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To the Graduate Council:

I am submitting herewith a dissertation written by G. Srinivasan entitled "A Comparison of Heritability Estimates Obtained by Different Methods." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

Robert R. Shrode
Major Professor

We have read this dissertation
and recommend its acceptance:

Richard M. Dowell

L. M. Josephson

Don O. Richardson

G. M. Merriman

P. L. Murphree

E. R. Tidwell

Accepted for the Council:

Hilton A. Smith
Vice Chancellor for
Graduate Studies and Research

# A COMPARISON OF HERITABILITY ESTIMATES OBTAINED BY DIFFERENT METHODS

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A Dissertation

Presented to

the Graduate Council of

The University of Tennessee

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In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

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by

G. Srinivasan

December 1969

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## ABSTRACT

Records of birth weight, average daily gain and 120-day weight of 447 purebred Hampshire lambs in 19 sire groups born from 1952 to 1968 at the Main Experiment Station of The University of Tennessee Agricultural Experiment Station were used to calculate estimates of heritability before and after least-squares adjustments of the records for the significant effects of age of dam, month of birth, sex of lamb, type of birth, type of rearing and year of birth. Estimates from unadjusted data were erratic and inexplicable, whereas, those from adjusted data were reasonable and consistently positive.

Estimates of heritability from regression of offspring on dam, from regression of offspring on mid-parent and from paternal half-sib correlation were very similar in magnitude, but estimates from regression of offspring on sire were much larger than the other regression estimates and had much larger standard errors reflecting larger sampling errors due to the small number of sires.

The heritability estimates ranged from 0.016 $\pm$ .038 to 0.388 $\pm$ .180 for birth weight, 0.101 $\pm$ .028 to 0.330 $\pm$ .320 for average daily gain and 0.099 $\pm$ .038 to 0.218 $\pm$ .261 for 120-day weight, the largest estimates being those obtained from the regression of offspring on sire. There

were no appreciable differences among the estimates obtained from regression of offspring on dam, regression of offspring on mid-parent and from paternal half-sib correlations, but the estimates obtained from regression on sire were much larger and had much larger standard errors than those obtained by other methods. It was concluded that heritability estimates based on regression of offspring on sire cannot be as accurate as estimates obtained by the other methods because of the much larger sampling errors to which they are subject as a result of small numbers of sires.

In view of non-significance of differences between estimates obtained using individual offspring values and those obtained using progeny means in the parent-offspring methods and some statistical advantages of using progeny means over using individual offspring values, it was concluded that use of progeny means is slightly preferable to use of individual offspring values.

There was no significant indication of the existence of variance due to maternal differences with respect to the three traits studied here as indicated by the lack of significance between paternal half-sib estimates of heritability, which receive no contribution from maternal variance, and parent-offspring estimates which contain a contribution from whatever maternal variance exists.

Extremely large estimates of genetic correlations were obtained (ranging from 0.76 to 0.98), and it was

concluded that these are gross overestimates of the respective parameters due to extremely large sampling errors to which estimates of genetic correlation are subject in data from samples of animals numbering many fewer than 1000 head.

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# CHAPTER I

## INTRODUCTION

Improving the level of expression of economic traits in animals through breeding depends on effective use of genetic variation. Pertinent to the effective use of this genetic variability is a knowledge of its magnitude as reflected by heritability and repeatability of traits. Also important are the genetic and environmental correlations among traits.

The first essential step in the application of genetics to livestock improvement is to determine the order of magnitude of the heritabilities of the traits the breeder desires to improve. The degree of heritability of a trait dictates the choice of breeding system to be used and permits estimation of the progress to be expected from selection based on individual merit alone. Such estimation provides the breeder a basis for determining the economic feasibility of using various supplements to individual merit such as information on the merit of ancestors, progeny or other relatives.

In determining heritability, large bodies of data are required to obtain reliable estimates which are reasonably free of sampling errors. Several methods are available to estimate the heritability of a trait, and all of them are,

in effect, based upon assessment of the extent to which closely related animals resemble each other more than do relatively unrelated animals.

Reported estimates of heritability of birth weight, average daily gain and weaning weight of sheep vary from low negative estimates to high positive estimates. Variation exists not only among estimates obtained from different sets of data but among estimates obtained from the same set of data by different methods. Such variation is confusing, to say the least, and deserves much more attention than it is usually given. Considerable discussion has been devoted to the theoretically expected differences between estimates obtained by different methods, but too little research effort has been directed toward examination of the differences actually existing among estimates obtained from the same data using different methods of calculation.

The objectives of the present study were: (1) to evaluate the effectiveness of adding least-squares constants as compared to using multiplicative correction factors to reduce environmental variation, (2) to estimate by various procedures the heritability of birth weight, average daily gain and 120-day weight of sheep, (3) to examine the differences among heritability estimates obtained by different methods in the light of theoretical expectations concerning such differences, (4) to assess maternal influences on offspring and (5) to evaluate the

phenotypic, genetic and environmental correlations among these traits.

# CHAPTER II

## REVIEW OF LITERATURE

Considerable research effort has been devoted to estimating heritability of production traits of sheep. However, little research has been devoted to study of the actual differences between estimates obtained from application of different methods to the same data.

Falconer (1960) discussed the theoretical composition of various estimates of heritability in terms of the amounts of environmental and various kinds of genetic variance and covariance included in the estimates. The parent-offspring and paternal half-sib resemblances are intended to provide an estimate of heritability in the narrow sense, which is defined as the fraction that additively genetic variance makes up of the phenotypic variance. However, the numerator of estimates obtained from parent-offspring and half-sib correlations may include a small fraction of any existing environmental contributions to the resemblance among these related animals. In addition to possible environmental contributions to the resemblance, some epistatic influences may contribute to the observed likeness to the extent that non-allelic gene interactions are involved in the inheritance of the trait in question. Generally, this contribution is believed to be small, and, hence, many investigators

consider the estimates of heritability obtained from parent-offspring and paternal half-sib data to be indicative of the magnitude of the additively genetic fraction of the phenotypic variance.

In the use of parent-offspring data, the question arises as to whether to use the performance of individual progeny or the mean of the progeny to represent the offspring in each parent-offspring pairing. Kempthorne and Tandom (1953) recommended that in data from multiple-offspring parents the parent record be repeated with each offspring's record if the phenotypic correlation among the offspring of a parent is zero or nearly so, but that the average of all offspring of each parent be used if the phenotypic correlation among members of the same parent group is substantially positive. Van Vleck (1966), in a study of milk production in dairy cattle, observed that analysis with one value in each sire-herd subclass gave the highest estimate of heritability from daughter-dam regression and the lowest estimate from the paternal half-sib correlation. Analysis with more than one value in each sire-herd subclass yielded approximately the same results from both methods.

Falconer (1960) stated that half-sib correlation and the regression of offspring on sire yield the most reliable estimates of heritability. The regression of offspring on dam may give a positively biased estimate as a result of

maternal effects. The use of full-sib correlations seldom does more than set an upper limit for the heritability because of the usually much larger environmental contributions to the resemblance between full sibs than to that between half sibs and between parent and offspring. Also, dominance-caused deviations from the linear regression of phenotype on genotype contribute to the resemblance between full sibs but not to that between half sibs and between parent and offspring. The regression of offspring on parent is not affected by change in variance among parents as a result of selection or deviations from random mating because the parent-offspring covariance is changed to an extent proportional to the change in the variance among the parents. Falconer (1960) emphasized the fact that the accuracy of the estimate of heritability from intra-sire regression of offspring on dam depends on the extent to which maternal effects contribute to the resemblance between offspring and dams. If maternal influences are appreciable, some method of adjusting the data to remove them must be employed if accurate estimates of heritability are to be obtained from dam-offspring data. Van Vleck and Hart (1965) reported that the existence of an environmental covariance between daughter and dam records, and the possibility of genetic maternal effects which would increase likeness between daughter and dam but not among paternal half sibs are the principle reasons for a difference in estimates of heritability from

daughter-dam regression and from correlations among paternal half sibs.

It was pointed out by Falconer (1960) that inequality of variances of males and females requires an adjustment if the heritability is to be estimated from the intra-sire regression of male offspring on dams. The regression coefficient obtained must be multiplied by the ratio of the phenotypic standard deviation of females to that of males. A similar complication arises in the use of regression of offspring on mid-parent if the variance of male parents is not equal to the variance of female parents. The genetic covariance of offspring and mid-parent is theoretically equal to the additively genetic variance provided the variances of the two sexes are equal. If they are not, the regression of offspring on mid-parent is not a valid estimate of heritability, and heritability must be estimated separately for each sex from regression of daughters on dams and of sons on sires.

Reeve (1952) suggested that assortive mating increases the variance of the mid-parent value, thereby making for a more precise estimate of heritability. Dawson (1964) pointed out that since many quantitative traits for which heritability estimates are desired involved maternal effects, heritability should be estimated from regression of offspring on sires, thus freeing the estimate of bias from maternal effects. He found that when mating is assortive,

heritability of a trait for which maternal effects are important will be over-estimated by offspring-on-parent regression if the regression is not intra-sire or intra-dam. In few situations with farm animal data would it be feasible to calculate intra-dam regressions of offspring on sire because of the extremely small maternal half-sib progeny groups and the consequent large sampling errors. Wilson et al. (1966) pointed out that the expectations of regression of offspring on mid-parent, regression of offspring on dam and regression of offspring on sire would be equal only if a perfect positive correlation between mates exists.

Rendel et al. (1955) pointed out that the half-sib method of estimating heritability is open to the objection that it is impossible to be certain that similarities between half sibs due to causes other than their common sires are eliminated. In cattle these arise mainly from year-to-year variation in climate and in management and from genetic trends within the herd. In such circumstances certain adjustments for environmental effects are possible and useful. Botkin et al. (1969) found that estimates of heritability of traits of sheep calculated from paternal half-sib correlations were generally higher and had lower standard errors than comparable estimates calculated by regression of offspring on sire.

Rice et al. (1967) emphasized the fact that estimates of heritability of weaning weight of sheep have varied

greatly. If variation in weaning weight of sheep results to an appreciable extent from variation in milk production of dams, then heritability estimates based on paternal half sib correlations would tend to be lower than heritability estimates based on regression of offspring on dam.

Estimates of heritability in sheep as reported in the literature range from -.14 to 0.72 for birth weight (Table I), from 0.18 to 0.84 for average daily gain (Table II) and from 0.00 to 0.77 for weaning weight (Table III). In view of the variation in estimates of heritability associated with differences in methods of calculation, it is desirable to investigate empirically this variation among methods as well as to propose theoretical explanation for the variation and to assess the effectiveness of various adjustment procedures in improving the estimates.

Estimates of genetic correlations among birth weight, average daily gain and weaning weight in sheep were not found in the literature. The cause of genetic correlation is chiefly pleiotropic action of genes, and the study of genetic correlation is useful in selection programs when two or more traits are combined. Though determination of genetic correlation is subject to large sampling error, it is related to the nature of the heritability of the traits involved. Van Vleck and Henderson (1961) showed that with small samples the accuracy of estimates of genetic correlations is low unless the heritabilities of the traits

TABLE I

PUBLISHED ESTIMATES OF HERITABILITY OF BIRTH WEIGHT

| Method | Estimate | Author |
|---|---|---|
| 1. Regression of offspring on dam: | 0.72 | Nelson and Venkatachalam (1949) |
| | 0.34 | Yao et al. (1953) |
| | 0.33 | Blackwell and Henderson (1955) |
| | 0.09 | Cassard and Weir (1956) |
| | -.14 | Butcher et al. (1964) |
| 2. Paternal half-sib correlation: | 0.30 | Chapman and Lush (1932) |
| | 0.15 | Nelson and Venkatachalam (1949) |
| | 0.18 | Yao et al. (1953) |
| | 0.10 | Butcher et al. (1964) |
| 3. Regression of offspring on mid-parent: | 0.25 | Yao et al. (1953) |

TABLE II

PUBLISHED ESTIMATES OF HERITABILITY
OF AVERAGE DAILY GAIN

| Method | Estimate | Author |
|---|---|---|
| 1. Regression of mean of the offspring on sire: | 0.22 | Shelton (1959) |
| 2. Paternal half-sib correlation: | 0.58 | Shelton et al. (1954) |
| | 0.84 | Botkin (1955) |
| | 0.20 | Hundley and Carter (1956) |
| | 0.33 | Dollahon and McGuire (1959) |
| | 0.18 | Givens et al. (1960) |

TABLE III

PUBLISHED ESTIMATES OF HERITABILITY OF WEANING WEIGHT

| Method | Estimate | Author |
|---|---|---|
| 1. Regression of offspring on dam: | 0.34 | Hazel and Terrill (1945) |
| | 0.29 | Nelson and Venkatachalam (1949) |
| | 0.07 | Blackwell and Henderson (1955) |
| | 0.41 | Cassard and Weir (1956) |
| | 0.14 | Felts et al. (1957) |
| | 0.02 | Butcher et al. (1964) |
| 2. Regression of average of offspring on dam: | 0.77 | Warwick and Cartwright (1957) |
| 3. Regression of offspring on sire: | 0.27 | Warwick and Cartwright (1957) |
| 4. Paternal half-sib correlation: | 0.27 | Hazel and Terrill (1945) |
| | 0.42 | Nelson and Venkatachalam (1949) |
| | 0.00 | Butcher et al. (1964) |
| 5. Regression of offspring on mid-parent: | 0.41 | Warwick and Cartwright (1957) |

involved are high. However, Robertson (1959) had said earlier that it is equally difficult to obtain useably accurate estimates of both heritability and genetic correlation, irrespective of the magnitude of heritability.

# CHAPTER III

## EXPERIMENTAL PROCEDURE

### Data Used

The data used for this study included records from 447 purebread Hampshire lambs in 19 sire groups born during the years 1952 to 1968, inclusive, at the Main Experiment Station of The University of Tennessee Agricultural Experiment Station. The breeding, feeding and management practices followed in the flock at this station throughout the years included in this study were not greatly different from those followed in any program of sheep production based on the best information available as to most effective practices. Some of the rams used during the period included in the study were raised in the flock, and some were purchased from breeders of purebred Hampshires. Since the actual performance records of these introduced rams were not available, the adjusted records supplied with them were used. A sire breeding group consisted of a random allotment of ewes. Rams were placed with the ewes at the beginning of August. They were taken away from the ewes in the middle of October. Lambing season in most years started in the middle of December. Ewes were culled only if they failed to lamb in two consecutive years or in two out of three years.

Statistical Analysis

Complete records were obtained on the performance of sires, dams and lambs with respect to birth weight, average daily gain and weaning weight. The weaning weight of sires, dams and lambs were adjusted linearly to a standard age of 120 days.

Least-squares estimates of the effects of age of dam, month of birth, sex of lamb, type of birth and year of birth upon birth weight of lambs and the effects of age of dam, month of birth, sex of lamb, type of rearing and year of birth upon average daily gain and 120-day weight were obtained by the method of fitting of constants as described by Harvey (1960). The model on which the analyses were based was: $Y_{ijklmno} = \mu + a_i + b_j + s_k + t_l + r_m + y_n + e_{ijklmno}$

Where:

$Y_{ijklmno}$ = is the observed value of a given trait, ijklmno-th individual

$\mu$ = the population mean with equal subclass numbers, i.e., an effect common to all individuals in the population sampled

$a_i$ = effect of i-th dam

$b_j$ = effect of j-th month of birth

$s_k$ = effect of k-th sex

$t_l$ = effect of l-th type of birth

$r_m$ = effect of m-th type of rearing (single raised as single, twin raised as single and twin raised as twin)

$y_n$ = effect of n-th year

$e_{ijklmno}$ = random error associated with an individual record.

For birth weight, the effect of type of rearing was deleted from the model, and for average daily gain and 120-day weight, type of birth was deleted.

The least-squares constants were used to adjust the data for the effects to place the records on a more comparable basis for estimation of heritability by different methods. Adjustment factors for Hampshires determined by Webb (1963) failed to remove the environmental effects from these data. In fact, instead of reducing the variance as effective adjustment factors must do, the variance among records adjusted by use of Webb's factors was greater than among the unadjusted records.

Both adjusted and unadjusted data were used to estimate heritability of birth weight, average daily gain and 120-day weight from regression of offspring on dam (using individual progeny and using the mean of the progeny), from regression of offspring on sire (using the average of the offspring), from regression of offspring on mid-parent (using individual progeny and using the mean of the progeny) and from paternal half-sib correlations as described by Becker (1968).

Since one sire can mate with several dams and each dam can produce several offspring, the sire effect is

removed by obtaining the regression of offspring on dam within sire for individual progeny as well as for the means of the dams' offspring. The accuracy of the estimate of heritability by this method depends on the extent to which maternal effects contribute to the resemblance between offspring and dam. Since there is no inequality of variances of male and female offspring in these data, the heritability estimates are not affected by such. For estimation of heritability from regression of offspring on sire, the average of the sire's progeny was used. In calculating the regression of offspring on mid-parent (the mean value of sire and dam), both individual progeny and the mean of the progeny were used to calculate separate estimates for comparison. Since, however, the variances among sires and among dams are unequal in the present data, heritability estimates were calculated also from regression of male offspring on sire and of female offspring on dam. In estimating heritability from the half-sib correlation method, paternal half-sib correlations are used rather than maternal half-sib correlations because there would be very few maternal half sibs in a set, making sampling errors extremely large. Also maternal effects would produce an environmental magnification of the phenotypic resemblance among maternal half sibs as compared to that among paternal half sibs.

The form of the analysis of variance used to obtain

the estimates of variance components for use in estimating heritability from paternal half-sib correlation (an intra-class correlation) is shown in Table IV. For calculation of standard errors of heritability estimates, procedures described by Becker (1968) were used.

Estimates of genetic correlations among birth weight, average daily gain and 120-day weight were calculated using the formula given by Becker (1968) viz.,

$$r_g = \frac{Cov_{S(XY)}}{\sqrt{s^2_{S(X)} \; s^2_{S(Y)}}}$$

Where:

$r_g$ = estimate of genetic correlation

$Cov_{S(XY)}$ = sire component of covariance of traits X and Y

$s^2_{S(X)}$ = sire component of variance of the trait X

$s^2_{S(Y)}$ = sire component of variance of the trait Y.

TABLE IV

FORM OF THE ANALYSIS OF VARIANCE IN ESTIMATING HERITABILITY FROM PATERNAL HALF-SIB CORRELATION

| Source of Variation | Degrees of Freedom | Composition of Mean Square |
|---|---|---|
| Between sires | (S-1) | $s_W^2 + k\, s_S^2$ |
| Within sires | (k. - S) | $s_W^2$ |

S = number of sires

k. = total number of offspring

$s_W^2$ = variance due to differences between offspring of same sire

$s_S^2$ = variance due to sire differences

$$k = \frac{\Sigma k_i}{S} - \frac{s_k^2}{\Sigma k_i} \quad \text{where } \Sigma k_i = k.$$

$k_i$ = number of offspring of i-th sire

$s_k^2$ = variance of number of offspring per sire

$$\text{Heritability} = \frac{4\, s_S^2}{s_S^2 + s_W^2}$$

# CHAPTER IV

## RESULTS AND DISCUSSION

Two mathematical models were used to determine the effects of various environmental factors affecting birth weight, average daily gain and 120-day weight of lambs. Least-squares analyses were conducted to determine the erfects of age of dam, month of birth, sex of lamb, type of birth and year of birth on birth weight. In the analyses of average daily gain and 120-day weight, type of rearing was included as an effect, but type of birth was excluded.

The analyses of variance of birth weight, average daily gain and 120-day weight and the least-squares constants are presented in Tables V, VI and VII, respectively. Age of dam, month of birth, sex of lamb, type of birth and year of birth had highly significant ($P<.01$) influences on birth weight of lambs. Similar results were reported by Blackwell and Henderson (1955), Harrington et al. (1958) and Smith and Lidvall (1964). Age of dam and month of birth had a significant ($P<.05$) effect on average daily gain and 120-day weight, whereas, sex of lamb, type of rearing and year of birth had highly significant ($P<.01$) effects on these traits. Evidence of such influences was found also by Hazel and Terrill (1946), Karam et al. (1953) and Smith and Lidvall (1964).

TABLE V

ANALYSIS OF VARIANCE OF BIRTH WEIGHT

| Source of Variation | Degrees of Freedom | Mean Square | F |
|---|---|---|---|
| Age of dam | 9 | 11.04 | 4.51** |
| Month of birth | 4 | 12.38 | 5.05** |
| Sex of lamb | 1 | 85.15 | 34.76** |
| Type of birth | 1 | 422.93 | 172.62** |
| Year of birth | 16 | 16.32 | 6.66** |
| Error | 415 | 2.45 | |
| Total | 446 | | |

**$P < .01$

TABLE VI

ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN AND 120-DAY WEIGHT

| Source of Variation | Degrees of Freedom | Mean Square | |
|---|---|---|---|
| | | Average Daily Gain | 120-day Weight |
| Age of dam | 9 | 0.015* | 196.96* |
| Month of birth | 4 | 0.019* | 261.24* |
| Sex of lamb | 1 | 0.673** | 11351.39** |
| Type of rearing | 2 | 0.352** | 7189.41** |
| Year of birth | 16 | 0.121** | 1953.36** |
| Error | 414 | 0.006 | 98.71 |
| Total | 446 | | |

*$P < .05$

**$P < .01$

TABLE VII

LEAST SQUARES ESTIMATES OF THE EFFECTS OF VARIOUS FACTORS ON BIRTH WEIGHT, AVERAGE DAILY GAIN AND 120-DAY WEIGHT

| Effects | Birth Weight (lb.) | Average Daily Gain (lb.) | 120-Day Weight (lb.) |
|---|---|---|---|
| Overall mean | 9.05 | 0.555 | 75.67 |
| Age of dam: | | | |
| 1. 2 year old | -1.28 | -.058 | -3.39 |
| 2. 3 year old | -.61 | 0.008 | 0.54 |
| 3. 4 year old | -.05 | 0.013 | 1.65 |
| 4. 5 year old | 0.26 | 0.021 | 2.89 |
| 5. 6 year old | 0.38 | 0.018 | 2.47 |
| 6. 7 year old | 0.24 | 0.111 | 1.28 |
| 7. 8 year old | 0.06 | 0.005 | 0.95 |
| 8. 9 year old | 0.07 | 0.006 | 0.72 |
| 9. 10 year old | -.39 | -.023 | -2.63 |
| 10. 11 year old | 1.32 | -.101 | -4.48 |
| Month of birth: | | | |
| 1. December | 0.14 | 0.029 | 3.24 |
| 2. January | 0.46 | 0.015 | 1.88 |
| 3. February | 0.60 | 0.003 | 0.13 |
| 4. March | -.21 | -.005 | -.79 |
| 5. April | -.99 | -.042 | -4.46 |
| Type of birth: | | | |
| 1. Single | 0.79 | - | - |
| 2. Twin | -.79 | - | - |
| Sex: | | | |
| 1. Female | -.34 | -.030 | -3.93 |
| 2. Male | 0.34 | 0.030 | 3.93 |

TABLE VII (continued)

| Effects | Birth Weight (lb.) | Average Daily Gain (lb.) | 120-Day Weight (lb.) |
|---|---|---|---|
| Type of rearing: | | | |
| 1. Single as single | - | 0.023 | 3.91 |
| 2. Twin as single | - | 0.018 | 1.68 |
| 3. Twin as twin | - | -.041 | -5.59 |
| Year of birth: | | | |
| 1. 1952 | -.56 | 0.017 | 1.62 |
| 2. 1953 | -.48 | -.034 | -4.66 |
| 3. 1954 | -.16 | -.148 | -17.82 |
| 4. 1955 | -.25 | 0.001 | -.08 |
| 5. 1956 | -.23 | 0.009 | 0.76 |
| 6. 1957 | 0.05 | -.064 | -8.13 |
| 7. 1958 | -.55 | 0.011 | 1.09 |
| 8. 1959 | -.69 | -.011 | -1.98 |
| 9. 1960 | 0.06 | -.047 | -5.39 |
| 10. 1961 | 0.43 | -.011 | -1.29 |
| 11. 1962 | -1.04 | -.004 | -1.41 |
| 12. 1963 | -.49 | -.017 | -2.32 |
| 13. 1964 | 0.19 | -.019 | -1.62 |
| 14. 1965 | 0.76 | 0.033 | 4.79 |
| 15. 1966 | 0.91 | 0.041 | 4.93 |
| 16. 1967 | 1.23 | 0.095 | 12.73 |
| 17. 1968 | 0.82 | 0.148 | 18.78 |

Since these analyses of variance demonstrated as significant the influence of various environmental effects, the least-squares constants were used to adjust the data and thus eliminate much of the environmental variation. However, to illustrate the influence of appropriate adjustment, heritability estimates were calculated using unadjusted data as well as adjusted data.

Since each lamb receives a sample half of the genes of each of its parents except for sex-linked genes which are negligible, the covariance between parent and offspring is expected to contain one-half of the additively genetic variance with respect to a trait, and, hence, the regression of offspring on parent represents one-half of heritability. Since relationship to only one of the two parents is involved, the regression must be multiplied by two to be used as an estimate of heritability. Since both parents are included in the regression of offspring on mid-parent, the regression itself is an estimate of heritability. The paternal half-sib correlation is multiplied by four to yield an estimate of heritability since the sire component of variance in the numerator of this intra-class correlation contains one-fourth of the additively genetic variance.

The estimates of heritability of birth weight, average daily gain and 120-day weight calculated by different methods (adjusted data) are shown in Tables VIII, IX and X, respectively. The analyses of variance from which

TABLE VIII

ESTIMATES OF HERITABILITY OF BIRTH WEIGHT*

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of offspring on dam: | |
| Individual progeny | 0.182 ± .102 |
| Mean of the progeny | 0.172 ± .114 |
| 2. Regression of offspring on sire | 0.388 ± .180 |
| 3. Regression of offspring on mid-parent: | |
| Individual progeny | 0.016 ± .038 |
| Mean of the progeny | 0.018 ± .049 |
| 4. Sib analysis: | |
| Paternal half-sib correlation | 0.104 ± .088 |

*Adjusted data

TABLE IX

ESTIMATES OF HERITABILITY OF AVERAGE DAILY GAIN*

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of offspring on dam: | |
| Individual progeny | 0.134 ± .112 |
| Mean of the progeny | 0.140 ± .126 |
| 2. Regression of offspring on sire | 0.330 ± .320 |
| 3. Regression of offspring on mid-parent: | |
| Individual progeny | 0.101 ± .028 |
| Mean of the progeny | 0.124 ± .037 |
| 4. Sib analysis: | |
| Paternal half-sib correlation | 0.160 ± .101 |

*Adjusted data

TABLE X

ESTIMATES OF HERITABILITY OF 120-DAY WEIGHT*

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of offspring on dam: | |
| Individual progeny | 0.178 ± .110 |
| Mean of the progeny | 0.188 ± .128 |
| 2. Regression of offspring on sire | 0.218 ± .261 |
| 3. Regression of offspring on mid-parent: | |
| Individual progeny | 0.104 ± .028 |
| Mean of the progeny | 0.099 ± .038 |
| 4. Sib analysis: | |
| Paternal half-sib correlation | 0.189 ± .189 |

*Adjusted data

paternal half-sib correlations were calculated, are given in Appendix Tables XVI to XXI.

The estimates of heritability obtained by using regression of offspring on sire are obviously inflated by larger sampling errors than are involved in other estimates. This extra sampling error is expected in view of the small number of sire groups and is reflected in the large standard errors of these estimates. The lower magnitude of estimates of heritability based on regression of offspring on mid-parent may be due to reduction in parental variance resulting from averaging the records of both parents. However, these estimates may be influenced in an unpredictable manner by differences in the variances of male and female parents. A test of homogeneity of these variances indicated significant ($P < .05$) differences between sire and dam variances. These differences between sire and dam variances probably resulted from the inability to adjust appropriately the sires' values for environmental effects using adjustments derived from analyses of data from this flock since six of the sires represented were developed in other flocks. In data from animals all of which were developed in the same flock the variance among dams would be expected to be larger than the variance among sires since any selection practiced, if effective, would reduce the variance among sires more than the variance among dams because selection among males is usually considerably more intense than that among

females. However, in the present study variances among sires were larger than variances among dams. The effect of selection was apparently more than offset by the fact that approximately a third of the sires involved were introduced from other flocks. In view of the fact that adjustments which might be applied to make the variances homogeneous would influence the portion of genetic variance remaining in the adjusted data, it seemed preferable to calculate separate estimates for each sex, i.e., by regressing male offspring on sire and female offspring on dam. The estimates of heritability thus obtained are shown in Table XI. The similarity of the two estimates for each trait can be considered circumstantial evidence for the validity of the estimates.

There is no statistical testing procedure available for comparing the heritability estimates obtained from paternal half-sib correlations to those obtained by the other methods which involved regression. However, it is possible to test statistically the differences among differences among different regression coefficient estimates and thus indirectly determine the significance of differences among estimates of heritability derived from different regression coefficient estimates. Such a test applied to the regression coefficients calculated here indicated no significant differences among the regression coefficients except for the coefficients of regression of offspring on

TABLE XI

ESTIMATES OF HERITABILITY*

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of male offspring on sire: | |
| Birth weight | 0.109 ± .091 |
| Average daily gain | 0.204 ± .116 |
| 120-day weight | 0.123 ± .131 |
| 2. Regression of female offspring on dam: | |
| Birth weight | 0.164 ± .102 |
| Average daily gain | 0.182 ± .069 |
| 120-day weight | 0.146 ± .098 |

*Adjusted data

sire which were significantly ($P < .05$) larger than the other regression coefficients for each trait. Even though it is not possible to test statistically the differences between the paternal half-sib estimates and the parent-offspring estimates, it seems likely that the paternal half-sib estimates are not significantly different from any of the parent-offspring estimates except the sire-offspring estimates since the paternal half-sib estimates are within the range of the parent-offspring estimates other than those obtained from the regression of offspring on sire.

The estimates of heritability from unadjusted data are presented in Tables XII, XIII and XIV. The only conclusion which can be drawn from observation of these estimates and comparison of them with estimates from adjusted data is that adjustment of data for statistically assessable effects is essential if reliable and meaningful estimates of heritability are to be obtained.

In the present study, there were no significant differences between heritability estimates obtained using individual progeny values and those obtained using progeny means in the regression of offspring on dam or in regression of offspring on mid-parent. Using individual progeny values necessitates repeating the parent value as an X value with each offspring's value as a Y value in computation of sums of squares and sums of products. This repetition of parent values could produce an artificial reduction in parent

TABLE XII

ESTIMATES OF HERITABILITY OF BIRTH WEIGHT (UNADJUSTED DATA)

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of offspring on dam: | |
| Individual progeny | 0.045 ± .108 |
| Mean of the progeny | -.053 ± .132 |
| 2. Regression of offspring on sire | -.094 ± .086 |
| 3. Regression of offspring on mid-parent: | |
| Individual progeny | -.041 ± .029 |
| Mean of the progeny | -.076 ± .035 |
| 4. Sib analysis: | |
| Paternal half-sib correlation | 0.057 ± .072 |

TABLE XIII

ESTIMATES OF HERITABILITY OF AVERAGE DAILY GAIN
(UNADJUSTED DATA)

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of offspring on dam: | |
| Individual progeny | -.035 ± .120 |
| Mean of the progeny | -.083 ± .046 |
| 2. Regression of offspring on sire | 0.508 ± .400 |
| 3. Regression of offspring on mid-parent: | |
| Individual progeny | 0.321 ± .021 |
| Mean of the progeny | 0.295 ± .031 |
| 4. Sib analysis: | |
| Paternal half-sib correlation | 0.292 ± .124 |

TABLE XIV

ESTIMATES OF HERITABILITY OF 120-DAY WEIGHT (UNADJUSTED DATA)

| Method of Estimation | Estimate ± Standard Error |
|---|---|
| 1. Regression of offspring on dam: | |
| Individual progeny | 0.036 ± .122 |
| Mean of the progeny | -.039 ± .150 |
| 2. Regression of offspring on sire | 0.468 ± .360 |
| 3. Regression of offspring on mid-parent: | |
| Individual progeny | 0.299 ± .025 |
| Mean of the progeny | 0.274 ± .098 |
| 4. Sib analysis: | |
| Paternal half-sib correlation | 0.189 ± .112 |

variance which would tend to bias positively the estimate of the regression coefficient. These statistical objections to the use of individual offspring values make the use of progeny means somewhat preferable even though the heritability estimates will be only slightly different using means from those obtained using individual values.

Reeve (1952) suggested that assortive mating increases the mid-parent variance, thereby increasing the precision of the estimate of heritability by the mid-parent methods as compared to other methods. Dawson (1964) disagreed with this and argued that random mating would be preferable to assortive mating, since using the mid-parent method data from assortive mating would permit overestimation of heritability to the extent that maternal effects are important. In the flock supplying the data used here ewes were randomly assigned to rams for breeding, and there were no significant differences between estimates based on regression on mid-parent and those obtained from intra-sire regression of offspring on dam. The results obtained here actually throw no light on this point of difference between Reeve (1952) and Dawson (1964) since the present results show no significant indication of variation in maternal influences in the case of any of the three traits studied.

The estimates of heritability obtained here clearly show that regression of offspring on sire should not be used as a basis for estimating heritability when the number of

sires represented is small. Even in data from large flocks with many more sires represented, estimates based on regression of offspring on sire would be subject to larger sampling errors than estimates based on regression of offspring on dam.

Since the estimates based on paternal half-sib correlations differ only slightly from those based on intra-sire regression of offspring on dam, the results of the present study provide no significant evidence that variation in maternal effects is important with respect to the three traits studied. However, the possible existence of important maternal variance would make estimates of heritability based on paternal half-sib correlations preferable to those based on regression of offspring on dam since maternal variance does not contribute to the correlation among paternal half-sibs, whereas, the covariance between dam and offspring contains one-half of whatever variance due to maternal differences exists in the data. It is unlikely that any logical adjustment for maternal effects would ever be perfectly effective in removing this variance from the data.

The phenotypic, genetic and environmental correlations among birth weight, average daily gain and 120-day weight are given in Table XV. Undoubtedly the genetic correlations obtained in this study contain large sampling errors because of relatively small size of the sample of

TABLE XV

PHENOTYPIC, GENETIC AND ENVIRONMENTAL CORRELATIONS AMONG BIRTH WEIGHT, AVERAGE DAILY GAIN AND 120-DAY WEIGHT OF LAMBS

| Traits | Phenotypic | Genetic | Environmental* |
|---|---|---|---|
| Birth weight - | | | |
| Average daily gain | 0.159 ± .211 | 0.759 ± .340 | -.215 |
| Birth weight - | | | |
| 120-day weight | 0.261 ± .259 | 0.911 ± .243 | -.271 |
| Average daily gain - | | | |
| 120-day weight | 0.910 ± .083 | 0.979 ± .042 | 0.878 |

*No appropriate formula for the standard error of an environmental correlation estimate has yet been developed.

data on which they were based. The values shown in Table XV are unexpectedly large and probably grossly overestimate the parameters. Van Vleck and Henderson (1961) stated that at least 1000 sets of observations are necessary to obtain reasonably accurate estimates of genetic correlations. Smaller sample sizes such as used here would yield more accurate estimates if the traits involved were highly heritable.

# CHAPTER V

## SUMMARY

Records of birth weight, average daily gain and 120-day weight of 447 purebred Hampshire lambs in 19 sire groups born from 1952 to 1968 at the Main Experiment Station of The University of Tennessee Agricultural Experiment Station were used to calculate estimates of heritability before and after least-squares adjustments of the records for the significant effects of age of dam, month of birth, sex of lamb, type of birth, type of rearing and year of birth. Estimates from unadjusted data were erratic and inexplicable, whereas, those from adjusted data were reasonable and consistently positive.

Estimates of heritability from regression of offspring on dam, from regression of offspring on mid-parent and from paternal half-sib correlation were very similar in magnitude, but estimates from regression of offspring on sire were much larger than the other regression estimates and had much larger standard errors reflecting larger sampling errors due to the small number of sires.

The heritability estimates ranged from 0.016 $\pm$ .038 to 0.388 $\pm$ .180 for birth weight, 0.101 $\pm$ .028 to 0.330 $\pm$ .320 for average daily gain and 0.099 $\pm$ .038 to 0.218 $\pm$ .261 for 120-day weight, the largest estimates being those

obtained from the regression of offspring on sire. There were no appreciable differences among the estimates obtained from regression of offspring on dam, regression of offspring on mid-parent and from paternal half-sib correlations, but the estimates obtained from regression on sire were much larger and had much larger standard errors than those obtained by other methods. It was concluded that heritability estimates based on regression of offspring on sire cannot be as accurate as estimates obtained by the other methods because of the much larger sampling errors to which they are subject as a result of small numbers of sires.

In view of non-significance of differences between estimates obtained using individual offspring values and those obtained using progeny means in the parent-offspring methods and some statistical advantages of using progeny means over using individual offspring values, it was concluded that use of progeny means is slightly preferable to use of individual offspring values.

There was no significant indication of the existence of variance due to maternal differences with respect to the three traits studied here as indicated by the lack of significance between paternal half-sib estimates of heritability, which receive no contribution from maternal variance, and parent-offspring estimates which contain a contribution from whatever maternal variance exists.

Extremely large estimates of genetic correlations

were obtained (ranging from 0.76 to 0.98), and it was concluded that these are gross overestimates of the respective parameters due to extremely large sampling errors to which estimates of genetic correlation are subject in data from samples of animals numbering many fewer than 1000 head.

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## LITERATURE CITED


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# APPENDIX

TABLE XVI

ANALYSIS OF VARIANCE OF BIRTH WEIGHT FOR CALCULATION OF PATERNAL HALF-SIB CORRELATION*

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | Composition of Mean Square |
|---|---|---|---|---|
| Between sires | 18 | 64.273 | 3.571 | $s^2 + k\, s_S^2$ |
| Within sires | 397 | 882.741 | 2.224 | $s^2$ |
| Total | 415** | 947.014 | | |

$k = 22.6$

$s_S^2 = 0.0596$

$$\text{Estimate of heritability} = \frac{4\ (0.0596)}{(0.0596 + 2.224)} = 0.104$$

*Analysis of adjusted data

**31 degrees of freedom sacrificed as a result of adjusting the records for environmental effects

TABLE XVII

ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN FOR CALCULATION OF PATERNAL HALF-SIB CORRELATION*

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | Composition of Mean Square |
|---|---|---|---|---|
| Between sires | 18 | 0.242 | 0.0134 | $s^2 + k\, s_S^2$ |
| Within sires | 396 | 2.724 | 0.00688 | $s^2$ |
| Total | 414** | 2.966 | | |

$k = 22.6$

$s_S^2 = 0.000287$

$$\text{Estimate of heritability} = \frac{4(0.000287)}{(0.000287+0.00688)} = 0.160$$

*Analysis of adjusted data

**32 degrees of freedom sacrificed as a result of adjusting the records for environmental effects

TABLE XVIII

ANALYSIS OF VARIANCE OF 120-DAY WEIGHT FOR CALCULATION OF PATERNAL HALF-SIB CORRELATION*

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | Composition of Mean Square |
|---|---|---|---|---|
| Between sires | 18 | 4272.91 | 237.38 | $s^2 + k\, s_S^2$ |
| Within sires | 396 | 44228.84 | 111.69 | $s^2$ |
| Total | 414** | 48501.75 | | |

$k = 22.6$

$s_S^2 = 5.562$

$$\text{Estimate of heritability} = \frac{4(5.562)}{(5.562 + 111.69)} = 0.189$$

*Analysis of adjusted data

**32 degrees of freedom sacrificed as a result of adjusting the records for environmental effects

TABLE XIX

ANALYSIS OF VARIANCE OF BIRTH WEIGHT FOR CALCULATION OF PATERNAL HALF-SIB CORRELATION (UNADJUSTED DATA)

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | Composition of Mean Square |
|---|---|---|---|---|
| Between sires | 18 | 70.75 | 3.93 | $s^2 + k\, s_S^2$ |
| Within sires | 428 | 1268.32 | 2.96 | $s^2$ |
| Total | 446 | 1339.07 | | |

$k = 22.6$

$s_S^2 = 0.043$

$$\text{Estimate of heritability} = \frac{4(0.043)}{(0.043 + 2.96)} = 0.057$$

TABLE XX

ANALYSIS OF VARIANCE OF AVERAGE DAILY GAIN FOR CALCULATION OF PATERNAL HALF-SIB CORRELATION (UNADJUSTED DATA)

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | Composition of Mean Square |
|---|---|---|---|---|
| Between sires | 18 | 1.610 | 0.089 | $s^2 + k\, s_S^2$ |
| Within sires | 428 | 13.716 | 0.032 | $s^2$ |
| Total | 446 | 15.326 | | |

$k = 22.6$

$s_S^2 = 0.00252$

$$\text{Estimate of heritability} = \frac{4(0.00252)}{(0.00252 + 0.032)} = 0.292$$

TABLE XXI

ANALYSIS OF VARIANCE OF 120-DAY WEIGHT FOR CALCULATION OF PATERNAL HALF-SIB CORRELATION (UNADJUSTED DATA)

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | Composition of Mean Square |
|---|---|---|---|---|
| Between sires | 18 | 5220.36 | 290.02 | $s^2 + k\, s_S^2$ |
| Within sires | 428 | 58495.58 | 136.67 | $s^2$ |
| Total | 446 | 63715.94 | | |

$k = 22.6$

$s_S^2 = 6.78$

$$\text{Estimate of heritability} = \frac{4(6.78)}{(6.78 + 136.67)} = 0.189$$

# VITA

G. Srinivasan was born in Madras State, India, on April 5, 1939. He was graduated from a Catholic High School in 1954. He attended the University of Madras and received a Bachelor of Veterinary Science degree in 1961. He worked as a Veterinarian in Madras State for two years. He obtained a Master of Veterinary Science degree from the University of Bombay with a major in Genetics and Animal Breeding.

He entered The University of Tennessee in September 1965 and received a Master of Science degree in December 1966 with a major in Animal Husbandry. He obtained a research assistantship to work toward an advanced degree in Animal Breeding. He obtained the Doctor of Philosophy degree in December 1969.

He is a member of the American Society of Animal Science and the American Genetic Association.