second, knowledge of the aims of Romney breeders indicates that until recently, probably less than a

decade, few if any of the ram breeding flocks have had a selection plan for fertility of the ewe, number of hogget oestrus or live weight characters of the sheep. Therefore, random breeding, practiced in the present flock by design, may well be a feature in effect, shared by many other Romney ram breeding flocks. Third, the calendar of farming and general management of this flock are similar to those found on other sheep farms in the surrounding areas. If the assumption of a general resemblance between this and other Romney flocks is reasonable as suggested above, it is proposed to consider briefly the application of present results, in the first instance, against a background of the existing methods of selection and then, in terms of the practical problems involved in putting them to work.

Although a higher level of fertility in Romney ewes is equally desirable either for the stud or the commercial flocks, the prospects of improvement by selection in this character appear to be better in the stud flocks. The main factors which may limit the rate of genetic improvement in the commercial flocks are the lack of permanent individual identification, thus making selection more difficult to apply and the reliance of sires bred in an outside flock as the major source of genetic improvement. Therefore a method of selection applicable under the conditions of a stud farm may well require modification before it can be effectively used in the typical commercial flock. As an example, a method of direct selection for lamb production has been available to the Romney stud breeders for a number of years (Rae 1958 a). Much can be said

in favour of this method. It is simple to use, requiring pedigree information on lambing performance of the ewe which is normally kept by a stud breeder, and has the effect of keeping the generation interval down to a minimum. However, modifications of this method are necessary if it is to be used in the commercial flock. This has led to a search for methods of genetic improvement which may be more easily applied to both types of flocks. In the report on face cover in Romney sheep (Cockrem, Barton and Rae 1956), some preliminary evidence of inheritance in this character and its phenotypic association with lambing per cent in particular, but with other characters as well, were presented; the implication was that 'an animal without wool on the face forward of the eyes' should be preferred in selection. More recently (see for example, Coop 1964) studies on the phenotypic association between the average live weight of the ewes in the breeding flock and the incidence of barrenness and twinning have led to the suggestion that live weight of the ewe near mating may be a useful criterion of her potential lambing performance in the same year. While both face cover and live weight of the ewe near mating may be useful as some indications of her more immediate lambing performance, the genetic correlation between each character and fertility of the Romney ewe is unknown. The results of the present study, therefore, may add something to that which is already available as methods of selection, both directly and indirectly for higher fertility in the ewe.

A more complete assessment of the applicability of the present results requires consideration of the monetary and other types of costs likely to be involved in putting them to work.

Specific information on this aspect of sheep breeding under New Zealand conditions, is not available at present. In the absence of information on this point, all that can be said is that the method must be simple to use and the performance of the animal easily measured. While these requirements, by themselves, do not necessarily mean efficiency or profitability, they are clearly the essential features of a practicable breeding plan. In these terms and other considerations aside, the record of a hogget body weight must rank, among the characters studied, as the easiest measurement to take under farming conditions. Taken after shearing, this measurement does not include the weight of a fleece as a source of inaccuracy and since the hoggets, having been mustered for shearing, would be readily available in or near the sheep yards, the work required for weighing at this time is kept down to a minimum.

The oestrous performance of the ewe hoggets may be recorded but less easily, and at the expense of a somewhat higher labour charge than is the case for hogget body weight. On the other hand, experience gained in the work during the course of the present investigation suggests that the necessary efforts can be minimised under certain conditions. For example, if occurrence of the first oestrus or puberty in the ewe hogget is the only criterion of selection, the work in recording of number of hogget oestrus reduces to that of identifying those individuals which fail to show evidence of oestrus, from the remainder. This procedure is likely to be applicable in the initial stages of selection, in view of the relatively low intensity of selection which is generally the case with the female sheep.

Without a doubt, whether the complete information on number of hogget oestrus is required or not, it would be easier to do the work under the conditions of a stud flock than those commonly found in commercial sheep flocks. For both sets of conditions, the use of sire-sine crayons as a labour-saving device of mating identification keeps the amount of work within reason.

In closing, it may be pointed out that mass selection has been implied in the above discussion. This, being the case, tends to reduce the need for permanent individual identification. For example, if single-character mass selection is to be used, only temporary individual identification is required; for hogget body weight, near shearing and for number of hogget oestrus, from the time of first occurrence of oestrus until selection. In the latter case, selection of the ewe hoggets may be carried out at various times during the breeding season. If on each occasion, the replacements selected are removed from the main mob, only the mating marks are needed for identification. Both of these characters, if used singly as criterion of selection, would lead to simple application and thus, may well be preferred under certain conditions such as those found on the hill country sheep farms.

Finally, it may be noted that the hogget characters investigated in this study are all heritable and each bears a similar degree of phenotypic and genetic correlation with fertility of ewe. In order to make more systematic use of this information, hogget selection indices have been constructed. In doing so, only two hogget characters, number of hogget oestrus and hogget body weight were included in the index so that simplicity,

normally found in association with the use of single-character selection methods, in some measure, is retained and at the same time, properties of the selection indices, are more tractable. In conclusion, the evidence presented in this thesis suggests that potential fertility of the ewe can be recognised early in life as indicated by the information on each hogget character. However, the use of a properly constructed hogget index ensures, to a greater degree, that the purpose of early recognition of fertility is more likely to be achieved in the current attempt to improve lamb production of the Romney Marsh ewe.

VI. SUMMARY

The study was primarily concerned with early recognition of fertility, as a method of improvement by selection for lamb production in the Romney Marsh ewe. The measurements of growth in live weight and oestrous behaviour which can be recorded at the hogget stage, four to 14 months in age, were investigated as possible criteria of potential fertility in the ewe. For this purpose, information was required and obtained on heritability of the characters and phenotypic and genetic correlations among them. The hogget characters used in the study were: weaning weight, live weight in March, live weight at the 'shortest-day' (21st, June) of the year and hogget body weight (post-shearing in October), each weight being measured to the nearest pound; and number of overt oestrus per ewe hogget during the first breeding season (March to early August) in the life of a ewe. The measurements of fertility were: number of lambs born per ewe at the first, over the first two and then three lambings, the last mentioned was considered as being the most important objective of improvement. The data were collected from an experimental Romney flock maintained at Massey University, Palmerston North, New Zealand and represented those available over a period of 11 years from 1955 to 1965 inclusive.

The study of environmental effects on hogget characters showed that type of birth and rearing effect was most marked on live weight characters but particularly for weaning weight, the average difference between singles and twins being about nine lb. at weaning. Presumably because of the severe handicap imposed pre-weaning, the twins showed compensatory growth post-weaning.

The effects due to age of dam and regression on age were moderate on the various characters, estimates of their values being comparable with those reported in the literature. Evidence of interaction between age of dam and type of birth and rearing was found in the data for weaning weight and live weight in March, but further analysis showed that the extent of departure from linearity was not serious, hence linear correction factors, being simpler to apply, were used in all cases. Some doubt existed as to whether the average difference in fertility between ewes themselves born as singles and twins (type of birth effect) could be regarded as environmental or genetic in origin. The results found in this study indicated that type of birth effect contained some genetic contribution and therefore, no adjustment was made to remove the type of birth effect in the fertility data. However, the fertility data were freed from age of dam effects prior to estimation of heritability and genetic correlations.

The genetic parameters were estimated using two relationships commonly available in sheep. The analysis based on the paternal half-sib relationship, was considered to be a more satisfactory method in view of the possible presence of maternal effect in the data. If the maternal effect was an important source of variation, the regression of daughter on dam, the second method of analysis, would be unsuitable without modification, for the purpose intended. In addition, particularly in relation to the analysis involving fertility of the ewe, the paternal half-sib method allowed a more complete utilisation of the available data. In the model used, the sires were nested within years.

The coefficient of the relationship among paternal half-sibs used to find the heritabilities and genetic correlations has the value of a quarter, being that expected from a Mendelian population under random mating. The estimates of heritability for the different characters were: weaning weight (0.30), March live weight (0.45), 'shortest-day' live weight (0.39), hogget body weight in October (0.51); number of hogget oestrus (0.24); number of lambs born per ewe for the first lambing at two years of age (0.05), over the first two lambings (0.13) and over the first three lambings (0.03). The genetic correlation between each pair of hogget characters was positive and the values ranged from 0.3 to 1 ; and those between a hogget character and the various measurements of fertility, all being positive, from 0.3 to 1 in value. These results are unlikely to be affected by the interaction between sires and 'years' which was studied for each hogget character and found to be a negligible source of variation in a sample of the present data.

The covariances and variances made available by the paternal half-sib analysis were used to find phenotypic correlations between each pair of hogget characters (range in value from 0.4 to 0.9); and between a hogget character and each measurement of fertility of the ewe (range in value from 0.1 to 0.2). The relative importance of weaning weight, post-weaning weight gains (weaning to March, March to the 'shortest-day') and age of the individual on variation in number of hogget oestrus was evaluated using the Path-coefficient analysis. The result showed that weaning weight was by far the most, and age of the individual, the least important factor in the determination of number of hogget oestrus.

This finding together with the information based on phenotypic and genetic correlations suggest a marked degree of dependence between growth and the phenomenon of oestrous behaviour in the ewe hogget.

The estimate of heritability for each character found by doubling the regression of daughter on dam with one exception, agreed closely with the corresponding value reported earlier by the paternal half-sib analysis. The empirical evidence therefore, indicated that the post-natal maternal environment or its carryover effect, if present, did not represent an important source of variation in so far as the estimates of heritability were concerned. On the other hand, a systematic inequality in value of the corresponding cross-covariances between dam and daughter was observed and further analysis showed that this was likely to have been caused by a carryover maternal effect. The problem of maternal and carryover maternal effect in the relationship between a dam and her daughter was investigated using, in the first instance, weaning weight data obtained from lambs which had been reared post-natally by 'foster' dams. The values of genetic correlations found according to a modified method which included the carryover maternal effect as a source of variation, were more comparable with the corresponding estimates from the paternal half-sib method, than those obtained by the usual analysis based on regression of daughter on dam. Point estimates of genetic correlations between maternal environment and characters used in this study, except in the case of number of hogget oestrus (0.11), were all negative in value (range from -0.2 to -0.8), and the largest absolute value, being that for maternal environment and weaning weight of the lamb.

In general, the results suggest that the hogget characters used in this investigation are all heritable, varying in value of heritability from 0.50 to 0.2. The fertility of the ewe, on the other hand, is a lowly heritable character, the present estimates of its heritability whether based on one, or more lambings, were all low in value, being in general agreement with those reported in the literature. Each hogget character was found to bear a similar and useful degree of phenotypic and genetic correlation with fertility of the ewe. The results, therefore, suggest that potential fertility of the ewe can be recognised early in life. In order to make a more systematic use of the information provided by the present data, selection indices were constructed each based on two hogget characters: number of hogget oestrus and hogget body weight (post-shearing at about 14 months in age). The likely consequences of the carryover maternal effect in response and correlated response to selection, were investigated by comparing the properties of a restricted selection index with those of an unrestricted selection index. The restriction imposed had the effect of keeping the additive genetic value of maternal environment constant, regardless of the direction or magnitude of the response to selection in either of the two hogget characters. The net result of the restriction was a small loss in the accuracy of prediction and a moderate reduction of the expected genetic gain in hogget body weight. The tentative conclusion is that worthwhile improvement in fertility of the ewe can be expected, despite the concession which has to be made in the presence of a carryover maternal influence. The practical

problems of indirect selection for higher fertility of the ewe were discussed and the need for simplicity in methods of selection and recording of animal performance was stressed. It may be concluded that the application of a simple and properly constructed hogget index is likely to provide a useful alternative, to direct selection for fertility in the current attempt to improve lamb production of the Romney Marsh ewe.

VII. LITERATURE CITED

- Allen, D.M. and Lamming, G.E. (1961) J. Agric. Sci. 57: 87.
- Apps, A.W.J. (1953) N.Z. J. Agric. 87: 112.
- Barnicoat, C.R., Logan, A.G. and Grant, A.I. (1949) J. Agric. Sci. 39: 44 and 237.
- Blackwell, R.L. and Henderson, C.R. (1955) J. Anim. Sci. 14: 831
- Bohren, B.B., McKean, H.E. and Yamada, Y. (1961 a and b) Biometrics 17: 481 and 626.
- Ch'ang, T.S. (1955) A Study of Some Aspects of Genetic Variation and Covariation of Fertility in a Flock of New Zealand Romney Ewes. Unpublished M. Agr. Sc. Thesis. Massey University Library.
- _____ (1960) Massey Sheepfarm. Ann. P.211.
- Ch'ang, T.S. and Raeside, J.I. (1957) Proc. N.Z.A.P.S. 17: 80.
- Ch'ang, T.S. and Rae, A.L. (1961) N.Z. J. Agric. Res. 4: 578.
- Chapman, A.B. (1946) Genetics 31: 494.
- Clarke, J.N. (1963) A Study of Some Aspects of Selection for the Fertility of New Zealand Romney Ewes. Unpublished M. Agr. Sc. Thesis. Massey University Library.
- Cochran, W.G. (1954) Biometrics 10: 417.
- Cockrem, F.R., Barton, R.A. and Rae, A.L. (1956) Proc. N.Z.A.P.S. 16: 59.
- Coop, I.E. (1964) Massey Sheepfarm. Ann. P.122.
- Dickerson, G.E. (1947) Res. Bull. No. 354. Agric. Expt. Sta. Iowa State College, Ames, Iowa.
- Dunlop, A.A. (1963) Aus. J. Agric. Res. 14: 690.
- Dunn, R.B. and Grewal, R.S. (1963) Aus. J. Exptal. Agric. and Anim. Hus. 3: 235.
- Falconer, D.S. (1960) "Introduction to Quantitative Genetics". Oliver and Boyd, Edinburgh and London.
- _____ (1965) Proc. XI International Congress of Genetics 3: 763.
- Fisher, R.A. and Yates, F. (1953) Statistical Tables for Biological, Agricultural and Medical Research. 4th Ed. Oliver and Boyd, Edinburgh.

- Hafez, E. S. E. (1952) J. Agric. Sci. 42: 189.
- Harvey, W. R. (1960) ARS-20-8, Agric. Res. Service, U. S. D. A.
- Hazel, L. N. (1943) Genetics 28: 476.
- Hazel, L. N. and Terrill, C. E. (1945) J. Anim. Sci. 4: 331.
- _____ (1946) J. Anim. Sci. 5: 318.
- Henderson, C. R. (1953) Biometrics 9: 276.
- Joubert, D. M. (1963) A. B. A. 31: 295.
- Karam, H. A. (1957) J. Anim. Sci. 16: 990.
- Kempthorne, O. (1952) "The Design and Analysis of Experiments". Wiley, New York.
- Kempthorne, O. and Tandon, O. B. (1953) Biometrics 9: 90.
- Kempthorne, O. and Nordskog, W. (1959) Biometrics 15: 10.
- Kennedy, J. P. (1959) M. Sc. Thesis. Univ. New South Wales.
(cited by Young, Turner and Dolling 1963).
- Koch, R. M. and Clark, R. T. (1955) J. Anim. Sci. 14: 979.
- Lerner, I. M. (1958) "The Genetic Basis of Selection". John Wiley and Sons, Inc. N. Y.
- Lewis, B. N. (1962) J. Roy. Stat. Soc. A. 125: 88.
- Lewis, K. H. C. (1959) Proc. N. Z. A. P. S. 19: 111.
- Lush, J. L. (1940) Amer. Soc. Anim. Prod. P. 293.
- Radford, H. M., Watson, R. H. and Wood, G. F. (1960) Aust. Vet. J. 36: 57.
- Rae, A. L. (1952) A. B. A. 20: 197.
- _____ (1956) The Genetics of the Sheep. Advances in Genetics 8: 189.
- _____ (1958 a) Massey Sheepfarm. Ann. P. 231.
- _____ (1958 b) N. Z. J. Agric. Res. 1: 104.
- Rae, A. L. and Ch'ang, T. S. (1955) Proc. N. Z. A. P. S. 15: 103.
- Reeve, F. C. R. and Robertson, F. W. (1953) A. B. A. 21: 211.
- Rendel, J. (1956) J. Anim. Sci. 15: 193.

- Roberts, E.M. (1957) The Practical Application of the Method of Selection Promising the Greatest Improvement in Merino Productivity. Ph.D. Thesis. Univ. New South Wales.
- Sidwell, G.M. (1956) J. Anim. Sci. 15: 202.
- Sidwell, G.M. and Grandstaff, J.O. (1949) J. Anim. Sci. 8: 373.
- Snedecor, G.W. (1950) "Statistical Methods". The Iowa State College Press. Ames, Iowa.
- Tallis, G.M. (1959) Aust. J. Stat. 1: 35.
- _____ (1962) Biometrics 18: 120.
- Turner, H.N., Hayman, R.H., Triffitt, L.K. and Prunster, R.W. (1962) Anim. Prod. 4: 165.
- Wallace, L.R. (1948) J. Agric. Sci. 38: 93.
- _____ (1964) Proc. Ruakura Farmers' Mtg. P.25.
- Wiggins, E.L. (1955) J. Anim. Sci. 14: 1260.
- Wilk, M.B. and Kempthorne, O. (1955) J. Amer. Stat. Ass. 50: 1144.
- Wilson, P.N. and Osbourn, D.F. (1960) Biological Review 35: 324.
- Wright, S. (1931) J. Amer. Stat. Ass. Supplement 26: 155.
- _____ (1934) Ann. Math. Stat. 5: 161.
- Yates, F. (1948) Biometrika 25: 176.
- Young, C.W., Legates, J.E. and Farthing, B.R. (1965) Genetics 52: 553.
- Young, S.S.Y., Turner, H.N. and Dolling, C.H.S. (1963) Aus. J. Agric. Res. 14: 460.