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FLEECE WEIGHT AND GRADE AND THE

REPEATABILITY OF GREASE FLEECE

WEIGHT IN SHEEP

By

RAM BARAN PRASAD

A THESIS

Submitted to the School of Graduate Studies of Michigan

State College of Agriculture and Applied Science

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

Department of Animal Husbandry

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Approved _P. H. Nelson_

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Abstract

Heritability estimates for grease fleece weight and grade and repeatability estimate for grease fleece weight were determined from sheep records from the Michigan State College sheep flock. The data included 1,599 records from 412 ewes of the Oxford, Shropshire, Hampshire and Southdown breeds, covering the period from 1933 to 1949. A study of the contribution of certain environmental factors to grease fleece weight was made and appropriate adjustments were indicated.

The study of environmental factors included the effects of age, number of lambs raised, breed and year on grease fleece weight. The least squares proceedure of analysis was used to study these environmental effects and the following is the estimate of the effects of different environmental factors:

Statistics	Grease Fleece Wt. (lbs.)
General Means (Constant Environment)	7.28
Deviation from General Means for age	2 years............ 0.36
	3 " 0.46
	4 " 0.20
	5 " 0.04
	6 " ....-0.42
	7 " ....-0.64

Deviation from General Means for Breed		
	Oxford............	0.94
	Hampshire.........	0.13
	Shropshire........	- 0.02
	Southdown.........	- 1.05

Deviation from General Means for No. of Lambs Raised		
	Single............	0.15
	Twin.............	0.02
	Triplet..........	-0.17

Deviation for General Mean for year of

from

Records made:-

1934.......0.151			1942......0.420
1935.......0.104			1943......0.320
1936.......0.727			1944......1.473
1937.......0.160			1945......1.304
1938.......0.583-			1946......0.343
1939.......0.636			1947......0.071
1940.......0.255			1948......0.211
1941.......0.165			1949......0.711

The analysis of variance was done by the method of fitting constants and only the environmental factors which accounted for at least 6 percent of the total variations were considered to be important enough to justify adjustment in a selection program. The environmental factors that needed adjustment were breed and years in grease fleece weight. On

comparison of the phenotypic parameters of grease fleece weight to grade it was found that the heaviest fleece weight was associated with the poorest grade. The phenotypic correlation coefficient between grease fleece weight and grade was estimated by correlating the two characters in the same animal and was found to be -0.35± 0.04.

Repeatability for grease fleece weight was estimated by the method of intra class correlation from records of 155 ewes of the Shropshire breed and this estimate was 0.44 ± 0.02.

Estimates of heritability, after adjusting for important environmental effects, were first made for each of the four breeds by the method of intra-sire regression of offspring on dam and intra-sire daughter-dam correlation. Then the weighted average of the four breeds and two methods were taken to give the best estimate of heritability. For grease fleece weight 169 daughter-dam pairs were used in analysis and the best estimate of heritability was found to be 0.38 ± 0.11. For grease fleece grade 167 daughter-dam pairs were used and the estimate of heritability was found to be 0.20 ± .10.

The genetic correlation was estimated by the formula:

$$r_{01\ 0j} = \frac{Cov_{12\ 11} + Cov_{12\ 11}}{\sqrt{(Cov_{12\ 11})(Cov_{12\ 11})}}$$

When the subscripts (1) and (2) represent the parental and
fillial generation respectively and i, j are two characters.
The estimate was found to be -0.37.

Under the assumption that 25 percent of the ewes are
replaced each year with ewe lambs from the best 50 percent of
the ewes and that the average loss due to death and accidents
is 15 percent; the anticipated gain for a flock of 100 ewes
in one year was estimated to be 0.17 pound for grease fleece
weight and a little less than 0.10 unit for grease fleece
grade. The gain in grade when interpreted in terms of the per-
centage of animals which may be expected to move up one grade
in one year is a little less than 10 percent.

ACKNOWLEDGMENT

TABLE OF CONTENTS

TABLE OF CONTENTS CONTD.

INTRODUCTION

(a) - General.

Biological investigations on sheep production have
tended to concentrate on the important problems of pathology,
parasitology, and nutrition. The impressive losses from
disease and drought have directed research to problems whose
solution was an immediate necessity. More recently the need
for basic information on genetic factors has been recognised.
The theoretical basis for genetic studies that might be
applied to most economic characters has been developed
largely by Fisher (1918, 1930) and Wright (1921, 1931).
The logical consequences of Mendelian inheritance, have
been interpreted in statistical terms, so that the results
of various systems of selection can be predicted with some
degree of accuracy. Lush (1935, 1945, and 1948) has de-
veloped applications of genetic theory to animal breeding
practice.

Since improvement in the genetic composition of one gener-
ation of a population is transmitted to succeeding generations,
each rung in the ladder of genetic improvement is permanent and
may be considered a capital gain. Hence, a small genetic ad-
vance is worth considerable effort because the expense incurred
in advancing one rung will yield dividends for many generations.

In order to better understand the genetic advance that can
be made in wool production, the purpose of this study was to
estimate heritability of grease fleece weight and grease fleece
grade, and repeatability of grease fleece weight.

Since genetic gain may be increased by the elimination of identifiable sources of environmental variation the following environmental effects on grease fleece weight were also studied:-

      1-Age of shearing.

      2-Breed.

      3-Number of lambs raised.

      4-Year in which the record was made.

Little need be said concerning the importance of fleece yield. Fleece contributes an important source of income in sheep production. Winter, etal. (1946) found that fleece yield was responsible for fifteen to twenty five percent of the income in sheep production.

The following discussion will explain concepts fundamental to this study. The phenotype of any individual organism is determined by its genotype and the environment in which it lives. Its phenotype will also be affected by interaction of genotype and environment; that is, the value of a given genotype will depend on the environment in which its possessor develops. In case of traits such as fleece weight, which are expressed more than once in an animals life, environment can be divided into two portions; one portion the effect of which is constant for all expressions of the trait, and another portion, the effect of which is variable for different expressions of the trait.

Let P symbolize the phenotypic measurment of a particular trait. For example, in the case of wool production, P would be the pounds of wool obtained in one shearing. If p is used to symbolize the phenotypic deviation from the population mean, (p=P - $\bar{P}$) the deviation may be expressed as a function of the contributing effects such that:

$$p_{ijk\alpha} = y_i + e_j + c_k + A_{fijk} + Z_{ijk\alpha}$$

where-

$p_{ijk\alpha}$ is the phenotypic deviation from the population mean for the α th expression of the k th individual with i th genotype developed in the j th environment.

y_i is the effect of the i th genotype

e_j is the effect of the j th environment

c_k is any environmental effect constant for all the expressions of the k th individual.

A_{fijk} is the sum of the interactions among the particular combination of y_i, e_j and c_k.

$Z_{ijk\alpha}$ is the error in measurement associated with the ijkα th expression.

Under the assumption that the genotypes occur among the various environments at random, the phenotypic variance σ_p^2, may be partitioned in the following manner;

$$\sigma_p^2 = \sigma_y^2 + \sigma_e^2 + \sigma_c^2 + \sigma_{Af}^2 + \sigma_z^2$$

For convenience let $\sigma_{\delta f}^2$ and $\sigma_{\bar{z}}^2$ be included in $\sigma_{\bar{e}}^2$ such that

$$\sigma_p^2 = \sigma_y^2 + \sigma_e^2 + \sigma_{\bar{e}}^2$$

Thus $\sigma_{\bar{e}}^2$ includes all the observed variance other than the portion attributable to constant differences between individuals.

Now consider the quantity y, which is the genotypic effect contributing to the phenotypic expression of the trait. Let g be the least squares approximation to y for this population on assigning additive effects to each gene replacement for all pairs of genes contributing to the expression of the trait. Let d be the deviation from g due to dominance, that is, d is the sum of the deviations from the additive scheme for each pair of genes because of dominant effects. Let r be the deviations from g because of interactions of non-allelic gene pairs such that

$$y = g + d + r$$

and the variance of y, σ_y^2 , is partitioned;

$$\sigma_y^2 = \sigma_g^2 + \sigma_d^2 + \sigma_r^2$$

where σ_y^2 is the total genotypic variance and σ_g^2, σ_d^2 and σ_r^2 are the variances due respectively to additive gene effects, dominance deviations and non-allelic gene interactions or epistatic effects.(Wright 1935).

(Wright 1935).

(b)-Heritability

In a broad sense, heritability (H_b) of a characteristic is then

$$H_b = \frac{\sigma^2 y}{\sigma^2 p}$$

This simply answers the question; what fraction of the observed phenotypic variance is due to hereditary differences between those individuals; heredity being considered as the whole combination of genes in each individual? Theoretically heritability can range from zero to 1.0, although actually these extremes are rarely encountered. A heritability estimate pertains to a particular characteristic in a certain population at some definite moment. It can be raised or lowered by any breeding system or practice or any alteration of environment which will increase or decrease either $\sigma^2 y$, $\sigma^2 c$ or $\sigma^2 e$.

Lush (1948) discussed the following features of heritability in the broad sense which seem to deserve mention here:-

(a) Presence or absence of a characteristic at birth is not a criterion of its heritability.

(b) Rarity or abundance is no criterion of heritability. Rarity or abundance comes into the picture only in that a rare contrast contributes little to the total varience in a population while if the same contrast were more abundant it would supply much variance.

(c) Dominance or recessiveness has nothing to do with heritability in the broad sense, although it does lower the resemblance between relatives. A completely recessive trait is as truly hereditary as a completely dominant one.

(d) Perfect heritability does not mean perfect likeness of parents and offspring. The sampling at segregation, and the fact that the individual has two parents not necessarily alike in the characteristic being considered, are enough to keep the resemblance between parent and individual offspring from being perfect, even when heritability is perfect.

As far as the animal itself is concerned its genotype functions as a whole. This actual functioning of the genotype as a whole is what is meant in the broad definition of heritability. But the gene, not the whole genotype is the unit in transmission from parent to offspring. If it is assumed that each gene substitution has, in every genotype, exactly the same effect as the average effect which it actually does have in that population, then by adding all these average effects of the constituent genes we can get an "expected" functioning or value for each genotype. Variance among these "expected" values constitutes the additively genetic variance in that population. Therefore, the narrowest definition of heritability, H_n, for a particular trait is defined as the fraction of the total phenotypic variance which is additively genetic, $H_n = \dfrac{\sigma_g^2}{\sigma_p^2}$.

Permanent improvement from phenotypic selection is proportional to this heritable fraction of the observed variance and varies from trait to trait (Lush 1935). **Thus**, heritability is important to the breeder because it represents the portion of superiority in selected parents which can be expected to be passed on to their offspring. This expected genetic gain, g_s, from a single cycle of selection for a single trait measured in terms of the **difference between the** expected mean performance of the offspring of selected parents and of the offspring of all possible parents may be estimated, ($\approx$), in the following manner;

$$g_s \ (\approx) \ sH$$

where the selection differential, s, is the mean difference in performance of selected parents and all possible parents.

When the economic value of an organism is a function of more than one characteristic, selection for a single trait may result in selection for or against or have no effect on other traits depending on the genetic correlations existing between the trait selected for and these other traits. Hazel and Lush (1942) showed that it is more efficient to base selection in every generation on an index involving all traits which affect the net merit of the organism provided each trait is given its proper weight relative to the others than to follow the plan of improving the individual traits one at a time or the plan of improving the traits simultane-

ously by the use of minimum culling levels. Heritability estimates are included in the information needed to arrive at optimum weights to be given to several traits in an index. Even in the other two methods of selection, heritability estimates would aid in properly weighting the various traits.

In addition, heritability estimates are essential in determining the efficiency and choice of different breeding systems (Wright, 1939). If heritability is high for the desired characteristics, the best method will be mass selection with little use for pedigree, relatives or progeny test selection. If heritability is low, a better plan would be to make considerable use of pedigree and some use of progeny tests, (Dickerson and Hazel, 1944) and of selection on the basis of family.

(c) - <u>Repeatability</u>

For traits which are expressed more than once by the same individual, repeatability may be defined as the regression of future performance or phenotype on past performance as measured by one expression of the trait. Using previous notations, repeatability, R, is defined such that;

$$R = \frac{\sigma_g^2 + \sigma_c^2}{\sigma_p^2}$$

which amounts to the fraction of the phenotypic variance that is attibutable to constant differences between individuals. This repeatable fraction of the total variance is the portion of the superiority in selected individuals that may be expected in future performance. Thus the expected gain, Ps, in

future performance from a single cycle of selection,
measured in terms of the mean difference between the ex-
pected future performance of selected individuals and
the performance of all individuals, may be estimated in
the following manner;

$$p_s \; (=) \; sR$$

s is again the selection differential which is defined as
the mean difference in performance of selected individuals
and all individuals of that population.

It may be worthwhile to mention the relationship
of heritability to repeatability. Since neither the genes,
nor the dominance, nor epistatic deviations change during
the individual's lifetime, repeatability should be at least
as large as heritability in the broad sense. Repeatability
may be still larger because it also includes the permanent
effects of environment. For example, the kinds of feeding
to which calves and young heifers are subjected, do affect
their production all through the rest of their lives.
These effects would be included in the repeatability but
they would not be heritable. Consequently repeatability
is useful in setting an upper limit to heritability.
Repeatability may not be much larger than heritability in
the broad sense but it can hardly be less. Using previous
notations the relationship can be represented as;

$$\frac{R}{H_n} = \frac{\sigma_g^2 + \sigma_d^2 + \sigma_n^2 + \sigma_e^2}{\sigma_g^2}$$

(d) - Means of increasing expected gain from selection.

When selection is based on an average of n records per individual the expected gain per cycle of selection is increased by the fraction

$$\frac{n}{1 + (n - 1)R} \quad \text{(Lush, 1947)}$$

such that

$$p_s \; (=) \; s \; \frac{nR}{1 + (n-1)R}$$

Similarly the expected genetic gain, g_s, from selection based on n records per individual is increased such that

$$g_s \; (=) \; s \; \frac{nH}{1 + (n-1)R}$$

However, the picture of increasing the gain by averaging records is not complete because the selection differentials are different for different values of n. For the purpose of illustration and in theoretical problems the selection differential may be defined such that

$$s = q\,\sigma_p$$

when q is the selection differential in units of the phenotypic standard deviation, σ_p, (Hazel and Lush, 1942). The magnitude of q depends on the portion of individuals selected and the size of the population.

Rewriting previous notations;

$$g_s \; (=) \; sH$$

$$H = \frac{\sigma_g^2}{\sigma_p^2}$$

$$s = q\,\sigma_p$$

And substituting

$$g_s (=) q \frac{\sigma_{\hat{g}}^2}{\sigma_{\hat{p}}}$$

which is equivalent to

$$g_s (=) q \frac{\sigma_{\hat{g}}^2}{\sqrt{\sigma_{\hat{g}}^2 + \sigma_{\hat{c}}^2 + \sigma_{\hat{e}}^2}}$$

The effect of averaging n records per individual in essence is to reduce $\sigma_{\hat{e}}^2$ to $\frac{\sigma_{\hat{e}}^2}{n}$; and the expected genetic gain for this condition, g_s (n), expressed as a fraction of the expected genetic gain for one record, g_s (1), is

$$\frac{g_s(n)}{g_s(1)} = \frac{\sqrt{\sigma_{\hat{g}}^2 + \sigma_{\hat{c}}^2 + \sigma_{\hat{e}}^2}}{\sqrt{\sigma_{\hat{g}}^2 + \sigma_{\hat{c}}^2 + \frac{\sigma_{\hat{e}}^2}{n}}}$$

which reduces to

$$g_s (n) = g_s (1) \sqrt{\frac{n}{1 + (n-1) R}}$$

q was assumed to be constant for this illustration. Thus it is seen that the effect of using n records is to increase genetic gain directly proportional to

$$\sqrt{\frac{n}{1 + (n-1) R}}$$

per cycle of selection. P_s is increased by the use of n records in the same manner.

Other means of increasing genetic gain are worthy of consideration. Since $g_s (=) q \frac{\sigma_{\hat{g}}^2}{\sigma_{\hat{p}}}$; g_s may be increased by increasing q or $\sigma_{\hat{g}}^2$ or by reducing $\sigma_{\hat{p}}$.

q may be increased by reducing the portion of individuals selected and/or by increasing the size of the

population. The latter condition is practically of no importance except that by increasing the size of the population the portion selected can possibly be reduced. However, these conditions depend on the reproduction rate and longevity of the species under consideration and the state of development of the population with respect to numbers, about which breeders generally have little control.

It has already been shown that σ_p may be reduced by the use of an average of n records per individual for the basis of selection. Carrying this concept one step further σ_p may be reduced by basing selection on averages of groups of individuals such that σ_p is reduced to $\sigma_{\bar{p}}$, the phenotypic standard deviation of means of groups of individuals. However, it should be pointed out if the use of averages of n records of an individual effectively reduces the number of cycles of selection over a period of time, then the total gain for the entire period could actually be reduced although the gain per cycle of selection was increased.

The method most readily available to the breeder for reducing σ_p has yet to be mentioned. Consider the quantity σ^2_e, which is the sum of all variances among phenotypic expressions other than those attributable to constant differences between individuals. Among these summed variances

there may be certain identifiable sources of environmental
variation which can be adjusted for. As an example, con-
sider that the year, the record was made, exerts considerable
influence on the grease fleece weight. If selection occurred
among individuals whose fleece weight occurred in the same
year, the effects of years would be automatically eliminated,
or if the weights occurred among different years they could
be adjusted for yearly differences. Let the environmental
portion eliminated be $\sigma_e^2(e)$ and let

Then
$$a = \frac{\sigma_e^2(e)}{\sigma_p^2}$$

$$g_s = q\,\frac{\sigma_g^2}{\sqrt{\sigma_p^2(1-a)}}$$

Thus the increase in g_s is directly proportional to
$\sqrt{\frac{1}{(1-a)}}$; where a is the fraction of the total variance ad-
justed for. The effect on H is

$$H = \frac{\sigma_g^2}{\sigma_p^2(1-a)}$$

and the increase in H is directly proportional to $\frac{1}{(1-a)}$.
Similar concepts hold for p_s and R. However, as would seem
logical, only adjustments that are practical for use in
routine selection programs should be applied to the data
in estimations of appropriate H and R.

METHODS AND MATERIAL

(a) Source of Data: - Data used in this study were obtained
from the flock of sheep at Michigan State College. The flock
contained the following breeds:

Shropshire, Hampshire, Oxford, Rambouillet, South-
down, Cotswold and Black top Delaine.

There were also some grades and cross breeds. The
feeding and management of the flock have been as good as
practicable in keeping with its objects of teaching, re-
search and extension demonstration. A general survey on
the productivity of the flock made by Venkatachalam (1949)
showed that of the two-year-old ewes, 65.3 percent gave
birth to singles; 33.7 percent to twins and one percent
to triplets and of the mature ewes, 51.2 percent gave
birth to singles; 46.4 percent to twins and 2.4 percent
to triplets. There has not been a major disease problem
among ewes since the early 30's; but there was high lamb
mortality during recent years. All sheep were usually
shorn about the middle of February. The lambing season
was from the middle of February to April.

The data included the shearing records made by the
college flock from the year 1933 to 1949. The records
from only medium-wooled breeds, Southdown, Oxford, Hamp-
shire, and Shropshire were used in this study. A grand
total of 1599 records from 412 ewes were used in the analysis.
Out of the 412 ewes, there were 240 Shropshire, 77 Hampshire,
38 Southdown and 57 Oxford ewes. The ewes that lambed as
yearlings were not included in this study. In order to
facilitate statistical analysis of grease fleece grade the

following numerical figures were assigned to the different
grades:

Grade	Numerical Figure Assigned
1/2 blood	5
3/8 blood	4
1/4 blood	3
low 1/4 blood	2
common	1
braid	O

(b) - Characters observed:

A series of characters, birth weight, weaning weight,
grease fleece weight and grade have been routinely recorded
in this flock.

Grease fleece weight: Grease fleece weight is the weight of
fleece immediately after shearing, expressed in pounds. The
weight includes not only wool substance, but also wool wax,
suint, dirt, vegetable matter, moisture and other materials.
Frenny and Turner, (1938) discussed factors which affect this
weight. In particular, the moisture content varies in dif-
ferent fleeces even at constant relative humidity. The lamb's
fleece was weighed at the first shearing (about 11-12 months
old). A year later when the sheep was about 23-24 months old
the second fleece was weighed and so on. Grease fleece weight
at the ages of one, two, three, four, five, six and seven
years have been included in this study. Machine shearing was
used.

Important errors in evaluating the fleece producing ability
of a sheep are likely to arise from less subtle causes such
as variations in shearing techniques, loss of portions of
fleece when weighing and errors in weighing and recording.

Grease fleece grade: - The fleece was graded in a warehouse
by a competent wool buyer. The grading was done by in-
spection and no laboratory methods were employed. The
American system of grading was used and the grade recorded
in the same terminology.

ESTIMATES OF PHENOTYPIC PARAMETERS

A - Phenotypic means, variances and correlation.

Data on grease fleece weight were available from 1599
shearing records made by 412 ewes. Data on grease fleece
grade were available from 1185 records made by 310 ewes.

The means and variances are shown in Table I, II and
III. In Table IV are given the average fleece weights of
ewes of different ages as published by different workers.
On studying Table I and Table IV it appears that the age of
heaviest fleece weight varied from two to four years of age
with the present data showing the heaviest fleece weight at
three years of age.

There was a gradual but steady decline in fleece weight
with increasing age after the ewes had reached the age of

Table I

Phenotypic Means, Variances, Standard Deviations

and Coefficients of Variations For Grease Fleece

Weight and Grade at Various Ages .

Trait	Group Estimate	D.F.	Means	Variance	S.D.	% C.V.
Grease Age	1 yr.	325	6.68	3.09	1.76	26.35
fleece	2 yr.	459	7.32	2.92	1.71	23.36
weight	3 yr.	369	7.43	2.32	1.52	20.46
	4 yr.	273	7.23	2.46	1.57	21.71
	5 yr.	161	7.01	2.40	1.55	22.11
	6 yr.	97	6.65	1.71	1.31	19.70
	7 yr.	48	6.50	1.93	1.93	21.38
Grease	1 yr.	193	3.64*	.28	.53	14.56
fleece	2 yr.	293	3.61*	.38	.62	17.17
grade	3 yr.	265	3.68*	.35	.59	16.03
	4 yr.	194	3.64*	.27	.52	14.28
	5 yr.	123	3.72*	.26	.51	13.71
	6 yr.	77	3.70*	.27	.52	14.05
	7 yr.	33	3.76*	.33	.57	15.16

* Low 3/8 blood.

Table II

Phenotypic Means, Variances, Standard Deviations and Coefficients of Variation of Weight and Grade for Number of Lambs Raised.

Trait	Group Estimate	D.F.	Means	Variance	S.D.	% C.V.
	No. of Lambs Raised					
Grease	Single	806	7.27	2.00	1.41	19.39
Fleece	Twin	568	7.14	2.97	1.72	24.09
Weight	Triplets	30	7.34	2.18	1.48	20.16
Grease	Single	543	3.64*	.29	.54	14.83
Fleece	Twin	431	3.64*	.51	.71	19.51
Grade	Triplets	20	3.67*	.39	.62	16.89

* Low 3/8 Blood.

Table III

Phenotypic Means, Variances, Standard Deviations and
Coefficients of Variation of Weight and Grade
for Breeds.

Trait	Group Estimate	D.F.	Means	Variance	S.D.	% C.V.
	Breed					
Grease	Oxford	207	8.33	2.74	1.65	19.81
Fleece	Hampshire	279	7.29	2.08	1.44	19.75
Weight	Shropshire	912	7.08	2.40	1.55	21.89
	Southdown	148	6.11	1.76	1.33	21.76
Grease	Oxford	151	3.14***	.12	.35	11.15
Fleece	Hampshire	279	3.56***	.29	.54	15.16
Grade	Shropshire	623	3.71*	.29	.54	14.55
	Southdown	128	4.22**	.14	.37	8.77

***   Over ¼ Blood

**   Over 3/8 Blood

*   Low 3/8 Blood

Table IV

Published Average Fleece Weight of Different Aged Ewes

Investigators	Breed	D.F.	Age in Yrs.	Av. Fleece wt
Jones etal. (1944)	Rambouillet	753	1	7.85
	B and C type	624	2	9.16
		508	3	9.40
		429	4	9.41
		351	5	9.16
		273	6	8.90
		202	7	8.63
Cockerham (1949)				
mixed breed	Mixed Breed		2	6.44
			3	6.38
			4	6.32
			5	6.01
			6	6.16
			7	5.33

AGE IN YEARS
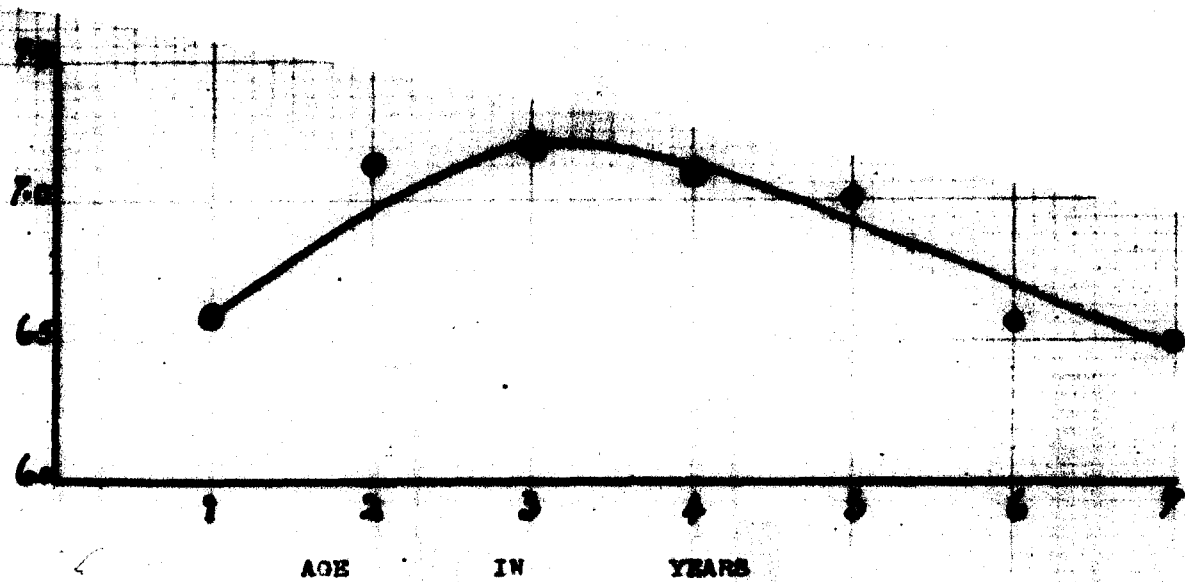
FIG. 1

Average fleece weight of different aged ewes.

AGE IN YEARS
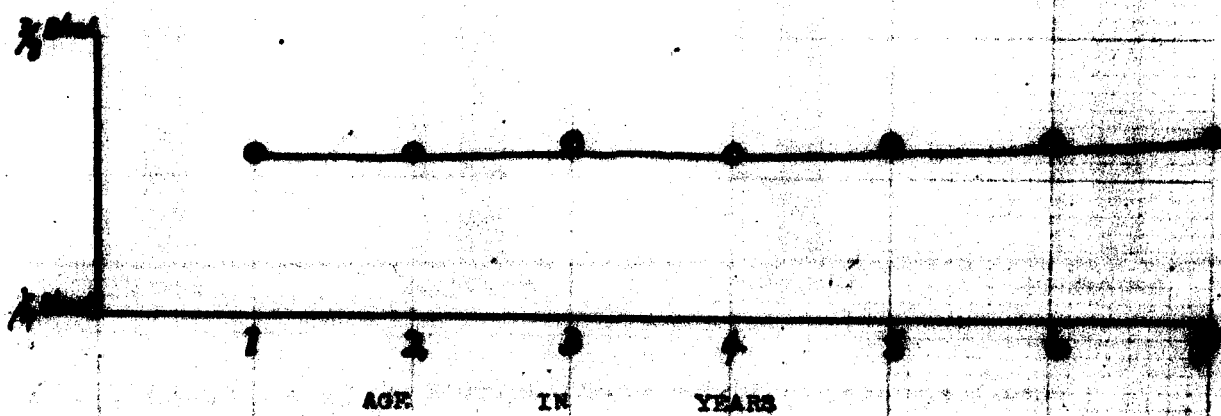
FIG. 2

Average fleece grade of different aged ewes.

KEY
Average fleece weight
Average fleece grade

Oxford   Hampshire   Shropshire   Southdown
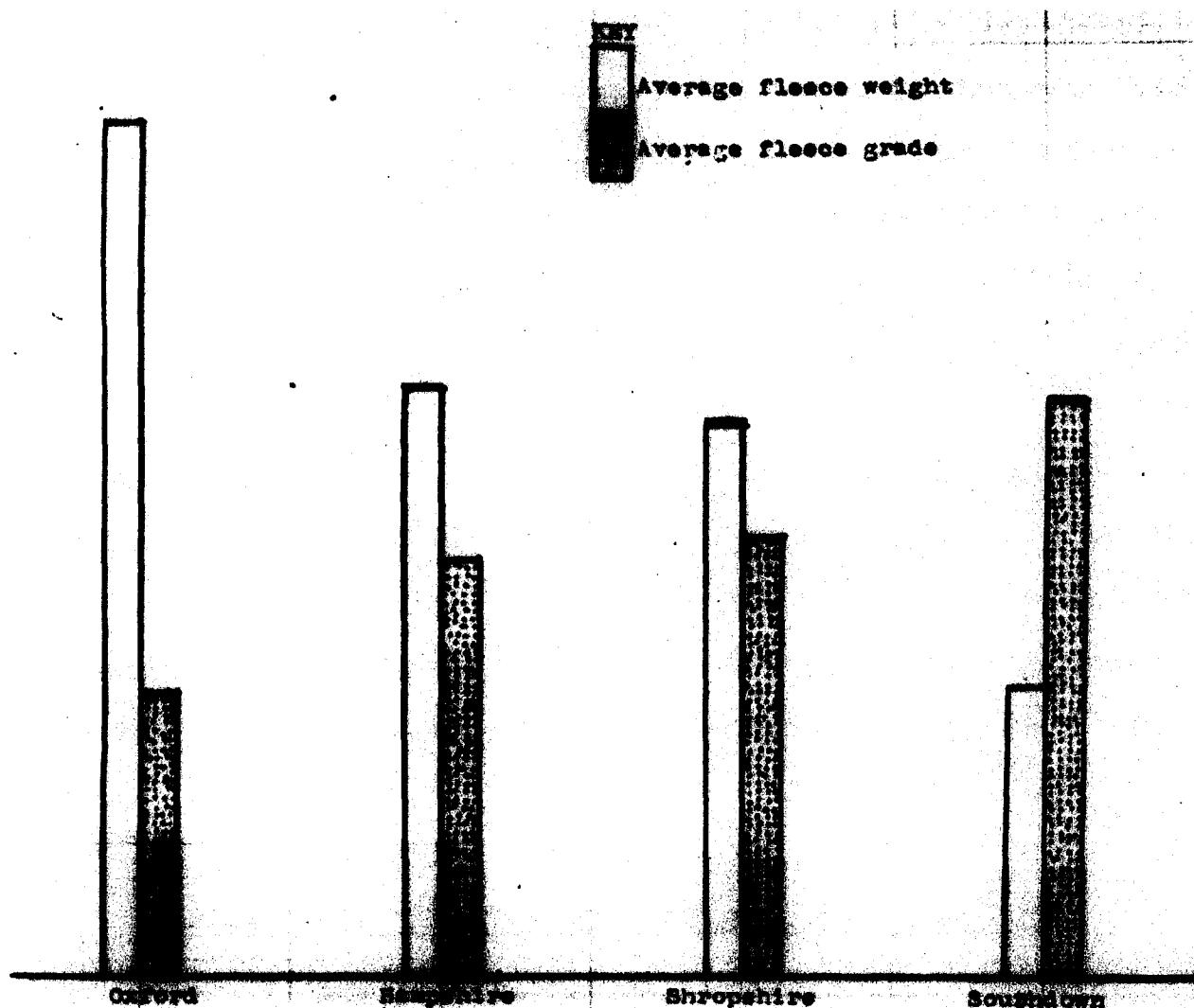
B R E E D S

FIG. 3

Comparison of the average fleece weight and average fleece
grade of the four breeds.

three years (Fig. 1). Similar declines were reported by Lush
and Jones (1923) and Spencer (1925). No significant difference
was found in the fleece weight of ewes raising single, twins,
or triplets. Among the four breeds under consideration,
Oxfords had the heaviest fleece weight and Southdowns had
the lowest while Hampshires and Shropshires were inter-
mediate. With regard to grease fleece grade, it is apparent
from Tables I, II and III that there was no significant dif-
ference in grease fleece grade among the ewes of different
ages (Fig. 2) and also among ewes raising different numbers
of lambs. But it was interesting to note the significant
differences among the breeds. In the four breeds studied it
was found that Oxfords, having the heaviest fleece weight,
had poorest fleece grade, while Southdowns, having lowest
fleece weight, had highest grade as shown in Table V and
Fig. 3.

Table V

Comparison of Average Grease Fleece Weight

and Grade of The Four Breeds

Breed	Grease Fleece Weight (lbs)	Grease Fleece Grade
Oxford	8.33	3.14 (over 1/4 blood)
Hampshire	7.29	3.56 (lower 3/8 blood)
Shropshire	7.08	3.71 (lower 3/8 blood)
Southdown	6.11	4.22 (over 3/8 blood)

The correlation coefficient between grease fleece weight and grease fleece grade was estimated by correlating the two characteristics on the same animal and was found to be $-.35 \pm 0.04$. Therefore, the individual with heaviest fleece weight might be expected to have poor fleece grade in this study.

B - Study of Environmental Effects on Fleece Weight

The data used for this study were collected from 1273 shearing records of 412 ewes belonging to Oxford, Hampshire, Shropshire and Southdown breeds. The effects of age, number of lambs raised, breed, and year on grease fleece weight were studied. For this study ewes were classified according to age, number of lambs raised, breed and year. Six age groups were considered, two through seven. Since the proportion of six year old and older ewes in a flock is small relative to the young aged ewes, there was some question as to whether they warranted inclusion. However, in the older records used for this study a good proportion of the older ewes had been retained in the flock and it was decided that the inclusion of six and seven year old ewes might present a clearer picture of the effect of age of ewe on the fleece weight and could strengthen trends observed in the younger ewes. Three groups, according to the number of lambs raised, were made as follows:- ewes raising single, twins, or triplets. It should be noted that generally ewes were shorn

a few days before lambing and, therefore, only the effects
of intra-uterine nourishing of foetus were studied. Four
breed groups were included, Oxford, Hampshire, Shropshire
and Southdown. For studying the effect of year, sixteen
year groups of ewes were made, 1934 through 1949.

Method of Analysis:- The least squares procedure of analysis
was used to study these environmental effects. Consider the
sample set of data of fleece weight in Table VI classified
according to breed and number of lambs raised.

A regression model can be written expressing each
figure in the data in terms of the effects to be considered
as follows:

$$Y_\alpha = u + b_j + c_k + e_\alpha \qquad (1)$$

Y_α is the observed fleece weight of the αth animal,

u is the effect common to all groups,

b_j is the effect common to all individuals,

of the jth breed group (j runs from 1 through 4)

b_1 - Oxford
b_2 - Hampshire
b_3 - Shropshire
b_4 - Southdown

c_k is the effect common to all individuals of kth
type of

"number of lambs raised". K runs from 1 through 3.

(c_1 - single
c_2 - twin
c_3 - triplet)

and e_α is the error in measurement of the grease fleece

Table VI

Sample set of data - Fleece Weight

No. of lambs raised K	BREED				
	Oxford j1	Hampshire j2	Shropshire j3	Southdown j4	Total
Single K_1	6.2	9.0	7.3	6.3	
	9.0	8.6	8.1	4.9	n=738
	---	---	7.8	5.8	yield=
	---	---	---	---	5411.0
	11.0	7.3	6.0	6.0	
	639.0	933.8	3527.9	1310.3	
	n=74	n=125	n=489	n=50	
Twins K_2	9.4	6.3	6.2	5.5	
	6.5	7.9	8.5	4.9	
	--- --	---	---	---	n=507
	---	---	---	---	yield=
	9.0	6.8	7.0	5.9	3664.3
	610.7	697.6	1988.0	368.0	
	n=75	n=93	n=279	n=60	
Triplets K_3	10.0	6.0	7.2	6.3	
	7.5	9.1	7.3	6.5	
	6.0	6.5	5.5	7.2	n=28
	---	8.3	---		yield=
	6.5	6.3	7.3		203.1
	76.6	36.2	70.3	20.00	
	n=10	n=5	n=10	n=3	
Total	n=159	n=223	n=778	n=113	n=1273
	Yield=	yield=	yield=	yield=	yield=
	1326.3	1667.6	5586.2	698.3	9278.4

weight for the α th animal.

By reference to Fisher (1946) and Snedcor (1946) it is found that the appropriate $\hat{b}$'s and $\hat{c}$'s (estimate of b's and c's) can be obtained. Hence u, b_j and c_k are unknown constants and e_α is expected to be zero. The method of least squares is to find the estimates of u, b_j and c_k; the particular values which minimize the sum of squares of deviations; i.e.

the sum of $(y_\alpha - u - b_j - c_k)^2$.

or as we write it $\sum_{jk} (y_\alpha - u - b_j - c_k)^2$.

The values of u, b_j and c_k, which minimizes this sum of squares are given by the so called normal equations which may be obtained by differentiation of the sum of squares with respect to u, the b_j's and the c_k's respectively.

In most cases, these equations can be written down by simple rules. To write out these equations, the number of observations in the jk th cell is denoted by n_{jk} and let

$$\sum_k n_{jk} = N_{j.}$$
$$\sum_j n_{jk} = N_{.k}$$
$$\sum_j \sum_k n_{jk} = N_{..}$$

Similarly

$$\sum_\alpha y_{jk\alpha} = Y_{jk.} \qquad \sum_j \sum_\alpha y_{jk\alpha} = Y_{.k.}$$
$$\sum_k \sum_\alpha y_{jk\alpha} = Y_{j..} \qquad \sum_j \sum_k \sum_\alpha y_{jk\alpha} = Y_{...}$$

Then the equations for

$$u: N_{..}u + N_{1.}b_1 + N_{2.}b_2 + N_{3.}b_3 + N_{4.}b_4 + N_{.1}c_1 + N_{.2}c_2 + N_{.3}c_3 = Y_{...}$$

b_1: $N_1.u + N_1.b_1 + N_2.b_2 + N_3.b_3 + N_4.b_4 + n_{11}c_1 + n_{12}c_2 + n_{13}c_3 = Y_1..$

b_2:

b_3:

b_4:

c_1:

c_2:

c_3: $N_{.3}u + n_{13}b_1 + n_{23}b_2 + n_{33}b_3 + n_{43}b_4 + N_{.1}c_1 + N_{.2}c_2 + N_{.3}c_3 - Y_{.3}.$

Thus, 8 simultaneous equations have been set up with eight unknowns which can be solved by several methods.

Now consider the set of data of grease fleece weight (in appendix 1) classified according to age, breed, number of lambs raised and year. The above regression model (1) can be extended to include all the variables expressing each in terms of the effects to be considered.

$$Y_\alpha = u + a_i + b_j + c_k + d_l + e_\alpha \qquad (2)$$

Y_α is the observed grease fleece weight of α th animal.

u is the effect common to all groups

a_i is the effect common to all individuals, of the i th age group

(i runs from 1 to 6)

a_1 = 2 years $\qquad$ a_4 = 5 years

a_2 = 3 years $\qquad$ a_5 = 6 years

a_3 = 4 years $\qquad$ a_6 = 7 years

b_j is the effect common to all individuals of the j th breed group; (j runs from 1 to 4)

b_1 - Oxford

b_2 - Hampshire

b_3 - Shropshire

b_4 - Southdown

c_k is the effect common to all individuals of the kth type of "number of lambs raised"; (k runs from 1 to 3)

c_1 - single

c_2 - twin

c_3 - triplet

d_l is the effect common to all individuals of the dth year group.

(l runs from 1 to 16)

d_1 is 1934

d_2 is 1935

. . . . . .

. . . . . .

d_{16} is 1949

e_α is again the error in measurment of the grease fleece weight for the αth animal.

Then following the above technique and by reference to Fisher (1946) and Snedcor) (1946) it is found that the appropriate $\hat{a}$'s, $\hat{b}$'s and $\hat{c}$'s and $\hat{d}$'s are obtained from simultaneous solutions of the following thirty equations.

Equations for

u: $N....u + N_1...a_1 + N_2...a_2 + N_3...a_3 + N_4...a_4 +$
$N_5...a_5 + N_6...a_6 + N.1..b_1 + N.2..b_2 + N.3..b_3 +$
$N.4..b_4 + N..1.c_1 + N..2.c_2 + N..3. c_3 + N...1d_1$

$$N...2d_2 + N...3d_3 + N...4d_4 + N...5d_5 + N...6d_6$$
$$N...7d_7 + N...8d_8 + N...9d_9 + N...10d_{10} + N...11d_{11}$$
$$N...12d_{12} + N...13d_{13} + N...14d_{14} + N...15d_{15} +$$
$$N...16d_{16} = Y.....$$

a_1: $\quad N_1...u + N_1...a_1 + n_{11}..b_1 + n_{12}..b_2 + n_{13}..b_3 +$
$\quad\quad n_{14}..b_4 + n_{111}.c_1 + n_{112}.c_2 + n_{113}.c_3 + n_{1111}d_1$
$\quad\quad n_{1112}d_2 + n_{1113}d_3 + n_{1114}d_4 + n_{1115}d_5 + n_{1116}d_6 + n_{1117}d_7$
$\quad\quad n_{1118}d_8 .... + n_{1116}d_{16} = Y_1...$

a_2:
$\quad \cdot$
$\quad \cdot$
$\quad \cdot$
$\quad \cdot$
$\quad \cdot$
$\quad \cdot$

d_{16}:-

A convenient and compact manner of writing the above
set of normal equations for the whole data is given in
appendix 1 in the form of u, a, b, c, d, matrix and 'Y'
column.

The figures under the matrix (u, a, b, c, d) represent
the coefficient of these constants respectively and the fig-
ures in the Y column represent the sum of the weights for
that particular equation. Although the constants are not
written in each equation, since they are constants for each
column, their mental inclusion is necessary to complete the
equations. In appendix 1, $uu = 1273$, is the total number
of weights; $a_1b_1 = 118$ is the number of weights for the South-
down breed and so on. Similarly, $Yu = 9278.4$ lbs. is the
sum of all weights; $Ya_1 = 3061.2$ lbs. is the sum of the
weights for the two year age group and so, on.

All the constants (u,a,b,c,d) may be solved for
directly. In this case a less laborious computational pro-
cedure than solving for all the constants directly is to
reduce the set of normal equations in such a manner that
the year effects along with u (for this example d_1 to d_{16}
and u) are eliminated and thus leaving thirteen equations
only. This elimination process may appear at first to be
quite a task but with a little practice one can soon de-
velop some systematic technique to facilitate reduction.
It may be remembered that the matrix is only a compact
manner of writing the normal equations and in the reduction
process the sum of weights, i.e. 'Y' column must also be
reduced. Then the coefficients of a_6 elements were sub-
tracted from a_1, a_2, a_3, a_4, a_5; b_4 from b_1, b_2 and b_3;
and c_3 from c_1 and c_2. Thus the thirteen equations were
reduced to ten equations. These ten unknowns with ten
simultaneous equations were solved by iterative method
(Hotelling, 1943). As these values are measured as devia-
tions about the mean, the sum of each class is zero, ($a_1 +$
$a_2 + a_3 + a_4 + a_5 + a_6 = 0$; $b_1 + b_2 + .. b_4 = 0$; $c_1 + c_2 + c_3 = 0$;
$d_1 + d_2 + ... d_{16} = 0.$) thereby enabling an estimate of a_6,
b_4 and c_3. Now it is a simple matter to substitute the
estimates of a_i; b_j; and c_k in the equations $(u + d_1)$....
$(u + d_{16})$ which were eliminated first and written in terms
of a_i, b_j and c_k. Thus the sum of all the sixteen equations
$(u + d_1)$ ...$(u + d_{16})$ were obtained. But using the relation

$(d_1 + d_2 \ldots d_{16} = 0)$, the sum of all the sixteen equations was equal to $16u$ and thereby the estimate of u was obtained. Then substituting the estimate of u in $(u + d_1) \ldots (u + d_{16})$ equations, the estimates of $d_1 \ldots d_{16}$ were obtained.

It is clear from the way the model has been set up that there are not unique solutions for all the constants. If all the a_i's are increased by a constant amount, say K and reduce by K, then the same prediction of the class mean will hold true. It may be noted that thirty unknowns in the thirty linear equations are not independent. The first equation is the same as the sum of a_i equations, and as the sum of the d_i equations. There is obviously no estimate of any a_i, b_j, or c_k by itself. The estimates of any quantities that can be estimated are given by the solutions of the least squares equations.

Then the analysis of variance was carried out by this method of fitting constants as suggested by Yates (1934), and Hazel (1946). It may be noted that in setting up the above regression model it was assumed that the effects combine additively or without interaction, i.e. differences in fleece weight due to age and number of lambs raised combine additively.

Results - The results of the analysis are given in Table Vll. The same trend for age and breed effects was found as was

given in Table I, II and III. As expected, the fleece
weight was found to decline with increase in the number
of lambs raised.

It is questionable if the time and labor involved
in estimating the environmental effects by the method
of fitting constants is worthwhile in face of the esti-
mates found in Table I. But the value of this method is
unquestionable for analysis of variance of data having
multiple classification table with unequal subclass num-
bers.

The percentage of variation attributed to each of
the environmental factors under study has been given in
Table VIII. Yearly differences were the most important
environmental source of variation accounting for 10.2 per-
cent of the total variation. Works by Terrill, Sidwell and
Hazel (1948, a and 1948, b) and Cockerham (1949) indicate
that years do appreciably affect the grease fleece weight.
Included in yearly effects are any differences in manage-
ment, nutrition, and others as well as climate.

Breed differences were another important factor,
accounting for 8.8 percent of total variation.

Age at shearing accounted for only 3.2 percent of total
variation, which is in line with the findings of Terrill,
Sidwell and Hazel (1948) who found it accounted for two

percent of total variation.

Number of lambs raised has very little effect on fleece weight, accounting for 0.2 percent of total variation. Summing up all the effects, it may be stated that the effects of these four factors account for 22.4 percent of the total variation for grease fleece weight. Many other factors of less tangible or measurable nature, such as sex, age of dam, type of birth, age at weaning, parasitism, (external or internal) etc. may also be expected to affect this trait.

Although the effects may be real, they must account for a substantial portion of the total variation in order that adjustment for them will effectively increase genetic gains from selection. From previous concepts, the expected gain for one cycle of selection is directly proportional to $\sqrt{\frac{1}{1-a}}$, where 'a' is the fraction of the total variance adjusted for. The following table gives a rough idea of the increase expected from adjusting for different percentages of the total variation.

A	B
Percent of total variation adjusted for)a)	Percent increase expected in genetic gain $(\sqrt{\frac{1}{1-a}} -)100$
2	1.0
6	3.2
10	5.4
20	11.8
30	19.5
40	29.1
50	41.4

From the above table it is readily seen that the rate
of increase in genetic gain increases with the percentage
of variation adjusted for. It does not seem that an adjust-
ment of less than six percent of the total variation would
be a very effective means of increasing genetic advance.

Under a restriction of six percent, fleece weights
were only affected enough by breed of ewes to justify ad-
justment. Yearly differences had also significent effects
which were probably worthy of adjustment.

Table VII

Statistics for Grease fleece Weight of Ewes

Statistics	Grease Fleece Weight (lb)
General mean (u)	7.28

Deviation from general mean for age

2 year (a_1)	0.36
3 year (a_2)	0.46
4 year (a_3)	0.20
5 year (a_4)	0.04
6 year (a_5)	-0.42
7 year (a_6)	-0.64

Deviation from general mean for breed

Oxford (b_1)	0.94
Hampshire (b_2)	0.13
Shropshire (b_3)	-0.02
Southdown (b_4)	-1.05

Deviation from general mean for no. of lambs raised.

Single (C_1)	0.15
Twin (C_2)	0.02
Triplet (C_3)	-0.17

Deviation from general mean for year of records made

1934 (d_1)	-0.151
1935 (d_2)	-0.104
1936 (d_3)	-0.727
1937 (d_4)	-0.160
1938 (d_5)	-0.583
1939 (d_6)	-0.636
1940 (d_7)	-0.253
1941 (d_8)	-0.165
1942 (d_9)	0.420
1943 (d_{10})	0.230
1944 (d_{11})	1.473
1945 (d_{12})	1.304
1946 (d_{13})	0.345
1947 (d_{14})	-0.071
1948 (d_{15})	-0.211
1949 (d_{16})	-0.711

Table VIII

Summary of Analysis of Variance Showing the Percentage of

Variation

Source of Variation	D.F.	S.S.
Total	1272	2957.6
Total reduction	29	659.6
Direct Effects:-		
Age	5	93.9
Percent of total	....	3.2
Breed	3	259.4
Percent of total	....	8.8
No. of lambs raised	2	6.5
Percent of total	....	0.2
Year	15	300.2
Percent of total	....	10.2

Page 36 lacking in numbering only.

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ESTIMATE OF REPEATABILITY

(a) - <u>Methods of Estimating Repeatability:</u> Since repeatability (R) is defined as the regression of future performance on phenotype as measured in one expression of the trait, it may logically be estimated by the regression of the second record on the first as was demonstrated by Stewart (1945). Let (1) and (2) denote the first and second records respectively by the same individual; then the regression coefficient is

$$b_{21} = \frac{\text{Cov. } 12}{S_1{}^2}$$

Cov. $_{12}$ estimates $\sigma^2{}_y + \sigma^2{}_c$ and $S_1{}^2$ estimates σ^2_p such that

$$b_{21} \; (=) \frac{\sigma^2_y + \sigma^2_c}{\sigma^2_p}$$

and b_{21} (=) R.

The correlation coefficient of the first and second record is: -
$$r_{21} = \frac{\text{Cov. } 21}{\sqrt{S_2{}^2 \; S_1{}^2}}$$

Provided there has been no selection the expectation of S_2^2 and S_1^2

are identical, and thus

$$r_{21} \; (=) \frac{\sigma^2_y + \sigma^2_c}{\sigma^2_p}$$

which is equivalent to the regression procedure.

Another means of estimating R which permits the use of all the records by each individual is the method of intra-class correlation (Snedcor 1946) demonstrated by

Lush and Mollin (1942). To illustrate this method consider
the following analysis of variance (Table IX) where the mean
squares are broken up into their expected component of
variances (Winsor and Clarke, 1940).

Table IX

Analysis of Variance Showing Mean Square Expectation

Source of Variation	Mean Square	Mean sq. expectation
Between individuals	m_1	$\sigma^2 + k\sigma_i^2$
Between records by the same individual	m_2	σ^2

K is the number of records per individual providing the
number is equal for all individuals otherwise K is something
less than the mean number of records per individual and
varies with the type of analysis (Snedcor, 1946). σ^2 is
the variance from record to record by the same individual
and estimates σ_e^2. σ_i^2 is the variance attributable to con-
stant differences between individuals and thus estimates
$\sigma_y^2 + \sigma_e^2$. The intra-class correlation coefficient, r_1, is
found such that

$$r_1 = \frac{m_1 - m_2}{m_1 + (K-1)m_2} \quad (=) \quad \frac{\sigma_i^2}{\sigma^2 + \sigma_i^2}$$

and substituting

$$r_1 \quad (=) \quad \frac{\sigma_y^2 + \sigma_e^2}{\sigma_p^2}$$

$$r_1 \quad (=) \quad R$$

(b) - Calculation of Repeatability:-Repeatability was estimat-
ed for grease fleece weight, by the method of intra class

correlation from 460 records of 155 Shropshire ewes. Since
Jones, etal. (1944) showed that rearing a lamb may lower
fleece weight, ewes were divided into groups according to
year of first record and fecundity so that all ewes in
each group were of the same age and had or had not reared
lambs in the same year. Analysis of variance was then
carried out in each of the eight groups resulting from this
classification. This procedure resulted in a separation of
the variance due to age, year and fecundity from the variance
due to permanent differences among ewes and to random devi-
ations from them. An example is provided in Table X by the
analysis of the second group in which each ewe had a record in
1946, 1947, 1948 and 1949. Each of the ewes in this group
reared a lamb during the year which the fleece was grown.

Table X

Analysis of Variance

Source of variation	D.F.	S.S.	M.S.
Between years	3	.98	
Between ewes	8	15.59	1.95
Error	24	8.58	.35
Total	35	25.05	

Now $(.\text{M.S. Ewes}) = \sigma_e^2 + K\sigma_1^2$

$(\text{M.S. Error}) = \sigma_e^2$

The S.S. among ewes and the S.S. error, were then pooled
to give the following combined analysis of variance in Table XI

Table XI

Combined Analysis of Variance

Source of variation	D.F.	S.S.	M.S.	M.S. Expectation
Ewes	147	392.30	2.67	$\sigma^2 + K\sigma_1^2$
Error	313	244.28	.78	σ^2

Then σ^2 and σ_1^2 were estimated to get an estimate of R.

Then Ewes (M.S. = 2.67) = $\sigma^2 + K\sigma_1^2 = \sigma^2 + \frac{460}{147}\sigma_1^2$

$$\sigma_1^2 = .61; \qquad \sigma^2 = .78$$

and $\qquad r = \dfrac{.61}{.78 + .61} = .438$

$$r \ (=) \ R \ (=) \ .438$$

An approximation of the sampling variance of R, V (R), when R is found in the above manner, is given by the following formula as used by Cockerham (1949):

$$V\ (R) = \frac{2(1-R)^2}{a\ Z\ K^2}\left[Z\left[1 + R\ (K-1)\right]^2 + a\left[1-R\ (K-1)\right]^2 \right]$$

When a and Z are the respective degrees of freedom for ewes and error.

The estimate of repeatability and its approximate standard error is .44 $\pm$ .02.

c-Comparison with Published Estimates

In comparing these findings with some of those in published material it was necessary to transform correlations between first record and total subsequent records to an

estimate of repeatability, using the formula

$$r_{xy} = R \sqrt{\frac{n}{1 + (n-1) R}}$$

Where r_{xy} = correlation between first record and the

total or average subsequent records.

R = repeatability

n = the number of subsequent records.

The value obtained is subject to considerable error, especially if the correlations between first and subsequent records is lower than other correlations.

Several estimates of repeatability are available for grease fleece weight. Lush and Jones (1923) obtained an average correlation of 0.61 between the weights of fleece of Rambouillet ewes in Texas. These authors did not correct for fecundity; but this would have caused little error, since most of the ewes lambed each year after their first shearing. Joseph (1928) obtained correlations of 0.29 to 0.84 between fleece at various ages. Joseph's figures could not be compared directly with the ones in this study. Rasmussen (1942) obtained estimates of 0.56 for Rambouillet and Corriedale ewes, and 0.43 for Romney crossbred ewes. Terrill(1939) obtained estimates which when transformed gave a repeatability of 0.45. Cockerham (1949) obtained a combined estimate of 0.60 for several breeds at the North Carolina Experiment Station.

In considering these estimates of repeatability one is impressed by the fact that the estimate obtained from this

data (.44 $\pm$ .02) is not greatly different from these
published estimates.

ESTIMATES OF HERITABILITY

a - Methods of Estimating Heritability

Estimates of heritability most commonly available for animals are those based on intra-sire regression of offspring on dam, intra-sire correlations between dam and offspring; and the sire component of variances among progeny of different sires (parental half-sib correlations). Lush (1940) discussed the methods of intra-sire regression and correlation. The regression is interpreted in the following manner. Let U and v represent records of offspring and dam respectively. Then the regression coefficient, b_{uv} is found as follows:

$$b_{uv} = \frac{\text{Cov. } uv}{S^2_v}$$

When Cov and S^2 are estimated coveriance and variance respectively.

Cov_{uv} estimates $\frac{1}{2} \sigma^2_g$ and S^2_v estimates σ^2_p so that

$$b_{uv} \; (\doteq) \; \frac{\frac{1}{2} \sigma^2_g}{\sigma^2_p}$$

and

$$H \; (=) \; 2b_{uv}$$

Provided that there has been no selection among parents the method of intra-sire correlation is for all practical purposes identical with the regression method. The correla-

tion coefficient,

is found such that

$$r_{uv} = \frac{Cov_{uv}}{\sqrt{S_u^2 \ S_v^2}}$$

The expectations of the variance among dams is

$$E\ (S_v^2) = \sigma_g^2 + \sigma_d^2 + \sigma_r^2 + \sigma_c^2 + \sigma_s^2 = \sigma_p^2$$

where $E\ (S_v^2)$ denotes expectation. The expectation of the
variance among daughters by the same sire is

$$E\ (S_u^2) = 3/4\ \sigma_g^2 + \sigma_d^2 + \sigma_r^2 + \sigma_c^2 + \sigma_s^2 = \sigma_p^2 - 1/4\ \sigma_g^2$$

$$R_{uv}\ (=)\ \frac{1/2\ \sigma_g^2}{\sqrt{\sigma_p^2\ (\sigma_p^2 - 1/4\ \sigma_g^2)}}$$

Since the additive genetic portion of the total variance
is generally small for traits of quantitative inheritance the
correlation procedure is for all practical purposes identical
with the regression procedure. Whether or not selection has
been practiced on the dams, the regression method gives an
unbiased estimate of heritability provided there are no en-
vironmental correlations between offspring and dam. This con-
dition is generally achieved when the regression is conducted
on a within sire basis. However, if individual sires occur
with different breeding groups, that is with different breeds
or at different locations, it is best to restrict the analysis
accordingly to avoid environmental correlation.

For the case where $\bar{V}$, the average of n records for each
dam, is used in the computation of the intra-sire regression
of offspring on dam, H is deduced from this regression in

the following manner:

$$H \; (=) \; 2b_{u v} \left[\frac{1 + (n-1)R}{n} \right]$$

(Lush and Straus, 1942). Averaging records for the off-
spring has no effect on the deviation of H.

Where data with progenies of different sires within
a breeding group are available the sire component of
variance is a handy tool to get intra-class correlation
for estimating heritability as demonstrated by Baker,
Hazel and Reinmuller (1943).

This method of paternal half-sib resemblence is
usually not as accurate as the previous method of parent-
offspring relationship. However, when the data are
analysed by the analysis of variance, the intra-class
correlation as outlined by Snedcor (1946) gives the re-
quired statistic which, on multiplying by four gives an
estimate of heritability. Here the statistic is multi-
plied by four because the relationship between half-sibs
is twenty five per cent. Even a small error when multi-
plied by four appears to be large, and hence the method
is often inaccurate.

Nelson (1941) demonstrated the mid-parent offspring
correlation or regression method to estimate heritability.
This method is the same as the parent-offspring relationship
method.

except that in the place of one parent the average of both the parents is used. There is not much literature on this method since most of the studies of heritability were concerned with characters which could be directly measured in one parent only. However, this mid-parent offspring method may be used if the trait can be measured in both parents; for example, fleece-weight. To get the estimate of heritability by this method, the regression or correlation coefficient is multiplied by 1.41 for the following reason:-

The correlation between the offspring and one of its parents is 0.5 for characters which are completely hereditary. According to the theory of path coefficients squaring this correlation gives 0.25 as the degree of determination of the offspring by one of its parents. Thus, the inheritance of the individual is twenty five percent, determined by each parent; and the degree of determination of the offspring by both parents is fifty percent. The square root of .5 gives .707 as the correlation between the parental average (mid-parent) and the offspring for traits which are completely hereditary. Consequently, the correlation (or the regression) between the offspring and the mid-parent would be multiplied by $\frac{1.0}{0.70}$ or 1.41 in place of $\frac{1.0}{0.5}$ or 2 as used for the correlation between the offspring and only one of its parents.

(b) - <u>Calculation of heritability of grease fleece weight</u>.

Of the four methods, the following three methods were chosen to be used for this study:

1 - Intra-sire regression of daughters on dams.

2 - Intra-sire daughter-dam correlations.

3 - Paternal half-sib correlations.

As previously pointed out the data needed adjustment for years and breeds in order to estimate heritability.

The difference in the records made in different years was tested for significance in each year seperately. It was found that the records made in 1944 and 1945 were significantly different from the rest of the years. Then there were three alternatives; one was to develop a conversion factor to correct the data to one standard year; or to adjust the estimate of heritability on the basis of percentage of variation accounted for by years according to formula on page 13 ; or to eliminate from the data the records made in the significantly different years. There were very few records made in these three years (13 in all) which would have been used in the analysis. Therefore, the data after eliminating these records were used for analysis. With regard to the adjustment for breed, the estimate of heritability was made seperately for each of the four breeds under study and then their weighted average was taken. It may be worthwhile to mention that only single records (two years old records) were used for both dams, and daughters so that the age and fecundity status was the same for all. Table XII gives the number of sire groups and the number of

daughter-dam pairs in each breed used in the calculation of heritability.

Table XII

Distribution of Records by Breeds

Breed	No. of Daughter-Dam Pairs	No. of Sires
Shropshire	65	12
Hampshire	60	9
Oxford	26	5
Southdown	618	4
Total	169	30

For this analysis, the fleece weight of dams was treated as one variable, X, and that of their daughters as the other variable Y. The fleece weight of the dam which had more than one daughter was repeated for each offspring for the analysis. The weights were grouped on an intra-sire basis. Then, the usual analysis of covariance was run between the two variables as outlined by Snedcor (1946). The results of the analysis of covariance of the four breeds are given seperately in Tables XIII, XIV, XV and XVI.

Table XIII

Analysis of Covariance of Fleece-Weight of Dams and Their Daughter for Hampshires

Source of Variation	Degrees of Freedom	Sum of Squares and Products		
		Sx^2(Dam)	Sxy	Sy^2(Offspring)
Total	59	114.09	1.17	137.63
Between sires	8	39.81	-13.73	33.95
Within sire (error)	51	74.28	14.90	103.68

Table XIV

Analysis of Covariance of Fleece Weight of Dams and Their Offspring for Shropshires

Source of Variation	Degrees of Freedom	Sum of Squares and Products		
		Sx^2(Dam)	Sxy	Sy^2(Offspring)
Total	64	182.65	55.69	263.20
Between sires	11	83.69	42.09	120.21
Within sires	53	98.96	13.60	142.99

Table XV

Analysis of Covariance of Fleece Weight of Dams and Their Offspring for Oxford

Source of Variation	Degrees of Freedom	Sum of Squares and Products		
		Sx^2(Dam)	Sxy	Sy^2(Offspring)
Total	25	83.58	-5.58	70.44
Between sires	4	27.58	-15.25	38.28
Within sire (error)	21	56.00	9.67	32.16

Table XVI

Analysis of Covariance of Fleece Weight of Dams and Their Offspring for Southdown

Source of Variation	Degrees of Freedom	Sum of Squares and Products		
		Sx^2(Dam)	Sxy	Sy^2(Offspring)
Total	17	7.96	4.74	17.36
Between Sires	3	.85	.29	3.66
Within Sire (error)	14	7.11	4.45	13.70

The following formulas were used to estimate regressions, correlations and their standard errors.

Dam-Daughter correlation coefficient $= r = \dfrac{Sxy}{\sqrt{Sx^2 \cdot Sy^2}}$

Standard Error of the correlation coefficient $= Sr = \dfrac{1-r^2}{\sqrt{n-2}}$

Regression coefficient of Daughter on Dam $= b = \dfrac{Sxy}{Sx^2}$

Standard Error of the regression coefficient $= S_b = \dfrac{\dfrac{Sy^2 - \dfrac{(Sxy)^2}{Sx^2}}{n-2}}{Sx^2}$

Half-sib correlation coefficient $= r_1 = \dfrac{S^2_m}{S^2 + S^2_m}$

where S^2 is the mean square of the error term

$S^2_m = \dfrac{\text{M.S. between sires - M.S. of Error term}}{\text{Average number in each sire group}}$

Standard error of the Half-sib correlation coefficient

$Sr_1 = \dfrac{1 - r^2}{\sqrt{n - 2}}$

As already pointed out heritability was estimated by doubling the regression coefficient and daughter-dam correlation coefficient and multiplying by four the half-sib

correlation coefficient. The respective standard error of heritability was calculated by doubling the standard error of regression and daughter-dam correlation coefficients and multiplying by four the standard error of half-sib correlation coefficient.

Table XVII summarizes the results and gives the estimate of heritability by breeds and methods separately.

Table XVII

Estimates of Heritability and Standard Errors
for the Fleece Weight

Breed	Intra-sire regression method		Intra-sire Correlation method		Paternal half-sib method	
	Heritability	Standard error	Heritability	Standard error	Heritability	Standard error
Shropshire	.274	.300	.228	.248	1.484	.436
Hampshire	.402	.304	.340	.256	.604	.512
Southdown	1.252	.618	.908	.398	.220	.996
Oxford	.345	.302	.456	.380	2.060.	.596

The large sampling error in the estimate of heritability is evident in the Paternal half-sib method and in Southdown breed. In view of this, the estimate of heritability calculated for each breed and by each of the three methods is not as accurate an estimate as an average of them all. Therefore, the values were averaged to get the best estimate for this set of data. These averages were calculated by weighting each of the individual estimates in Table XVII (above) by the reciprocal of its squared standard error, as outlined by Hazel

(1945). Although this method of **weighting has some error it**
gives greater weight to those estimates which are based on
the largest number of data.

The weighted average of heritability was obtained by the
use of the formula as follows:

Weighted average heritability. $= \dfrac{(\frac{h_1}{Sh_1})^2 + (\frac{h_2}{Sh_2})^2 + \ldots (\frac{h_n}{S^2_{hn}})^2}{(\frac{1}{S^2_{h_1}}) + (\frac{1}{S^2_{h_2}}) + \ldots (\frac{1}{S^2_{hn}})}$

where $h_1 \ldots h_n$ = heritability estimates, and

$\quad$ $Sh_1 \ldots Sh_n$ = Standard error of heritability.

The weighted average of the standard error of herit-
ability was calculated by the following formula:

Weighted Average error
$\quad$ of heritability $= \sqrt{\dfrac{1}{(\frac{1}{S^2_{h_1}}) + (\frac{1}{S^2_{h_2}}) + \ldots (\frac{1}{S^2_{hn}})}}$

where $Sh_1 \ldots Sh_n$ are the individual standard errors of heritability.

In order to facilitate the calculations, the squared
standard errors and their reciprocals for the individual
estimates of heritability found in Table XVII were first
calculated and entered in Table XVIII. Then substituting
the corresponding values from Table XVII and XVIII the
weighted average of four breeds and the weighted average
of three methods and four breeds was obtained. In view of
a large sampling error in the estimate of heritability by
the paternal half-sib method, it was decided to take the
weighted average of four breeds and two methods only

(Intra-sire regression and Daughter-Dam Correlation) as the best estimate of heritability of fleece weight in this flock and it was found to be 0.38 $\pm$ .11. It should be pointed out that the intra-sire regression of daughter on dam and intra-sire daughter-dam correlation are not actually two different methods of estimating heritability. Therefore, it does not seem fundamentally sound to weight the estimates derived from the two for one estimate since both are based on the same data.

Table XVIII

Squared Standard Errors and Their Reciprocals of the Heritability of Fleece Weight

Breed	Half-sib method		Intra-sire regression method		Dam-daughter correlation method		Reciprocal sum of three methods
	S^2h_1	$1/Sh_1^2$	S^2h_2	$1/S^2h_2$	S^2h_3	$1/S^2h_3$	
Oxford	.35	2.82	.09	10.96	.14	6.93	20.71
Shropshire	.19	5.26	.09	11.11	.06	16.26	32.63
Hampshire	.26	3.85	.09	10.87	.05	17.95	32.67
Southdown	.99	1.01	1.58	0.63	.16	6.31	7.95
Reciprocal sum of four breeds		12.94		33.57		47.45	93.96

Table XIX

Weighted Average Heritability Estimate

of Four Breeds (Fleece Weight)

Method	Heritability	Standard Error
Intra-sire regression	.36	.17
Intra-sire dam-daughter correlation	.39	.14
Paternal Half-sib correlation	1.25	.28

Table XX

Weighted Average Heritability Estimate

of Three Methods and Four Breeds

Trait	Heritability	Standard Error
Grease-fleece Weight	0.50	0.10

Table XXI

Weighted Average Heritability Estimate

of Two Methods (Intra-Sire

Regression and Intra-Sire Correlation) and Four Breeds

Trait	Heritability	Standard Error
Grease-fleece Weight	0.38	0.11

Calculation of Heritability of Grease-fleece Grade.

Of the four methods, the following two methods were chosen to be used for the set of data available for this estimate:—

Intra-sire regression of Daughter on Dam and Intra-Sire Daughter-Dam correlation method.

Paternal Half-sib correlation method was not used due to the large sampling errors associated with it in such small number of data,(particularly a small error when multiplied by 4 becomes serious). The data suitable for this estimate were available in three breedsonly. The heritability was estimated seperately for each of the three breeds and then their weighted average was taken. Only single records (two year old records) were used for both dams and daughters.

Table XXII gives the distribution of records by breeds which shows the number of sire groups and the number of daughter-dam pairs used in the calculation.

Table XXII

Distribution of Records by Breeds

Breed	No. of Pairs of Dam-Daughter	No. of Sires
Shropshire	75	11
Hampshire	66	9
Oxford	26	4
Total	167	24

For the purpose of analysis, the fleece grade of dams was treated as one variable, X, and that of their daughter as the other variable Y. The fleece grade of the dam which had more than one daughter was repeated for each daughter. The weights were grouped on an intra-sire basis. Then the usual analysis of covariance was run between the two variables and the results of the three breeds are given seperately in Tables XXIII, XXIV and XXV.

Table XXIII

Analysis of Covariance of Fleece Grade of Dams and Their Daughters for Shropshires

Source of Variation	D.F.	Sum of Squares and Products		
		Sx^2 (Dam	Sxy	Sy^2 (Offspring)
Total	74	27.1	2.0	16.7
Between Sires	10	8.6	- .2	3.4
Within sire (error)	64	18.5	2.2	13.3

Table XXIV

Analysis of Covariance of Fleece Grade of Dams and their Daughters for Hampshires

Source of Variation	D.F.	Sum of Squares and Products		
		Sx^2(Dam)	Sxy	Sy^2(Offspring)
Total	65	15.3	-2.2	15.9
Between Sires	8	6.5	-2.9	4.8
Within Sire (error)	57	8.8	.7	11.1

Table XXV

Analysis of Covariance of Fleece Grade of Dams and Their Daughters For Oxfords

Source of Variation	D.F.	Sum of Squares and Products		
		Sx^2(Dam)	Sxy	Sy^2(Offspring)
Total	25	2.7	.3	4.6
Between sires	3	.2	.2	2.0
Within sire (error)	22	2.5	.1	2.6

According to the formulas as given in the section of "Calculation of Heritability of Fleece Weight" the estimates of heritability and standard error were calculated.

Table XXVI summarises the results and gives the estimate of heritability by breeds and methods seperately.

Table XXVI

Estimates of Heritability and Standard

Error for the Fleece Grade

Breed	Inter-sire regression method		Intra-sire Daughter-dam Correlation method	
	Herit-ability	Standard Error	Herit-ability	Standard Error
Shropshire	.24	.18	.28	.22
Hampshire	.16	.28	.14	.24
Oxford	.08	.41	.08	.40

Following the method of weighted average as outlined above in the section of Calculation of heritability of fleece weight; the weighted average of three breeds and the weighted average of three breeds and two methods was obtained as the best estimate of heritability of grease fleece grade in the flock and it was found to be .20 ± .10.

Table XXVII

Weighted average of three breeds (Fleece grade heritability)

Method	Heritability	Standard error
Intra-sire regression	.20	.14
Intra-sire Daughter-Dam correlation	.20	.15

Table XXVIII

Weighted Average of Three Breeds and Two Methods
- (Fleece-grade Heritability)

Trait	Heritability	Standard error
Grease fleece grade	.20	.10

Comparison with Published Results.

Comparison of observed values of heritability of
fleece weight with those of other workers indicates rather
good agreement, considering that breeds and environment
differ so widely. The estimates are set out for comparison
in Table XXIX. Heritability as estimated in these studies
is not a fixed parameter, but rather a description of the
relative importance of heredity and environment in determin-

ing differences among individuals in a particular environment belonging to a particular breed and at a particular time. The relative importance of sources of variation may differ depending upon the control of environmental variation and the gene frequency characteristic of the population studied.

The discrepancy in heritability of fleece weight in the Romney as compared with the Rambouillet and the estimate found in this study seem to be a fairly clear example of a true breed difference. Environmental differences and previous selection for fleece weight are some of the probable reasons for breed differences. This discrepancy draws attention to the possibility of error in applying to one breed values of heritability which were obtained in another. There may even be station to station differences in this respect.

Table XXIX

Some Estimates of Heritability for the Grease-fleece

weight from the literature.

(After Morley, 1950)

Estimate	Reference	Breed	Remarks
.40	Rasmussen (1943)	Rambouillet	70prs: parent+off.
.28	Hazel & Terril (1943)	"	1622 prs: parent-off.
.24	Rasmussen (1943)	Corriedale	173 prs: parent-off.
.40	Cockerhan (1949)	Mixed breeds	233 prs: parent-off.
.14	Rasmussen (1943)	Romney cross	213 prs: parent-off.
.39	Morley (1950)	Aust. Merino	529 prs: parent-off.
.10-.15	McMohen (1943)	N.Z. Romneys	Ext. data, but year diff. confounded

ESTIMATE OF GENETIC CORRELATION

a- Definition: The linear relationships between a set
of variables may be described by the variance and covari-
ances; similarly the relationships between the genic
(additively genetic) causes of variation and covariation
in different characters may be described by genetic
variances and covariances. A genetic correlation is
thus a description of the relationship between the addi-
tive deviations caused by genes in the two characters.
In rather more precise terms a genetic correlation is
the ratio of the genetic covariance between two charact-
ers to the product of their genetic standard deviations;

$$\text{i.e.} \qquad r_{Gi\,Gj} = \frac{\text{Cov. } Gi\,Gj}{\sigma_{Gi}\,\sigma_{Gj}}$$

when Gi and Gj are the genic values of individuals for
traits i and j. The most important cause of genetic
correlations would be that some of the genes which af-
fect one trait also affect the other. This is what is
meant by pleiotropy. Other usually minor causes include
linkage and that previous selection may have been practised
with varying emphasis in different partially isolated por-
tions of the population.

b- Calculation of genetic correlation: Hazel (1943) de-
scribed the basis of methods of calculating genetic cor-

relation and gave the following formula:

$$r_{Gi\ Gj} = \sqrt{\frac{(Cov\ i_2j_1)\ (Cov\ j_2i_1)}{(Cov\ i_2i_1)\ (Cov\ j_2j_1)}}$$

When the subscripts (1) and (2) represent the parental
and filial generation respectively and i, j, are two
characters. Lush (1948) stated that sampling errors of r
when computed thus are large and likely to be complex.
He suggested taking the arithmetic mean of the numerator
rather than the geometric mean as indicated here, es-
pecially when sampling errors are a major concern or when
the volume of data is small. That would avoid such dif-
ficulties as arise when one of the observed covariances
in the numerator is negative and the other is positive.
Therefore the following formula was used with the same
meaning of the subscripts:

$$r_{Gi\ Gj} = \frac{\dfrac{Cov\ i_2j_1 \neq Cov\ j_2i_1}{2}}{\sqrt{(Cov\ i_2i_1)\ (Cov\ j_2j_1)}}$$

The statistics to be used for the estimate of
genetic correlation are given in Table XXX, XXXI, XXXII
and XXXIII.

Table XXX

Statistics for the Estimation of Covariance of Fleece Grade

Breed	Number	Sum of Dam's Grade	Sum of Off-spring's Grade	Sum of Cross-Product
Shropshire	65	237.0	238.0	894.0
Hampshire	60	225.0	205.0	742.0
Oxford	24	73.0	77.0	241.0
Total	149	535.0	520.0	1877.0

Intrabreed Covariance = .04

Table XXXI

Statistics for the Estimation of Covariance of Fleece Weight

Breed	Number	Sum of Dam's Grade	Sum of Off-spring's Grade	Sum of Cross Product
Hampshire	60	447.2	452.7	3410.6
Shropshire	65	514.2	480.1	3898.6
Oxford	24	214.5	216.5	1944.7
Total	149	1175.9	1149.3	9253.9

Intrabreed Covariance = 1.01

Table XXXII

Statistics for the Estimation of Covariance of Fleece
Weight of Dam and Fleece Grade of Offspring.

Breed	Number	Sum of Dam's Fleece Weight	Sum of Offspring's Fleece Grade	Sum of Cross Product
Hampshire	60	451.6	207.0	1558.6
Shropshire	65	538.8	233.0	1930.6
Oxford	24	216.5	74.0	663.1
Total	149	1206.9	514.0	4152.3

Intrabreed Covariance = -.04

Table XXXIII

Statistics forthe Estimation of Covariance of Fleece Grade
of Dam and Fleece Weight of Offspring.

Breed	Number	Sum of Dam's Fleece Grade	Sum of Offspring Fleece Weight	Sum of Cross-Products
Hampshire	60	220.0	458.7	1674.1
Shropshire	65	241.0	509.4	1878.4
Oxford	24	76.0	219.0	694.7
Total	149	537.0	1187.1	4247.2

Intrabreed Covariance = -.11

substituting these values of covariances in the formula:

$$r_{Gi \; Gj} = \frac{\dfrac{Cov \; i_2j_1 + Cov \; j_2i_1}{2}}{\sqrt{(Cov \; i_2i_1)(Cov \; j_2j_1)}}$$

$$= \frac{\dfrac{(-0.11) + (-0.04)}{2}}{\sqrt{(1.01)(.04)}} = \frac{-.075}{.2} = -.37$$

Therefore the genetic correlation between grease fleece weight and grease fleece grade is -.37.

DISCUSSION

The effects of environmental factors and phenotypic parameters have already been discussed in the appropriate section. A discussion of estimates of repeatability and heritability may become somewhat abstract unless a clear concept of their meaning and application is kept in mind. Although defined and developed somewhat differently to withstand a rigorous proof, repeatability is simply the average rate of change in future performance per unit change in present performance; and heritability is the average rate of change in performance of offspring per unit change in performance of parents. When estimates of repeatability and heritability are not accompanied by standard errors which warrant a great deal of confidence in them, as is true for the estimate of heritability, a comparison of the estimates with those of other workers may aid considerably in conditioning one's evidence.

The estimate of 0.44 for repeatability of grease-fleece weight is well within the limits of the findings of other workers given on page 41. This estimate for these data indicates that the methods of shearing, weighing, recording etc. of fleece weight (temporary environmental factors) are not accurate and improved techniques to control these factors may raise the repeatability of this

character. But this finding is unimportant for when repeatability is high, repeated observations are unlikely to be important aids to selection. In general the use of repeated observations will delay decisions. Variation due to years and age were removed from these data by analysis of variance. The breeder makes his selection of young stock on a within-year basis, before the young ewes are mated. Therefore he does not have to consider years, age or fecundity in his selections, except in so far as he may base part of his selection on the dams of these ewes. Further this estimate gives a fair indication of improvement that might be expected from selection under practical conditions.

The heritability estimate of .38 compares favorably with the estimates found by different workers given in Table XXVI. Although it is within the limits of the above estimates, it may be high.

In any case, heritability of fleece weight seems to be high enough for considerable improvement to be made by selection and without doubt would warrant a position in a selection programme for sheep, particularly since fleece weight is also of direct economic importance.

The value obtained for genetic correlation is unsatisfactory because of the limited number of degrees of freedom available; hence general conclusions are probably

not justifiable. Nevertheless it does give some indica-
tions of the pattern of relationship among the characters
considered.

Accepting the computed estimates of genetic cor-
relation (of -.37) at their face value, it seems that
selection for increased fleece weight will be accompanied
by decrease in fineness. Lush (1948, chap. 26) suggested
that past selection for two or more traits is likely to
have caused genetic correlations to become prevailingly
negative rather than positive, where the direction of
past selection has been positive. The hypothesis requires
that pleotropic effects of genes be reasonably common,
and that selection has increased the frequencies of genes
favorable to all traits to near untiy. Most of the genetic
variance will then come from genes with frequencies near
0.5. For gene frequencies to remain near 0.5 in spite
of continued selection requires that genes affect one
character favorably, the other unfavorably. The situa-
tion then would appear as a paradox wherein genetic vari-
ance would still exist for each character, but possible
improvement in both characters simultaneously would be
limited or even zero.

Dobzhansky (1927) found that ten out of twelve
mutants studied in Drosophila were associated with changes
in the shape of spermatheca. The mutants studied were
not previously suspected of having any effects upon internal

organs and certainly not on spermatheca shape. Results
such as these could have been caused by closely linked
genes but critical experiments to test whether any gene
has manifold effects were not possible.

Dobzhansky (1941) discussed the evidence for mani-
fold effects of genes and expressed the opinion:

> "There is . . . no evidence that every gene
> has a circumscribed province of action, in-
> cluding only a single character of physio-
> logical function. This problem belongs to
> the field of developmental genetics, and
> concerns us here only in connection with
> the so called neutral characters. Differ-
> ences between races, species, and genera
> frequently involve characters whose value
> in the struggle for existence is uncertain.
> Yet the prevalence of manifold effects of
> genes makes caution necessary in reaching
> the conclusion that a given property of an
> organism is devoid of any adaptive significance."

It would be indeed surprising if some of the
characters studied were not determined in part by the
same genes. For example, the weight of fleece is partly
determined by diameter of fibres composing the fleece,
so that genes affecting fibre diameter would probably also
affect fleece weight.

Mather (1943) suggested an alternative reason for
unfavorable correlated responses. Polygenic combinations,
in which a balance was achieved by linkage of plus and
minus genes along the chromosome, were postulated. Se-
lection imposed on a population in equilibrium will tend
to destroy the balance of polygenes, so that unfavorable

combinations for apparently unrelated characters may limit progress until new favorable combinations are formed by selection of suitable cross over types.

But there appears to be an important distinction between the results expected from selection in Drosophila and in domestic animals. Because of the small number of chromosomes and because there is no crossing over in the male, Drosophila has relatively few segregating units. Extremely intense selection can be practiced and there is a distinct possibility that the effect of linkage may be important. Selection in sheep, which have several times the number of segregating units, is unlikely to be affected by linkage to the same extent. In sheep selection for any one segregating unit is unlikely to be sufficiently intense to seriously distort the random order of gene combinations. In Drosophila, it possibly could be so intense that individuals with the preferred linkage combinations would have more descendents than those with "unbalanced" combinations. Mather's theory seems unlikely to apply to domestic animals because in them selection for desirable linked combinations must necessarily be weak, particularly where large numbers of genes influence the character in question. Yet another possible reason for negative genetic correlations is provided by physiological limitations. If two traits

both require a substrate which is available only in limited quantities, then selection for genes favoring the expression of one trait must also cause a decrease in the other.

Heritability of fleece weight seems high, but the nature of genetic correlation may limit progress. Consequently breeders may have to be satisfied with an intermediate expression in any particular characteristic in order to achieve greatest overall performance for their livestock.

APPLICATION

The breeder, confronted with the problem of improving his flock by selection requires answers to the following questions:

1- What characters should be considered in a selection program? Probably no two breeders are wholly agreed on this question, which is perhaps a fortunate situation, for no single authority is likely to be completely correct. Some diversity of ideals will assure diversity of selected types, thereby creating reservoirs of desirable germ plasm which would be valuable should price structures change radically in directions not predicted by the majority of breeders. In this study only two traits, grease fleece weight and grade, have been considered which account for fifteen to twenty five percent of the productive rating in sheep. There are other important economic characters as mentioned by Winter et al (1946) which must be considered in selection programs .

2- What progress may be expected with the information available in this study? The actual advance that one may make by mass selection for a trait can be estimated by computing the anticipated progress from a single cycle of selection. As was previously pointed out the estimates used in the computation of expected advances should be adjusted for the environmental effects and only the environ-

mental effects that are to be eliminated in the routine breeding program. These effects may be eliminated in two ways, first if selection occurs among animals which do not differ with respect to the environmental effects considered, then the effects are automatically eliminated. This is the most accurate method of adjustment. Examples are, fleece weights which occured in the same year need no adjustment for yearly differences and lamb weights taken at a constant age need no adjustment for age. The latter case is an excellent example of how a little forethought in record keeping may materially aid in a selection program. The second method is to actually adjust the records to a common basis for the differences in environment. Using this method, if the fleece weights occured in different years, they would be adjusted to a common year by computing the average fleece weight for each year and the overall average fleece weight and adjusting the records for the average yearly differences to this overall average.

To illustrate the method of computing anticipated progress by selection, the expected gain per year will be estimated for grease-fleece weight and grade in a flock of 100 ewes. Assuming that the lamb crops average one hundred percent and that half the ewe lambs are retained, then about 25 percent of the ewes are replaced each year.

This replacement is made with ewe lambs from the best 50 percent of the ewes having ewe lambs. It may be assumed further that the sires of ewe lambs are of same genetic ability as dams. Death and other accidents would eliminate about fifteen percent leaving about 85 percent of the entire flock to select from. If 75 percent of the flock must be retained and only 85 percent of the flock is available to select from, then the proportion that may be selected is actually ($\frac{.75}{.85}$) or .88 or 88 percent.

When 88 percent of the individuals are selected the average performance of the selected individuals would be expected to deviate about 0.2 standard deviation, σ_p , from the average performance of the entire flock. (Lush, 1947, pp. 148). The σ_p is the standard deviation of fleece weight corrected for years. The σ_p^2 adjusted for years may be estimated from $\sigma_i^2 + \sigma^2$ for fleece weight in Table XI such that:

$$\sigma_p^2 = (.61 - .78) = 1.39$$

and $\sigma_p = 1.18$

Therefore, the average fleece weight of the selected ewes (i.e. 88% of the ewes) is (.2 x 1.18) or .24 pounds above the flock average. Since these ewes constitute only 75 percent of the entire flock, the expected increase in fleece weight that this group will bring about would be (75 x .24) or 0.18 pounds above flock average.

But the expected production the next year would be
(0.18 x .44) or .08 pounds above the flock average of
the previous year. (0.44 being the estimate of repeat-
ability)

The remaining e 25 percent of the flock is con-
stituted by the ewe lambs from the best 50 percent of
ewes. The average fleece weight of this 50 percent of
ewes is expected to deviate about 0.8 standard deviation,
σ_p, from the average performance of the flock. There-
fore, the average fleece weight of these ewes would be
expected to be (.8 x 1.18) or .94 lb. above flock aver-
age. The expected production of the offspring of these
ewes is the product of the selection differential of
the dams selected and the heritability estimate. Actual-
ly, the selection differential, which is the main dif-
ference in performance of selected individuals and all
individuals among which selection was practiced, has
already been estimated to be 0.94 pounds above flock
average. The best estimate of heritability for grease
fleece weight in this flock is 0.38. Therefore, the ex-
pected average fleece weight of ewe lambs next year is
(.94 x .38) or .36 pounds above flock average this year.
Since the ewe lambs constitute 25 percent of the entire
flock the expected increase in fleece weight that this
group will bring about would be (.25 x .36) or .09 pounds

above the flock average previous year.

Thus the total expected progress per year may be obtained by summing up the gains made in the ewes-group constituting 75 percent of the flock and in ewe-lamb-group constituting the rest of the 25 percent of the flock. In other words, the expected flock average fleece weight next year would be (.09 + .08) or .17 pounds above flock average of this year.

Similarly, the anticipated progress in grease fleece grade can also be worked out. Its phenotypic standard deviation is 0.56 and estimate of heritability is .20. The expected increase in grade of ewes constituting 75 percent of the entire flock would be (.2 x .56) .75 or .08 units above the flock average and expected increase in grade of ewe lambs constituting 25 percent of the entire flock would be (.8 x .56 x .20) x .25 or .02 units above flock average the previous year. By summing them the expected flock average fleece grade next year is estimated to be (.08 + .02) or .10 units above flock average this year. But the estimate of repeatability for grease fleece grade was not found in this study and, hence, could not be used in computing the anticipated gain. Therefore, the expected gain in one year in fleece grade would be a little less than .10 units as estimated above. The gain in grade may be interpreted in terms of

the percentage of animals which may be expected to move up one grade in one year and it is estimated to be a little less than 10 percent.

SUMMARY

Heritability estimates for grease-fleece weight and grease-fleece grade, and repeatability estimate for grease fleece weight were determined from sheep records from the Michigan State College sheep flock. The data included 1599 records from 412 ewes of Oxford, Shropshire, Hampshire and Southdown breeds covering the period from 1933 to 1949. A study of the contributions of certain environmental factors to grease fleece weight was made and appropriate adjustments were indicated.

The study of environmental factors included the effects of age, number of lambs borad, breed, and year on grease-fleece weight. Only the environmental effects which accounted for at least six percent of the total variation were considered to be important enough to justify adjustment in a selection program. The factors found to be important enough on grease fleece weight to justify adjustment were breeds and years. The phenotypic correlation between grease fleece weight and grease fleece grade was found to be -0.35 $\pm$ 0.04.

Repeatability estimates after adjusting for the important environmental effects, were determined by the method of intraclass correlation and the estimate for grease-fleece weight was 0.44 $\pm$ 0.02.

Estimates of heritability after adjusting for important environmental effects, were deduced from the weighted average of the heritability calculated by intra-sire regression of offspring on dam and intra-sire daughter-dam correlations, on 169 daughter-dam pairs for grease fleece weight and 167 daughter-dam pairs for grease fleece grade. The best estimate of heritability for grease fleece weight was 0.38 $\pm$ .11 and for grease fleece grade was 0.20 $\pm$ .10.

Estimate of genetic correlation between fleece weight and grade was found to be -0.37. The causes of negative genetic correlation were discussed. Under the assumption that 25 percent of the ewes are replaced each year with ewe lambs from the best 50 percent of the ewes and that the average loss due to death and accidents is 15 per cent; the anticipated gain for a flock of 100 ewes in one year was estimated to be .17 lb. for grease fleece weight and a little less than .10 unit for grease fleece grade when selection was based entirely on one or the other of these traits.

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		a1	a2	a3	a4	a5	a6	b1	b2	b3	b4	c1	c2	c3	d1	d2	d3	d4
	1273	412	336	247	147	89	42	113	159	778	223	738	507	28	8	13	32	51
a1	412	412	0	0	0	0	0	38	57	240	77	297	111	4	6	5	19	14
a2	336	0	336	0	0	0	0	30	37	211	58	187	142	7	0	8	7	23
a3	247	0	0	247	0	0	0	17	31	162	37	129	112	6	1	0	6	7
a4	147	0	0	0	147	0	0	15	17	92	23	67	72	8	1	0	0	7
a5	89	0	0	0	0	89	0	9	10	51	19	40	49	0	0	0	0	0
a6	42	0	0	0	0	0	42	4	7	22	19	18	21	3	0	0	0	0
b1	113	38	30	17	15	9	4	113	0	0	0	50	60	3	2	1	3	5
b2	159	57	37	31	17	10	7	0	159	0	0	74	75	10	0	0	1	4
b3	778	240	211	162	92	51	22	0	0	778	0	489	279	10	5	7	20	30
b4	223	77	58	37	23	19	9	0	0	0	223	125	93	5	1	5	8	12
c1	738	297	187	129	67	40	18	50	74	489	125	738	0	0	4	8	19	32
c2	507	111	142	112	72	49	21	60	75	279	93	0	507	0	4	5	12	17
c3	28	4	7	6	8	0	3	3	10	10	5	0	0	28	0	0	1	2
d1	8	6	0	1	1	0	0	2	0	5	1	4	4	0	8	0	0	0
d2	13	5	8	0	0	0	0	1	0	7	5	8	5	0	0	13	0	0
d3	32	19	7	6	0	0	0	3	1	20	8	19	12	1	0	0	32	0
d4	51	14	23	7	7	0	0	5	4	30	12	32	17	2	0	0	0	51
d5	146	75	28	30	6	7	0	8	9	113	14	105	40	1	0	0	0	0
d6	197	62	72	26	30	2	5	16	15	145	21	123	73	1	0	0	0	0
d7	165	33	51	50	18	12	1	13	15	117	20	84	77	4	0	0	0	0
d8	136	44	23	31	28	13	3	15	12	86	23	78	58	0	0	0	0	0
d9	69	17	18	10	9	9	6	2	12	34	21	39	28	2	0	0	0	0
d10	58	14	13	13	5	8	5	8	12	22	16	25	31	2	0	0	0	0
d11	31	8	9	6	5	1	2	4	9	17	1	17	13	1	0	0	0	0
d12	71	31	10	15	8	6	1	4	14	33	20	34	36	1	0	0	0	0
d13	77	23	26	8	9	7	4	7	14	34	22	38	35	4	0	0	0	0
d14	73	20	14	22	6	6	5	9	13	34	17	46	22	5	0	0	0	0
d15	70	21	15	10	13	5	6	8	14	42	6	41	27	2	0	0	0	0
d16	76	20	19	12	8	13	4	8	15	37	16	45	29	2	0	0	0	0

b_2	b_3	b_4	c_1	c_2	c_3	d_1	d_2	d_3	d_4	d_5	d_6	d_7	d_8	d_9	d_{10}	d_{11}	d_{12}	d_{13}	d_{14}	d_{15}	d_{16}	yield
159	778	223	738	507	28	8	13	32	51	146	197	165	136	69	58	31	71	77	73	70	76	9278.4
57	240	77	297	111	4	6	5	19	14	75	62	33	44	17	14	8	31	23	20	21	20	3061.2
37	211	58	187	142	7	0	8	7	23	28	72	51	23	18	13	9	10	26	14	15	19	2506.6
31	162	37	129	112	6	1	0	6	7	30	26	50	31	10	13	6	15	8	22	10	12	1797.5
17	92	23	67	72	8	1	0	0	7	6	30	18	22	9	5	5	8	9	6	13	8	1042.1
10	51	19	40	49	0	0	0	0	0	7	2	12	13	9	8	1	6	7	6	5	13	595.3
7	22	9	18	21	3	0	0	0	0	0	5	1	3	6	5	2	1	4	5	6	4	275.7
0	0	0	50	60	3	2	1	3	5	8	16	13	15	2	8	4	4	7	9	18	8	698.3
159	0	0	74	75	10	0	0	1	4	9	15	15	12	12	12	9	14	14	13	14	15	1326.3
0	778	0	489	279	10	5	7	20	30	115	145	117	86	34	22	17	33	34	34	42	37	5586.3
0	0	223	125	93	5	1	5	8	12	14	21	20	23	21	16	1	20	22	17	6	16	1667.6
74	489	125	738	0	0	4	8	19	32	105	123	84	78	39	25	17	34	38	46	41	45	5411.0
75	279	93	0	507	0	4	5	12	17	40	73	77	58	28	31	13	36	35	22	27	29	3664.3
10	10	5	0	0	28	0	0	1	2	1	1	4	0	2	2	1	1	4	5	2	2	203.1
0	5	1	4	4	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57.2
0	7	5	8	5	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	96.6
1	20	8	19	12	1	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	214.5
4	30	12	32	17	2	0	0	51	0	0	0	0	0	0	0	0	0	0	0	0	0	373.2
9	115	14	105	40	1	0	0	0	146	0	0	0	0	0	0	0	0	0	0	0	0	1004.4
15	145	21	123	73	1	0	0	0	0	197	0	0	0	0	0	0	0	0	0	0	0	1356.0
15	117	20	84	77	4	0	0	0	0	0	165	0	0	0	0	0	0	0	0	0	0	1177.2
12	86	23	78	58	0	0	0	0	0	0	0	136	0	0	0	0	0	0	0	0	0	973.0
12	34	21	39	28	2	0	0	0	0	0	0	0	69	0	0	0	0	0	0	0	0	542.2
12	22	16	25	31	2	0	0	0	0	0	0	0	0	58	0	0	0	0	0	0	0	438.4
9	17	1	17	13	1	0	0	0	0	0	0	0	0	0	31	0	0	0	0	0	0	277.8
14	33	20	34	36	1	0	0	0	0	0	0	0	0	0	0	71	0	0	0	0	0	626.1
14	34	22	38	35	4	0	0	0	0	0	0	0	0	0	0	0	77	0	0	0	0	600.6
13	34	17	46	22	5	0	0	0	0	0	0	0	0	0	0	0	0	73	0	0	0	533.2
14	42	6	41	27	2	0	0	0	0	0	0	0	0	0	0	0	0	0	70	0	0	501.2
15	37	16	45	29	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	76	0	506.8