A STUDY OF SOME ASPECTS OF THE GENETIC VARIATION AND COVARIATION OF FERTILITY IN A FLOCK OF NEW ZEALAND ROMNEY EWES

by

T.S. CH'ANG

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I. INTRODUCTION

"Fertility" is a term generally used to denote the expression of reproductive performance. Any precise definition of "Fertility", however, must depend ultimately on the purpose for which it is intended and the criterion by which it is measured. For the present purpose "Fertility" may be regarded as the rate of reproduction which is measured by some form of a lambing percentage.

The economic importance of fertility in sheep production has not been, until recently, fully appreciated, but still less has its significance in the genetic improvement of sheep been realised.

Many breeds, in particular, the New Zealand Romney* are regarded as dual purpose sheep. They are expected to produce meat and wool. In a flock of sheep, gross financial returns depend on the total amount of meat and wool available for sale. This is a simple function of the production per sheep and the number of sheep. In a self-contained flock, the number of surplus sheep in a given financial year is determined almost solely by the lambing per cent of that year. Thus, it can not be denied that lambing per cent or fertility contributes substantially to the returns from sheep. At

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* The term "New Zealand Romney" is used here to indicate that they are grade sheep, the offspring of many generations of Romney Marsh rams.

same time other economic characters, such as fleece weight, and fleece style in sheep production, must not be neglected.

In order to apportion the importance of each character in terms of its contribution to the gross financial return of a flock, it is necessary to measure its relative economic value. The relative economic value of a character may be defined as the increase in gross financial return per unit change in the expression of the character. Rae (1954) reported the following relative economic values for the New Zealand Romney.

Table I. The Relative economic values of Fleece and Carcass Characters

Fleece weight	1 lb. more increases returns by	47d
Quality number	1 quality finer " " "	12½d
Style	1 grade better " " "	48d
Fertility	1 lamb more " " "	518d
Carcass weight	1 lb. more " " "	17d
Body weight	1 lb. more " " "	8d
Carcass grade	1 grade better " " "	21d
Body conformation	1 grade better " " "	7d

The outstanding feature of the above table is clearly the high relative economic value of fertility. In addition, Rae (1954) presented the following table which shows the increased return per sheep as a result of one generation of selection, if all the selection potential were used on each of the characters singly.

Table II. Increased return per sheep as a result of one generation of Selection

Fleece weight	10d
Quality number	7d
Style	10d
Fertility	20d
Body weight	7d
Body Conformation	3d

Thus, from these two tables, the objectives of breeding for increased productivity in the New Zealand Romney have been outlined. Most important for present purposes is that increasing fertility leads to by far the greatest improvement in the financial returns of the Romney breed.

Most animal breeders consider selection or the existence of a differential rate of reproduction as the main, if not the only, force at their command for changing the genetic composition of their individual flocks or of a whole breed. Selection for one or several characters, however, depends on both the genetic variability of the population from which selections are made and the proportion of available animals that are required for breeding purposes. Satisfactory reproductive performance or fertility, therefore, results in larger populations from which a given number of animals may be selected and leads to more rapid genetic improvement.

It is thus evident that high fertility <u>per se</u> is an important economic character in sheep but still more, owing to its genetic ramifications through selection, it provides a foundation on which the greater genetic improvement of other economic traits is made possible.

In view of these features of fertility, its place in a sheep breeding programme is undeniable. There are many selection methods which may either be used alone or in combination in a breeding programme. The choice of a particular selection method, however, depends largely on the heritability of the character concerned. In reality, often more than one character is under selection. Some knowledge of correlated responses, but in particular, possible genetic antagonisms between characters of economic importancce is necessary before the most effective breeding programme can be devised. This investigation is, therefore, mainly concerned with the statistical estimation of the genetic variation and covariation of fertility in a flock of New Zealand Romney ewes.

The following aspects will be considered in detail:

1. The effects of age and year on the incidence of barrenness, single births, and multiple births.

2. The estimation of repeatability of the number of lambs born.

3. The estimation of heritability of the number of lambs born.

4. The estimation of the phenotypic covariation between the number of lambs born and weaned and the greasy fleece weight of the ewe.

5. The estimation of the genetic covariation between the number of lambs born and weaned and greasy fleece weight.

6. Applications of the present findings will be discussed.

II. DEFINITION AND DISCUSSION OF TERMS TO BE USED

A. Fertility of the ewe

In popular usage fertility depicts the ability of an animal to produce large numbers of living young. The inability to produce any offspring at all is termed sterility. There are many criteria by which fertility is measured. Various measurements of fertility, however, may not be strictly comparable. Goot (1950) found that a difference of 30 per cent in lambing per cent could be due, simply to the different methods of measurement. It is obvious that the term "fertility" should not be used without adequate definition.

In general, fertility of the ewe may be measured at several different phases of the reproductive cycle. These measurements are usually made at stages where numerical expressions are possible, e.g. the number of Graafian follicles, the number of ova shed, fertilised and implanted, the number of foetuses surviving at different times during pregnancy, the number of lambs born at birth, at docking, weaning and finally reaching breeding age. Ideally, for studies of inheritance, measurements at breeding age are most useful. It is obvious that if all the young died before reaching breeding age, studies of inheritance, in particular the inheritance of fertility, are not possible. On most sheep farms in New Zealand and the present flock is no exception, disposal of some or all wether lambs and surplus ewe lambs takes place either before or shortly after weaning. As a result, collection of data at first breeding age of the young is usually not feasible. Thus, data collected at weaning appear to be a necessary compromise between the ideal and current management practices.

On the other hand, in the present state of physiological knowledge, the number of lambs born* is the earliest visible and measurable expression of fertility in ewes. In addition, given that identical twins are infrequent in sheep (Johansson 1933, Johansson and Hansson 1943 and Barton 1949) the number of lambs born is, in effect, an estimate of the minimum number of ova shed by the ewe at her last ovulation. Since ovulation rates can not be measured without slaughtering the animal, the number of lambs born at birth is a useful substitute. Measurements taken subsequent to the one at birth are likely to be confounded by effects of weather, shepherding and other managemental practices, and thus are less suitable as a measure of fertility in the ewe.

While the number of lambs born and weaned are useful indices of fertility for individual ewes, on a flock basis, lambing per cent is the usually accepted measure. In the

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*Number of lambs born dead or alive but apparently carried to the full term of gestation.

present study, lambing per cent will be calculated as:

(a) the lambing per cent at birth

$$\frac{\text{The total number of lambs born} \times 100}{\text{The total number of ewes put to the ram}}$$

and (b) the lambing per cent at weaning

$$\frac{\text{The total number of lambs weaned} \times 100}{\text{The total number of ewes put to the ram}}$$

B. Fertility of the ram

In this study, effects due to the fertility of the ram will be assumed to be distributed at random. This assumption appears to be reasonable in the present data. As will be described later, a total of 27 rams has been used and they were mated to ewes chosen at random. Unless otherwise specified, fertility of the ram will be treated simply as a component of the environment to which the ewes are exposed.

C. Terms used in relation to the age of sheep

For the sake of clarity, the correspondence between age of sheep and the measurements of fertility and fleece weight will be described separately.

Lambing in this flock generally commences in August. Lambs are usually weaned in January when they are four to five months old. A two-tooth lambing record corresponds to the age of two years and the four-tooth, six-tooth and eight-tooth records are made respectively at three years, four years and five years of age.

Hoggets are normally shorn in October when they are about 14 to 15 months old. Ewes are generally shorn in December, approximately a month before weaning. A two-tooth fleece weight represents approximately 14 to 15 months' wool growth. Thereafter, four-tooth, six-tooth and eight-tooth fleece weights are collected at yearly intervals.

III. SOURCE OF DATA

A. History and Management of the flock

This flock was originally established in 1944 for the purpose of investigating the inheritance of many fleece and carcass characters of the Romney Marsh breed. Information pertaining to various other economic characters, including the reproductive performance of the ewes, was gathered as a part of this investigation. Data used in this study were collected over eight consecutive years from 1946 to 1953 inclusive.

From 1946 to 1948 this flock was run on the Pahiatua Block of the Massey College sheep farm. The details of this area and management have been adequately described by Rae (1950). However, early in 1949 the flock was transferred to the Tuapaka Block also of the College. Of the 1,050 acres which comprise Tuapaka approximately 800 acres are hills and 250 acres flats. This flock was chiefly run on these flats which will be briefly described presently.

Tuapaka was taken over by the College in 1938 and since then a considerable amount of pasture and other improvement has been made. By the time this flock was transferred to Tuapaka in 1949, the pasture and other amenities were brought up to a status more or less comparable with that of the Pahiatua Block. In addition, management and shepherding were kept on a similar standard and from 1949 to the present time no perceptible change in all aspects of husbandry has been observed.

The soil at Tuapaka is a yellowish-grey silt loam with underlying clay sub-soil. Natural drainage was poor and tile drains and some mole drains were laid. The average rainfall is in the region of 40 inches per annum with a reasonable seasonal distribution. Pastures, since sowing down some 10 to 15 years ago, have been maintained predominantly as a perennial rye - white clover association. On the average a topdressing of five cwt. of lime and one cwt. of superphosphate was given annually on all paddocks. Except during the winter months normal complements of beef breeding cows were also kept on these flats. It is estimated that these flats have a carrying capacity of three and a half to four ewes per acre (Hewitt 1955). It must be emphasised that in general this flock has been kept in an environment which is typical of sheep farms in the Manawatu area.

B. Collection and Arrangement of the Data

Ewes in the flock were shorn annually and their greasy fleece weights recorded. The information available from the fertility data includes:

1. Birth date of lamb.
2. Birth rank of lamb.
3. Sex of lamb.
4. Birth weight of lamb.
5. Ear tag number of the dam.
6. Number of lambs weaned per ewe

7. Weaning dates and weaning weights of lambs.
8. Remarks.

To facilitate the computation of phenotypic and genetic parameters, it was found convenient to record on cards the information listed above. In addition, the sire of the lamb was also recorded. These cards were perforated on all sides and various classifications were made by slitting some pre-determined perforations. The sorting, for the purpose of either tabulation or computation directly from these cards, was aided by the use of a needle. Thus, for each ewe entering the flock there was correspondingly a card recording the reproductive performances and greasy fleece weights throughout her life-time.*

C. Certain features of the data relevant to the present investigation

While various assumptions involved in the application of statistical procedures are difficult to evaluate, much can be done during the experimental period so that these seemingly restrictive assumptions may become inherent in the data collected. In this respect the following features of the data are worth mentioning.

(1) Surplus replacement ewes, if any, were culled at random. In fact, no selection for any character was prac-

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*As a rule, ewes are cast for age at approximately 5½ years old.

tised. This renders these data equally suitable to regression as well as correlation techniques. Similar data gathered either from Surveys or stud books are, however, subject to some possible bias through false returns or selective registration. This feature leaves inference from those data uncertain if not impossible.

(2) Ten rams were used over the whole flock in each year from 1944 to 1945 inclusive; thereafter the number was reduced to seven. Rams were normally discarded after three consecutive years in use and fresh ones purchased. In selecting them the rams were deliberately procured from widely different sources. This feature thus permits the assumption that inbreeding does not affect the outcome of these data.

(3) The number of ewes in each mating group was virtually the same within each mating season. The size of the mating groups between seasons was, however, variable, depending on the number of rams used and the total number of ewes available. The age composition of ewes in each mating group was kept as uniform as was possible. Ewes were assigned at random to each mating group. This feature favours the assumption that this flock is a population bred at random.

(4) Ewes were rotationally grazed in mobs all the year round except during the mating season when mating groups

were confined to their respective paddocks for a period varying from six to eight weeks and again during lambing when they were drafted into three mobs, early, mid or late, according to the mating dates. Through these practices it was hoped that no two groups of animals received better or worse than average treatment for any length of time. More important, however, this feature of the data supports the assumption that there is no environmental correlation between daughters and dams or between groups of ewes which are half-sibs.

IV. REVIEW OF LITERATURE

A. Effects of Age and Other Environmental Factors on the Fertility of Ewes

Fertility as measured by some form of a lambing percentage is primarily determined by its components, i.e. frequency of barren ewes and frequency of single and multiple births. In general, most workers have reported the effects of age and other environmental factors on these components of lambing per cent rather than on lambing per cent as such. For the sake of clarity some work concerning the effects of age on the components of lambing per cent is reported first and other environmental factors will be reviewed later.

Barton (1947) reported the incidence of barrenness to be 15.8% in a flock of stud Romney Marsh ewes. The percentages of barren ewes in each age group were given as follows:

Age of Ewes at Lambing	$\frac{\text{No. of Barren ewes} \times 100}{\text{Total No. of Ewes}}$
2 yr. old	25.2%
3 yr. old	13.5%
4 yr. old	11.5%
5 yr. old	10.8%
6 yr. old	7.1%
7 yr. old	10.8%
8 yr. old	7.1%

Goot (1952) showed that age accounted for approximately 43% of the total variance in barrenness in two flocks of Romney Marsh ewes. The mean percentage of barren ewes was found to be 10.2%. By age groups the incidence of barren ewes was distributed as follows:-

Age of Ewes at Lambing	$\frac{\text{No. of Barren ewes x 100}}{\text{Total No. of Ewes}}$
2 yr. old	16.6%
3 yr. old	11.2%
4 yr. old	5.8%
5 yr. old	5.9%
6 yr. old and over	5.5%

Nichols (1924), analysing returns from a questionnaire, noted that age had a very important effect on barrenness among many British breeds of sheep. From these reports it may be concluded that the incidence of barrenness is highest in young ewes and decreases with advancing age.

Little or no attention has been paid to the effects of age on single births. Consequently, no literature seems to be available on this subject.

The incidence of twin or multiple births has been, comparatively speaking, subject to much study in connection with the problem of fertility in sheep. Literature on factors affecting multiple births in sheep has been reviewed recently by Reeve and Robertson (1953). Marshall and

Potts (1921) found that the frequency of twins in pure bred Southdown ewes increased with age up to five or six years old. Terrill and Stoehr (1939) reported the same trend in studies on Rambouillet, Corriedale, Columbia and Targhee ewes. Roberts (1921) working with American Shropshire sheep stated that multiple births increased with age up to four years, and remained fairly constant from then on until eight years of age. Jones and Rouse (1920),analysing flock records of the University of Wisconsin, confirmed an earlier report by Carlyle and McConnell (1902) that the highest per cent of multiple births occurred among five-year-old ewes. Lopyrin (1938) concluded from work in Russia that ewes of late-maturing breeds showed the highest number of multiple births at five to six years of age, whereas the ewes of early-maturing breeds reached their maximum at three years. Kelley (undated) reported that in an Australian stud Merino flock twins were most frequent when the ewes were six to ten years old. Nikoljskii (1933), studying fertility on Karakuls in an Askania flock, reported twinning rates of 17 per cent in four-year-old ewes compared with 3 - 7 per cent in younger ewes. In a detailed study of the records of the registered flocks of Oxford Down, Shropshire, Cheviot and Landrace breeds in Sweden, Johansson and Hansson (1943) showed that there was generally a steady rise in the average number of lambs per birth in all breeds up till five to six years of age, with a gradual reduction thereafter.

In addition, they presented regression coefficients measuring the average increase in number of lambs at the second birth for a unit increase at the first birth. These regression coefficients which clearly show the effect of age are tabulated below.

Table III. Coefficients of Regression of the Number of Lambs Born at different parturitions of the same ewe.

Breed	No. of Ewes	No. of lambs per birth at 2 & 3 years of age of the ewe Regression Coefficients (Within flocks)	No. of Ewes	Av. No. of lambs per birth at 2-3 & 4-5 years of age of the ewe Regression Coefficients (Within flocks)
Shropshire	2488	0.162**	1414	0.276**
Cheviot	3696	0.193**	2111	0.289**
Landrace (F)	575	0.187**	436	0.295**
Average Within Breeds		0.180**		0.285**

** $P \leq 0.01$

It can be seen that a difference of one lamb at two years of age was followed by an increase of 0.180 lamb per birth at the following lambing. Similarly an average increase of one lamb at two and three years of age was accompanied by an increase of 0.285 lamb per birth at four and five years of age.

Desai and Winters (1951a), working with mixed breeds, analysed the effect of age on lambing percentages (number of lambs born per one hundred lambings) and found that it accounted for 6.39 per cent of the total variation. In general, they stated that the lambing percentage rises at an average rate of 0.1405 lambs per year up to the fifth year of age and then there would be decline.

In view of the effects of age on fertility, it is worth noting that comparison of lambing percentages, either between years within the same flock or between flocks, unless based on similar age-compositions, could be very misleading.

Unlike age, specific effects of the environment on fertility are generally difficult to isolate and measure. Temperature, rainfall, light, soil, pastures, management practices and many others, at one time or another have been reported by various workers as environmental factors affecting fertility in sheep. To review each in detail is not warranted for present purposes. Only those considered useful to this study will be reported.

In many studies of lambing per cent, differences between years have been considered. Variations due to year would include differences in climate resulting both from its direct effects on the animal and from its indirect effects through soil and pasture. In addition, differences in management and possibly, if the flock is under selection, differences in average genetic merit of the animals may also contribute to yearly variations. Still more yearly variations may contain many other environmental differences. Their effects are, however, not known in the present state of knowledge.

Goot (1952) found that 11 per cent of the total variance of barrenness was due to differences between years. Desai and Winters (1951a) computed the partial regression coefficient of lambing average on year (holding age constant) and found it to be -0.0698 lamb per year. No explanation was advanced for this finding.

That environment has an important effect on fertility was shown by the work of White and Roberts (1927). Among other things they were able to demonstrate differences in fertility of Welsh Mountain sheep under mountain, intermediate and lowland conditions.

Finally, that "flushing" appears to increase fertility in many breeds of sheep has been reported by Marshall and Potts (1921), Nichols (1924), Underwood and Sheir (1941), Johansson and Hansson (1943) and recently by Vita (1951) and Wallace (1951).

B. Repeatability of Reproductive Performance of the Ewe

Repeatability measures the consistency of performance of the same individual at different times. It may be computed either as an intra- or inter-class correlation coefficient. Computing the repeatability as an intra-class correlation, however, requires the assumption that variances at different occasions be equal. Failure to satisfy this assumption will result in some under-estimation when compared with the result from the inter-class correlation (Lush and Molln, 1942).

The size of repeatability is of considerable importance in a selection programme. High estimates of repeatability generally indicate that the use of early records alone is sufficiently accurate to achieve satisfactory progress from selection. Consequently, the delay in waiting for later records, as would be necessary if the repeatability were low, is avoided. Once estimated, however, repeatability is useful in at least two other aspects. Firstly, it indicates the upper limit of heritability of the character. Secondly, the discrepancy between repeatability and heritability serves to expose the importance of dominance and epistasis in addition to maternal influence and other permanent environmental agencies affecting the character.

Literature concerning the repeatability of the number of lambs born per birth is scanty. Estimates of repeatability that have been reviewed, are summarised in the following table.

Table IV. Estimates of Repeatability of Reproductive Performance

Estimates of Repeatability	Breed	Age	Notes	Reference
0.0498 ± 0.0263	Mixed Breed	Mixed ages	Age effect corrected. Intra-class correlation 2,696 lambings from 962 ewes	Desai & Winters (1951b)
0.148**	Shropshire	Between 2yr & 3 yr old lambing records	Calculated on within flock basis. Inter-class Correlation 2488 ewes	Johansson & Hansson (1943)
0.173**	Cheviot	"	" 3696 ewes	"
0.194**	Landrace (F)	"	" 575 ewes	"
0.249**	Shropshire	Between averages of 2-3 yr old & 4-5 yr old lambing record	" 1414 ewes	"
0.257**	Cheviot	"	" 2111 ewes	"
0.275**	Landrace (F)	"	" 436 ewes	"
0.141**	Shropshire	Mixed ages	Calculated on within flock & age basis. Intra-class Correlation. 213 ewes	"
0.171**	Cheviot	"	" 393 ewes	"
0.236**	Landrace(F)	"	" 368 ewes	"
0.06 ± 0.03	-	-	-	Cockerham (1949) as quoted by Desai & Winters (1951b)

**P ≤ 0.01

C. Heritability of Reproductive Performance of the Ewe

Heritability is defined by Lush (1949) as the fraction of the observed or phenotypic variance which was caused by differences between the genes or the genotypes of the individual. More precisely, the definition of heritability in the narrow sense is:

$$\frac{\sigma_g^2}{\sigma_g^2 + \sigma_d^2 + \sigma_i^2 + \sigma_e^2 + \sigma_j^2}$$

and, in the broad sense, it is:

$$\frac{\sigma_g^2 + \sigma_d^2 + \sigma_i^2}{\sigma_g^2 + \sigma_d^2 + \sigma_i^2 + \sigma_e^2 + \sigma_j^2}$$

where: σ_g^2 is the variance due to the additive effects of the genes in the population.

σ_d^2 is the variance caused by non-additive effects of allelic genes; i.e. the dominance deviations.

σ_i^2 is the variance caused by non-additive interactions between genes which are not allelic, i.e. the epistatic variance.

σ_e^2 is the variance caused by the environmental conditions under which the animal's record was made.

σ_j^2 is the variance caused by joint effects or non-additive interactions of heredity and environment.

The two definitions differ only in respect of the consideration given to the dominance and epistatic variance. The effects due to dominance and epistasis depend on the particular combinations of genes. At each Mendelian segregation, genes recombine. Consequently, under random mating, effects which the genes have only in certain combinations are transmitted to their offspring only in part if at all. It is therefore the heritability in the narrow sense that is of interest from the point of view of selection.

Depending on the method used, an actual numerical estimate of heritability is usually between the narrow and broad definitions (Lush, 1948). The estimate almost always includes a little of the epistatic variance and sometimes a little of the dominance variance.

Early studies on the inheritance of fertility were reported mainly as parent-offspring correlations or regressions. The following tables summarise the results of some previous investigations on the inheritance of fertility in sheep.

Table V(a). Estimates of Heritability of the Number of Lambs at Birth

Estimates of Heritability	Breed	Age	Notes	Reference
0.10 ± 0.05	-	-	-	Cockerham (1949) as quoted by Desai & Winters (1951b)
0.0306 ± 0.0102	Mixed Breeds	Mixed Ages	Average of all lines. Intra-sire Dtr-Dam regression 542 prs. By Procedure 1.	Desai & Winters (1951b)
0.0736 ± 0.0152	Mixed Breeds	Mixed Ages	Average of all lines. Intra-Sire Dtr.-Dam regression. 639 prs. By Procedure 2.	"

Table V(b). Daughter-Dam Correlation Coefficients of the Number of Lambs at Birth.

Parent-Offspring Correlation	Breed	Age	Notes	Reference
0.0869 ± 0.0065	Shropshire	Mixed Ages	Correlation between size of litter in which offspring are born and size of litter in which dams are born. 10532prs.	Rietz & Roberts (1915)
0.21 - 0.31	Rambouillet	-	Correlation between twinning tendencies of Dtr. and Dam	Joseph (1931)
0.285 ± 0.045	Cheviot	Av. of first three lambings	Dtr. - Dam Correlation 421prs	Johansson (1933)
0.111 ± 0.047	Shropshire	"	Dtr. - Dam Correlation 441prs	"
0.022[4]	Cheviot	2 yr. old	Within flocks Av. Dtr.-Dam Correlation 1324prs	Johansson & Hansson (1943)
0.090[2]	"	"	Total Dtr.-Dam Correlation 1324prs	"
0.082[4]	Oxford Down	Av. of 3 lambings at 2-6yrs old	Within flocks Av. Dtr.-Dam Correlation 156prs	"
0.130[3]	"	"	Total Dtr.-Dam Correlation 156prs	"
0.159[1]	Shropshire	"	Within flocks Av. Dtr.-Dam Correlation 455prs	"

Table Vb (Contd.)

Parent-Offspring Correlation	Breed	Age	Notes	Reference
0.230^{1}	Shropshire	Av. of 3 lambings at 2-6yrs old	Total Dtr.-Dam Correlation 455 prs.	Johansson & Hansson (1943)
0.087^{3}	Cheviot	"	Within flocks Av. Dtr.-Dam Correlation 657prs.	"
0.255^{1}	"	"	Total Dtr.-Dam Correlation 659prs.	"
0.134^{4}	Landrace (F)	"	Within flocks Av. Dtr.-Dam Correlation 100prs.	"
0.273^{3}	"	"	Total Dtr.-Dam Correlation 100prs.	"

⌿ Probable error $^{1}p \leq 0.001$ $^{2}p \leq 0.01$ $^{3}p \leq 0.05$ $^{4}p \leq 0.1$

Table V(c) Daughter on Dam Regression Coefficients of the Number of Lambs at Birth

Parent-Offspring Regression	Breed	Age	Notes	Reference
0.022	Cheviot	2 yr. old	Within flocks Av. Dtr.-Dam regression 1324 prs	Johansson & Hansson (1943)
0.091	"	"	Total Dtr.-Dam regression 1324 prs.	"
0.086	Oxford Down	Av. of 3 lambings at 2-6 yrs old	Within flocks Av. Dtr.-Dam regression 156 prs.	"
0.145	"	"	Total Dtr.-Dam regression 156 prs	"
0.128	Shropshire	"	Within flocks Av. Dtr.-Dam regression 455 prs.	"
0.193	"	"	Total Dtr.-Dam regression 455 prs.	"
0.089	Cheviot	"	Within flocks Av. Dtr.-Dam regression 659 prs.	"
0.255	"	"	Total Dtr.-Dam regression 659 prs.	"
0.117	Landrace (F)	"	Within flocks are Dtr.-Dam regression 100 prs.	"
0.216	"	"	Total Dtr.-Dam regression 100 prs.	"

D. Phenotypic Covariation Between Fleece Weight and Reproductive Performance of the Ewe

The phenotypic covariation between a pair of productive characteristics may be expressed either as a regression or as a correlation. Purposes of measuring phenotypic covariation, however, may be outlined as follows:

(1) Phenotypic correlations are needed for constructing selection indices to obtain maximum rate of genetic improvement (Hazel, 1943).

(2) Phenotypic regressions as well as correlations may be used for predictive purposes. If a character is expensive or otherwise difficult to measure, its relationship to an easily measurable character or a combination of such characters can be used as a means of predicting it.

(3) Phenotypic correlations provide a description of the concomitant variation between pairs of characters in a given population.

Studies of phenotypic covariation between many fleece characters have been made by various workers. Literature concerning the phenotypic covariation between fleece weight and the number of lambs weaned in sheep, is, however, almost non-existent. What appears to be available is included in this review.

Terrill and Stoehr (1942) analysing life-time production records of Columbia, Corriedale and Rambouillet ewes, suggested that there was an inverse, although low relationship between average life-time fleece weight and pounds of lamb weaned per ewe year. In a different part of the same report, they stated that the pounds of lamb weaned per ewe year were due more to a higher per cent of lambs weaned than to heavier weaning weights. Winters *et al*. (1946) in their study on the factors affecting productivity in breeding sheep concluded that gross fleece production appeared to be somewhat negatively associated with total lamb production. Stevens and Wright (1951) reported that in a flock of Romney Marsh stud ewes the average greasy fleece weight for barren ewes was 10.8 lb.,ewes with single lambs and twin lambs being 9.8 lb. and 9.4 lb. respectively. These averages were based on 141 (barren ewes), 1673 (single birth), and 932 (twin births) records and over a period of eight years.

E. Genetic covariation between Fleece Weight and Reproductive Performance of the Ewe

A genetic correlation is a measure of the tendency for the additive genetic values of two different characters to vary together, whereas a phenotypic correlation may also contain contributions from environmental sources or from dominance or gene interactions. More precisely, the genetic correlation between two characters may be defined as the ratio of the genetic covariance to the product of their genetic standard deviations.

$$r_{G_iG_j} = \frac{\text{Cov. } G_iG_j}{\sigma_{G_i} \cdot \sigma_{G_j}}$$

where G_i and G_j are the additive genetic values for characters i and j.

Application of genetic correlations to animal selection problems was first made by Hazel (1943). He recognised that for predictions based on heritability alone to be reasonably accurate, it is necessary that selection be for this one trait only or that the trait be uncorrelated genetically with any of the others affecting productivity or fitness of the animal. Since selection for only one trait is seldom the aim or rarely feasible in animal breeding, it is obvious that heritabilities are, by themselves, not sufficient to characterise adequately the genetic properties of a population. Consequently genetic correlations play an important role in selection programmes.

The theoretical basis of genetic correlations rests essentially on the assumption of pleiotropy of genes. This, together with other explanations of genetic correlations will be discussed in detail later.

Validity of the theory of genetic correlation has been tested by Falconer (1954) in a mouse selection programme. He concluded that from his data no serious disagreement was found between the calculated genetic correlation and the observed correlated response between body weight and tail length.

A positive genetic correlation indicates that improvement through selection of one trait will be accompanied by some improvement in the other trait. A negative genetic correlation, however, implies that selection for one trait will itself cause some deterioration of the other. Thus, the knowledge of genetic correlations between economically important characters, e.g. fleece weight and the number of lambs weaned, is of considerable interest. Nevertheless, no previous attempt has been made to measure the genetic covariation between fleece weight and the number of lambs. The only work that has been done on the Romney Marsh sheep was by Rae (1950) who reported genetic correlations between various fleece and carcass characters.

V. METHODS OF ANALYSIS AND RESULTS

A. Effects of Age and Year on the Incidence of Barren Ewes, Single Births and Twin Births

(a) Method of Analysis

At the end of a lambing season ewes may be divided into two mutually exclusive classes:

(1) Barren ewes, and

(2) Ewes that have lambed.

However, among the ewes that have lambed, there are again two further mutually exclusive classes:

(3) Ewes that produced single lambs at birth, and

(4) Ewes that produced twin lambs at birth.

(Triplets or higher births are negligible in the present data and thus excluded from the analysis.)

The incidence of barren ewes, single births or twin births may be expressed as a fraction or a percentage of total ewes. The nature of the variation in percentage data of this type has been discussed by Cochran (1943).

Let n_i be the denominator on which an observed fraction or percentage is based, and let $f_i = \frac{a_i}{n_i}$ be the observed fraction. If p_i is the true fraction for this observation i.e. if $E\ (f_i) = p_i$, the variance of f_i i.e. $V(f_i)$ about p_i is the binomial variance $^{p_i\ q_i}/_{n_i}$, where $q_i = (1 - p_i)$. The true fraction p_i, however, will frequently vary from observation to observation. Where present, such variation may contribute to the experimental error on which z, F or t- tests are made. Thus, the total variance of an observed fraction may be expressed as, $V(f_i) = \frac{p_i q_i}{n_i} + \sigma^2_i$, where the first term represents the binomial variation and the second term the extraneous variation. Consequently, percentage data may contain both the binomial as well as the extraneous variation. Depending on the relative amount of each variation present different methods of weighting can be applied. Where the variation is nearly all binomial, weighting proportional to the denominator of the percentage is used. If the variation is largely extraneous, weighting should be independent of the denominator. The weighting used in the present analysis is that of binomial.

A further point to note is the disproportion of sub-class numbers and the occurrence of vacant sub-classes in the present data. This was mainly due to the fact that in any year the number of ewes in each age group was unequal. The method of fitting constants by least squares as described by Kempthorne (1952) was used to eliminate these discrepancies.

The linear model chosen to represent the present data is assumed to be:

$$y_{ij} = \mu + b_i + t_j + e_{ij} \qquad i = 1.....p, \quad j = 1.....q$$

$$\text{with weights } W_{ij} = n_{ij}$$

where: y_{ij} is the number of ewes of a given attribute in the i^{th} age group and j^{th} year, e.g. y_{ij} may represent the number of two-tooth barren ewes in the year 1946.

μ is a constant effect common to all ewes.

b_i is an effect common to all ewes in the i^{th} age group.

t_j is an effect common to all ewes in the j^{th} year.

e_{ij} is the error or residual associated with y_{ij}.

If it is assumed that

$$E(e_{ij}) = 0, \quad E(e_{ij})^2 = \sigma^2_e \text{ and } E(e_{ij}, e'_{ij}) = 0$$

or in words, the error terms are to have zero mean, a constant variance and are not correlated; the following least square equations will yield estimates which are unbiased and "best" in the sense that no other unbiased linear estimates which could be computed from the data, have a smaller variance. These equations are:-

$$\begin{array}{llllll}
\mu : & \sum_{ij} n_{ij}\,\mu + & \sum_{i} n_{i.} b_i + & \sum_{j} n_{.j}\, t_j & = & \sum_{ij} n_{ij}\, y_{ij} \\
b_i : & n_i\,\mu + & n_{i.} b_i + & \sum_{j} n_{ij}\, t_j & = & \sum_{j} n_{ij}\, y_{ij} \\
t_i : & n_{.j}\,\mu + & \sum_{i} n_{ij} b_i + & n_{.j}\, t_j & = & \sum_{i} n_{ij}\, y_{ij}
\end{array}$$

The equations as they stand, of course, have no unique solution since the matrix of coefficients is not of full rank. Some restrictions have to be imposed on the parameters in order that they may be estimated. The following two sets of restrictions have been investigated:

Set (a) $\sum b_i = 0$, $\sum t_j = 0$;

and set (b) $\sum_i n_{i.} b_i = 0$, $\sum_j n_{.j} t_j = 0$

Although the type of restrictions imposed has no effect on the size of the estimates and does not affect the sum of squares computed in an analysis of variance, interpretation of μ, nevertheless differs between these two sets of restrictions. Under set (a), μ is the mean of a hypothetical population in which all subclass numbers are equal. Under set (b), however, μ is the mean of a population in which the distribution of subclass numbers is the same as that actually found in the population. The restriction used in the present data is set (b).

In order to test the statistical significance of these Least Square estimates, a further assumption on the distributional properties of the error term (e_{ij}) in the linear model is necessary. It is assumed that e_{ij} are distributed normally. This may seem to be inconsistent with the assumption underlying the binomial weighting, however, departure from normality does not appear to introduce any serious errors in the significance level of the F-test. (Cochran, 1947). Non-normality is likely to be accompanied by a loss of efficiency in the estimation of treatment effects. More serious though, is the possible correlation between the mean and the variance in the data. It is appreciated that, in view of these possible discrepancies between the assumptions and the data, the efficiency of the analysis of variance will not be as high as if all the assumptions were exactly met. However, as pointed out by Cochran (1947) an experimenter could rarely, if ever, convince himself that all the assumptions were exactly satisfied in his data; consequently, the technique of analysis of variance must be regarded as approximate rather than exact. It is based on these remarks and reservations that the present treatment of the data appears to be not unreasonable.

Briefly, the actual computation was carried out in the following order:

(1) absorbing t_j equations into b_i equations.

(2) solving b_i equations for the estimates of b_i with the restriction that $\sum_i n_{i.} b_i = 0$

(3) estimating t_j similarly and with the restriction that $\sum_j n_{.j} t_j = 0$

(4) Sums of squares used in the analysis of variance were obtained by the reduction in the sum of squares due to fitting several sets of parameters minus the reduction in the sum of squares due to fitting all sets of parameters except the one set whose significance is to be tested, e.g. the sum of squares due to age is found by subtracting the sum of squares due to fitting the mean and year from the sum of squares due to fitting the

mean, year and age.

(b) Results

The analysis of variance was done separately for the effects of age and year on the incidence of barren ewes, single births and twin births. Tables showing the number of barren ewes (B), single births (S) and twin births (T) in each sub-class, together with their respective analysis of variance, are given below.

Table VI. Number of Barren Ewes Classified according to Age and Year.

AGE	2-tooth		4-tooth		6-tooth		8-tooth		Total	
YEAR	n	B	n	B	n	B	n	B	n	B
1946	133	9	-	-	-	-	-	-	133	9
1947	188	46	167	21	-	-	-	-	355	67
1948	24	3	188	9	153	13	-	-	365	25
1949	87	6	18	0	162	4	128	5	395	15
1950	125	26	81	9	2	0	24	5	232	40
1951	211	23	120	9	79	5	-	-	410	37
1952	25	4	199	25	120	16	71	7	415	52
1953	86	7	20	1	180	5	104	2	390	15
Total	879	124	793	74	696	43	327	19	2695	260

Table VII. Analysis of Variance for the Incidence of Barren Ewes

Source of Variation Due to	S.S.	d.f.	M.S.	F
$R(\mu, t_j)$	28.1585	8		
Ages $R(\mu, b_i, t_j) - R(\mu, t_j)$	6.6198	3	2.2066	44.488**
$R(\mu, b_i)$	32.3160	4		
Years $R(\mu, b_i, t_j) - R(\mu, b_i)$	2.4623	7	0.3517	7.091**
$R(\mu, b_i, t_j)$	34.7783	11		
Remainder	0.6945	14	0.0496	
Total	35.4728	25		

** $p \leq 0.01$

Table VIII. Number of Single Births Classified according to Age and Year

AGE	2-tooth		4-tooth		6-tooth		8-tooth		Total	
YEAR	n	S	n	S	n	S	n	S	n	S
1946	133	79	-	-	-	-	-	-	133	79
1947	188	91	167	80	-	-	-	-	355	171
1948	24	18	188	147	153	98	-	-	365	263
1949	87	55	18	9	162	77	128	37	395	178
1950	125	72	81	24	2	1	24	6	232	103
1951	211	150	120	70	79	37	-	-	410	257
1952	25	19	199	112	120	55	71	26	415	212
1953	86	54	20	11	180	77	104	46	390	188
Total	879	538	793	453	696	345	327	115	2695	1451

Table IX. Analysis of Variance for the Incidence of Single Births

Source of Variation Due to	S.S.	d.f.	M.S.	F
$R(\mu, t_j)$	799.5196	8		
Ages $R(\mu, b_i, t_j) - R(\mu, t_j)$	23.6265	3	7.8755	23.190**
$R(\mu, b_i)$	804.7584	4		
Years $R(\mu, b_i, t_j) - R(\mu, b_i)$	18.3877	7	2.6268	7.735**
$R(\mu, b_i, t_j)$	823.1461	11		
Remainder	4.7541	14	0.3396	
Total	827.9002	25		

** $p \leq 0.01$

Table X. Number of Twin Births Classified according to Age and Year

AGE	2-tooth		4-tooth		6-tooth		8-tooth		Total	
YEAR	n	T	n	T	n	T	n	T	n	T
1946	133	45	-	-	-	-	-	-	133	45
1947	188	51	167	66	-	-	-	-	355	117
1948	24	3	188	32	153	42	-	-	365	77
1949	87	26	18	9	162	81	128	86	395	202
1950	125	27	81	48	2	1	24	13	232	89
1951	211	38	120	41	79	37	-	-	410	116
1952	25	2	199	62	120	49	71	38	415	151
1953	86	25	20	8	180	98	104	56	390	187
Total	879	217	793	266	696	308	327	193	2695	984

Table XI. Analysis of Variance for the Incidence of Twin Births

Source of Variation due to	S.S.	d.f.	M.S.	F
$R(\mu, t_j)$	393.0069	8		
Ages $R(\mu, b_i, t_j) - R(\mu, t_j)$	21.6170	3	7.2057	45.404**
$R(\mu, b_i)$	384.8991	4		
Years $R(\mu, b_i, t_j) - R(\mu, b_i)$	29.7248	7	4.2464	26.757**
$R(\mu, b_i, t_j)$	414.6239	11		
Remainder	2.2221	14	0.1587	
Total	416.8460	25		

** $p \leq 0.01$

(c) Discussion

Effects due to Age and Year on the incidence of barrenness and different types of births are statistically significant at the 1 per cent level. This agrees with most of the similar studies reviewed but in particular, with the report by Goot (1952) who worked with the Romney Marsh breed in New Zealand. Results of the present data suggest that adjustment should be made for both the effects due to Age and Year in subsequent analyses. As will be shown later, this has been accomplished by doing the analysis separately for each age group on an intra-year basis.

B. Estimates of Repeatability of the Number of Lambs Born

(a) Methods of Analysis

Techniques appropriate for measuring the amount of association in discrete data are little developed, and those that are available appear to suffer from certain limitations. For the lack of better and more precise techniques, Karl Person's Coefficient of Mean Square Contingency (1904, 1913) and the correlation method given by Peters and Van Voorhis (1940) were used. A full discussion on the assumptions and limitations of these two methods has been given by Rae (1946) and will not be repeated here.

In addition, the ordinary product-moment method (Snedecor 1950) was also used to compute the correlation between: (1) the number of lambs born to two-tooth ewes and the average number of lambs born to them in subsequent three lambings i.e. the average of their four-tooth, six-tooth and eight-tooth lambing records.

(2) the average number of lambs born to two-tooth and four-tooth ewes and the average of their subsequent lambings at six-tooth and eight-tooth.

Strictly speaking, the product-moment Correlation method is satisfactory only for continuous variates. The consequences of its application to the present data are not known. It is necessary to regard the results thus obtained as approximations.

(b) Results

Table XII summarises the results obtained by Pearson's Coefficient of Mean Square Contingency Method. Results derived from the method of Peters and Van Voorhis are given in Table XIII. There is no method available for testing the statistical significance of coefficients obtained by the latter method. The numbers of pairs of observations for each coefficient are included in both Tables.

Table XII. Estimates of Repeatability of the Number of Lambs Born

Coefficients / No. of pairs of observations	2th	4th	6th	8th
2th		0.135*	0.246**	0.165
4th	540		0.247**	0.135
6th	475	532		0.124
8th	195	220	228	

* $p \leq 0.05$ ** $p \leq 0.01$

Table XIII. Estimates of Repeatability of the Number of Lambs Born

Coefficients / No. of pairs of observations	2th	4th	6th	8th
2th		0.132	0.166	0.101
4th	540		0.166	-0.023
6th	475	532		-0.019
8th	195	220	228	

The correlation between the number of lambs born to two-tooth ewes and the average number of lambs born to them at four-tooth, six-tooth and eight-tooth is 0.132. This, with 269 degrees of freedom is significant at the

5 per cent level. The correlation between the average number of lambs born to two-tooth and four-tooth and the average of their subsequent lambings at six-tooth and eight-tooth is 0.192. This, with 269 degrees of freedom is significant at the 1 per cent level.

(c) Discussion

The ranking of the repeatability at comparable ages is similar in Table XII and Table XIII. Both methods appear to give reasonably consistent results. Two negative estimates in Table XIII are probably due to sampling errors. It may be noted that they are based on a smaller number of observations.

No previous investigation of this aspect in the New Zealand Romney has been reported. Consequently comparison of results can only be made with other breeds. Of the estimates of repeatability presented in Table IV in the review of literature, only part of Johansson and Hansson's (1943) findings are comparable with the present results. They reported the values 0.148 (Shropshire), 0.173 (Cheviot) and 0.194 (Landrace F) as estimates of repeatability between two-year- and three-year-old lambing records. The comparable values from the present study are 0.135 and 0.132. Their estimates of repeatability between averages of two-and three-year-old and four-and five-year- old lambing records are 0.249 (Shropshire), 0.257 (Cheviot) and 0.275 (Landrace F). The present estimate is 0.192. It is noticeable that in all cases their values are higher than those of the present study. Reasons for this difference are not clear. Their results were, however, based on a considerably larger amount of data. It is also possible that the relatively low repeatability of the number of lambs born is a breed characteristic of the New Zealand Romney. In general, it may be concluded that repeatability of the number of lambs born is low in the present data.

That the character - number of lambs born per ewe - is greatly influenced by environmental factors may be inferred both from the present estimates of repeatability and the knowledge of reproductive physiology in sheep. These effects due to environment tend to confuse the sheep breeder in his attempt to select animals of satisfactory breeding value. By using the average of repeated observations in a selection programme, some but not all of the temporary environmental effects will have a chance to cancel out. The expectation is that only $^1/_n$ of the variance caused by random environmental changes will remain in averages of n observations. Cancelling part of the temporary environmental variance reduces the total phenotypic variance and therefore the heritability of the remaining differences will be higher. If, however, the differences between repeated observations are largely due to permanent environmental effects, epistasis or dominance, heritability will remain low.

While considerations from repeatability alone suggest the use of the average of repeated observations to increase the accuracy of selection, the fact that this results in an increase in the generation interval must not be overlooked. Dickerson and Hazel (1944) have discussed at length the relationship between generation interval and the genetic progress per unit of time. The necessary delay in waiting for yet another lambing record prolongs the generation interval and in general, this may result in reduction of the expected genetic progress per year. If the present estimates of repeatability were taken at their face value, comparison between the expected gains from selection, based on one record and the average of two records, may be made. When selection is based on two-tooth lambing records alone, approximately nine more lambs per 100 ewes put to the ram can be expected from the average of the next three consecutive lambings. This is indicated by the regression coefficient 0.087 ± 0.040. On the other hand, if selection is based on the average of the first two records, the gain expected from the subsequent two lambings is 19 lambs per 100 ewes put to the ram. The corresponding regression coefficient is 0.191 ± 0.060. Thus a considerable gain results from waiting for a second record.

If it is decided to wait for two records, then two possible methods of selection are available. Firstly, all ewes are retained until they have had two records, the average of the two records being used as a basis for selection. Secondly, a plan of sequential culling could be used. In this plan, some culling is done after the first record is available and the remaining selection potential is used at the completion of the second record. The expectated gains from selection by these two methods are not the same but the consequences of sequential culling in the present data have not been worked out.

C. Estimation of Heritability of the Number of Lambs Born

Methods of Analysis

All methods of estimating heritability rest in one way or another on measuring the extent to which related individuals are more alike than unrelated ones. In principle, the conceptual model underlying the estimation of heritability is assumed to be linear; $P = H + E + J$

where, P is the phenotype of the individual

H is heredity in the broad sense

E is environment, and

J represents the joint effects due to heredity and environment

The difference between two individuals is usually ascribed partly to the difference in their heredity and partly to the difference in their environment, for example,

$$P_1 - P_2 = (H_1 - H_2) + (E_1 - E_2).$$

The joint effects due to heredity and environment are those which can not be ascribed to either heredity or environment alone and are often called the non-linear interactions between heredity and environment. Non-linear interactions may take several forms and according to Mather (1949) they are:

(1) Environmental factors which may interact with one another. This should be examined only in so far as it improves the accuracy of measurement.

(2) Interaction between allelic genes or Dominance.

(3) Interaction between non-allelic genes or Epistasis, and (4) Heredity and environment interaction.

From the view point of the estimation of heritability, it is desirable that the choice of a scale of measurement or in statistical terms, a transformation should be aimed at minimising and where possible, eliminating all interactions. Given independent and sufficiently detailed knowledge of the modes of gene action, an appropriate scale could be devised. Unfortunately, present knowledge of polygenic action is too meagre to enable a scale to be constructed having the above properties. Usually, a scale is chosen empirically and mainly from considerations of convenience: for instance, the scale of zero, one, two or three lambs born per birth. Consequently, the linear model of estimation based on an empirical scale is only an approximation to the scale on which the genes actually work.

Choice of a scale according to the "interaction" criterion is not possible. There are, however, other criteria which have been investigated and may be useful for a particular purpose. Thus Rae (1950) reported a technique of finding the scale by maximising the regression of offspring on parent. By doubling the value of the regression coefficient, the heritability estimate can be found. This technique is then equivalent to finding the scale to maximise the heritability of the character being measured. Since genetic progress depends much on the size of heritability, the criterion of maximising the heritability is a useful one.

Method I. Finding Scales to Maximise the Regression of Daughter on Dam

(a) Method of Analysis

The mathematical model assumed to represent the data is:

$$y_i = a + b(x_i - \bar{x}) + e_i \qquad i = 1 \ldots . n$$

where, y_i is the observation on the i^{th} offspring.

a is the population mean of the y value

b is the regression coefficient

x_i is the observation on the i^{th} dam

$\bar{x}$ is the mean of all dams

e_i is the error associated with the y_i.

The problem is essentially one of predictive estimation i.e. to predict the breeding value of the parent from its offspring. The present estimation of heritability was done separately for each age group. In other words, the dam's reproductive performance at a given age was compared with her daughter's performance at the same age. Arguments in favour of calculating the regression and eventually the heritability separately for each age group are:

(a) An estimate of heritability is a description of a particular characteristic in a certain population at some definite moment (Lush, 1948).

(b) Genetic variance of the character may vary with age if some genes have effects which are manifested only at certain age or stage of development of the animal, e.g. genes for baldness or gray hair in man or genes affecting the soundness of udder attachment in dairy cattle. A change in genetic variance will alter the value of heritability.

(c) Earlier analysis on the incidences of barrenness, single births and twin births in the present data, has shown that they were influenced to a considerable extent by the effects due to age. A further point to note is that where a dam has more than one daughter, the dam's record was used repeatedly to form the daughter-dam pair. Kempthorne and Tandon (1953) have devised a more efficient weighting method in dealing with this situation in the data. However, only a few dams have more than one daughter in the present data, little can be gained by using this more sophisticated technique.

Finding the scale to maximise the daughter-dam regression is essentially the adjustment of various values of x_i and y_i so that b is as large as the data will permit. The derivation of the maximising process, however, as shown by Rae (1950) is briefly as follows:

The data are arranged in a contingency table with the grades for dams on one axis and those of the daughters on the other. Arbitrary scores, t_i, are assigned to the grades $(i,j = 1....p)$. Let n_{ij} be the number of daughter-dam pairs in which the score of the dam is t_i and that of the daughter t_j. In addition, let $n_{i.} = \sum_j n_{ij}$, $n_{.j} = \sum_i n_{ij}$ and $n_{..} = \sum_{ij} n_{ij}$, then the sum of crossproducts (P) are

$$\sum_{ij} n_{ij}t_it_j - \frac{(\sum_i n_{i.}t_i)(\sum_j n_{.j}\ t_j)}{n_{..}}$$

and the sum of squares for dams (S) are

$$\sum_i n_{i.}\ t_i^2 - \frac{(\sum_i n_{i.}\ t_i)^2}{n_{..}}$$

The regression coefficient $b = {}^{P}/S$ is to be maximised by the choice of the appropriate t_i. On differentiating with respect to the t_i and setting the resulting equations equal to zero, the following expressions are obtained:

$$\frac{\partial b}{\partial t_i} = \frac{S\frac{\partial P}{\partial t_i} - P\frac{\partial S}{\partial t_i}}{S^2} \quad \text{or} \quad \frac{\partial P}{\partial t_i} = \frac{P}{S} \cdot \frac{\partial S}{\partial t_i}$$

Thus, $\frac{\partial P}{\partial t_i} - \frac{\partial S}{\partial t_i} b = 0$

A system of linear homogeneous equations may be derived from the expression above. The necessary and sufficient conditions for their solution are that the determinant

$\left| \frac{\partial P}{\partial t_i} - \frac{\partial S}{\partial t_i} b \right|$ be equal to zero.

The regression is maximised by taking b as equal to the largest root of the above determinantal equation. In order to find the largest root, the iterative method given by Aitken (1936-37) may be used. The product matrix

$\left[\frac{\partial S}{\partial t_i}\right]^{-1}\left[\frac{\partial P}{\partial t_i}\right]$ is formed and its transpose is repeatedly pre-multiplied by an arbitrary vector. The largest root is found by taking the ratio of corresponding elements of the last two vectors after a sufficient number of pre-multiplications. Twice the value of the largest root thus found, gives the estimates of the heritability.

In order to solve for t_i, the largest root b is substituted back in the determinantal equation. This results in another set of linear equations and as they stand, there is no unique solution for the t_i (since the value of b is found so that the determinant shall be equal to zero). It is convenient to fix t_o at zero and t_p at some value, say 1 or 100. Unique values for the remaining t_i can then be found. The values obtained for t_i are subject to errors of sampling. No exact test of significance is available for testing the differences between any two sets of scales thus obtained. Little is known about the statistical properties of scales derived in the above manner.

(b) Results

The following example was chosen to illustrate the computational processes involved in finding the scales to maximise the regression of daughter on dam.

Ewes classified according to the number of lambs born at their two-tooth lambing are arranged in a contingency table below.

Dtr. Dam	t_o	t_1	t_2	t_3	Sums
t_o	16	26	14	0	56
t_1	31	191	58	0	280
t_2	13	105	39	0	157
t_3	0	2	0	0	2
Sums	60	324	111	0	495

where t_i ($i = 0 \ldots 3$) denote the scores for the grades according to which ewes are classified i.e. barren ewes, single, twin and triplet births. Earlier analysis has shown that effects due to year have some influence on the incidences of barrenness and single and twin births in the present data. Thus, by computing the regression b on a intra- year basis, the complications arising from the effects due to year are avoided. No new principles are involved except the regression coefficient is now equal to;

$$b = \frac{\text{Total cross products - Year crossproducts}}{\text{Total Sum of Squares for Dams -Year Sum of Squares for dams}}$$

It is computationally convenient to leave crossproducts and sum of squares in the form of matrices. Thus,
Total crossproducts = $\sum_{ij} n_{ij}\, t_i\, t_j = 16\, t_0^2 + 57\, t_0 t_1 + \ldots\ldots + 39\, t_2^{\,2} + \ldots\ldots + o\, t_3^{\,3}$ may be written as:

	t_o	t_1	t_2	t_3
t_o	16	57	27	0
t_1		191	163	2
t_2			39	0
t_3				0

Year Cross products = $\dfrac{(\sum_i n_{i.} t_i)(\sum_j n_{.j}\, t_j)}{n_{..}}$

	t_0	t_1	t_2	t_3
t_0	6.787879	33.939394	19.030303	0.242424
t_1	36.654545	183.272727	102.763636	1.309091
t_2	12.557576	62.787879	35.206061	0.448485
t_3	0	0	0	0

For instance, the value in the first element of the leading diagonal of the matrix was obtained as follows:

$$\frac{60 \times 56}{495} = 6.787879$$

Total cross product - Age cross product = P

Substracting element by element, the following matrix P was obtained:

	t_0	t_1	t_2	t_3
t_0	9.212121	-13.593939	-4.587879	-0.242424
t_1		7.727273	-2.551515	0.690909
t_2			3.793939	-0.448485
t_3				0.000000

= | P |

Differentiating P with respect to t_i resulted in,

t_0	t_1	t_2	t_3
18.424242	-13.593939	-4.587879	-0.242424
-13.593939	15.454546	-2.551515	0.690909
-4.587879	-2.551515	7.587878	-0.448485
-0.242424	0.690909	-0.448485	0.000000

$$= \left|\frac{\partial P}{\partial t_i}\right|$$

Similarly, total sum of squares for dams and year sum of squares for dams were computed. Substracting element by element and differentiating Matrix S with respect to t_i, the following expression was obtained.

t_0	t_1	t_2	t_3
99.329292	-63.353536	-35.523232	-0.452526
-63.353536	243.232324	-177.616162	-2.262626
-35.523232	-177.616162	214.408080	-1.268686
- 0.452526	-2.262626	-1.268686	3.983838

$$= \left|\frac{\partial S}{\partial t_i}\right|$$

The equations for estimating the t_i are not independent since they sum to zero over any row or column. The simplest way to make them independent is to place t_1 equal to zero which results in the deletion of the first row and column in the last two tables ($\left|\frac{\partial P}{\partial t_i}\right|$ and $\left|\frac{\partial S}{\partial t_i}\right|$).

The determinantal equations were then:

$$\left|\frac{\partial P}{\partial t_i}-\frac{\partial S}{\partial t_i}b\right| = \begin{vmatrix} 15.454546-243.232324b, & -2.551515+177.616162b, & 0.690909+2.262626b \\ -2.551515+177.616162b, & 7.587878-214.408080b, & -0.448485+1.268686b \\ 0.690909+\ 2.262626b, & -0.448485+\ 1.268686b, & 0.000000-3.983838b \end{vmatrix} = 0$$

The product matrix $\left[\frac{\partial S}{\partial t_i}\right]^{-1}\left[\frac{\partial P}{\partial t_i}\right]$ **being**

$$\begin{vmatrix} 0.148967, & 0.036411, & 0.003398 \\ 0.113256, & 0.065125, & 0.000737 \\ 0.294108, & -0.071156, & 0.002165 \end{vmatrix} = \left[\frac{\partial S}{\partial t_i}\right]^{-1}\left[\frac{\partial P}{\partial t_i}\right]$$

The transpose of $\left[\frac{\partial S}{\partial t_i}\right]^{-1}\left[\frac{\partial P}{\partial t_i}\right]$ **was found and it was pre-multiplied by a chosen vector as below:**

$$\begin{array}{lcccccccc} & & \text{Chosen Vector} & & \text{I} & \text{II} & \text{III} & \text{IV} \\ \left|\begin{array}{l} 0.148967,0.113256,0.294108 \\ 0.036411,0.065125,-0.071156 \\ 0.003398,0.000737,0.002165 \end{array}\right| & \cdot & \left|\begin{array}{c} 1 \\ 1 \\ 1 \end{array}\right| & = & \left|\begin{array}{c} 0.188776 \\ 0.179118 \\ 0.225117 \end{array}\right| & \left.\begin{array}{c} 0.035408 \\ 0.033211 \\ 0.043263 \end{array}\right| & \left.\begin{array}{c} 0.006631 \\ 0.006205 \\ 0.008144 \end{array}\right| & \left.\begin{array}{c} 0.001241 \\ 0.001161 \\ 0.001526 \end{array}\right| \end{array}$$

The first value in Column I was obtained as follows:-

$0.148967 \times 1 + 0.036411 \times 1 + 0.003398 \times 1 = 0.188776.$

Values in Column II were found similarly,

e.g. $0.035408 = 0.148967 \times 0.188776 + 0.036411 \times 0.179118$

$+ 0.003398 \times 0.225117$

Ratios between corresponding values in successive columns have been listed below.

$^{II}/_{I}$	$^{III}/_{II}$	$^{IV}/_{III}$
0.187566	0.187274	0.187151
0.185414	0.186836	0.187107
0.192180	0.188244	0.187377

It can be seen that in $^{IV}/III$, the ratios are practically equal in size which indicate that no further iteration is necessary. This is the value of the largest root. Thus $b = 0.187$. The estimate of heritability is twice the regression coefficient and is 0.374. The value 0.187 was then substituted back in $\left|\frac{\partial P}{\partial t_i} - \frac{\partial S}{\partial t_i} b\right|$ to solve for t_i. However, since the value of b was found so that the determinantal equation shall be equal to zero, there is no unique solution for the t_i. This may be overcome by fixing t_4 at some convenient number say 1 or 100. Having done this and solved the set of simultaneous equations, t_1 and t_2 were found to be 0.813 and 0.761 respectively. This, however, is not the easiest method of computation to obtain

t_1. The iterative method used gives the values of t_1 and t_2 directly in addition to the value of the largest root. Thus the value for t_1 can be found by dividing the first number in Column IV by the last number in that column, i.e. $^{0.001241}/_{0.001526} = 0.813$ and t_2 is equal to $^{0.001161}/_{0.001526} = 0.761$.

The following table is a summary of results obtained in a similar manner to that described above. In addition, for the purpose of comparison regression coefficients were computed by the product-moment method using the same data on the empirical scale of measurement, i.e. 0, 1, 2 or 3 lambs born per birth.

Table XIV. Estimates of Heritability for the Number of Lambs Born.

(b = Maximised Regression Coefficient, $\hat{H}$ = Estimate of Heritability based on the calculated scale, b' = product moment regression, $\hat{H}'$ = Estimate of Heritability based on the empirical scale)

AGE	N(pr_s)	t_0	t_1	t_2	t_3	b	$\hat{H}$	b'	$\hat{H}'$
2th	495	0	0.813	0.761	1.000	0.187	0.374	0.086	0.172
4th	420	0	0.973	1.000	1.000	0.050	0.100	0.033	0.066
6th	356	0	1.291	1.118	1.000	0.123	0.246	-0.046	0.000
8th	77	0	1.704	0.491	1.000	-0.127	0.000	-0.185	0.000

Furthermore, it was thought that the small number of observations in the triplet birth class or t_3 may unduly influence the regression slope. Consequently, heritabilities were re-estimated excluding the triplet birth class. The results are presented in the following table.

Table XV. Estimate of Heritability for the Number of Lambs Born.

(b = Maximised Regression Coefficient, $\hat{H}$ - Estimate of Heritability based on the calculated scale, b' = product-moment regression, $\hat{H}'$ - Estimate of Heritability based on the empirical scale)

AGE	N(prs.)	t_0	t_1	t_2	b	$\hat{H}$	b'	$\hat{H}'$
2th	493	0	1.063	1.000	0.186	0.372	0.091	0.182
4th	409	0	1.013	1.000	0.130	0.260	0.002	0.004
6th	341	0	1.146	1.000	0.135	0.270	-0.041	0.000
8th	75	0	0.924	1.000	-0.025	0.000	-0.068	0.000

(c) Discussion

The value of the largest root of the determinantal equation and scales obtained from it is a property of the data and not a consequence of the way in which it was determined. The procedure of maximising the regression of offspring on dam does not appear to introduce difficulties of genetic interpretation of the results since:

(1) the data were from a random bred population, and

(2) the environments of dam and offspring were assumed to be uncorrelated.

Heritabilities thus estimated include some of the epistatic variance in addition to the genic variance. Consequently, unless the epistatic variance is zero, it may not be inferred that scales found are such that the ratio of the additively genetic variance to the total variance is maximised.

It should be realised that strictly speaking heritability estimates presented in Tables XIV and XV are associated with and have meaning only in relation to the scales accompanying them. Size of sampling errors of these scales is, however, not known. Thus, interpretation of these scales is difficult. Nevertheless, they do indicate that barren ewes i.e. t_0 and other ewes i.e. t_1, t_2 and t_3 are probably more different from the genetic viewpoint than is usually recognised.

In general, within any given age group, the estimate of the regression coefficient by the maximising procedure is larger than that found by assigning the scores at equal intervals i.e. 0, 1, 2 and 3. Maximised regression coefficients also are subject to sampling errors and at present, no method is available to determine their size.

Method II. Paternal Half-sib Correlation

The paternal half-sib correlation is usually calculated as an intra-class correlation from an analysis of variance of the following type:

Source of Variation	d.f.	Expectation of Sums of Squares
Between Sires	$k - 1$	$(k-1)B + n(k-1)A$
Within Sires	$k(n - 1)$	$k(n - 1)B$

where; k is the number of Sires

n is the number of offspring in each sire group

B represents the variance between offspring which have the same sire, i.e. paternal half-sibs.

A The additional variance between offspring by different Sires.

The paternal half-sib correlation is $\frac{A}{A + B}$. Multiplying this correlation by four gives an estimate of heritability which contains the genic variance, a small portion of the epistatic variance if that exists but nothing from either dominance or maternal effects.

Method IIa. Finding scales to Maximise the Paternal Half-sib Correlation

(a) Method of Analysis

The approach used in this method is essentially the same as that of finding scales to maximise the regression of daughter on dam. However, to maximise the correlation

$\frac{A}{A+B}$, it is necessary to find the scale which makes the A component as large as possible and the B component as small as possible. This may be done by finding the scale so that the ratio of the sum of squares between sires to the total sum of squares is maximised. The theory involved here is the same as that given by Fisher (1950). Thus only a numerical example will be given to illustrate the arithmetical handling of the data. Correlations on an intra-year basis were computed separately for each age group.

(b) Results

The table shows data on 792 four-tooth ewes classified according to Sires and according to the number of lambs born. The scores t_0, t_1, t_2 and t_3 are to be found by the maximising process.

SIRE	t_0	t_1	t_2	t_3	Sums
A	6	34	11	0	51
B	2	26	9	0	37
C	2	2	5	2	11
D	2	8	7	0	17
E	5	27	13	1	46
F	1	25	10	0	36
G	3	26	13	0	42
H	3	21	6	0	30
I	3	7	5	0	15
J	1	30	15	0	46
K	10	27	20	1	58
L	2	23	8	0	33
M	0	2	2	0	4
N	9	29	25	0	63
O	7	34	14	0	55
P	2	33	23	0	58
Q	1	36	21	0	58
R	7	31	18	0	56
S	7	21	27	1	56
T	0	1	1	0	2
U	1	1	1	0	3
V	0	2	0	0	2
W	0	3	5	0	8
X	0	1	1	0	2
Y	0	3	0	0	3
Sums	74	453	260	5	792

t_0 was fixed at 0 and t_3 was fixed at 1, i.e. $t_0 = 0$ and $t_3 = 1$.

Total sum of squares;

	t_1	t_2	1
t_1	453		
t_2		260	
1			5

Correction factor for effects due to year;

	t_1	t_2	1
t_1	259.102272	148.712121	2.859848
t_2	148.712121	85.353535	1.641414
1	2.859848	1.641414	0.031566

Total sum of squares - Correction factor for effects due to year;

	t_1	t_2	1
t_1	193.897728	-148.712121	-2.859848
t_2	-148.712121	174.646465	-1.641414
1	-2.859848	-1.641414	4.968434

Sum of Squares between Sires: By squaring the number of daughters in each classification or multiplying the number of daughters in each pair of classifications and dividing by the total number in the sire group and summing over all sires the following array was obtained.

	t_1	t_2	1
t_1	269.482731	142.266199	1.791110
t_2	142.266199	91.256548	2.018670
1	1.791110	2.018670	0.420474

e.g. Coefficient of $t_1^2 = (\frac{34}{51})^2 + (\frac{26}{37})^2 + \ldots . + (\frac{1}{2})^2 + (\frac{3}{3})^2$

$$= 269.482731$$

or Coefficient of $t_1 t_2 = (\frac{34 \times 11}{51}) + (\frac{26 \times 9}{37}) + \ldots + (\frac{1 \times 1}{2})$

$$+ (\frac{3 \times 0}{3}) = 142.266199$$

Sums of squares between sires - Correction factor for effects due to year:

	t_1	t_2	1
t_1	10.380459	-6.445922	-1.068738
t_2	-6.445922	5.903013	0.377256
1	-1.068738	0.377256	0.388908

To find the values of t_1 and t_2 which will make the ratio

$$= \frac{\text{Year corrected sum of squares between sires}}{\text{Year corrected total sum of squares}}$$

a maximum, it was necessary to solve the following determinantal equation for its largest root .

$$\begin{vmatrix} 10.380459-193.897728\theta, & -6.445922+148.712121\theta, & -1.068738+2.859848\theta \\ -6.445922+148.712121\theta, & 5.903013-174.646465\theta, & 0.377256+1.641414\theta \\ -1.068738+2.859848\theta, & 0.377256+1.641414\theta, & 0.388908-4.968434\theta \end{vmatrix} = 0$$

The largest root of the equation was found to be $\theta =$ 0.096 with scales $t_1 = -0.155$ and $t_2 = -0.063$. Computational techniques used to find the largest root and scales were the same as that used in the Daughter-Dam regression.

An approximate test of significance of the differences between sire groups, which was at the same time a test of significance of the intra-class correlation, followed directly from the definition of θ without the necessity of recalculation.

Analysis of Variance

Source of Variation	d.f.	Sums of Squares	Mean Squares
Between Sires	26	0.0963	0.0037**
Within Sires	765	0.9037	0.0012
Total	791	1.0000	

** $p \leq 0.01$

Two degrees of freedom for the two adjustable coefficients t_1 and t_2 were added to the degrees of freedom between sires which were equal to 24, while two were substracted from the degrees of freedom within sires. Fisher (1950) has demonstrated an approximate test of significance for scales so obtained. Briefly, it consists of computing an analysis of covariance between a given scale and that found by maximising the ratio of the sums of squares to show whether the given scale was sufficient to explain the apparent differences between sires. Bartlett (1951-52) has developed a more precise test of significance for these scales. The present purpose is, however, to find the correlation and to estimate the heritability, consequently, it did not warrant the computational labour to test the significance of these scales.

The following table is a summary of results obtained in the same manner as described above. For the purpose of comparison intra-class correlation coefficients (r) were computed using the equally spaced empirical scales, i.e. 0, 1, 2 and 3.

Table KVI. Estimates of Heritability of the Number of Lambs Born

(θ = Maximised intra-class correlation, $\hat{H}$ = Estimate of Heritability based on the calculated scale, r = Intra-class correlation based on the empirical scale, $\hat{H}'$ = Estimated Heritability based on the empirical scale)

AGE	N	No. of Sires	t_0	t_1	t_2	t_3	θ	$\hat{H}$	r	$\hat{H}'$
2th	No Triplet Birth among this Age group						-	-	-	-
4th	792	25	0	-0.155	-0.063	1.000	0.096	0.384	0.032	0.128
6th	695	18	0	-2.819	-0.359	1.000	0.066	0.264	0.053	0.212
8th	327	18	0	0.375	0.540	1.000	0.073	0.292	0.071	0.284

After excluding the triplet birth-class owing to its small frequency, the following results were obtained.

Table XVII. Estimates of Heritability of the Number of Lambs born

(θ = Maximised intra-class correlation, $\hat{H}$ = Estimate of Heritability based on the calculated scale, r = Intra-class correlation based on the empirical scale, $\hat{H}'$ = Estimate of Heritability based on the empirical scale)

AGE	N	No.of Sires	t_0	t_1	t_2	θ	$\hat{H}$	r	$\hat{H}'$
2th	887	26	0	-2.556	1.000	0.041	0.164	0.023	0.092
4th	787	25	0	2.520	1.000	0.052	0.208	0.028	0.112
6th	684	18	0	6.500	1.000	0.063	0.252	0.052	0.208
8th	321	18	0	0.619	1.000	0.075	0.300	0.075	0.300

(c) Discussion

The reliability of heritability estimates derived from the analysis of variance depends more on the number of sires than on the number of offspring in each sire group. The present data contain from 19 to 26 sires, varying from age group to age group.

When the equally spaced empirical scales were used, estimates of heritability appeared to increase with age. This may indicate that an individual's breeding value for the expression of number of lambs born reaches its maximum when it is four or five years old. However, lack of accurate measure of sampling errors of these estimates does not warrant further conjecture in this direction.

Negative values obtained for the scales may have been due to sampling errors, but in general, they are difficult to explain.

Multiplication of the correlation between half-sibs by four in order to estimate heritability is a serious drawback to this method. It magnifies any sampling error which may be in the estimate. It, nevertheless, introduces no systematic bias but merely either over- or under-estimates the true heritability. By increasing the number of sires and the number of daughters in the sire groups, these sampling errors can be reduced. The present degrees of freedom between sires are relatively small as compared with the number of degrees of freedom used in the regression of daughter on dam, consequently, estimates of heritability derived from the latter method are considered to be more reliable.

Method II(b) Analysis of Variance on the Assumption of Binomial Distribution of the Data

(a) Method of Analysis

In the present method, it is assumed that the data are distributed binomially. The nature of the binomial variation has already been discussed and will not be repeated here.

The present statistical model used is that given by Lush, Lamoreux and Hazel (1948). It is essentially an analysis of variance of the same type as the one given earlier in this section. The minor modification of the present model lies in the composition of the expectation of Mean Squares. For the sake of clarity, the whole analysis of variance table is outlined as follows:

Analysis of Variance

Source of Variation	d.f.	Sums of Squares	Expectation of Mean Squares
Total	$N - 1$	$\frac{(T - A)A}{T}$	
Between Sires	$k - 1$	By difference	$W + \bar{S}B$
Within Sires	$N - k$	$\sum_i \frac{(t_i - a_i)a_i}{t_i}$	W

Where $N = T$ and is the total number of offspring

k is the number of sires

A is the total number of ewes of a given attribute, e.g. barren ewes

The derivation of the total sum of squares can be shown as follows:

Total sum of squares $= \sum x^2 - \frac{(\Sigma x)^2}{N}$ as for a continuous variate.

Let barren ewes have a value of 1 and other ewes 0, the total sum of squares is then equal to

$$A - \frac{A^2}{T} = \frac{AT-A^2}{T} = \frac{A(T-A)}{T}$$

Similar reasoning leads to the expression for computing within sires sums of squares

$$\sum_i \frac{(t_i - a_i)a_i}{t_i} \quad i = 1 \ldots.k$$

Where t_i is the number of offspring in a sire group and
a_i is the number of offspring of a given attribute,
e.g. barren ewes.

In addition, W represents the variance between offspring which have the same sire, i.e. paternal half-sibs.

B is the additional variance between offspring by different sires.

$\bar{S}$ is the weighted average number of offspring in each sire group and is computed as

$$\bar{S} = \frac{N - \frac{\sum t_i^2}{N}}{k-1}$$

Likewise, the paternal half-sib correlation is defined as $\frac{B}{W+B}$. Multiplying this ratio by four gives the heritability estimate.

The variance in binomial data is correlated with the mean and thus becomes very small when the proportion of individuals in either one of the two mutually exclusive classes approaches zero. This relationship makes the estimates of heritability based on observed data dependent, in part, upon the average incidence of the attribute. Consequently, a correction is required in order that various estimates of heritability based on different incidences of a given attribute may be compared. This correction as given by Lush et al. (1948) is made by multiplying the estimate of heritability by a factor $\frac{p(1 - p)}{z^2}$

where, p is the fraction of ewes of a given attribute, e.g. barren ewes, and

z is the height of the ordinate which truncates p of the area of the Normal curve.

The presence of z in the correction factor implies that the additive genetic values of the character are distributed normally, although their phenotypes are of an all-or-none kind. This correction transforms the estimate of heritability from the actually observed percentage scale to the genetically more accurate heritability on the probit scale. (Lush et al. 1948).

In order to avoid the problem of proper weight in the present data, sire groups with less than 10 daughters were excluded from the analysis. Data thus discarded were of an insignificant amount.

(b) Results

The following Tables XVIII and XIX summarise the estimates of heritability of barrenness (H_b) and twinning tendency (H_t).

Table XVIII. Estimates of Heritability for Barrenness

AGE	No. of Sires	% of Barren Ewes	$\hat{H}_b$ (Percent. Scale)	$\hat{H}_b$ (Probit Scale)
2th	25	13.95	0.097	0.234
4th	18	9.57	0.042	0.124
6th	18	6.29	0.108	0.417
8th	15	5.52	0.000	0.000

Table XIX. Estimates of Heritability for Twin Births

AGE	No. of Sires	% of Twin Births	$\hat{H}_t$ (Percent. Scale)	$\hat{H}_t$ (Probit Scale)
2th	25	28.33	0.055	0.098
4th	18	36.23	0.066	0.108
6th	18	46.18	0.178	0.280
8th	15	62.20	0.008	0.014

(c) Discussion

The merit of the method given by Lush _et_ _al_. (1948) lies perhaps mainly in their awareness of the possible application of the probit transformation, rather than the development of a special technique for genetical analysis of an all-or-none trait. Robertson & Lerner (1949) working on a similar problem have this to say:

> "They have introduced the concept of 'heritability on the probit scale', which, however, is not the real heritability of sensitivity but the genetic variance. The assumption implicit in their reasoning is that the probit units for the whole population and for the individual genotypes are the same, whereas in reality they are different. The probit for individual genotypes takes as its unit of measurement the environmental standard deviation on the sensitivity scale. That for the whole population takes as its unit the total phenotypic standard deviation. In terms of variance the latter is $(1 + \sigma_x^2)$ times the former. Thus heritability on the sensitivity scale is equal to $\sigma_x^2/1 + \sigma_x^2$ rather than to σ_x^2 as considered by Lush, Lamoreux and Hazel (1948)."

In view of this comment, the method developed by Robertson and Lerner (1949) for approximate determination of the degree of heritability of traits expressed in an all-or-none manner was tried out on the present data. Robertson and Lerner's approach may be outlined as follows, using the present data as an example.

In a flock of sheep where no artificial selection has been practised, there exists a natural selection. Ewes with a genotype for low fertility will have a lower chance of leaving offspring to become parents of the next generation than the ewes with a genotype for high fertility. The improvement in the average genotype by natural selection may be calculated thus enabling the calculation of heritability for barrenness and also twinning tendency.

Let the genotypic value for reproductive performance of the m^{th} individual in a given generation be p_m where

$m = 1 \ldots n$ with mean $\bar{p}$ and variance σ_p^2. The phenotype for reproductive performance of the m^{th} ewe will then be $p_m + e_m$ where e_m is the environmental component. This phenotype may be scored either as 0 i.e. barren or 1 i.e. fertile. The mean genotype of fertile ewes will be denoted by ${}_1\bar{p}$ in contrast with $\bar{p}$ which is the mean genotype of all ewes.

$${}_1\bar{p} = \frac{\sum_1^n p_m(p_m + e_m)}{\sum_1^n (p_m + e_m)} \qquad \text{where } m = 1 \ldots .n$$

If ewes are kept under conditions in which there is no correlation between genotype and environment, then:

$$E\left(\sum_1^n e_m\right) = 0 \text{ and } E\left(\sum_1^n p_m e_m\right) = 0$$

$$\text{Thus, } E({}_1\bar{p}) = \frac{E\left(\sum_1^n p_m^2\right)}{E\left(\sum_1^n p_m\right)}$$

The expected gain over the previous generation is:

$$E({}_1\bar{p} - \bar{p}) = \frac{E\left(\sum_1^n p_m^2\right)}{E\left(\sum_1^n p_m\right)} - \bar{p}$$

$$\because \sigma_p^2 = \sum_1^n (p_m - \bar{p})^2 \Big/ n \text{ and } \sum_1^n p_m^2 = n(\sigma_p^2 + \bar{p}^2)$$

where σ_p^2 is the genotypic variance

$$\therefore E\left({}_1\bar{p} - \bar{p}\right) = \frac{n(\sigma_p^2 + \bar{p}^2)}{n\,\bar{p}} - \bar{p}$$

$$= \frac{\sigma_p^2}{\bar{p}}$$

The phenotypic selection differential can be shown as equal to $1 - \bar{p}$, being the difference between the mean phenotype of all fertile ewes (taken as unity) and the mean phenotype of the population.

$$\text{Mean phenotype of the population} = \frac{\sum_1^n (p_m + e_m)}{n}$$

$$E(\text{Mean phenotype of the population}) = E\left[\frac{\sum_1^n (p_m + e_m)}{n}\right]$$

$$= \frac{\sum_1^n p_m}{n} = \bar{p}$$

Thus heritability may be estimated according to the following relationship:

$$\text{Heritability} = \frac{\text{genetic improvement}}{\text{phenotypic selection differential}}$$

$$= \frac{\sigma_p^2}{\bar{p}\,(1 - \bar{p})}$$

By applying the technique of analysis of variance, the genotypic variance σ_p^2 may be determined according to the relationship $\sigma_s^2 = r\,\sigma_p^2$, where;

σ_s^2 is the variance between offspring by different sires and r is the genetic relationship among the offspring of a sire. In a random bred population, $r = \frac{1}{4}$.

The computational method used in the present data is given below.

The data may be arranged in a 2 x s table:

e.g.

Sires	Barren ewes	Total
A	a_1	n_1
B	a_2	n_2
.	.	.
.	.	.
.	.	.
.	.	.
S	a_s	n_s
Σ	Σa_i	$\Sigma n_i = N \quad i = 1 \ldots s$

The sum of squares between sires is: $\sum_1^s \frac{a_i^2}{n_i} - \frac{(\Sigma a_i)^2}{\Sigma n_i}$

E (sum of squares between sires) = $(s-1)\ \bar{p}\ (1-\bar{p}) + n_o\ \sigma_s^2$

where: $n_o = \Sigma n_i - \frac{\Sigma n_i^2}{\Sigma n_i} - (s - 1)$

The within sire component is $\bar{p}(1 - \bar{p})$, which is the usual expression for the variance of a binomial distribution.

Thus; $$\sigma_p^2 = \frac{\left[\sum_1^s \frac{a_i^2}{n_i} - \frac{(\Sigma a_i)^2}{\Sigma n_i}\right] - (s-1)\ \bar{p}(1-\bar{p})}{r\ n_o}$$

Heritability is

$$H_b = \frac{\sigma_p^2}{\bar{p}(1-\bar{p})} = \left[\frac{\sum_1^s \frac{a_i^2}{n_i} - \frac{(\Sigma a_i)^2}{\Sigma n_i}}{\bar{p}(1-\bar{p})} - (s-1) \right] \bigg/ r\, n_o$$

The expression $\dfrac{\sum_1^s \frac{a_i}{n_i} - \frac{(\Sigma a_i)^2}{\Sigma n_i}}{\bar{p}\,(1-\bar{p})}$ is the heterogeneity χ^2 in the 2 x s table. The mean value of χ^2 for (s - 1) d.f. is (s - 1). Hence the expression

$\dfrac{\sum_1^s \frac{a_i}{n_i} - \frac{(\Sigma a_i)^2}{\Sigma n_i}}{\bar{p}\,(1-\bar{p})} - (s - 1)$ is the excess of the observed χ^2 above its expected value. The composition of the heritability and hence its relation to χ^2 indicate that it would be unwise to include in the computation any subclass with less than five observations. Accordingly in the present data, subclasses with less than five observations were excluded.

Heritabilities of barrenness $(\widehat{H}_b)$ and of twin births $(\widehat{H}_t)$ were estimated separately for each age group and results were summarised in the following tables.

Table XX. Estimates of Heritability for Barrenness

AGE	No. of Sires	% of Barren Ewes	σ_p^2	$\hat{H}_b$
2th	25	13.95	0.0115	0.096
4th	18	9.57	0.0038	0.045
6th	18	6.29	0.0063	0.107
8th	15	5.52	0.0000	0.000

Table XXI. Estimates of Heritability for Twin Births

AGE	No. of Sires	% of Twin Births	σ_p^2	$\hat{H}_t$
2th	25	28.33	0.0112	0.055
4th	18	36.23	0.0151	0.066
6th	18	48.18	0.0446	0.180
8th	15	62.20	0.0022	0.009

Heritabilities of barrenness and twin births estimated according to the method of Robertson and Lerner (1949) are in all cases much lower than corresponding heritabilities on probit scale obtained by method given by Lush *et al*. (1948). When compared with heritabilities on percentage scale, however, results by these two methods are practically the same. This is not unexpected since the way in which the sums of squares are calculated is identical in each case. This may be shown as follows: Sums of squares between sires $= \sum \frac{a_i^2}{n_i} - \frac{(\sum a_i)^2}{\sum n_i}$ was given by Robertson and Lerner (1949).

Lush _et al_. (1948) used a different notation but it can be easily identified with that used by Robertson and Lerner. Lush _et al_. gave: total sum of squares $= \frac{A\ (T-A)}{T}$ where $A = \sum a_i$, $T = \sum n_i$ and $i = 1 \ldots s$.

Therefore, total sum of squares $= A - \frac{A^2}{T} = \sum a_i - \frac{(\sum a_i)^2}{\sum n_i}$

Lush _et al_. also gave:

sum of squares within sires $= \sum \frac{a_i(t_i - a_i)}{t_i}$ where $t_i = n_i$

Therefore, sum of squares within sires $= \sum a_i - \sum \frac{a_i^2}{n_i}$.

Using the relationship that total sum of squares - sum of squares within sires = sum of squares between sires it can be shown that the formula used to compute the sum of squares between sires by Lush _et al_. is exactly the same as that used by Robertson and Lerner, as below:

Total sum of squares - sum of squares within sires

$$= \sum a_i - \frac{(\sum a_i)^2}{\sum n_i} - \left(\sum a_i - \sum \frac{a_i^2}{n_i}\right)$$

$$= \sum \frac{a_i^2}{n_i} - \frac{(\sum a_i)^2}{\sum n_i}$$

= Sum of squares between sires.

However, the difference that does exist between them appears to be the consideration given to the correlation between the mean and the variance in binomial data. Both recognised the possible occurrence of such a correlation in their data but the remedy prescribed was not the same. Lush et al. (1948) used the "probit" transformation. Robertson and Lerner (1949) considered the genotypic variance (σ^2_p) being so small in their data that instead of using the arc-sine transformation to overcome the correlation between the mean and variance, the raw data were used in computation. Genotypic variances for different age groups of the present data have been presented in Column 4 of Tables XX and XXI; and they are within the range of the genotypic variances in Robertson and Lerner's data. It may be concluded that both methods have some merit but neither is entirely satisfactory.

Discussion

Present estimates of heritability by regressions of daughter on dam are, in general, lower than those based on paternal half-sib correlations. This discrepancy is probably, in part, due to the magnified sampling errors in the paternal half-sib correlation. Present estimates of heritability based on daughter-dam regressions are, however, higher than those reported by Desai and Winters

(1951b) and Cockerham (1949). It should be noted that their data were collected from mixed breeds under different environmental conditions. On the other hand, present results are within the range of estimates reported by Johansson and Hansson (1943). No reports are available for comparison with the estimates of heritability derived from paternal half-sib correlations. The assumption that the present data were distributed binomially, led to the estimation of heritability of barrenness and twin births. No previous work is available for comparison. However, estimates of heritability of barrenness and twin births are consistent with the conclusion that the heritability of the number of lambs born is low.

There are several factors both genetic and non-genetic which tend to contribute to the low estimates of heritability. It has been stated earlier that present estimates of heritability are somewhere between its narrow sense definition i.e. $\frac{\sigma_g^2}{\sigma_g^2 + \sigma_d^2 + \sigma_i^2 + \sigma_e^2 + \sigma_j^2}$ and its broad sense definition i.e. $\frac{\sigma_g^2 + \sigma_d^2 + \sigma_i^2}{\sigma_g^2 + \sigma_d^2 + \sigma_i^2 + \sigma_e^2 + \sigma_j^2}$

Estimates of heritability will be low if the denominator is far in excess of the numerator. Hence, by examining some of the variance components, part of the explanation for the present results may be found.

(1) σ_g^2: σ_g^2, the additive genetic variance may be

very small. In theory, this is brought about if all the genes concerned are homozygous or nearly so. Inbreeding together with artificial selection will give rise to homozygosity. However, inbreeding is assumed to have no effects on the present data. Nevertheless, one may choose to recognise that individuals with a higher fertility would have had greater chances to be represented by their offspring in the next generation. Hence selection for fertility by nature has been taking place all the time. If natural selection had been effective, it is expected that most of the additive genetic variance would have been exhausted by now, thus σ_g^2 would be zero or nearly so. This situation is indicated in the present study by the size of the genotypic variances for barrenness and for twin births at various ages. However, the determination of their sampling errors based on more data is needed before any definite conclusions can be drawn.

(2) σ_d^2 and σ_i^2 : The magnitude and importance of these non-additive genetic variances in the present data are not known. If heterosis is used as a criterion, it is possible to infer from cross breeding results that non-additive genetic variances may be of importance. Thus Whitehurst et al. (1947) reported that in crossing Columbia rams to native Florida ewes, the number of lambs born per ewe was 0.68 (Columbia) 1.30 (F_1) and 0.99

(native ewes) respectively. Peren et al. (1951) comparing lambing per cent between Romney and Cheviot x Romney over seven years (from 1944 to 1950 inclusive) found a difference of 31 per cent in favour of the crossbred. However, as stressed by Robertson (1949), results from crossbreeding must be interpreted with some qualification. There are certain conditions which must be met before data are useful in elucidating the factors in and effects of crossbreeding. Firstly, parent breeds and crossbreds must be reared under the same general environmental conditions. Secondly, the gene complement of the crossbred must be comparable with the genes carried by the purebreds. Evidence can also be found from work on litter size in swine that lends support to the importance of non-additive genetic variances in reproductive performance. Dickerson (1952) in a review article stated that effects of inbreeding and crossbreeding indicate that the degree of heterozygosity exerts a major influence on the important performance characters. A high degree, either of dominance or of epistasis due to deviations from an optimum genetic intermediate, or both, characterises the genetic variability in performance. Moreover, the apparent ineffectiveness of selection for litter size in swine, in spite of the size of heritability estimates, also points in the direction that most of the hereditary variance of litter size is probably non-additive.

(3) σ_e^2: Environmental variances may be large. This could result from numerous causes. Variations in climate, pasture growth and management, as described earlier in the review of literature, contribute to the size of these environmental variances.

(4) σ_j^2: Very little is known about σ_j^2. In the linear model used, σ_j^2 absorbs various non-linear interaction between heredity and environment. It may be large in the present data if the genotype of fertility interacts with environment in different years.

To conclude, it may be summarised that these data suggest that heritability of the number of lambs born, barrenness and twin births are not high. More data than available, at present, are required to narrow the confidence interval of these estimates of heritability.

D. Phenotypic Regression of Fleece Weight on the Number of Lambs Born and Weaned per Ewe

(a) Method of Analysis

Although the variate, fleece weight, is distributed continuously, the other variate, the number of lambs born or weaned, is discrete. Consequently, the correlation technique is not satisfactory for measuring the relationship between these two variates. If, however, the number of lambs born or weaned is chosen as the independent variate, a regression analysis can be validly used to measure the covariation in these data. The regression model assumed to represent the data is

$$y_i = \mu + \beta x_i + e_i \qquad i = 1 \ldots n$$

where, y_i is the greasy fleece weight in pounds.

μ is the population mean

x_i is the number of lambs

e_i is the random error about the mean μ.

and β is the phenotypic regression coefficient of greasy fleece weight on either the number of lambs born or weaned.

Regression coefficients were computed on an intra-year basis and separately for each age group. The regression of fleece weight on the number of lambs weaned is defined as!

$$= \frac{\text{Total sums of crossproducts} - \text{sums of crossproducts for years}}{\text{Total sums of squares} - \text{sums of squares for years}}$$

The regression coefficient of the hogget fleece weight on the number of lambs born to them at two-tooth was calculated slightly differently. In it, the effects of birth-rank as well as the effects of years were eliminated. This regression coefficient is defined as:

$$= \frac{\text{Total sums of crossproducts}}{\text{Total sums of squares}}$$

$$\frac{-\text{ sums of crossproducts for years}}{-\text{ sum of squares for years}}$$

$$\frac{-\text{ sum of crossproducts for birth-rank}}{-\text{ sum of squares for birth-rank}}$$

By birth-rank is meant whether the ewe itself was born as a single or as one of a twin pair. This adjustment for the effects of birth-rank was considered unnecessary for ewes beyond the hogget stage, since Rae (1950), working with the same flock, reported that birth-rank ceases to have any direct effect on fleece weight after weaning, although it may have carry-over effects.

It may be pointed out that the range of the independent variate x_i is limited since in the present data, the number of lambs born or weaned per ewe seldom exceeded three. This is not a serious disadvantage. Extrapolation beyond the actual range of the variate x_i is both unwise and biological ly unwarranted. No such extrapolation is, however, intended.

(b) Results

The following Table is a summary of results obtained in the manner described above.

Table XXII. Estimates of Phenotypic Regression of Fleece Weight on the Number of Lambs Born and Weaned

AGE	d.f.	xy	x^2	y^2	$\hat{\beta}$	Test of significance
Hogget	859	93.747	304.838	569.725	0.307 ± 0.045	**
2th	643	-3.934	272.914	1089.280	-0.014 ± 0.079	N.S.
4th	659	-65.151	266.344	1083.130	-0.245 ± 0.078	**
6th	646	-102.700	271.296	1209.560	-0.379 ± 0.082	**
8th	286	-50.120	131.828	424.240	-0.380 ± 0.104	**

** $p \leq 0.01$

(c) Discussion

No previous reports giving phenotypic regression of fleece weight on either the number of lambs born or weaned per ewe are available for comparison.

The present regression coefficient at the hogget stage is 0.307. This indicates that for every extra lamb born at two-tooth lambing, there was correspondingly a 0.307 lb. greater greasy fleece weight per sheep at hogget shearing. An exact physiological explanation of this phenomenon is not available; however, some indirect evidence will be discussed in proposing a tentative explanation for the present result. Work by Esplin, Madsen and Phillips (1940) on the range breeding ewes in Utah, showed that better fed and consequently better grown ewe hoggets during their first winter yielded more wool and produced more lambs at the two-tooth age. They argued that the higher lambing per cent could not have been due to the effects of "flushing", since the average live weight of all ewe-groups was practically the same at the time of mating. The higher lambing per cent, as they suggested, might be due to:

(1) better development of reproductive organs,

and/or (2) greater storage of some essential element or elements in the body of the ewes of the better fed groups.

The work of Terrill and Stoehr (1942) on Columbia, Corriedale and Rambouillet breeds, also led them to the conclusion that ewes which were heavier in the fall as yearlings, on the average, weaned more pounds of lamb per ewe during their lifetime. This greater lamb production was due more to a higher per cent of lambs weaned rather than to heavier weaning weights. In addition, it may be noted that Hafez (1951), working with Suffolk sheep, reported that for the manifestation of oestrus in ewe lambs it was necessary for them to surpass a certain threshold of live weight. From the above evidence it can be reasoned that better growth and more advanced development of the animal at the hogget age tend to promote a greater fleece production in addition to providing a physiological basis for better reproductive performance at a later age. Thus it may be surmised that the positive covariation between hogget fleece weight and two-tooth reproductive performance in the present data is due to such a "growth effect".

The regression of fleece weight on the number of lambs weaned per ewe at two-tooth is -0.014. This estimate is not significantly different from zero at the 5 per cent level. The regressions at other ages are -0.245 (four-tooth), -0.379 (six-tooth) and -0.380 (eight-tooth). They show that for every extra lamb weaned, there is a correspondingly 0.254 lb. (four-tooth) 0.379 lb. (six-tooth) and 0.380 lb. (eight-tooth) lower fleece weight per ewe. These regression coefficients are all significantly different from zero at the 1 per cent level.

If the explanation of the "growth effect" was to hold for the entire productive life of the ewe the regression coefficients of various age groups are expected to be positive in sign. The fact that they are not does not necessarily prove that the "growth effect" is not the explanation for the positive regression at hogget stage. It should be realised that the hogget fleece is grown under somewhat different circumstances from those of older ewes.

Examination of the data reveals that hogget fleece weight represents the wool growth from lamb shearing to hogget shearing; a period during which complication of pregnancy and lactation normally do not arise. On the other hand, fleece weight of the older ewes was usually collected about a month before weaning of the lambs. It is therefore plausible that the effects of pregnancy and lactation are responsible for the negative regression of fleece weight on the number of lambs weaned. Evidence that pregnancy and lactation do adversely affect wool production may be drawn from the work by Bosman (1935).

He reported a reduction in fibre fineness which caused a decrease in the weight of scoured fleece in lactating Merino ewes. Stevens and Wright (1951) also reported that in a Romney Marsh stud flock barren ewes clipped, on the average, 1.0 lb. more fleece than ewes producing single lambs and these latter ewes clipped 0.4 lb. more fleece than ewes raising twins. The theory of the "priority of partition of nutrients according to metabolic rate" by Hammond (1950) probably forms the underlying physiological mechanism. Wallace's work (1948) showed that early stages of placentation and lactation in sheep have a high priority for nutrients. Presumably then, the growth of the gravid uterus (particularly in the latter half of the pregnancy) and the initiation and maintenance of milk production at some stage had utilised nutrients which would otherwise have been available for wool production.

In summary, the relationship between fleece weight and the number of lambs born and weaned in these data, is as follows:

At hogget stage the "growth effect" is more important and results in a positive regression of fleece weight on the number of lambs born to them at two-tooth. At two-tooth stage, the "growth effect" is probably still operative and tends to produce a positive regression.

However, because the effects of pregnancy and lactation on wool growth are working in the opposite direction, the regression, as obtained, is not significantly different from zero at the 5 per cent level. At four-tooth and later ages the "growth effect" either has ceased or is negligible when compared with the effects of pregnancy and lactation on wool growth. Consequently, the observed results of negative regression of fleece weight on the number of lambs weaned were obtained.

E. Genetic Covariation of Fleece Weight on the Number of Lambs Born and Weaned per Ewe

(a) Method of Analysis

The variate, fleece weight, is continuous; the other variate, the number of lambs born or weaned is, however, discrete. Consequently, the techniques developed by Hazel (1943) for computing genetic correlations are not directly applicable. The genetic covariation between these two variates, nevertheless, can be measured by a regression analysis in which the number of lambs is regarded as the independent variate and fleece weight, the dependent variate, e.g. the regression of the fleece weight of dams on the number of lambs born to their daughters. The model in this regression analysis is assumed to be:

$Pw_i = M + BPm_i + e_i$

where, Pw_i is the phenotypic measure of the character fleece weight in pounds. In particular dPw_i and oPw_i represent the fleece weight of the dam and the fleece weight of her daughter; subscripts d and o denote the dam and the daughter respectively.

M is the population mean

Pm_i is the phenotypic measure of the number of lambs in discrete numbers e.g. 0, 1 and 2. Similarly, the subscripts d and o in dPm_i and oPm_i denote the dam and the daughter respectively.

e_i is the random error about the mean M.

B is the regression coefficient.

e.g.

$$\hat{B} = \frac{\widehat{\text{Cov. } oPw \cdot dPm}}{\hat{\sigma}^2_{dPm}} = \frac{\widehat{\text{Cov. } dPw \cdot oPm}}{\hat{\sigma}^2_{oPm}}$$

In particular, B_1 is the regression of the dams' fleece weight on the number of lambs born to their daughters.

B_2 is the regression of the daughters' fleece weight on the number of lambs born to their dams.

The above formulation can be applied to include the measure of genetic covariation between fleece weight and

and the number of lambs weaned. Nothing new is involved except in the definition of the regression coefficients:-

B_3 is the regression of the dam's fleece weight on the number of lambs weaned by their daughter and

B_4 is the regression of the daughters fleece weight on the number of lambs weaned by their dams.

In the derivation to follow, no distinction will be made for particular situations pertaining to B_1, B_2, B_3 or B_4.

The genetic regression of the fleece weight on the number of lambs may be defined as

$$\beta_{Gw \cdot Gm} = \frac{\text{Cov. } Gw \,.\, Gm}{\sigma^2_{Gm}}$$

where, $\beta_{Gw.Gm}$ is the genetic regression

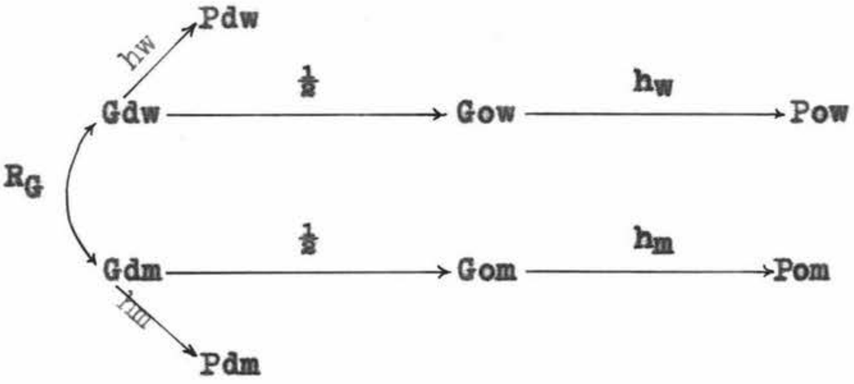
Cov. $Gw \cdot Gm$ is the genetic covariance between fleece weight and the number of lambs

and σ^2_{Gm} is the genetic variance of the number of lambs.

It can be shown that $\beta_{Gw \cdot Gm} = \frac{2\,B}{h^2 m}$, for instance,

$$\beta_{Gw \cdot Gm} = \frac{2 \,.\, B_{dPw \cdot oPm}}{h^2_m}$$

The Path-coefficient diagram representing the method is as follows:



The environment between daughter (o) and dam (d) is assumed to be uncorrelated and for the present purpose environmental paths need not be drawn. The symbols in the diagram are:-

G denoting genotype

P denoting phenotype

R_G the genetic correlation between fleece weight and the number of lambs and is defined as

$$R_G = \frac{\text{Cov. } G_w \cdot G_m}{\sigma_{Gw} \cdot \sigma_{Gm}}$$

h being $\sqrt{\text{heritability}}$

Subscript d denotes dam

o denotes daughter

w denotes fleece weight

and m denotes the number of lambs.

From the Path-coefficient diagram the correlation between dPw and oPm is:

$$R_{dPw\cdot oPm} = \tfrac{1}{2}R_G \cdot h_w \cdot h_m$$

$$= \tfrac{1}{2}\,\frac{\text{Cov. } Gw \,.\, Gm}{\sigma_{Gw}\cdot\sigma_{Gm}}\cdot\frac{\sigma_{Gw}}{\sigma_{Pw}}\cdot\frac{\sigma_{Gm}}{\sigma_{Pm}} \quad \because h_w = \frac{\sigma_{Gw}}{\sigma_{Pw}} \text{ and } h_m = \frac{\sigma_{Gm}}{\sigma_{Pm}}$$

Since $B_{dPw\cdot oPm} = R_{dPw\cdot oPm}\cdot\frac{\sigma\ dPw}{\sigma\ oPm}$

$$\therefore B_{dPw\cdot oPm} = \tfrac{1}{2}\,\frac{\text{Cov. } Gw \,.\, Gm}{\sigma_{Gw}\cdot\sigma_{Gm}}\cdot\frac{\sigma_{Gw}}{\sigma_{Pw}}\cdot\frac{\sigma_{Gm}}{\sigma_{Pm}}\cdot\frac{\sigma\ dPw}{\sigma\ oPm}$$

Assuming, $\sigma_{Pw} = \sigma_{dPw}$ and $\sigma_{Pm} = \sigma_{\ oPm}$

then $\text{Cov. } Gw \,.\, Gm = 2 \,.\, B_{dPw\cdot oPm}\cdot\sigma^2_{Pm}$

Dividing both sides by σ^2_{Gm}, the following result is evident,

$$\hat{\beta}_{GwGm} = \frac{\widehat{\text{Cov. } Gw \,.\, Gm}}{\hat{\sigma}^2_{Gm}} = \frac{2\,.\,\hat{B}_{dPw\cdot oPm}}{\hat{h}^2_m}$$

The genetic regression coefficients corresponding to B_1, B_2, B_3 and B_4 are denoted by the symbols β_1, β_2, β_3, and β_4. It may be anticipated that $\hat{\beta}_2$ and $\hat{\beta}_4$ will be slightly less reliable than $\hat{\beta}_1$ and $\hat{\beta}_3$ since the fleece weights of daughters may possibly have been affected by their own birth-rank which is at the same time the number of lambs born to or weaned by their dams. Such possibilities are, however, excluded from the estimation of β_1 and β_3. This regression analysis was done separately for each age and year effects were duly adjusted. The method of computation of sums of squares and cross products was the same as that for phenotypic regressions.

(b) Results

Table XXIII. Estimates of the Genetic Regression of Fleece Weight on the Number of Lambs Born per Ewe

AGE	d.f.	$\widehat{B}_1$	$\widehat{B}_2$	$\widehat{h}^2_m$ *	$\widehat{\beta}_1$	$\widehat{\beta}_2$
2th	457	-0.167		0.15	-2.227	
4th	390	0.082		0.15	1.093	
6th	344	-0.227		0.15	-3.027	
8th	66	0.326		0.15	4.347	
2th	464		0.039	0.15		0.520
4th	386		-0.053	0.15		-0.707
6th	344		-0.264	0.15		-3.520
8th	69		-0.259	0.15		-3.453

* $\widehat{h}^2_m$ is the estimate of heritability for the number of lambs born and is chosen to be equal to 0.15 on the basis of evidence presented in Section C.

Table XXIV. Estimates of the Genetic Regressions of Fleece Weight on the Number of Lambs Weaned per Ewe

AGE	d.f.	$\hat{B}_3$	$\hat{B}_4$	$\hat{h}^2_m$ *	$\hat{\beta}_3$	$\hat{\beta}_4$
2th	298	-0.198		0.15	-2.640	
4th	302	0.077		0.15	1.027	
6th	313	-0.200		0.15	-2.667	
8th	54	0.270		0.15	3.600	
2th	321		0.010	0.15		0.133
4th	357		-0.078	0.15		-1.040
6th	343		-0.302	0.15		-4.027
8th	69		-0.195	0.15		-2.600

* $\hat{h}^2_m$ is the estimate of heritability for the number of lambs born and is chosen to be equal to 0.15 on the basis of evidence presented in Section c.

(c) Discussion

Estimates of genetic regressions presented in Tables XXIII and XXIV include all the deviations due to the additive effects of genes and probably some epistatic effects if these exist but no dominance deviations. Estimates of β_1 and β_3 and β_2 and β_4 are in fairly good agreement. Differences between the values of $\hat{\beta}_1$ and $\hat{\beta}_3$

and $\hat{\beta}_2$ and $\hat{\beta}_4$ are solely due to the effects of lamb mortality from birth to weaning. This, however, did not alter the pattern of covariation in any age group, the signs of the estimates of genetic covariances being unchanged.

Each estimate of the genetic regressions presented in Tables XXIII and XXIV is based on two statistics i.e. the $\hat{B}_s$ and $\hat{h}^2_m$ each of which has its own sampling errors, for instance the $\hat{B}_1$, $\hat{B}_2$, $\hat{B}_3$ and $\hat{B}_4$ together with their standard errors are given below:

AGE	$\hat{B}_1$	$\hat{B}_2$	$\hat{B}_3$	$\hat{B}_4$
2th	-0.167±0.114	0.039±0.097	-0.198±0.146	0.010±0.107
4th	0.082±0.103	-0.053±0.110	0.077±0.113	-0.078±0.106
6th	-0.227±0.127	-0.264±0.120	-0.200±0.110	-0.302±0.119
8th	0.326±0.242	-0.259±0.228	0.270±0.205	-0.195±0.177

Consequently, sampling errors in the estimates of genetic regressions are not expected to be small. More observations than available at present are needed to reduce these sampling errors so that more confidence can be placed on these estimates of genetic regressions.

Although the present estimates of genetic regressions are unsatisfactory, it is reasonably clear that most of them are negative in sign. Thus, selection for increased fleece weight will bring about a correlated response in the direction of reduced fertility, i.e. less number of lambs born and weaned per ewe. Likewise, selection for higher fertility will result in some decrease of fleece weight.

The remainder of this discussion will be devoted to an attempt to find and suggest the causes of this observed correlated response between fleece weight and fertility in the ewe.

Possible causes of correlated responses in selection have been put forward by several workers. Basically, there appears to exist two schools of thought in regard to the genetic mechanism through which the observed correlated response is brought about. One school believes that the pleiotropy of genes i.e. genes having effects on more than one character, is the underlying genetic mechanism while the other school postulates that breaking-up of the balanced linked gene combinations leads to correlated responses.

(1) Pleiotropy of genes

There is ample evidence in the literature on Genetics to support the existence of the pleiotropy of genes. The best known example in sheep is, however, the discovery of pleiotropic effects of the N-gene in the

Romney sheep by Dry (1946). The most noticeable effect of the N-gene is the grossly hairy birth coat in the lamb. The same gene is also responsible for the growth of horns in rams (Dry, Fraser and Wright, 1947). In addition, Dry and Fraser (1947) reported that among other characters, the presence of brown patches especially on the back of the neck and to a less extent, at the root of the tail of the individual, is also due to the effects of this N-gene. The physiological and developmental paths of the N-gene have been subjected to detailed studies. Consequently, the mode of physiological behaviour of this gene is reasonably well established. On the other hand, both characters, the fleece weight and the number of lambs born or weaned, are assumed to be influenced by a large number of genes, each having a small effect. Furthermore, the present knowledge of developmental and reproductive physiology is insufficient to relate the end expression such as fleece weight and the number of lambs to the primary actions of genes. Thus, in spite of the evidences from the pleiotropy of the N-gene, the suggestion that pleiotropy is the cause of the present negative genetic covariation between fleece weight and the number of lambs born or weaned, appears to be premature.

While still assuming that pleiotropy is the basic genetic mechanism of correlated response between two characters, Lush (1948) has suggested that if past selection has been effective, it may be instrumental in producing negative genetic correlations. The frequencies of genes which have favourable effects on both characters and of genes with favourable effects on only one character but neutral to the other, will have been raised by selection to a sufficiently high level so that they contribute little to the genic variance. Genes which are beneficial for one but deleterious to the other character will on the other hand have reached the intermediate level (say 0.5) through continued selection. These genes will contribute more to the genic variance but at the same time result in a negative genetic correlation. It is doubtful whether the effects of selection as postulated by Lush are actually realised in these data. It is unlikely that effects of past selection could, as yet, adequately account for the present genetic antagonism between fleece weight and fertility.

(2) Crossing over and Recombination of genes

Mather (1943) and Mather and Harrison (1949) have suggested that natural selection penalises extreme gene combinations. Thus, in an unselected population i.e. not subject to artificial selection; balanced linked combination of polygenes are built up. However, under directional selection, i.e. artificial selection, the unbalanced combinations have selective advantages i.e. extremes are favoured. Crossing over and recombination are necessary to increase the proportion of these unbalanced combinations. Crossing over within a chromosome will bring out recombination not only within the polygenic combination affecting the character which is being selected, but also within other polygenic combinations which are intermingled with it along the chromosome. Thus, selection for changed combination in one set of genes will bring about a correlated response in other combinations which are not being selected. This could produce either a negative or a positive correlated response.

The above postulate is mainly based on work with Drosophila. Drosophila have characteristically:

(i) a small number of chromosomes,
(ii) no crossing over in the male,
(iii) frequent inversions.

Selection intensity can also be made high in Drosophila. It may be noted that these features are not likely to occur in sheep. In addition, Wright (1945) has shown that in a random bred population, if crossing over is at the usual rate, the frequency of coupling and repulsion heterozygotes is soon equalised and recombination is at random. In view of these reasons, the concept on the balanced linked gene combinations does not appear to be useful in elucidating the present negative genetic covariation between fleece weight and fertility in sheep.

There is yet another explanation for negative genetic correlations. This explanation has been put forward by Lerner (1950). He suggested that if the secondary character,i.e. the unselected character, forms an important component of total fitness, it might be expected to decline in response to selection of the primary character in either direction. Briefly, this is brought about if one considers the fact that present-day domestic animals are end-products of centuries of natural selection towards the fittest type. The mean value of the primary character in a population thus far not subject to artificial selection is, therefore, the optimum for fitness under the conditions prevailing. Any departure from this optimum through artificial selection will be accompanied by a reduction in fitness, i.e. some reduction in the secondary character.

Fleece weight for the present purpose may be regarded as the primary character and the number of lambs as the secondary character. There is little doubt that fleece weight has long been subject to artificial selection. The number of lambs for all intents and purposes has, on the other hand, not been strongly selected for by breeders. The amount of genetic improvement in fleece weight presumably measures the extent of the departure from its evolutionary optimum. However, evidence to indicate the amount of improvement in fleece weight as a result of selection is lacking. Theoretical considerations from estimates of the intensity of selection, heritability of fleece weight (Rae 1950) and the survey results on the size and duration of the New Zealand Romney Marsh stud flocks (Stevens 1948) indicate that genetic improvement in fleece weight is likely to be slow. Nevertheless, some genetic improvement has doubtless taken place and the present value of fleece weight is unlikely to be at its evolutionary optimum. Consequently it is expected that a correlated reduction in total fitness will have taken place and this has led to some deterioration in the reproductive performance. The above pattern of causes and effects applies generally to the Romney sheep as a breed. It should be realised that the Romney sheep in New Zealand originally came from the Romney Marsh district in England. The obvious and vast difference in environment must not be overlooked. The importance of the "prevailing conditions" is implicit in Lerner's reasoning. Therefore, not only the difference in environment between the Romney Marsh district in England and New Zealand but also the difference existing between the present environment for the New Zealand Romney and that of some sixty to seventy years ago when these sheep first arrived in this country, must be taken into account. There is little doubt that a change in environment has taken place. This being the case, on assuming that selection for fleece weight has not been effective, it is possible that the mean fleece weight for fitness is no longer at its evolutionary optimum on account of this vast change in environment. Thus, a reduction in total fitness could have taken place and with it a deterioration in the reproductive performance.

Thus far, in discussing Lerner's exposition on the negative correlated responses, the environment has been assumed to remain unchanged at first and the correlated responses are brought about by selection for fleece weight and secondly, the selection for fleece weight has been assumed to be ineffective and the change in environment is considered as the cause of the negative correlated responses between fleece weight and the reproductive performance. In reality, however, both the environment and the genetic composition of a character such as fleece weight are dynamic in nature and are continuously changing. The equilibrium between the fitness of an individual and its environment is probably never exactly established. The process of physiological homeostasis (as termed by Brody 1945) in an individual probably acts as an immediate buffer for any relatively small disequilibrium between the fitness of the individual and its environment. Thus, phenotypically all those individuals that survive, appear to be in equilibrium with their environment. This visible equilibrium may be maintained in spite of the possibility that some reduction in total fitness has taken place through a change in either the genetic composition of the character in question or the environment or both but at a different rate and/or direction. The reduction in fitness, if occurring at all among some individuals,will be transmitted in some measure to their offspring. After many generations, if such a tendency persisted, the reduction in fitness, however small it may be, will gradually manifest itself phenotypically among the offspring. Since reproductive performance is an important component of total fitness, some deterioration in reproductive performance is not altogether unexpected. The present observed negative genetic covariation between fleece weight and reproductive performance may well be regarded as some evidence for the above exposition. Any definite conclusion must, however, await further investigation.

In conclusion, it may be emphasised that pleiotropy is a likely genetic mechanism underlying the explanation of the present findings, but Lerner's postulate is particularly pertinent in view of the unique importance of reproductive performance in relation to the definition of selection - the existence of a differential rate of reproduction.

VI. DISCUSSION AND APPLICATIONS

A. Introduction

The value of the results obtained in this study depends much on their accuracy and usefulness. Aspects of their accuracy have already been dealt with in previous Sections. Their usefulness remains to be assessed.

The usefulness of the present results may be examined from the following two aspects:

(1) To what extent can they be generalised.

(2) To what extent can they be applied.

(1) Estimates of phenotypic and genetic parameters obtained in this study are descriptive of the properties of the flock from which the present data have been collected. Several reasons, however, suggest that these estimates may be generalised to describe the genetic as well as the phenotypic properties of other Romney sheep flocks in the Manawatu area. Firstly, the ewes which founded the flock in 1944 were drawn from flocks in the Manawatu (Rae, 1950). The majority of the rams which have been used were purchased from Romney stud flocks in the same area but a few rams were procured from studs in the Wairarapa. Secondly, the agreement between results of the present study of environmental effects, i.e. age and year on the reproductive performance of ewes and that reported by Goot (1952) who worked with different flocks

in the Manawatu, suggests that this flock and other flocks in the same area are much alike. Thirdly, general management practices in the present flock have been similar to those found among most sheep farms in this locality. More precisely, the present data may be regarded as a sample from a population comprising the daughters of Romney Marsh rams sold for use in the Manawatu and possibly the Wairarapa areas where the environmental conditions are similar to those in this flock. As such, the generalisation of the present findings to be applicable to other flocks in the Manawatu does not appear to be unreasonable. The validity of this generalisation, nevertheless, can be tested only by further investigation on other flocks from the same area.

(2) Application of the present results is, to a large extent, dependent upon the organisation and structure of the Romney sheep breed in New Zealand. In addition, the vital statistics of lambing per cent, death rates in all classes of stock and the annual replacement rate of the two-tooth ewes are needed to compute the expected gains and to compare the efficiency of various selection plans. Some of the information listed above is now being gathered by the New Zealand Meat and Wool Board's Economic Service, while the organisation and structure of the Romney breed in New Zealand has been surveyed by Stevens (1948). The

information pertinent for present purposes is that essentially three types of Romney flocks may be distinguished (Stevens 1948). They are the nucleus, propagating and commercial flocks. Both the nucleus and propagating flocks are registered with the New Zealand Romney Marsh Sheep Breeders Association. Generally, registered flocks are situated on the more fertile lowland and the commercial flocks are located on the hills. This locality difference renders the application of the present results to the commercial flocks uncertain in view of the possible interaction between heredity and environment.

In general, a high proportion of the sires in the nucleus flock is selected from within the flock whereas the propagating flocks secure most of their sires from either the nucleus or other propagating flocks. While these two types of flocks differ in the method of procuring sires, both, as a rule, select replacement ewes from the young ewes bred in the flock.

On account of these features of the Romney breed in New Zealand, ready application of the present findings appears to be restricted to the registered flocks. Owners of commercial flocks, however, will benefit to the extent in learning that the trait - the number of lambs born - is lowly heritable and that the genetic antagonism between fleece weight and fertility is likely to render their efforts of selecting simultaneously for both fleece weight and fertility less effective or, selecting for either character alone will be accompanied by some deterioration of the other.

B. Methods of Selection for Increased Number of Lambs per Ewe

In order to appreciate the value of various selection methods to be discussed, the genetic premise upon which the selection for reproductive performance in ewes is based will be briefly described.

The character - the number of lambs born per ewe, may be regarded as a threshold character, with more than one threshold. Its underlying genetic mechanism may be similar to that of the number of digits in guinea pigs, as reported by Wright (1934). The additive genetic values of the number of lambs born per ewe may be numerous and continuously distributed but owing to the nature of the character, its phenotypic expression can be measured only on a discontinuous or discrete scale. Consequently, there is no phenotypic difference between two genetically different individuals which are both on the same side of the pertinent threshold. All individuals with additive genetic values below that threshold are phenotypically the same, while all with additive genetic values above that threshold are phenotypically like each other and different from those below the threshold. A genetic change will produce no phenotypic effect unless it moves the individual across the threshold. If it does that, even a very small genetic change will have large phenotypic effects (Lush, 1948). The first threshold postulated in the present data is located at a "single birth per ewe" and the second threshold at "twin births per ewe". The probit scale is used to approximate the underlying continuously distributed genetic scale. The estimates of heritability for barrenness and twin births to be used in discussing various selection methods will be that transformed to the probit scale as presented in Tables XVIII and XIX.

(a) Individual or Mass Selection

The difference between the average of barren ewes and the average of the ewes that have lambed has been given by Lush (1948) as Z^2/p_1 on the observed scale. In it, p_1 represents the ewes that have lambed as a proportion of the total number of ewes, $(1 - p_1)$ being the corresponding levels of barrenness and Z is the height of the ordinate which truncates p_1 of the area of the normal curve. Assuming that:

(i) selection against barrenness is based on one lambing record only,

(ii) ewes only are under selection and they have been mated to rams that are near the average of their generation for fertility,

(iii) it is physiologically possible for the margin of reserve for fertility* to be built so high that the incidence of barrenness is nil,

then the expected reduction of barrenness in per cent in the next generation as a result of mass selection will be $\frac{Z^2}{(1-p_i)} \times \frac{1}{2} \widehat{H}_{Pb}$, where $\widehat{H}_{Pb}$ is the estimate of heritability of barrenness on the probit scale. Using a heritability estimate of barrenness on the probit scale, averaging 0.17 as in the present data, the expected reduction in barrenness from one generation of such mass selection, starting at various levels of barrenness is,

Initial level of barrenness (per cent)	Expected reduction/generation (per cent)
50	2.75
40	2.11
30	1.47
20	0.83
10	0.29
5	0.09

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*Used here to denote the opposite of "barrenness".

These figures suggest that the effectiveness of mass selection for such a threshold character, even under highly favourable conditions, falls off rapidly as the incidence of barrenness becomes low. These expected reductions may also be looked upon as the effectiveness of natural selection against barrenness. If the initial level of barrenness is taken at between 10 to 20 per cent, the expected reduction of barrenness due to natural selection against barrenness is somewhere between 0.29 and 0.83 per cent per generation. These expected reductions suggest that natural selection against barrenness is relatively ineffective.

What happens when more than one lambing record (c.f. assumption (i)) is used as a basis of selection has not yet been investigated. With regard to assumption (iii), it is perhaps more realistic to suppose that there is an irreducible minimum of barrenness from accidents, e.g. rams to which ewes are mated, may be sterile or deaths from some ewes put to the ram. In other words, although the ewes leave no offspring, this is not due to their sterility. This irreducible minimum of barrenness is without, or has possibly a different genetic basis to that of true barrenness. This, however, will lower the effectiveness of mass selection a little even when the incidence of barrenness is as high as 40 or 50 per cent.

The size of this irreducible minimum will, of course, be variable. The general conclusion on the effectiveness of mass selection against barrenness, is nevertheless clearly that it is relatively effective when the average incidence of barrenness is high but approached zero rapidly as the average incidence of barrenness falls under 30 per cent.

On the other hand, selection for twin births can be carried out simultaneously with selection against barrenness to enhance the over-all effectiveness of mass selection for the characteristic - the number of lambs born per ewe. Based on similar assumptions and reasoning as in the case of barrenness, the following figures show the expected gain in per cent from mass selection for twin births in ewes.

Initial average incidence of twin-birth (per cent)	Expected gain /generation* (per cent)
5	0.07
10	0.22
20	0.68
30	1.12
40	1.61
50	2.07

*Estimate of heritability on the probit scale for twin births is approximately 0.13 in these data.

These figures clearly show that for mass selection to be relatively effective, the average incidence of twin births must be reasonably high. Assuming that the initial incidence of barrenness and twin births is 10 per cent and 20 per cent respectively, the expected gain per generation from mass selection for the number of lambs born per ewe is approximately one lamb per 100 ewes or 1 per cent.

(b) Family Selection

A family is a group of individuals related by descent. Thus, members of a family are, by definition, genetically related. Commonly, in a flock of sheep bred at random, most families consist of paternal half-sibs whose genetic relationship is 0.25.

Selection for higher fertility i.e. lambing per cent, based on family merit alone, implies that all the ewes required for breeding will be selected from families of the highest lambing per cent. An example to illustrate the information required if family selection is used for selecting fertility in sheep is given in the table below.

Table XXV. Example of Family Selection

Paternal half sib families	Frequency of barren ewes	Frequency of single birth	Frequency of twin births	Total No. of lambs	Total No. of ewes	Lambing per cent
A	3	15	2	19	20	95
B	6	14	0	14	20	70
C	4	13	3	19	20	95
D	2	15	3	21	20	105
E	5	12	3	18	20	90
Total	20	69	11	91	100	91

Based on one lambing record as shown in the table and assuming 60 ewes are required for breeding, using family selection alone, these 60 ewes will come from families D, C and A.

In general, family selection is likely to be somewhat more effective than individual selection but particularly so when selection is either against barrenness or for twin births. This is because individual selection for either of these two components of fertility depends much on the average incidence of each. At low levels of incidence of barrenness or twin births individual selection is almost ineffective. In these circumstances, however, family selection is still effective.

A further possibility is the use of the optimum combination of family and individual selection. It has been shown by Lush (1947) that it produces genetic improvement in characters distributed continuously at a rate $\sqrt{1 + \frac{(r-t)^2}{1-t} \cdot \frac{(n-1)}{1+(n-1)t}}$ times as fast as could be achieved by individual selection alone. In the above formula, n is the number in the family, r is the genetic relationship between members of the family and t is the phenotypic correlation between members of the family. In order to achieve this optimum combination of family and individual selection, the family average should receive $\frac{n}{1 + (n-1)t} \cdot \frac{r-t}{1-r}$ times as much attention as individual's phenotype (Lush, 1947). Although the details of using the optimum combination of family and individual selection for fertility in sheep have not been worked out, it may be anticipated that it also applies to the present problem. With reference to Table XXV it can be seen that if individual selection alone is used, 60 ewes required for breeding will consist of the 11 ewes that produced twin lambs and the remaining 49 ewes will be chosen at random from ewes that have produced single lambs. If selection is based on individual as well as family selection, it is likely that those 11 ewes producing twins will be chosen and the remaining 49 ewes will be selected from families of the highest lambing per cent. The problem of families differing in size has not been considered in the example. Where family size is variable then each family should be weighted according to the deviation of its lambing per cent from the total lambing per cent by the ratio $\frac{n}{1 + (n-1)t}$. (Lush et al. 1948).

An additional point to note is that the effectiveness of family selection may be increased, irrespective of the average incidence of barrenness or twin births by increasing the value of the genetic relationship (r) between members of the same family. In a flock of sheep where no inbreeding has been practised, the value of r is usually about 0.25 which is the genetic relationship between non-inbred half-sibs. Since there may be some contemporary full-sibs (r = 0.50) in a flock, r may be a little larger than 0.25 but not very much. To increase the value of r much beyond 0.25 in a sheep flock, it is necessary to practise inbreeding. Inbreeding, however, has been reported to be usually accompanied by some reduction of litter size (Dickerson 1952) and its effects on the fertility in sheep await detailed investigation.

(c) Progeny Test

Usually a ewe does not have enough offspring to make it possible to progeny test her. A progeny test for the character - the number of lambs born per ewe, on rams is really outside the scope of the present study which is concerned largely with the selection of ewes. However, it may be noted in passing that if the first crop of offspring is born when the ram is two years of age, the earliest information from the progeny test will usually not be available until the ram is four years of age. The first opportunity to use the ram occurs only when the ram is about four years and seven months old. Hence the ram will be five years of age when its first offspring is born. This tends to lengthen the generation interval which in turn will reduce the expected genetic gain per year (Dickerson and Hazel, 1944). It thus appears that the progeny test is of no value as an aid to selection for increased number of lambs per ewe.

(d) A Fertility Index of the Ewe

An increased number of lambs per ewe may be of little advantage if they are of poor viability or if the ewe's milk production is insufficient to provide for the adequate growth of these lambs. This problem could possibly be overcome by using information on the live weight of lambs taken at weaning or some other appropriate time. This information on the live weight of lambs together with the number of lambs per ewe could be used to form a fertility index of the following type:

$$I = aN + bW$$

where I is the fertility index of the ewe,

N is the number of lambs weaned

W is the live weight per lamb at weaning or some other appropriate time

a and b are weights determined by the respective importance of N and W e.g. a and b may represent the relative economic value of N and W.

An index of the above type can take into account not only the phenotypic and genetic correlations between N and W but also the respective heritabilities of N and W. Detailed investigation on the merit of such an index will be carried out in the near future.

C. Selection Index for Fertility and Fleece Weight

Selection for fertility is only one aspect of the problem in selecting for productivity in sheep. It can not be over-emphasised that it is the productivity of sheep rather than some aspects of it that is the ultimate concern in sheep breeding. Hazel and Lush (1943) have shown that selection for an index which gives proper weight to each trait is more efficient than selection for one trait at a time or for several traits with an independent culling level for each trait. To actually construct such an index based on both the trait - fertility, and the trait - fleece weight, requires information which is not available at present. Some problems likely to be encountered in constructing such an index, however, can be deduced as a result of the present study.

(i) The principles on the construction of selection indices as outlined by Hazel (1943) provide specifically for characters that are distributed continuously and the effects due to the inclusion of a character, such as the number of lambs, measured on a discrete scale, need to be investigated.

(ii) If the selection index is based on only fleece weight and fertility (number of lambs) in view of the negative genetic covariation between them, the heritability of the index is likely to be very low. However, the relative economic value of fertility, i.e. the number of lambs, is high as compared with that of the fleece weight; consequently, the heritability of the index probably will not be zero but is likely to be lower than that of either fertility or fleece weight alone. This will tend to make genetic progress slower than if the heritability of the index is relatively high.

In conclusion, one may well be reminded by quoting Hazel (1943) that:

> "While these considerations do not indicate much possibility of phenomenally rapid improvement in animal populations from selection alone, the progress which can be made with properly constructed indices is considerably greater than can be expected when the ideals toward which selection is directed are confused or erroneous."

VII. REFERENCES

Aitken, A.C. (1936-37). Proc. Roy. Soc. Edin. 57: 172,269.

Bartlett, M.S. (1951-52). Ann. Eugenics 16: 199.

Barton, R.A. (1947). Proc. 10th Ann. Mtg. Sheepfarmers, Massey Agricultural College, 113.

___________ (1949) N.Z. J. Sci. & Tech. 31:(A) 24.

Bosman, V. (1935). Ondp. J. Vet. Sci & Anim. Ind. 4: 551.

Brody, S. (1945). Bioenergetics and Growth. Waverley Press, Baltimore, MD.

Carlyle, W.L. & McConnell, T.F. (1902). Uni. Wisconsin Agr. Expt. Sta. Bull. 95, 1.

Cochran, W.G. (1943). J. Amer. Stat. Ass. 38: 287.

___________ (1947). Biometrics 3: 22.

Cockerham, C.C. (1949). Unpublished M.S. Thesis. (As quoted by Desai and Winters 1951b).

Desai, R.N. & Winters, L.M. (1951a). Ind. J. Vet. Sci. & Anim. Hus. 21; Pt. 3, 177.

___________ (1951b). Ind. J. Vet. Sci. & Anim. Hus. 21; Pt. 3 191.

Dickerson, G.E. and Hazel, L.N. (1944). J. Agri. Res. 69: 459.

Dickerson, G.E. (1952) Heterosis 330. Iowa State College Press.

Dry, F.W. (1946). Proc. N.Z. Soc. Anim. Prod. 6th Ann. Conf. 6: 95.

Dry, F.W. and Fraser, A.S. (1947). Proc. N.Z. Sci. Cong. 243.

Dry, F.W., Fraser, A.S., and Wright, G.M. (1947). Nature 160: 646.

Esplin, A.C., Madsen, M.A. and Phillips, R.W. (1940). Bull. Utah Agri. Exp. Sta. No. 292.

Falconer, D.S. (1954). J. Heredity 55: 42.

Fisher, R.A. (1950) Statistical Methods for Research Workers. 11th Ed. Oliver & Boyd Ltd. Sec. 49 2.

Goot, H. (1950). J. Agr. Sci. 41: 1.

———— (1952). N.Z. J. Sci. & Tech. (A) 34: 97.

Hafez, E.S.E. (1951). Nature 168, 1046.

Hammond, J. (1950). Proc. Roy. Soc. B, 137: 452.

Hazel, L.N. (1943). Genetics 28: 476.

Hazel, L.N. and Lush, J.L. (1943). J. Hered. 33: 393.

Hewitt, W.R.R. (1955). Private Communication.

Johansson, I. (1933). Proc. Amer. Soc. Anim. Prod. 25th Ann. Mtg. 285.

Johansson, I. and Hansson, A. (1943). Lantbr-Hogskol. Ann. (Uppsala) 11: 145. (A.B.A. 13: 35).

Jones, S.V.H. and Rouse, J.E. (1920). J.D. Sci. 3: 260.

Joseph, W.E. (1931). Proc. Amer. Soc. Anim. Prod. 24th Ann. Mtg. 219.

Kelley, R.B. (1943). Pamphl. Aust. Wool Bd. No. 2, 23. (A.B.A. 12: 27).

Kempthorne, O. (1952). The Design and Analysis of Experiments. John Wiley & Sons, Inc.

Kempthorne O. and Tandon, O.B. (1953). Biometrics 9: 90.

Lerner, I.M. (1950). Population Genetics and Animal Improvement. Cambridge Uni. Press.

Lopyrin, A.I. (1938). Moscow: Seljhozgiz. (A.B.A. 6:210).

Lush, J.L. and Molln, A.E. (1942). U.S.D.A. Tech. Bull. 836.

Lush, J.L. (1947). Amer. Naturalist, 81: 241, 362.

———— (1948). The Genetics of Populations. Ames, Iowa. Mimeographed.

Lush, J.L., Lamoreux, W.F., and Hazel, L.N. (1948). Poultry Sci. 27: 375.

Lush, J.L. (1949). Proc. 8th Int. Cong. Genetics, 356.

Marshall F.R. and Potts, C.G. (1921). Bull. U.S.D.A. No. 996.

Mather, K. (1943). Biol. Rev. 18: 32.

——————— (1949). Proc. 8th Int. Cong. Genetics. 376.

Mather, K. and Harrison, B.J. (1949). Heredity 3: 1, 131.

Nichols, J.E. (1924). J. Min. Agr. 31: 835.

Nikoljskii, N.F. (1933). Abstract. (A.B.A. 2: 121).

Pearson, K. (1913). Biometrika, 9: 116.

——————— (1940). Draper's Co. Research Memoirs. (Abstract).

Peren, G.S., Hewitt, W.R.R., Ballard, H.V. and Phillips, T.O. (1951). Proc. 14th Ann. Mtg. Sheepfarmers, Massey Agricultural College, 111.

Peters, C.C. and Van Voorhis, W.R. (1940). Statistical Procedures and Their Mathematical Bases. McGraw-Hill Book Coy.

Rae, A.L. (1946). Unpublished M. Agr. Sc. Thesis, Massey Agricultural College.

——————— (1950). Unpublished Ph.D. Thesis. Iowa State College.

——————— (1954). Proc. 17th Ann. Mtg. Sheepfarmers, Massey Agricultural College, 155.

Reeve, E.C.R. and Robertson, F.W. (1953). A.B.A. 21: 211.

Rietz, H.L. and Roberts, E. (1915). J. Agri.Res. 4:479.

Roberts, E. (1921). J. Agri. Res. 22: 231.

Robertson, A. (1949). A.B.A. 17: 201.

Robertson, A. and Lerner, I.M. (1949). Genetics, 34: 395.

Stevens, P.G. (1948). Lincoln Coll. Tech. Bull. 2.

Stevens, P.G. and Wright, G.M. (1951). Proc. N.Z. Soc. Anim. Prod. 11th Ann. Conf. 11: 18.

Snedecor, G.W. (1950). Statistical Methods. The Iowa State College Press. Ames, Iowa.

Terrill, C.E. and Stoehr, J.A. (1939). Proc. Amer. Soc. Anim. Prod., 32nd Ann. Mtg., 369.

———————————— (1942). J. Anim. Sci. 1: 221.

Underwood, E.J. and Sheir, F.L. (1941). J. Dept. Agri. W. Australia, 18: 13.

Vita, A. (1951). Zootec e Vet., 6: 528. (A.B.A. 20, 50).

Wallace, L.R. (1948). J. Agri. Sc. 38: 93, 243, 367.

—————— (1949). Proc. N.Z. Soc. Anim. Prod. 9th Ann. Conf. 85.

—————— (1951). N.Z. J. Agri. 83: 377.

White, R.G. and Roberts, J.A.F. (1927). Welsh J. Agri. 3: 70.

Whitehurst, V.E., Crown, R.M., Phillips, R.W. and Spencer, D.A. (1947). Bull. 429 Fla. Agri. Expt. Sta.

Winters, L.M., Dailey, D.L., Kiser, O.M., Jordan, P.S., Hodgson, R.E. and Green, W.W. (1946). Tech. Bull. 174. Uni. Minn. Agri. Expt. Sta.

Wright, S. (1934). Genetics 19: 506, 537.

———— (1945). Ecology, 26: 415.

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