ESTIMATES OF HERITABILITY OF BIRTH WEIGHT AND WEANING WEIGHT OF LAMBS

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INTRODUCTION

Both heredity and environment play an important role in the ultimate make-up of a characteristic in an individual. The question of whether heredity or environment is the more important one for that particular trait in a particular population may be answered by the estimates of heritability of that trait.

Definition of Heritability

The heritability of a trait may be defined as the ratio of the amount of genetic variation to the total variation observed in the population. In other words, it is that part of the variability which would be lost if all the individuals of a population had one and the same genotype.

Lush (1940) defines heritability as the fraction of the observed variance which was caused by differences in heredity. This fraction is a statistic describing a particular population.

Let S_H^2 = that part of the variance caused by differences in the heredity which different individuals have

S_E^2 = that part of the variance caused by differences in the environments under which different individuals developed

$S_H^2 + S_E^2$ = Total variance observed.

Then, the fraction $\frac{S_H^2}{S_H^2 + S_E^2}$ is the portion of the observed variance for which differences in heredity are responsible. When this fraction is large, the characteristic is said to be highly hereditary; when it is small, then the characteristic is said to be slightly hereditary or largely environmental.

"The narrowest definition includes as hereditary only the additively genetic variance. The broadest definition of heritability includes as hereditary the differences caused by epistatic and dominance deviations and even by the joint non-linear interactions of heredity and environment." Lush (1940).

Why Estimate Heritability?

The rate of improvement of the future generations of livestock over the present generation that can be brought about through selection depends on the extent to which the variations in the characteristics concerned are transmissible from parent to offspring. Thus, an estimate of heritability of a trait is important and useful to the breeder as it indicates the amount of improvement which will, on the average, be transmitted to the offspring of selected parents, and also, it estimates the probable genetic improvement which is permanent as against the progress through environment. (Lush, 1935).

In addition, estimates of heritability are essential in planning efficient breeding systems. A breeding program successful for characters where variability is largely genetic, may be unsuccessful if most of the variability is environmental (Wright, 1939). While choosing an efficient breeding system, an estimate of heritability of the economically most important traits is the first thing a breeder needs to know after he has decided upon his goal. If the desired traits are highly hereditary the best method will be mass selection (phenotypic selection), paying little attention to pedigree, relatives, progeny test or inbreeding. If heritability is low, but there is not much epistatic variance, then considerable use of pedigree, progeny tests and selection on a family basis would be a better plan.

If there is much of epistatic variance a considerable amount of inbreeding may be practiced in order to create new lines distinct from each other (Lush, 1940).

Finally, a knowledge of heritability is useful in setting up accurate criteria for the selection indexes and also, in determining the relative emphasis due each of several traits when breeding animals are selected (Hazel, 1943).

The purpose of the present study was to estimate the heritability of birth weight and weaning weight of lambs of different breeds raised in the Michigan State College flock.

REVIEW OF LITERATURE

Different Methods of Estimating Heritability

Lush (1940) has given various ways of estimating heritability. All methods of estimating heritability are fundamentally based on the relationship between the individuals. Since related animals are more likely to have received some of the same genes from common ancestors they may be expected to be more alike in their hereditary traits than are the unrelated individuals. The methods rest on measuring how much more closely animals with similar genotypes resemble each other than do the less closely related animals. Relatives such as parents and offspring, full-sibs and half-sibs are most useful for this purpose.

The method used depends on the material one has to work with, that is, whether genetically pure lines are available; the mating systems, such as inbreeding, which may have been practiced; or the nature of the data which has already been collected for other purposes and from which you must make your estimate. If it is a trait which has not previously been investigated several methods or several sources for separate estimates would be desirable in order to have a check on the figure since sampling errors may have quite a large effect on a single estimate that is based on a small volume of data.

Isogenic Line Method

Variation within isogenic lines is wholly environmental. If genetically pure (homozygous) individuals or lines (identical twins if at all there are any in farm animals) are available the method of isogenic lines is a method likely to measure all the genetic variance due to epistasis, dominance and additive effects. The procedure is similar to the intra-class correlation method of comparing the observed variance between isogenic lines with the variance in the population being studied and thus, derive a direct estimate of heritability. Since the relationship between two individuals having the same genotype, or between the identical twins is 100 per cent the calculated ratio of the variance or the correlation coefficient is the estimate of heritability.

The disadvantages of this method are (1) there may be a tendency for the individuals within the isogenic line to receive a more uniform environment than those in the population, as a whole. This might result in an over-estimate of heritability; and (2) in livestock, isogenic lines are usually unavailable. Identical twins are one source of such isogenic lines but they are very rare and hard to identify. In the course of this paper, statistical evidence will be presented to show that identical twins in sheep are rare if they exist at all. It would probably be possible to produce inbred lines homozygous enough to be used but it would take a long time to get them inbred enough to make the method practicable.

Selection Experiment Method

This method may be used if the data were collected from the parents selected for a particular trait for which a heritability estimate is desired. In order to get the estimate, the difference between the average of the offspring of the selected parents and the average of the generation in which the selected parents were born is divided by the difference between the average of the selected parents and the average of the generation in which they were born. The result multiplied by 2 gives the estimate of heritability.

If selection continues for more than one generation, then the replacements must come from within each line itself. In other words, there should be no interchange of individuals between the two lines. A disadvantage of this method is that the individuals may not have been selected strictly for just one character. Further, for adequate control of environment it is usually necessary that selection in the opposite direction shall be practiced in a contemporary control line. This method is not often available to the breeder, since he can rarely afford to select in the undesired direction just to get information on heritability.

Intra-sire Daughter-Dam Correlation or Regression Method

Sewall Wright (1921, 1934) illustrates the principles of this method in his works. It was by the method of path coefficients that Wright proved that the correlation between the parent and offspring was half of the estimate of heritability ($r_{po} = 1/2\ h^2$). Therefore, we multiply the correlation between parent and offspring by 2 to get the measure of heritability. The main basis of the following intra-sire regression or correlation method is the theory of path coefficients.

This is the most frequently used method for most data available in the field of animal husbandry because of certain distinct advantages in estimating heritability by computing the correlation or regression of offspring on dam within groups of offspring by the same sire. This is essentially a parent-offspring resemblance but computing it on an intra-sire basis reduces most of the environmental differences and any peculiarities of the mating system (Lush, 1940). The intra-sire regression dodges most of the environmental correlations because (1) the daughters and mates of a sire are nearly always kept in the same herd and therefore, the effects of heterogeneity of management from herd to herd would be left in the differences between sires, and (2) the offspring of one sire are usually nearly contemporary. Selection of the dams will tend to lower the correlation coefficient but will not bias the regression of offspring on dam. Since some selection of dams is usually practiced in most flocks the regression method is preferable to correlation.

The correlation and regression figures are obtained from the analysis of covariance of the data grouped on an intra-sire basis. These figures are multiplied by 2 to get the estimates of heritability because the relationship between parent and offspring is fifty per cent as a limit. In other words, each parent contributes, on the average, only half of the inheritance to the offspring.

Half-sib Correlation Method

This method of paternal half-sib or maternal half-sib relationship is usually not as accurate as the previous method of parent-offspring relationship. However, when the data are analyzed by the analysis of variance, the intra-class correlation as outlined by Snedecor (1946), gives the required statistic which, on multiplying by 4 gives an estimate of heritability. Here, we multiply the statistic by 4 because the relationship between half-sibs is 25 per cent. Even a small error when multiplied by 4 appears to be large and hence, the method is often inaccurate. In the case of the full-sib correlation method, the statistic is multiplied by 2.

Mid-parent-Offspring Correlation or Regression Method

This method is the same as the parent-offspring relationship method except that in the place of one parent you take the average of both parents. There is not much literature on this method to review 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. By this method, the statistic is multiplied by 1.41 to get the estimate of heritability for the following reason.

The correlation between the offspring and one of its parents is 0.5 for characters which are completely hereditary. Squaring this correlation gives 0.25 as the degree of determination of the offspring by one of its parents, by the theory of path coefficients. Thus, the inheritance of the individual is 25 per cent determined by each parent; and the degree of determination of the offspring by both parents is 50 per cent. The square root of 0.5 gives 0.707 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 1.0/0.707 or 1.41 in place of 1.0/0.5 or 2 used for the correlation between the offspring and only one of its parents (Nelson, 1941).

Of these methods, only the following ones were chosen as the best for the set of data available for this study.

1. Paternal Half-sib Correlation Method,
2. Intra-sire Regression of Daughter on Dam Method, and
3. Intra-sire Daughter-Dam Correlation Method.

Ultimately, to arrive at the best estimate, the weighted average of these three methods, the weighted average of five breeds and the weighted average of three methods and five breeds have been calculated. This will be described in the course of the paper.

Heritability Estimates for Various Traits in Sheep

The review on this topic is well condensed by the table published by Phillips (1943-1947). Hence, the table has been reproduced here. In this study, the traits for which the heritability estimates found are the birth weight and the weaning weight of lambs.

TABLE 1. ESTIMATES OF HERITABILITY FOR VARIOUS CHARACTERS IN SHEEP (After Phillips)

Character	Herita-bility (per-cent)	Method used to determine heritability	Reference
Birth weight	30	Paternal half sib	Chapman and Lush (1932)
Yearling staple length	36	Intrasire regression	Terrill and Hazel (1943)
Yearling weight of clean wool	38 28	Intrasire regreesion	Terrill and Hazel (1943) Terrill and Hazel (1943)
Yearling body weight	40	Intrasire regression	Terrill and Hazel (1943)

TABLE I. (Continued)

Character	Heritability (percent)	Method used to determine heritability	Reference
Yearling body score	12	Intrasire regression	Terrill and Hazel (1943)
Face covering	32	Intrasire regression	Terrill and Hazel (1943)
Neck folds	26	Intrasire regression	Terrill and Hazel (1943)
Body folds	37	Intrasire regression	Terrill and Hazel (1943)
Weaning weight	26.9	Paternal half sib	Hazel and Terrill (1945)
Staple length at weaning	17.0	Average 3 breeds, 2 methods	Hazel and Terrill (1946a)
	33.9	Intrasire regression	Hazel and Terrill (1945)
	30	Weighted average of 2 methods	Hazel and Terrill (1945)
	41	Paternal half sib	Hazel and Terrill (1945)
	38.7	Intrasire regression	Hazel and Terrill (1945)
	40	Weighted average of 2 methods	Hazel and Terrill (1945)
	43.0	Average 3 breeds, 2 methods	Hazel and Terrill (1946a)
Type score at weaning	15.2	Paternal half sib	Hazel and Terrill (1946)
	6.8	Intrasire regression	Hazel and Terrill (1946)
	13.0	Weighted average of 2 methods	Hazel and Terrill (1946)
	7.0	Average 3 breeds, 2 methods	Hazel and Terrill (1946a)

TABLE I. (Continued)

Character	Heritability (percent)	Method used to determine heritability	Reference
Condition score at weaning	2.4	Paternal half sib	Hazel and Terrill (1946)
	13.8	Intrasire regression	Hazel and Terrill (1946)
	4	Weighted average of 2 methods	Hazel and Terrill (1946)
Skin folds	45.6	Average of 4 methods	Jones et al. (1946)
	51.2	Average of 4 methods, within year	Jones et al. (1946)
Neck folds	36.2	Paternal half sib	Terrill and Hazel (1946)
	45.1	Intrasire regression	Terrill and Hazel (1946)
	39	Weighted average of 2 methods	Terrill and Hazel (1946)
	8	Average 3 breeds, 2 methods	Hazel and Terrill (1946a)
Face covering	51.0	Paternal half sib	Terrill and Hazel (1946)
	60.3	Intrasire regression	Terrill and Hazel (1946)
	56	Weighted average of 2 methods	Terrill and Hazel (1946)
	46.0	Average 3 breeds, 2 methods	Hazel and Terrill (1946a)
Number of nipples	14.4	Intrasire correlation	Phillips, et al. (1945)
Number of functional nipples	26	Intrasire correlation	Phillips, et al. (1945)
	22	Intrasire regression	Phillips, et al. (1945)

The variations in the estimates of heritability of various characters are due to sampling errors and environmental differences; and in some of the early studies, the system of mating has not been taken into consideration. Reference to the original paper of Chapman and Lush (1932) showed that 30 per cent of heritability of birth weight of lambs was obtained by the half-sib method from the records of 361 sets of twins born from 1915 to 1930 inclusive. The data collected over a long period of years are likely to contain most of the environmental variations due to changes in feed and management. If the estimates were made on the adjusted data it is probable that the real heritability of birth weight of lambs would be more than 30 per cent.

Hazel and Terrill (1945) estimated that the heritability of weaning weight of lambs was $0.269 \pm .05$ by the half-sib method and $0.339 \pm .08$ by the intra-sire regression method; and $0.30 \pm .04$ by the weighted average of the two methods. He found that about 50 per cent of the variance in weaning weight was due to environmental factors such as sex, age of dam, type of birth, age at weaning and per cent inbreeding for which proper corrections were made before the calculation of heritability.

The review of literature on sex ratios and the environmental factors that affect the birth weight and weaning weight of lambs is discussed in the course of the analysis of data.

ANALYSIS OF DATA

Source of Data

The data used in this study were taken from the Michigan State College flock of sheep, which contained the following breeds: Shropshire, Hampshire, Oxford, Rambouillet, Southdown, Cotswold, and Black Top Delaine. There were also some grades and crossbreds. The records date back to 1930. A total of 4470 lambs of these different breeds and crossbreds was available for the preliminary study of sex ratios. A total of 3484 lambs out of 2305 pregnancies was used for estimating the percentages of different types of births at different ages of ewes. Some of these records were taken from the sheep flock at the Kellogg Farm, a branch station of Michigan State College. Since the numbers in some breeds were extremely small for a thorough and detailed study it was decided to include only those breeds which had reliable and complete informations. For the study of the estimates of heritability of birth weight and weaning weight of lambs, only the records of the five breeds in the Michigan State College flock for the period from 1945 through 1948 were used. The breeds were Hampshire, Oxford, Rambouillet, Shropshire and Southdown.

Flock Survey

A general survey of the flock was made mainly to find out the percentages of different types of births at different ages of ewes in each breed and then in the entire flock. For this, a table was set up for two-year-old ewes and mature ewes each with three types of births, viz., singles, twins and triplets. The records of the yearling ewes were excluded from this study. In other words, the ewe had to start her first lambing when two years old. All ewes over two years of age were grouped under mature ewes. The records which did not contain the date of birth of the ewe were also excluded. An attempt was made to include only those ewes which had at least two lambing records.

Table 2 shows the number of lambs based on the age of ewe and the type of birth in different breeds.

TABLE 2. NUMBER OF BIRTHS ACCORDING TO THE AGE OF EWE AND THE TYPE OF BIRTH IN VARIOUS BREEDS

Breed	Two-year-old Ewes			Mature Ewes		
	Singles	Twins	Triplets	Singles	Twins	Triplets
Hampshire	93	70	2	138	167	14
Oxford	32	33	2	51	49	8
Rambouillet	41	16	0	61	90	8
Shropshire	159	50	2	246	253	12
Southdown	27	25	1	36	57	2
Cotswold	16	14	0	29	26	0
Crossbred	106	37	0	146	182	4
Total	474	245	7	707	824	48

Table 3 gives the percentages of different types of birth at different ages of ewes in the entire flock. Out of a total of 2305 pregnancies in all breeds, about 51 per cent were single births and about 49 per cent multiple births of which 2.4 per cent were triplets. It is interesting to note that the two-year-old ewes drop, on the average, more singles than twins.

Most of the twins and triplets are born to the mature ewes. These results agree with the previous works of Jones (1920). She reported that 4 per cent triplets and 54 per cent twins were born out of a total of 1194 births. The percentage of twin and triplet births increased with the age of the ewe. The largest percentages of single and multiple births were produced respectively by two-year-old and mature ewes.

TABLE 3. PERCENTAGES OF DIFFERENT TYPES OF BIRTHS AT DIFFERENT AGES OF EWES

Type of Birth	Two-year-old Ewes		Mature Ewes		Total	
	Number of Pregnancies	Per cent	Number of Pregnancies	Per cent	Number of Pregnancies	Per cent
Singles	474	65.3	707	44.8	1181	51.2
Twins	245	33.7	824	52.2	1069	46.4
Triplets	7	1.0	48	3.0	55	2.4

Sex Ratios

The sex ratio in a species of animals may be expressed as the percentage of males at birth. For a matter of convenience, the sex ratios could be considered at three different stages in the life history of animals, namely, at conception, birth and maturity. Sex ratios at these stages are usually spoken of as primary, secondary and tertiary, respectively. The ratios reported in this study are based on the number of offspring born (including still births), that is, the secondary sex ratio which will be, hereafter, referred to merely as the sex ratio.

The lambing records of all the available ewes were used without any discrimination for the study of the sex ratio in the flock. The number of ram lambs and ewe lambs is given in table 4.

TABLE 4. NUMBER OF MALES AND FEMALES IN DIFFERENT TYPES OF BIRTHS

Type of Birth	Total Pregnancies	Pregnancies with Sex Recorded	Males	Females
Singles	1687	1676	856	820
Twins	1333	1316	1298	1334
Triplets	58	54	73	89
Total	3078	3046	2227	2243

It is considered that the lambing records are the most reliable source of data for the study of sex ratio and that the data obtained from herd books and breeders' replies do not possess the necessary accuracy for a study of sex ratios and frequency of sex combinations in multiple births. From a total of 4470 lambs, a male percentage of 49.8 ± 0.75* was obtained in this flock. This shows a slightly less number of males, which agrees with previous reports. Henning (1939) reported a male percentage of 48.96 ± 0.14 on a total of 127587 lambs from various sources.

Twin Sex Ratio

Twinning in sheep is of considerable importance to both sheep men and scientists from the point of view of economy and research, respectively. However, the latter is much interested in the identical (monozygotic) twins

*Standard error of the percentage was calculated by using the formula $\sqrt{PQ/N}$. Interpretation of the standard error: Male 49.8% ± 0.75 means that if we repeat the study using a number of samples, we would expect the percentage of male in approximately two-thirds of the results to fall in the range from (49.8 - 0.75) = 49.05% to (49.8 + 0.75) = 50.55%.

in farm animals, which are very rare and difficult to identify if, at all, there are any. The sheep seems to be intermediate between uniparous and multiparous mammals. That it is better adapted to multiple births than the cow is shown by a lower rate of premature births and a lower postnatal mortality as a result of multiparity. In cattle, multiple births are considered as disadvantageous but in mutton breeds of sheep, they are very desirable from an economic point of view (Johansson, 1932).

It is a well-known fact that twinning may occur as the result of either of two distinct processes. (1) Monozygotic twins resulting from the splitting of a single fertilized ovum. Twins of this type are called identical twins, since they have the same genotype. Hence, the variance observed within the sets of identical twins is wholly environmental. (2) Dizygotic twins or fraternal twins result from the fertilization of two ova; and they are the same as ordinary full sibs in genetic variability.

Lush (1937) is of the opinion that the diagnosis of identical (monozygotic) twins rests on the similarity in a long series of characteristics, each of which is determined to a considerable extent by heredity. Fraternal (dizygotic) twins might, of course, happen to be as like each other as identicals in one or a few characteristics but as the number of characteristics is increased it becomes more and more improbable that fraternal twins would happen to be alike in all the genes involved, whereas that is to be expected of twins arising from a single fertilized egg. Kronacher (1936) tries to show how one can be sure that a particular pair of twins are in fact identical and not fraternal. The methods that he used to identify identical twins in cattle were the similarity quotients, the post-mortem measurements of stature, and the analysis of blood and hormone characteristics.

An attempt has been made in this study to present statistical evidence to show that, in sheep, we are dealing almost exclusively with fraternal twins. A study of the sex combinations in twins may be used to estimate the frequency of identical twins. Assuming the sex ratio to be equal, the ratios of the three possible sex combinations would be approximately 1 ♂♂ : 2 ♂♀ : 1 ♀♀ , derived from the binomial distribution formula $(a + b)^2$ where a is the proportion of males and b, the proportion of females. One possible cause of deviation from this ratio would be the frequent occurrence of identical twins which would increase the proportion of like-sexed twins.

Twin sex combinations were tabulated for different breeds separately. Despite the small sample numbers in most breeds it is interesting to note that the twin sex combination ratio 1 : 2 : 1 consistently holds true in each case. Table 5 shows the twin sex ratios in various breeds.

TABLE 5. TWIN SEX RATIOS IN DIFFERENT BREEDS OF SHEEP

Breed	Twin Combinations		
	Both Rams ♂♂	Ram and Ewe ♂♀	Both Ewes ♀♀
Black Top Delaine	5	12	6
Cotswold	10	20	9
Southdown	18	41	23
Oxford	23	39	18
Rambouillet	19	60	23
Hampshire	81	145	69
Shropshire	97	239	119
Crossbreds and Grades	55	126	59
Total	308	682	326

Table 6 shows the observed numbers of twins of each sex combination and the corresponding numbers expected on the basis (1) of the sex ratio among these twins, (2) of the sex ratio in this whole flock and (3) of assumed equal sex ratio in sheep. The sex ratio from 1316 twins is 49.3 ± 0.97. The expected numbers of twins were calculated as follows:

Let a = % of male

(1) Sex ratio from twins = 49.3 = a

(2) Sex ratio from the flock = 49.8 = a

(3) Assumed equal sex ratio = 50.0 = a

Value of a	♂♂ a^2	♂♀ $2a(1-a)$	♀♀ $(1-a)^2$
.493	.243	.50	.257
.498	.248	.50	.252
.500	.250	.50	.250

Multiply the ratios in the table by the total number of twins (1316) to get the expected number in each class.

TABLE 6. ACTUAL AND EXPECTED NUMBERS OF TWINS OF DIFFERENT SEX COMBINATIONS

Type of Twin	Observed Number	Expected Numbers		
		From Sex Ratio in Twins	From Sex Ratio in Flock	From Assumed Equal Sex Ratio
Both Rams	308	320	326	329
Ram and Ewe	682	658	658	658
Both Ewes	326	338	332	329

Since the proportion of the unlike-sexed twins is in excess it is concluded that identical twins in sheep must be a rare and odd phenomenon. This, however, does not rule out the possibility of identical twins in sheep since Henning (1937) produced a strong evidence in favor of amonovular origin of two fetuses by finding a single corpus luteum, where the fetuses were of like sex and they were very similar in other respects. The twin sex ratio in this flock was 308 ♂♂: 682♂♀ : 326♀♀ . Clark (1931) reported a ratio of 129♂♂: 273 ♂♀ : 121 ♀♀. Chapman and Lush (1932) observed a

ratio of 87 ♂♂: 184 ♂♀: 90 ♀♀ . Johansson (1932) observed 1164 ♂♂: 2685 ♂♀ : 1239 ♀♀ .

BIRTH WEIGHT AND CONVERSION FACTORS

Birth Weight

The growth of lambs may be said to consist of an intra-uterine phase and an extra-uterine phase. The former could be measured by the birth weight and the latter, by the weaning weight. The data on birth weight included those lambs which were born alive as well as dead; but the dead ones included only the still births carried full time and not the premature births. The birth weights were taken within about 24 hours after parturition. It is hoped that the bias in the weight of the wet lamb immediately after birth will compensate for the dry lamb weighed after a few hours of growth in vitro. The mean and standard deviation of the birth weight of the five breeds are given in table 7 as a preliminary routine study.

TABLE 7. MEAN AND STANDARD DEVIATION OF THE UNCORRECTED BIRTH WEIGHT OF LAMBS OF FIVE BREEDS (1945-1948)

Breed	Number of Lambs	Mean Weight ± Standard Error	Standard Deviation ± Standard Error
Hampshire	137	9.38 ± 0.19	2.24 ± 0.14
Oxford	89	9.01 ± 0.26	2.44 ± 0.18
Rambouillet	51	8.69 ± 0.19	1.38 ± 0.14
Shropshire	170	7.61 ± 0.12	1.61 ± 0.09
Southdown	51	7.52 ± 0.20	1.46 ± 0.14

The average standard deviation of the birth weights for the combination of all the breeds was 2.09 pounds, and it will be used later for estimating the expected increase in birth weight per generation, with certain intensities of selection. The values from table 7 were taken for the following calculation of the standard deviation.

Standard deviation of the combined sets of data for the uncorrected birth weight:

$$S_x^2 = \frac{Sn_i(S_i^2 + \overline{X}_i^2)}{N} - \left[\frac{(Sn_i X_i)}{N}\right]^2$$

$$= 1/498\Big[137(2.24^2 + 9.38^2) + 89(2.44^2 + 9.01^2) + 51(1.38^2 + 8.69^2) + 170(1.61^2 + 7.61^2) + 51(1.46^2 + 7.52^2)\Big] - (4207.36/498)^2$$

$$= 4.372$$

$$S_x = \sqrt{4.372} = 2.09$$

Conversion Factor

The question of conversion factor arose because certain environmental factors conceal the actual genetic merit of the individuals, thereby confusing the breeder in his selection of animals. For example, two animals which have the same genotype or equal breeding value may differ considerably in their phenotype because of the effect of the differences in age of dam, type of birth and sex. In order to eliminate or control some of these environmental variations, an adjustment factor was deemed desirable, which would place all animals on a comparable basis. The correction factor applies to the group as a whole and not to the individuals within the heterogeneous group. Sex, age of dam and type of birth were the factors adjusted for in this study of birth weight of lambs. All the years were thrown together as there was no significant year difference.

The birth weights of lambs were grouped under two-year-old ewes and mature ewes which, in turn, were sub-classed into singles and multiples, males and females since the object was to bring the weight of all lambs to an equivalent basis of ewe lamb, single birth and mature dam. On the average the males outweighed the females consistently in each breed. Lambs born as singles were heavier than the individuals in twins and triplets. Mature ewes dropped heavier lambs than the two-year-old ewes. These differences were observed in all breeds, but there was no significant difference in the average weights from year to year. In order to get a common conversion factor for all the breeds it was decided to combine the average differences and adopt the multiplicative method instead of the additive method of correction. By the multiplicative method, the heavy breeds and the light breeds are equally adjusted in proportion to the size of the lamb.

The combined average birth weight of ram lambs was 0.5 lb. more than that of ewe lambs; the multiple births weighed 1.62 lbs. less than the singles, and the lambs from mature ewes averaged 0.53 lb. more than those of the two-year-old ewes. The conversion factors for the multiplicative method were obtained by figuring the average differences as follows:

<u>Sex</u>

The average birth weight of all female lambs from mature dams divided by that of all male lambs from mature dams is 8.63/9.23 = 0.935. The average birth weight of all female lambs from two-year-old dams divided by that of all male lambs from two-year-old dams is 8.19/8.55 = 0.959. The average of these two values is 0.947, which is the conversion factor for sex.

Age of Dam

The average birth weight of all single lambs from the mature dams divided by that of all singles from the two-year-old dams is 10.231/9.391 = 1.089. The average birth weight of all twins and triplets from the mature dams divided by that of all multiples from the two-year-old dams is 8.474/7.596 = 1.115. The average of these two values is 1.102 which is the conversion factor for age of dam.

Type of Birth

The average birth weight of all singles from two-year-old dams divided by that of all multiples from two-year-old dams is 9.391/7.596 = 1.236. The average birth weight of all singles from mature dams divided by that of all multiples from mature dams is 10.231/8.474 = 1.207. The average of these two values is 1.222, which is the conversion factor for type of birth.

Conversion for Sex = -5.3 per cent

Conversion for Age of Dam = 10.2 per cent

Conversion for Type of Birth = 22.2 per cent

These percentages of adjustment for the environmental differences in birth weight were consistent in all the breeds, and were used for adjusting the data. For example, the birth weights of males were reduced by 5.3 per cent to bring them to the female basis. A ram lamb weighing 10 lbs. would be converted to 10 x 0.947 = 9.47 lbs. to place it on a comparable basis with ewe lambs. Likewise, lambs from multiple births will be increased by 22.2 per cent, that is, a twin lamb weighing 10 lbs. will be raised to 10 x 1.222 = 12.22 lbs. to bring it to a single lamb basis. The weight of lambs from two-year-old ewes will be increased by 10.2 per cent. A single lamb from a two-year-old ewe, weighing 10 lbs. will be corrected to 10 x 1.102 = 11.02 lbs. to bring it to the mature ewe basis. Thus, a male twin lamb from a two-year-old ewe, weighing 10 lbs. was adjusted to 10 x 1.271 = 12.71 lbs. on a female, single and mature ewe basis.

CALCULATION OF HERITABILITY OF BIRTH WEIGHT

The calculations for the half-sib method, and the intra-sire regression and correlation methods were carried out from the values in the tables of analysis of covariance. For this, the corrected birth weight of dams was treated as one variable, X, and that of their offspring as the other variable, Y. The birth weight of the dam which had more than one offspring was repeated for each offspring for the analysis. Thus, some of the X-variables were repeated. The weights were grouped on an intra-sire basis. Then, the usual analysis of covariance was run between the X- and Y-variables as outlined by Snedecor (1946). Their sums, sums of squares and products are given in table 8a. For a detailed explanation of the procedures, one breed, namely, Oxford, was chosen at random. The completed analysis of covariance for Oxfords is given in table 8b.

TABLE 8a. PRELIMINARY DATA FOR THE STATISTICS OF BIRTH WEIGHT OF OXFORDS

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	34	320.6	3169.64	327.6	3453.80	3198.57
II	26	277.3	3010.83	276.6	3089.98	2925.45
III	27	286.1	3118.25	300.3	3432.53	3209.64
IV	4	38.1	363.05	46.1	537.23	439.87
Total	91	922.1	9661.77	950.6	10513.54	9773.53

Calculation Procedures:

Correction for X = $(922.1)^2/91$ = 9343.61

Correction for Y = $(950.6)^2/91$ = 9930.11

Correction for XY = (922.1)(950.6)/91 = 9632.40

Total

Sum of Squares for X = 9661.77 - correction = 318.16

Sum of Squares for Y = 10513.54 - correction = 583.43

Sum of Products for XY = 9773.53 - correction = 141.13

Between Sires

Sum of Squares for X = $(320.6)^2/34 + \text{---} + (38.1)^2/4$ - correction = 31.47

Sum of Squares for Y = $(327.6)^2/34 + \text{---} + (46.1)^2/4$ - correction = 40.31

Sum of Products for XY = (320.6)(327.6)/34 + --- + (38.1)(46.1)/4 - correction

= 27.88

TABLE 8b. ANALYSIS OF COVARIANCE OF BIRTH WEIGHT OF DAMS AND THEIR OFFSPRING FOR OXFORDS

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	90	318.16	141.13	583.43
Between Sires	3	31.47	27.88	40.31
Within Sires (or Error)	87	286.69	113.25	543.12

TABLE 8c. ANALYSIS OF VARIANCE OF BIRTH WEIGHT OF DAMS (X) IN OXFORDS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	90	318.16		
Between Sires	3	31.47	10.49	3.19*
Within Sires (or Error)	87	286.69	3.29	

* Signifies probability of chance occurrence at less than 5% level.

TABLE 8d. ANALYSIS OF VARIANCE OF BIRTH WEIGHT OF OFFSPRING (Y) IN OXFORDS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	90	583.43		
Between Sires	3	40.31	13.44	2.15
Within Sires (or Error)	87	543.12	6.24	

From the data of the analysis of covariance table 8b, a preliminary analysis of variance of the birth weight of dams (X) was made as shown in table 8c. The F-value between sires was significant at 5 per cent level indicating that the average birth weight of one group of dams was significantly different from that of the other groups of dams mated to different sires. The calculation of correlations and regressions on an intra-sire basis which minimizes the variance due to different groups of dams is thus justified. Likewise, the analysis of variance of the birth weight of offspring (Y) was made as shown in table 8d. Here, the F-test did not show any significant difference in the average birth weights of different groups of offspring sired by different rams, indicating that there was no significant year to year difference in the average birth weights of different groups of offspring.

TABLE 8e. CORRELATION AND REGRESSION DATA FOR THE FOUR OXFORD SIRES (B.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	33	146.57	109.50	297.28	0.5246	0.7470
II	25	53.32	-24.59	147.38	-0.2774	-0.4611
III	26	86.65	27.57	92.53	0.3081	0.3181
IV	3	0.15	0.77	5.93	0.8164	5.1333
Total	87	286.69	113.25	543.12	0.2870	0.3950

The correlation and regression data were calculated separately for each sire group and entered in table 8e. The notable features of this table are: (1) the totals in the three columns Sx^2, Sxy and Sy^2 are the same as the values for the within sires term in the analysis of covariance table 8b. This checks the calculations in both tables. Also, the within sires regression of table 8b is an average of the four sire group regressions of table 8e. The values of either of these tables were used for the following calculation of the required statistic.

$$\text{Correlation Coefficient} = r = Sxy/\sqrt{Sx^2 \cdot Sy^2} = 113.25/\sqrt{(286.69)(543.12)} = 0.2870$$

Standard error of the correlation coefficient was calculated by using the formula: $S_r = 1-r^2/\sqrt{n-2} = 1 - (0.287)^2/\sqrt{91-2} = 0.9176/\sqrt{89} = 0.0972$

The heritability estimate is obtained by multiplying this correlation coefficient by 2, which is equal to 2 x 0.2870 = 0.5740. The standard error of heritability is, likewise, obtained by multiplying the standard error of correlation coefficient by 2, which is equal to 2 x 0.0972 = 0.1944. Thus, the heritability of birth weight of Oxford lambs by the intra-sire correlation method is 0.5740 ± 0.1944.

Regression of offspring on dam is the required regression coefficient.

Regression Coefficient = b = Sxy/Sx^2 = 113.25/286.69 = 0.3950

Standard error of the regression coefficient was calculated as follows:

$$S_b^2 = \frac{\text{S.S. of Standard error of estimate of the error term}/n-2}{\text{Sum of squares of x of the error term}}$$

$$= \frac{\frac{Sy^2 - (Sxy)^2/Sx^2}{n-2}}{Sx^2} \quad \frac{\frac{543.12 - (113.25)^2/286.69}{91 - 2}}{286.69} = \frac{5.599}{286.69} = 0.01953$$

$$S_b = \sqrt{0.01953} = 0.1397$$

The above regression coefficient when multiplied by 2 gives the estimate of heritability, which is equal to 2 x 0.395 = 0.790. Similarly, the standard error of the regression was multiplied by 2 to get the standard error of heritability, which is 2 x 0.1397 = 0.2794. Thus, the heritability of birth weight of Oxford lambs by the intra-sire regression method is 0.790 ± 0.2794.

Half-sib Method

The intraclass correlation was calculated from the data in table 8d, Analysis of Variance of Birth Weight of Offspring (Y). Intraclass correlation $= r_1 = S_m^2/(S^2 + S_m^2)$ where S^2 = the mean square of the error term.

$$S_m^2 = \frac{\text{Mean square between sires - Mean square of error term}}{\text{Average number in each sire group}}$$

First, calculate the average number as follows:

$K_o = (1/\ n-1)(Sk\ -\ Sk^2/Sk)$ where n = number of sire groups, and k = number in each sire group.

$K_o = (1/\ 4-1)(91\ -\ 34^2+26^2+27^2+4^2/91) = 20.89$

Now, substituting in the intraclass correlation formula, we get the half-sib correlation: $S^2 = 6.24$

$$S_m^2 = \frac{13.44-6.24}{20.89} = 0.3447$$

$r_1 = 0.3447/(6.24+0.3447) = 0.0523$

Standard error of this correlation was calculated by the previous formula as shown below:

$S_{r_1} = (1-r_1{}^2)/\sqrt{n-2} = (1-0.523^2)/\sqrt{91-2} = 0.9973/9.434 = 0.1057$

The half-sib correlation 0.0523 was multiplied by 4 to get the estimate of heritability, which is equal to 0.2092. Likewise, the standard error of heritability was obtained by multiplying the standard error of half-sib correlation by 4, which was equal to 4 x 0.1057 = 0.4228. Thus, the heritability of birth weight of Oxford lambs by the paternal half-sib correlation method is 0.2092 ± 0.4228.

The calculations for the other four breeds were identically the same as described above for Oxford. Hence, only the data of preliminary calculations, the analysis of covariance and the correlation and regression values are given in the succeeding tables. Tables 9a, b and c pertain to Hampshire; tables 10a, b and c to Rambouillet; tables 11a, b and c to Shropshire; and tables 12a, b and c to Southdown.

TABLE 9a. PRELIMINARY DATA FOR THE STATISTICS OF BIRTH WEIGHT OF HAMPSHIRE

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	60	635.1	6937.73	644.7	7346.55	6930.66
II	9	101.8	1159.30	101.2	1213.06	1160.35
III	40	449.8	5141.62	448.2	5177.10	5068.59
IV	6	61.9	644.31	60.6	619.68	623.08
V	11	118.6	1315.30	113.1	1186.71	1239.39
VI	8	93.1	1104.69	90.0	1019.32	1047.62
VII	3	32.6	357.66	34.4	396.66	371.09
Total	137	1492.9	16660.61	1492.2	16959.08	16440.18

TABLE 9b. ANALYSIS OF COVARIANCE OF BIRTH WEIGHT OF DAMS AND THEIR OFFSPRING OF HAMPSHIRE

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	136	392.36	179.56	706.08
Between Sires	6	18.77	14.00	16.20
Within Sires	130	373.59	165.56	689.88

TABLE 9c. CORRELATION AND REGRESSION DATA FOR THE SEVEN HAMPSHIRE SIRES (B.Wt.)

Sires	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	59	215.20	105.91	419.25	0.3526	0.4921
II	8	7.83	15.67	75.12	0.6461	2.0012
III	39	83.62	28.59	155.02	0.2511	0.3419
IV	5	5.71	-2.11	7.62	-0.3199	-0.3695
V	10	36.58	19.97	23.84	0.6763	0.5459
VI	7	21.24	0.25	6.82	0.0208	0.0112
VII	2	3.41	-2.72	2.21	-0.9905	-0.7976
Total	130	373.59	165.56	689.88	0.3261	0.4431

TABLE 10a. PRELIMINARY DATA FOR THE STATISTICS OF BIRTH WEIGHT OF RAMBOUILLET

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	32	331.7	3499.07	320.3	3266.87	3345.96
II	22	226.4	2359.82	254.2	2983.44	2619.10
Total	54	558.1	5858.89	574.5	6250.31	5965.06

TABLE 10b. ANALYSIS OF COVARIANCE OF BIRTH WEIGHT OF DAMS AND THEIR OFFSPRING OF RAMBOUILLET

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	53	90.82	27.50	138.27
Between Sires	1	0.08	-1.50	31.12
Within Sires	52	90.74	29.00	107.15

TABLE 10c. CORRELATION AND REGRESSION DATA FOR THE TWO RAMBOUILLET SIRES (B.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	31	60.79	25.85	60.87	0.4250	0.4252
II	21	29.96	3.15	46.28	0.0846	0.1051
Total	52	90.75	29.00	107.15	0.2941	0.3196

TABLE 11a. PRELIMINARY DATA FOR THE STATISTICS OF BIRTH WEIGHT OF SHROPSHIRE

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	30	271.6	2559.48	274.1	2590.59	2493.98
II	46	408.3	3682.63	423.2	4029.58	3779.85
III	48	428.8	4004.90	429.2	4047.24	3924.16
IV	11	95.0	841.08	106.0	1031.08	914.15
V	11	107.9	1081.51	100.0	956.58	1003.92
VI	5	41.9	360.35	42.8	374.02	365.73
VII	20	189.6	1829.24	188.9	1834.65	1782.35
Total	171	1543.1	14359.19	1564.2	14863.74	14264.14

TABLE 11b. ANALYSIS OF COVARIANCE OF BIRTH WEIGHT OF DAMS AND THEIR OFFSPRING OF SHROPSHIRE

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	170	434.29	148.84	555.43
Between Sires	6	16.07	2.56	8.32
Within Sires	164	418.22	146.28	547.11

TABLE 11c. CORRELATION AND REGRESSION DATA FOR THE SEVEN SHROPSHIRE SIRES (B.Wt.)

Sires	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	29	100.60	12.46	86.23	0.1337	0.1238
II	45	58.53	23.49	136.14	0.2631	0.4013
III	47	174.29	89.97	209.48	0.4708	0.5162
IV	10	20.63	-1.30	9.63	-0.0923	-0.0630
V	10	23.11	23.01	47.49	0.6947	0.9956
VI	4	9.23	7.07	7.65	0.8414	0.7659
VII	19	31.83	-8.42	50.49	-0.2100	-0.2645
Total	164	418.22	146.28	547.11	0.3058	0.3497

TABLE 12a. PRELIMINARY DATA FOR THE STATISTICS OF BIRTH WEIGHT OF SOUTHDOWN

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	16	142.8	1313.28	137.7	1222.93	1249.44
II	11	105.4	1019.90	97.9	876.59	941.91
III	9	75.4	679.84	73.7	618.45	640.12
IV	7	58.1	496.45	55.8	454.48	462.90
V	6	46.9	383.81	53.5	481.47	410.98
VI	2	12.2	74.42	18.6	172.98	113.46
Total	51	440.8	3967.70	437.2	3826.90	3818.81

TABLE 12b. ANALYSIS OF COVARIANCE OF BIRTH WEIGHT OF DAMS AND THEIR OFFSPRING OF SOUTHDOWN

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	50	157.81	40.03	78.98
Between Sires	5	29.45	0.48	6.81
Within Sires	45	128.36	39.55	72.17

TABLE 12c. CORRELATION AND REGRESSION DATA FOR THE SIX SOUTHDOWN SIRES (B.Wt.)

Sires	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	15	38.79	20.47	37.85	0.5343	0.5277
II	10	9.98	3.85	5.28	0.5304	0.3857
III	8	48.16	22.68	14.93	0.8458	0.4709
IV	6	14.22	-0.24	9.68	-0.0205	-0.0169
V	5	17.21	-7.21	4.43	-0.8257	-0.4189
VI	1	0	0	0	0	0
Total	45	128.36	39.55	72.17	0.4109	0.3081

To summarize the results of the various breeds it was thought pertinent to give the data of the various statistics in a separate table. Table 13 gives the distribution of records by breeds, which enables the reader to find at a glance, the number of sire groups and the number of pairs of dam-offspring used in the calculation of heritability of birth weight and weaning weight. Tables 14 and 15 give the required estimates of heritability by breeds and methods separately.

TABLE 13. DISTRIBUTION OF RECORDS BY BREEDS (1945-1948).

Breed	No. of pairs of Dam-offspring for Birth Weight	No. of Sires	No. of pairs of Dam-offspring for Weaning Weight
Hampshire	137	7	85
Oxford	91	4	51
Rambouillet	54	2	36
Shropshire	171	7	137
Southdown	51	6	39
Total	504	26	348

TABLE 14. CORRELATIONS, REGRESSION AND STANDARD ERRORS OF THE CORRECTED BIRTH WEIGHT OF LAMBS

Breed	Paternal half-sib correlation		Intra-sire regression		Intra-sire correlation	
	r_1	S_{r_1}	b	S_b	r	S_r
Hampshire	-0.0314	0.0859	0.4431	0.1105	0.3261	0.0769
Oxford	.0523	.1057	.3950	.1397	.2870	.0972
Rambouillet	.3509	.1216	.3196	.1439	.2941	.1266
Shropshire	-.0264	.0768	.3497	.0837	.3058	.0697
Southdown	-.0185	.1428	.3081	.0976	.4109	.1187

TABLE 15. ESTIMATES OF HERITABILITY AND STANDARD ERRORS FOR THE CORRECTED BIRTH WEIGHT

Breed	Paternal half-sib method		Intra-sire regression method		Intra-sire correlation method	
	Herit-ability	Standard error	Herit-ability	Standard error	Herit-ability	Standard error
Hampshire	-.1256	.3436	.8862	.2210	.6522	.1538
Oxford	.2092	.4228	.7900	.2794	.5740	.1944
Rambouillet	1.4036	.4864	.6392	.2878	.5882	.2532
Shropshire	-.1056	.3072	.6994	.1674	.6116	.1394
Southdown	-.0740	.5712	.6162	.1952	.8218	.2374

In view of the large sampling errors, the estimates of heritability calculated for each breed and by each of the three methods may not be as accurate an estimate as if they were all averaged. 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 15 by the reciprocal of its squared standard error, as outlined by Hazel (1945). Although this method of weighting has some errors 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:

$$\text{Weighted Average Heritability} = \frac{(h_1/S^2_{h_1}) + (h_2/S^2_{h_2}) + \text{---} + (hn/S^2_{h_n})}{(1/S^2_{h_1}) + (1/S^2_{h_2}) + \text{---} + (1/S^2_{h_n})}$$

where h_1 --- hn = heritability estimates, and S_{h_1} --- S_{h_n} = standard errors of heritability.

The weighted average of the standard errors of heritability was calculated by the following formula:

$$\text{Weighted Average Error of Heritability} = \sqrt{\frac{1}{(1/S^2_{h_1}) + (1/S^2_{h_2}) + \cdots + (1/S^2_{hn})}}$$

where S_{h_1} --- S_{hn} are the individual standard errors of heritability.

TABLE 16. SQUARED STANDARD ERRORS AND THEIR RECIPROCALS OF THE HERITABILITY OF BIRTH WEIGHT

Breed	Half-sib method		Intra-sire regression method		Intra-sire correlation method		Reciprocal sum of 3 methods
	$S^2_{h_1}$	$1/S^2_{h_1}$	$S^2_{h_2}$	$1/S^2_{h_2}$	$S^2_{h_3}$	$1/S^2_{h_3}$	$S(1/S^2_h)$
Hampshire	.1181	8.5	.0488	20.5	.0237	42.2	71.2
Oxford	.1788	5.6	.0781	12.8	.0378	26.5	44.9
Rambouillet	.2366	4.2	.0828	12.1	.0641	15.6	31.9
Shropshire	.0944	10.6	.0280	35.7	.0194	51.5	97.8
Southdown	.3263	3.1	.0381	26.1	.0564	17.7	46.9
Reciprocal sum of 5 breeds		32.0		107.2		153.5	292.7

In order to facilitate the calculations, the squared standard errors and their reciprocals for the individual estimates of heritability found in table 15 were first calculated and entered in table 16. Then, substituting in the formula, the corresponding values from tables 15 and 16, the weighted average of three methods, the weighted average of five breeds, and, in turn, the weighted average of 3 methods and 5 breeds were obtained. These results are summarized in tables 17a, b and c. As a result of this method of weighting, the best estimate of heritability of birth weight of lambs in this flock was found to be 0.61 ± .06.

TABLE 17a. WEIGHTED AVERAGE OF THREE METHODS (Birth Weight)

Breed	Heritability	Standard error
Hampshire	0.6267	0.1185
Oxford	.5901	.1492
Rambouillet	.7149	.1771
Shropshire	.5659	.1011
Southdown	.6482	.1460

TABLE 17b. WEIGHTED AVERAGE OF FIVE BREEDS

Method	Heritability	Standard error
Paternal half-sib correlation	0.1453	0.1768
Intra-sire regression	.7189	.0966
Intra-sire correlation	.6381	.0807

TABLE 17c. WEIGHTED AVERAGE OF 3 METHODS AND 5 BREEDS

Trait	Heritability	Standard error
Birth Weight	0.6138	0.0584

WEANING WEIGHT AND INFLUENCE OF ENVIRONMENTAL FACTORS

Weaning Weight is important in lambs because it is soon after weaning that ewe lambs are selected to add to the breeding flock, and the remainder sent to market. Weaning weight is one of the measures of the producing ability of ewes. The weaning weights reported in this study are 120-day weights.

All lambs were weighed when they were 120 $\pm$ 4 days of age. A small correction was made for those lambs which were weighed a few days before or after the exact 120th day. Thus, the weights were all brought to a standard for comparison. The average weaning weights and their standard deviations for the five breeds were calculated as a preliminary routine study and entered in table 18. The average standard deviation for the five breeds combined was found to be 14.5 lbs. This will be used, later, for estimating the expected gain per generation in weaning weight with certain intensities of selection.

TABLE 18. MEAN AND STANDARD DEVIATION OF THE UNCORRECTED WEANING WEIGHT OF LAMBS OF FIVE BREEDS (1945-1948)

Breed	Number of Lambs	Mean Weight $\pm$ Standard error	Standard Deviation $\pm$ Standard error
Hampshire	95	70.08 $\pm$ 1.52	14.79 $\pm$ 1.07
Oxford	59	67.24 $\pm$ 2.31	17.76 $\pm$ 1.63
Rambouillet	50	62.10 $\pm$ 1.59	11.22 $\pm$ 1.12
Shropshire	175	59.14 $\pm$ 0.86	11.39 $\pm$ 0.61
Southdown	39	50.18 $\pm$ 1.78	11.11 $\pm$ 1.26

From the values in table 18, the standard deviation for all the breeds combined was calculated as follows:

$$Sx^2 = Sni(S_i^2 + \bar{X}_i^2)/N - (Sni\bar{X}i/N)^2$$

$$= 1/418\left[95(14.79^2+70.08^2) + 59(17.76^2+67.24^2) + 50(11.22^2+62.10^2) + 175(11.39^2+59.14^2) + 39(11.11^2+50.18^2)\right] - (26036.28/418)^2$$

$$= 210.2155$$

$$S_X = \sqrt{210.2155} = 14.50$$

Influence of Various Factors on Weaning Weight

An adjustment for environmental factors which influenced the weaning weight was found necessary because of the differences in weight due to sex, age of dam, type of birth and type of rearing. The early works of Hazel and Terrill (1945a, 1946b); and Terrill et al. (1947) indicated that generally ram lambs, single lambs and lambs from mature dams were superior in growth rate to ewe lambs, twin lambs and lambs from two-year-old dams, respectively. Hazel and Terrill (1945a) found that about 50 per cent of the total variation in weaning weight was due to the environmental factors. They reported that ram lambs were 8.3 lbs. heavier than ewe lambs; single lambs were 9.2 lbs. heavier than twin lambs; and the lambs from mature ewes weighed 6.1 lbs. more than the lambs from two-year-old ewes. A difference of 2.5 lbs. between singles and twins raised singly was observed in favor of singles.

In this study, the weaning weights were grouped according to the sex, age of dam, type of birth and type of rearing. The type of rearing was of three kinds: (1) singles, (2) twins raised together, and (3) twins raised singly. The twins raised singly were expected to gain more than the twins raised together. If the two individuals of a twin lived more than 30 days on the mother's milk they were considered as a twin raised together. If one of them was dead or separated then, the other lamb was considered as a twin raised singly.

There was no significant difference in the average weaning weight of lambs from one year to another. Hence, the data for all the years were analyzed together. In each breed, the ram lambs outweighed the ewe lambs. Twins were lighter than the singles; and the lambs from mature dams averaged more than those of the two-year-old dams. The average of all the five breeds combined showed that ram lambs weighed 3.8 lbs. more than ewe lambs; single lambs weighed 6.7 lbs. more than twin lambs; and lambs from mature dams were heavier by 2.8 lbs. than lambs from two-year-old dams. There was no significant difference in the average weaning weight of single lambs and twins raised singly in this flock. Therefore, the singles and twins raised singly were combined for the study.

The conversion factors were found by the straight average method for the five breeds combined; and the multiplicative method was adopted to convert the weaning weight to the equivalent basis of ram lamb, mature dam and single lamb.

The average weaning weight of all the singles and all the twins raised singly divided by that of all the twins raised together is 66.72/57.13 = 1.168. The conversion factor for the type of rearing is 16.8 per cent. The average weaning weight all the males divided by that of all the females is 64.17/60.35 = 1.063. The conversion factor for sex is 6.3 per cent. The average weaning weight of lambs from all mature dams divided by that of lambs from two-year-old dams is 62.89/60.13 = 1.046. The conversion factor for the age of dam is 4.6 per cent. These conversion factors were used to adjust for the environmental variations in weaning weight due to these three factors. For example, the weaning weight say, 70 pounds of a twin ewe lamb born to a two-year-old dam and raised together will be adjusted to 70 x 1.277 = 89.39 lbs. to bring it to the equivalent basis of single, male lamb and mature dam.

CALCULATION OF HERITABILITY OF WEANING WEIGHT

The method of calculation was identically the same as for the calculation of heritability of birth weight. Hence, the repetition of the same statements has been avoided as far as possible. The adjusted weaning weights were grouped on an intra-sire basis. The weaning weight of dam was treated as one variable - X, and that of offspring as the other variable - Y. Some of the X-variables were repeated and the analysis of covariance was made between X and Y. As an example, Rambouillet was chosen at random to describe the procedures in detail.

TABLE 19a. PRELIMINARY DATA FOR THE STATISTICS OF WEANING WEIGHT OF RAMBOUILLET

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	22	1566.5	113045.09	1669.6	129175.02	119240.07
II	14	1044.3	78740.35	958.3	66281.37	71545.07
Total	36	2610.8	191785.44	2627.9	195456.39	190785.14

Calculation Procedures from Table 19a

Correction for X = $(2610.8)^2/36$ = 189341.01

Correction for Y = $(2627.9)^2/36$ = 191829.40

Correction for XY = (2610.8)(2627.9) / 36 = 190581.14

Total

Sum of Squares for X = 191785.44 - correction = 2444.43

Sum of Squares for Y = 195456.39 - correction = 3626.99

Sum of Products for XY = 190785.14 - correction = 204.00

<u>Between Sires</u>

Sum of Squares for X = $(1566.5)^2/22 + (1044.3)^2/14$ - correction = 98.23

Sum of Squares for Y = $(1669.6)^2/22 + (958.3)^2/14$ - correction = 473.69

Sum of Products for XY = (1566.5)(1669.6) / 22 + (1044.3)(958.3) / 14

- correction = -215.71

TABLE 19b. ANALYSIS OF COVARIANCE OF WEANING WEIGHT OF DAMS AND THEIR OFFSPRING OF RAMBOUILLET

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	35	2444.43	204.00	3626.99
Between Sires	1	98.23	-215.71	473.69
Within Sires (or error)	34	2346.20	419.71	3153.30

TABLE 19c. ANALYSIS OF VARIANCE OF WEANING WEIGHT OF DAMS (X) IN RAMBOUILLET

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	35	2444.43		
Between Sires	1	98.23	98.23	1.42
Within Sires (or Error)	34	2346.20	69.00	

TABLE 19d. ANALYSIS OF VARIANCE OF WEANING WEIGHT OF OFFSPRING (Y) IN RAMBOUILLET

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	35	3626.99		
Between Sires	1	473.69	473.69	5.1*
Within Sires (or Error)	34	3153.30	92.74	

* Signifies probability of chance occurrence at less than 5% level.

TABLE 19e. CORRELATION AND REGRESSION DATA FOR THE TWO RAMBOUILLET SIRES (W.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	21	1503.17	356.97	2467.56	0.1853	0.2374
II	13	843.03	62.74	685.74	0.0825	0.0744
Total	34	2346.20	419.71	3153.30	0.1543	0.1788

Correlation coefficient = $r = Sxy/\sqrt{Sx^2 \cdot Sy^2} = 419.71/\sqrt{(2346.2)(3153.30)}$

$= 0.1543$

Standard error of the correlation coefficient was calculated by using the formula: $S_r = (1-r^2)/\sqrt{n-2} = (1-0.1543^2)/\sqrt{36-2} = 0.9762/\sqrt{34} = 0.1674$

The heritability estimate is obtained by multiplying this correlation coefficient by 2, which is equal to 2 x 0.1543 = 0.3086. The standard error of heritability is, likewise, obtained by multiplying the standard error or correlation coefficient by 2, which is equal to 2 x 0.1674 = 0.3348. Thus, the heritability of weaning weight of Rambouillet lambs by the intra-sire correlation method is 0.3086 ± 0.3348.

Regression of offspring on dam is the required regression coefficient.
Regression coefficient = $b = Sxy/Sx^2 = 419.71/2346.20 = 0.1788$

Standard error of the regression coefficient was calculated as follows:

$$S_b^2 = \frac{\text{S.S. of Standard error of estimate of the error term}/n-2}{\text{Sum of squares of X of the error term}}$$

$$= \frac{\dfrac{Sy^2 - (Sxy)^2/Sx^2}{n-2}}{Sx^2}$$

$$= \frac{\dfrac{3153.30 - (419.71)^2/2346.20}{36-2}}{2346.20}$$

$$= 90.53/2346.20 = 0.03858$$

$$S_b = \sqrt{0.03858} = 0.1964$$

The heritability estimate is obtained by multiplying this regression coefficient by 2, which is equal to 2 x 0.1788 = 0.3576. Similarly, the standard error of heritability is calculated by multiplying the standard error of regression by 2, which is equal to 2 x 0.1964 = 0.3928. Thus, the heritability of weaning weight of Rambouillet lambs by the intra-sire regression method is 0.3576 ± 0.3926.

Half-sib Method

The intra-class correlation was calculated from the data in table 8d. - Analysis of Variance of Birth Weight of Offspring (Y).

Intraclass correlation = $r_1 = S_m^2/(S^2+S_m^2)$ where S^2 = the mean square of the error term.

$$S_m^2 = \frac{\text{Mean square between sires - Mean square of error term}}{\text{Average number in each sire group}}$$

First, calculate the average number as follows:

$K_o = 1/(n-1) \cdot (Sk - Sk^2/Sk)$ where n = number of sire groups, and k = number in each sire group.

$K_o = 1/(2-1) \cdot (36 - 22^2+14^2/36) = 17.1$

Now, substituting in the intraclass correlation formula, we get the half-sib correlation:

$S^2 = 92.74$

$S_m^2 = (473.69-92.74)/17.1 = 22.28$

$r_1 = 22.28/(92.74+22.28) = 0.1937$

Standard error of this correlation was calculated by the formula as shown below:

$S_{r1} = (1-r_1^2)/\sqrt{n-2} = (1 - 0.1937^2)/\sqrt{36-2} = 0.963/\sqrt{34} = 0.1652$

This half-sib correlation and its error are separately multiplied by 4 to get the estimate of heritability and the standard error of heritability. Thus, the heritability of weaning weight of Rambouillet lambs by the half-sib method is $4 \times 0.1937 = 0.7748$ and the corresponding standard error of heritability is $4 \times 0.1652 = 0.6608$.

The calculations were made in the same manner for the other four breeds and hence, only the data of sums, sums of squares and products, the analysis of covariance and the correlation and regression data for each sire group are given in the following tables. Tables 20a, b and c pertain to the breed Hampshire; tables 21a, b and c to Oxford; tables 22a, b and c to Shropshire; tables 23a, b and c to Southdown.

TABLE 20a. PRELIMINARY DATA FOR THE STATISTICS OF WEANING WEIGHT OF HAMPSHIRE

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	37	3071.5	259715.49	2830.6	223789.14	235033.45
II	4	356.8	31868.40	311.3	24896.67	27870.64
III	28	2309.1	194773.91	2274.5	189920.55	188346.40
IV	2	142.1	10118.65	139.0	10501.00	10013.30
V	7	552.2	44604.10	524.6	41189.12	41549.19
VI	4	363.7	33551.45	324.0	26488.56	29708.86
VII	3	205.6	14253.10	275.7	25602.69	18687.49
Total	85	7001.0	588885.10	6679.7	542387.73	551209.33

TABLE 20b. ANALYSIS OF COVARIANCE OF WEANING WEIGHT OF DAMS AND THEIR OFFSPRING OF HAMPSHIRE

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	84	12249.80	1037.81 ok	17465.48
Between Sires	6	1410.54 ok	-238.64 ok	1172.07
Within Sires	78	10839.26	1276.45	16293.41

TABLE 20c. CORRELATION AND REGRESSION DATA FOR THE SEVEN HAMPSHIRE SIRES (W.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	36	4739.49	55.40	7240.59	0.0095	0.0117
II	3	41.84	102.68	669.75	0.6134	2.4541
III	27	4347.39	773.26	5158.05	0.1633	0.1778
IV	1	22.45	137.35	840.50	1.0000	6.1180
V	6	1043.41	165.75	1874.10	0.1185	0.1588
VI	3	482.03	249.16	244.56	0.7257	0.5168
VII	2	162.65	-207.15	265.86	-0.9959	-1.2735
Total	78	10839.26	1276.45	16293.41	0.0960	0.1177

TABLE 21a. PRELIMINARY DATA FOR THE STATISTICS OF WEANING WEIGHT OF OXFORD

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	20	1556.4	123545.86	1551.5	129717.25	123637.10
II	12	1017.0	86756.10	871.6	66768.38	73622.29
III	17	1416.0	123295.28	1230.0	91539.34	101708.88
IV	2	125.4	8046.90	146.4	11070.26	9434.64
Total	51	4114.8	341644.14	3799.5	299095.23	308402.91

TABLE 21b. ANALYSIS OF COVARIANCE OF WEANING WEIGHT OF DAMS AND THEIR OFFSPRING OF OXFORD

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	50	9652.40	1850.31	16032.48
Between Sires	3	1125.40	-315.73	312.66
Within Sires	47	8527.00	2166.04	15719.82

TABLE 21c. CORRELATION AND REGRESSION DATA FOR THE FOUR OXFORD SIRES (W.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	19	2426.82	2899.37	9359.64	0.6083	1.1947
II	11	565.35	-245.35	3461.17	-0.1756	-0.4346
III	16	5350.81	-742.88	2545.23	-0.2013	-0.1388
IV	1	184.32	255.36	353.78	1.0000	1.3854
Total	47	8527.30	2166.14	15719.82	0.1871	0.2540

TABLE 22a. PRELIMINARY DATA FOR THE STATISTICS OF WEANING WEIGHT OF SHROPSHIRE

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	26	1603.4	100516.26	1787.0	126835.38	109840.96
II	33	2259.5	157363.09	2182.1	149543.67	147721.09
III	42	2600.9	164685.63	2719.3	182002.29	169527.85
IV	9	571.8	37152.44	583.8	38641.38	37298.25
V	8	503.3	32204.33	440.6	24568.52	27610.46
VI	5	303.3	18399.15	260.1	14060.35	15758.25
VII	14	934.1	63269.51	831.0	50247.56	55421.17
Total	137	8776.3	573590.41	8803.9	585899.15	563178.03

TABLE 22b. ANALYSIS OF COVARIANCE OF WEANING WEIGHT OF DAMS AND THEIR OFFSPRING OF SHROPSHIRE

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	136	11375.51	-804.94	20142.55
Between Sires	6	1151.51	56.70	2408.08
Within Sires	130	10224.00	-861.64	17734.47

TABLE 22c. CORRELATION AND REGRESSION DATA FOR THE SEVEN SHROPSHIRE SIRES (W.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	25	1635.82	-361.95	4013.50	-0.1412	-0.2212
II	32	2655.81	-1686.63	5253.97	-0.4515	-0.6350
III	41	3621.81	1131.97	5940.57	0.2440	0.3125
IV	8	824.08	207.49	772.22	0.2601	0.2517
V	7	540.47	-108.78	302.48	-0.2690	-0.2012
VI	4	0.98	-19.41	529.95	-0.8513	-19.800
VII	13	945.03	-24.33	921.78	-0.0261	-0.0257
Total	130	10224.00	-861.64	17734.47	-0.0639	-0.0842

TABLE 23a. PRELIMINARY DATA FOR THE STATISTICS OF WEANING WEIGHT OF SOUTHDOWN

Sire	Number of Pairs of Dam Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	10	561.4	32238.88	596.8	36512.20	34032.48
II	8	474.8	28415.32	406.8	20835.30	24183.22
III	8	458.6	26664.34	485.0	30594.80	28337.80
IV	5	232.7	10855.71	212.8	9369.30	9979.49
V	6	295.8	14684.42	406.1	27746.87	19925.72
VI	2	93.6	4380.48	122.6	7567.40	5737.68
Total	39	2116.9	117239.17	2230.1	132625.87	122196.39

TABLE 23b. ANALYSIS OF COVARIANCE OF WEANING WEIGHT OF DAMS AND THEIR OFFSPRING OF SOUTHDOWN

Source of Variation	Degrees of Freedom	Sums of Squares and Products		
		Sx^2	Sxy	Sy^2
Total	38	2334.93	1147.71	5104.18
Between Sires	5	874.64	63.99	2242.57
Within Sires	33	1460.29	1083.72	2861.61

TABLE 23c. CORRELATION AND REGRESSION DATA FOR THE SIX SOUTHDOWN SIRES (W.Wt.)

Sire	Degrees of Freedom	Sums of Squares and Products			Correlation Coefficient	Regression Coefficient
		Sx^2	Sxy	Sy^2		
I	9	721.89	528.13	895.18	0.6568	0.7316
II	7	235.94	39.64	149.52	0.2110	0.1680
III	7	375.12	535.18	1191.68	0.8004	1.4266
IV	4	25.86	75.78	312.54	0.8429	2.9292
V	5	101.48	-95.01	260.67	-0.5843	-0.9362
VI	1	0	0	52.02	0	0
Total	33	1460.29	1083.72	2861.61	0.5301	0.7421

The main statistics required for the estimates of heritability are summarized in table 24, whence the desired results are tabulated in table 25 for all the five breeds. The best estimate of heritability was found by the average of the three methods, by the average of the five breeds and then, by the average of 3 methods and 5 breeds. These averages were taken by weighting each of the individual estimates by the reciprocal of its squared standard error. Likewise, the weighted average of the standard errors of heritability was calculated by taking the square root of the reciprocal of the sum of the reciprocals of the squared standard errors.

TABLE 24. CORRELATIONS, REGRESSION AND STANDARD ERRORS OF THE CORRECTED WEANING WEIGHT OF LAMBS

Breed	Paternal half-sib correlation		Intra-sire regression		Intra-sire correlation	
	ri	S_{ri}	b	S_b	r	S_r
Hampshire	-0.0066	0.1097	0.1177	0.1339	0.0960	0.1087
Oxford	-.0635	.1423	.2540	.1905	.1871	.1378
Rambouillet	.1937	.1652	.1788	.1964	.1543	.1674
Shropshire	.0969	.0853	-.0843	.1131	-.0640	.0857
Southdown	.3984	.1383	.7421	.1951	.5302	.1182

TABLE 25. ESTIMATES OF HERITABILITY AND STANDARD ERRORS FOR THE CORRECTED WEANING WEIGHT

Breed	Paternal half-sib method		Intra-sire regression method		Intra-sire correlation method	
	Herit-ability	Standard error	Herit-ability	Standard error	Herit-ability	Standard error
Hampshire	-.0264	.4388	.2354	.2678	.1920	.2174
Oxford	-.2540	.5692	.5080	.3810	.3742	.2756
Rambouillet	.7748	.6608	.3576	.3928	.3086	.3348
Shropshire	.3876	.3412	-.1686	.2262	-.1280	.1714
Southdown	1.5936	.5532	1.4842	.3902	1.0604	.2364

The weighted average heritability = $(S \cdot hn/S^2_{hn}) \;/\; (S \cdot 1/S^2_{hn})$

The weighted average standard error of heritability =

$\sqrt{1/(S \cdot 1/S^2_{hn})}$ where hn = heritability; and S_{hn} = standard error of heritability. In order to facilitate this calculation, the necessary data are given in table 26. The figures in tables 25 and 26 were used to get the final average values of heritability as shown in tables 27a, b and c. Thus, the best estimate of heritability of weaning weight of lambs was found to be 0.30 ± 0.08 by the weighted average of 3 methods and 5 breeds.

TABLE 26. SQUARED STANDARD ERRORS AND THEIR RECIPROCALS OF THE HERITABILITY OF WEANING WEIGHT

Breed	Half-sib method		Intra-sire regression method		Intra-sire correlation method		Reciprocal sum of 3 methods
	S^2_{h1}	$1/S^2_{h1}$	S^2_{h2}	$1/S^2_{h2}$	S^2_{h3}	$1/S^2_{h3}$	$S(1/S^2_h)$
Hampshire	.1925	5.2	.0717	13.9	.0473	21.1	40.2
Oxford	.3240	3.1	.1452	6.9	.0760	13.2	23.2
Rambouillet	.4367	2.3	.1543	6.5	.1121	8.9	17.7
Shropshire	.1164	8.6	.0512	19.5	.0294	34.0	62.1
Southdown	.3060	3.3	.1523	6.6	.0559	17.9	27.8
Reciprocal sum of 5 breeds		22.5		53.4		95.1	171.0

TABLE 27a. WEIGHTED AVERAGE OF THREE METHODS (Weaning Weight)

Breed	Heritability	Standard error
Hampshire	0.1788	0.1577
Oxford	.3301	.2076
Rambouillet	.3872	.2377
Shropshire	-.0693	.1269
Southdown	1.2243	.1897

TABLE 27b. WEIGHTED AVERAGE OF FIVE BREEDS

Method	Heritability	Standard error
Paternal half-sib correlation	0.4200	0.2108
Intra-sire regression	.2923	.1369
Intra-sire correlation	.2772	.1026

TABLE 27c. WEIGHTED AVERAGE OF 3 METHODS AND 5 BREEDS

Trait	Heritability	Standard error
Weaning Weight	0.3007	0.0765

DISCUSSION OF RESULTS

The individual estimates of heritability of adjusted birth weight range from negative values to over 100 per cent by the half-sib method. These are obviously due to sampling errors since the negative results cannot be interpreted except that these amount to zero value or no heritability. Anything over 100 per cent is meaningless since the limit is 100 per cent. However, the weighted average of 5 breeds by the half-sib method is approximately $0.15 \pm .18$ for birth weight. Evidently, the advantage of taking a weighted average of several breeds is to at least partly remove the sampling errors. The standard error of heritability by this method is greater than the heritability itself, which indicates the large sampling error. On account of the negative values for three out of five breeds the average result is very low when compared with the estimates by the other two methods.

The individual estimates by the intra-sire regression and correlation methods are consistently uniform although the range is 57 to 88 per cent. The average of 3 methods and 5 breeds, which is $0.61 \pm .06$, seems to be the best estimate of heritability of adjusted birth weight of lambs in this flock. In order to show how much practical confidence one can put in these values, the fiducial limits at 99 per cent are calculated as follows: Limit $= h \pm t_{.01} \times S_h = 0.6138 \pm 2.568 \times 0.0584 = 0.6138 \pm 0.15$. The "t" value at 1 per cent level should be taken for (n-2) degrees of freedom, where n = total number of pairs. Here, n = 504. Therefore, the 99 per cent fiducial limits are 0.4638 and 0.7638. This means that the chances are very good (99 out of 100) that the real heritability of adjusted birth weight lies within these limits.

The heritability of adjusted weaning weight for Southdown is consistently over 100 per cent by the three methods, which is, again, probably due to the smallest sample number in the group. However, the average heritability by 3 methods and 5 breeds seems to be the best estimate and is 0.30 ± .08 for adjusted weaning weight. The 99 per cent fiducial limits, in this case, are 0.3007 ± 2.592 x 0.0765 which are 0.1024 and 0.4990. (The n-value, here, is 348). The real heritability of adjusted weaning weight of lambs probably lies between 10 per cent and 50 per cent.

Sources of Errors

1. Negative results of heritability and estimates over 100 per cent are obviously an error which could be attributed mainly to the size and nature of the sample. In this study a small sample number is a chief source of error. These sampling errors may also include certain unknown environmental circumstances.

2. In the half-sib method, the necessary adjustment for the presence of twins is not made. The twins are genetically full-sibs and not half-sibs. However, the error due to this source may be insignificantly small since the number of full-sib comparisons is too small a proportion of the total comparisons.

3. System of mating (inbreeding) requires an additional correction depending upon the amount of inbreeding practiced in the flock. The error due to this source is very small since there has been no inbreeding in this

flock except a small amount in the Rambouillets. For all practical purposes, the flock is considered non-inbred.

Inbreeding increases the homozygosity and reduces the genetic variance for a particular trait. This would show a lower estimate of heritability for the inbred stock than in a non-inbred population. If there is considerable amount of inbreeding practiced in the flock from which the data are obtained for the study of heritability, then, a correction must be made as outlined by Hazel and Terrill (1945).

4. The error due to the source of the environmental differences has been practically eliminated in this study by following the method on the intra-sire basis. Moreover, the usual practice in the flock has been to use one or two sires in a breed each year. The management in the college herd would vary less from time to time than would be the case in the average sheepman's flock where much depends on his crop yields, the market price he receives for, and so on. Although it is practically impossible to control the environment absolutely and perfectly, the error due to this source is negligibly small.

Practical Applications

In the light of the differences in weaning weight of lambs due to environmental factors, it seems highly recommendable as a good management practice to separate the lambs into groups according to sex, type of birth and age of dam. This would enable the breeder to make selection of lambs on a more comparable basis on the real genetic merit of the individuals.

The twin sex ratio of 308♂♂: 682♂♀: 326♀♀ in this flock gives no positive proof of the existence of any identical twins in sheep. Hence, there is no point in seeking like-sexed twins for controlling genetic variance in experiments on nutrition and management of sheep.

The expected gain in birth weight or weaning weight per generation would be proportional to half the product of the percentage of heritability, the standard deviation and the total selection differentials. Assuming that the replacement rates in a static population are about 50 per cent for ewe lambs and about 3 per cent for ram lambs, the corresponding selection differentials are 0.80 and 2.27, respectively, in a normally distributed population (Lush, 1945). Since the average standard deviation of birth weight is 2.09 pounds and the average heritability of birth weight is 61 per cent, the expected gain per generation would be equal to $(0.61)(2.09)(0.80+2.27)/2 = 1.96$ pounds if all the selection were directed toward the improvement of birth weight alone. Likewise, since the average standard deviation of weaning weight is 14.50 lbs. and the average heritability of weaning weight is 30 per cent, the expected gain per generation would be equal to $(0.30)(14.50)(0.80+2.27)/2 = 6.68$ lbs., granting that the selection was made for the improvement of weaning weight alone.

These gains are the estimates per generation. In sheep, since the average interval between generations, that is, the average age of ewes when their offspring are born is between 4 and 4-1/2 years according to Lush, the maximum gain or improvement per year would be less than 0.5 pound in birth weight and less than 1.5 pound in weaning weight. Hazel and Lush (1942) have shown that with n equally important but uncorrelated traits, the gain possible in any trait is only $1/\sqrt{n}$ times as great as if all selection were directed toward improving one trait alone. So, when allowance is made for emphasis on other traits, as is necessary in a properly balanced breeding program, it seems probable that the gains actually made will be considerably less than the figures deduced above.

SUMMARY

1. A study of the lambing records of Hampshire, Oxford, Rambouillet, Shropshire, Southdown, Cotswold, crossbreds and grades kept at the Michigan State College flock from 1930 to 1948 showed that 51.2 per cent of a total of 2305 pregnancies were singles, 46.4 per cent were twins and 2.4 per cent triplets.

2. About 65 per cent of the births in the two-year-old ewes were all singles as against only 45 per cent singles in the mature ewes, showing that multiple births increased as the age of the ewe advanced.

3. A total of 4470 lambs gave a male percentage of 49.8 ± 0.75.

4. Identical twins in sheep appear to be very rare, as evidenced by the twin sex ratio of 308 ♂♂ : 682 ♂♀ : 326 ♀♀.

5. Only the records of Hampshire, Oxford, Rambouillet, Shropshire and Southdown from 1945 through 1948 were used to study the estimates of heritability. The heritability estimates by the weighted average of 3 methods and 5 breeds was 0.61 ± 0.06 for birth weight and 0.30 ± 0.08 for weaning weight.

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