GENETIC PARAMETERS OF CARCASS TRAITS IN THE NEW ZEALAND ROMNEY

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ABSTRACT

The data used in the present study were collected from wether lambs of a flock of New Zealand Romney sheep started at Massey Agricultural College, Palmerston North, in 1944. The lambs, 474 in number, were the progeny of 12 mixed-age rams born over a period of three years from 1944 to 1947. Altogether, 25 carcass traits were analysed.

A linear mathematical model, which included sire, year and type of birth and rearing as the main effects, a sire-year interaction term and age at slaughter as a covariate, was used to describe the data. The estimates of the various terms in the model were derived by least-squares procedures. Preliminary analyses included determining the significance of the sire-year interaction in each of the 25 traits. In traits where the sire-year interaction were found not significant, the main effects and regression term were estimated.

Variance components were estimated using Henderson's Method III. Heritability was estimated by paternal half-sib correlation. The procedures used in the estimation of covariance components were, in many ways, similar to those used in the analysis of variance components. In the former, the sums of crossproducts for the appropriate effects were computed from the difference

between two reductions in sums of crossproducts.

Sire-year interaction was found to be significant in four traits, namely width of gigot (G) and the ratio of the weight of the forequarter to the hindquarter (FQ/HQ) at the 1% level of probability and, carcass grade and cannon bone weight at the 5% level of probability.

Estimates of heritability of carcass traits are as follows:

Internal measurements: A, 1.11 ± 0.27; B, 0.20 ± 0.12; C, 0.31 ± 0.14; D, 0.27 ± 0.13; X, 0.09 ± 0.08; Y, 0.28 ± 0.14; J, 0.35 ± 0.15.

Measurements indicative of bone length and weight: F, 0.73 ± 0.22; T, 0.62 ± 0.20; R, 0.55 ± 0.19; P, 0.70 ± 0.22; Cannon bone length, 0.80 ± 0.23; cannon bone weight, 1.01 ± 0.26.

Measurements indicative of width or depth of body: G, 0.41 ± 0.17; WR, 0.14 ± 0.10; WF, 0.09 ± 0.08; WTh, 0.37 ± 0.16; Th, 0.67 ± 0.21.

Measurements indicative of length of body: K, 0.34 ± 0.15; L, 0.55 ± 0.19; H, 0.20 ± 0.12.

"Other" carcass traits: carcass weight, 0.03 ± 0.04; carcass grade, -0.04; carcass total, 0.34 ± 0.15; FQ/HQ, 0.00.

Estimates of genetic correlations showed large sampling errors. The correlations between the ratio of the weight of the forequarter to the hindquarter (FQ/HQ) and the other carcass traits were not included because the sampling errors were very large. In the majority of cases, the genetic correlations were of the same sign as the phenotypic correlations.

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CHAPTER 1

INTRODUCTION

The development of reliable methods for identifying the desirable carcass is of paramount importance to the sheep industry and is an essential prerequisite to any selection programme aimed at improving carcass quality. The methods must be based on sound research findings. Only then can the traits found to contribute significantly to carcass quality be incorporated in selection and production programmes. Unfortunately, not all this information is available currently.

From the available information, it appears that there is little to be gained by means of crossbreeding for carcass quality. According to Bradford (1967), "...available information supports the conclusion that breed differences in carcass characteristics are not large ..." He added that "... if, as generally believed, heterosis in carcass characteristics is not important, then breeding for improved carcass quality reduces to a problem of within-breed selection ..." At present, information on the genetic parameters of carcass traits in sheep is lacking and many important questions are still unanswered. Botkin, Field, Riley, Nolan and Roehrkasse (1969) stated that more information is available on fleece traits than on carcass traits of lambs and attributed this to the fact that fleece traits are easier to measure and/or, to select for visually. To this may be added the high cost of progeny testing for carcass traits. The limited evidence available so far on sheep and other species indicate that carcass traits have heritabilities in the medium to high range.

Reliable estimates of heritabilities of carcass traits are essential in determining whether single-trait selection will be effective in altering the traits and for the optimum design of selection programmes. In the latter context, selection on the basis of individual performance is the best for traits with high heritabilities and would yield the most rapid progress. For traits of low heritabilities, selection on the basis of family information would be the usual choice. However, for the improvement of carcass quality, selection of breeding individuals cannot be made on the basis of their own performance because the traits can only be measured on carcasses and meat, not on live animals. Therefore, selection must be made from the information provided by their progeny. The details of the procedures involved in progeny testing will not be dealt with here. It suffices to say that this method is not only time- and labour-consuming but also very costly. Over a short period of time, progeny testing may appear to be of little benefit but long-term considerations might very well indicate that it is an economically justifiable proposition.

Estimates of genetic correlations among carcass traits in lambs, although they are of extreme importance, are also lacking at present. They are useful for predicting the kinds of problems that may arise as a result of intense directional selection for specific traits. They may also bring to light those traits which, due to their low heritabilities, may not be responsive to direct selection, but may be improved by indirect selection applied to other traits. It can be shown that indirect selection has the advantage over direct selection when the "secondary" character has a much higher heritability than the desired character, when the genetic correlation between the two traits is high, and when a higher intensity of selection can be applied to the secondary character than to the desired character.

An improvement programme for carcass traits is bound to involve selection for several traits simultaneously. For this purpose, three methods are available. The first, "tandem" selection involves selecting in turn for each trait singly. In the second method, called "independent culling levels", the characters are selected simultaneously, rejecting all individuals that fail to come up to a certain level for each character regardless of what their values are for the other characters. The third method involves selection for several characters on the basis of a selection index. Hazel and Lush (1943) have shown that index selection is the most efficient of the three when proper weight is given for each trait. The construction of a selection index requires estimates of the following parameters:

i). phenotypic and additive genetic variances of each trait,

ii). phenotypic and additive genetic covariances between each pair of traits and,

iii). relative economic values of each trait.

Aspects of progeny testing of rams and estimation of genetic parameters of fleece characters in the New Zealand Romney sheep have been investigated by Rae (1946, 1957). Estimation of genetic parameters of some carcass traits in this breed forms the main objective of the present study.

CHAPTER 2

REVIEW OF LITERATURE

I. CARCASS WEIGHT AND CARCASS MEASUREMENTS AS INDICES OF CARCASS COMPOSITION

A. Carcass weight as an index of carcass composition

A knowledge of any existing relationship between carcass weight and carcass components would be highly desirable in many animal production experiments. Barton and Kirton (1958) stated that in many of these experiments, "...carcass weight is used as the sole criterion for the effectiveness of the treatments and of the nutritional status of the animals involved. In these experiments some knowledge of the carcass components would be desirable in order to assess any effects on the various tissues."

Smith-Pilling and Barton (1954), and Kirton (1957) noted that the high correlation between carcass weight and weight of carcass fat indicated that this tissue was a major factor influencing carcass weight in the mature ewe. As a result of their studies to determine the nutritive value of New Zealand lamb and mutton, Shorland, de la Mare, Sorrel and Barnicoat (1947) concluded that weight of carcass may be used as a simple indicator of carcass composition, but in general, would not distinguish between animals of different breed, sex or growth rate. Clarke and McMeekan (1952) noted that, within quality grades in lambs, there is a decrease in the proportion of fat with increasing carcass weight. Earlier, McMeekan (1940), studying the influence of the plane of nutrition on the growth and development of pigs, noted a similar change in carcass components with increase in carcass weight.

Barton and Kirton (1958) reported that the correlation between carcass weight and dissectible fat was 0.94 in wether lambs, 0.87 in ewe lambs and 0.94 in mature ewes, while that between carcass weight and dissectible muscle was 0.95, 0.89 and 0.87 respectively. From these findings they concluded that carcass weight could be used to predict carcass composition with an acceptable degree of accuracy. However for a more accurate estimation of carcass composition, Kirton and Barton (1962) recommended the complete dissection of any one of the four parts of the right side, namely leg, loin, rib cut and fore part. The positive correlations existing between carcass weight and carcass composition were also reported by Khandekar, Golstone and McManus (1965), and Timon and Bichard (1965).

Work on lamb carcasses belonging to several breeds, performed by Southam and Field (1969) in the United States, showed that as carcass weight increased there was an increase in percent kidney fat, fat depth over l.dorsi and bodywall thickness. As a result of increased fat, there was a decrease in the estimated percent retail yield. Consumer preference studies showed that retail cuts from 30 kg.

carcasses were preferred over those from 23 kg carcasses, although both were within the same finish group. As a result of these findings, the workers suggested that retailers process more heavy, properly-finished carcasses because they would benefit from the increased weight of salable cuts per unit cost when compared to carcass weights which they then preferred.

B. Carcass measurements as indices of carcass bone content

Linear measurements on the carcass are, in general more indicative of the amount of bone than of the other two major tissues, muscle and fat. Realizing this fact, McMeekan (1941) stated that "... the reasons for this view are simply that all such measurements will depend largely upon the size of the animal, which is due in a very large measure to its 'frame' or skeletal size." However, he cautioned that "... the very fact that such measures are affected to some extent by the flesh cover of the animal will reduce their reliability even as indices of skeletal development." His work on bacon-pig carcasses showed that no external measurements were highly enough correlated with the total weight of skeleton for any of them to be used individually for predictive purposes. Length of leg and length of fore trotter + arm were the two length measurements most highly correlated with the amount of bone in the carcass.

The two most commonly used external measurements on the carcass as indices of skeletal weight in sheep are length of leg (F) and length of tibia + tarsus (T). Of these two, length of tibia + tarsus gives a direct measure of bone length and is more useful since it can be measured with greater precision, and is not as much affected by flesh cover as measurement F. As stated by Pálsson (1939), "... the weight of a bone depends on its length, thickness and density. In the limb bones ..., length growth is likely to contribute more to their weight than thickness growth." It would, therefore, be too much to expect a perfect correlation between the length measurement of any bone and total skeletal weight in the carcass. Thus, with such an expectation, it did not come as a surprise to Pálsson when he found that length of tibia + tarsus was the only external carcass measurement strongly correlated ($r = 0.82$) with total weight of bone in wether lambs. However, the relationship was not significant in wether hoggets. He attributed this difference to the fact that length growth in bones was an early-developing character. In lambs, the tibia and tarsus were still actively growing in length while in hoggets at about one year of age, these bones had practically reached their ultimate lengths while still actively growing in thickness. Walker and McMeekan (1944) showed that in Canterbury lamb the product of this measurement and width of gigots (T X G) provided a better index of total weight of bone than measurement T alone.

Recent evidence supporting the usefulness of employing length of leg and length of tibia + tarsus as indicators of carcass bone content came from the work of Khandekar et al. (1965) and Barton (1976, unpublished data). It is, therefore, surprising to find that Timon and Bichard (1965) were able to provide evidence which disagreed with the findings of Pálsson. In their work involving Clun Forest wether lambs, length of leg and length of tibia were poorly correlated with carcass bone weight as well as carcass bone percentage regardless of carcass weight. In their opinion, the higher correlations obtained by Pálsson could be due to the greater weight range (40 to 60 lb) in the carcasses he used and the widely divergent nature of the breeds.

Linear measurements, such as F and T, are only estimates of the length of bones. For greater accuracy, it is desirable to make measurements directly on the entire bone, cleaned of the remaining muscle, fat and other tissues. In his search for the bones to be used as indices of carcass skeletal development, Hammond (1932) suggested that "... as the proportions of the body change with age and other circumstances, the best bone to use would be one which developed late in life, such as the femur ... Practical considerations, however, prevent the use of this bone as it is situated deep in the carcass and surrounded by meat." Alternatively, he recommended the connon bone since, among other things, it could be obtained without damaging the carcass, is reasonably large and could be easily cleaned. However, he cautioned that as the cannon bone is early-developing, its use to estimate total weight of bone in the carcass is only possible when a scale is prepared showing the relation of the cannon to total bone weight of the carcass at different ages. In estimating total bone weight in the carcass, Hammond worked out the ratio: total bones of carcass/one femur and total bones of carcass/one cannon.

Pálsson (1939) made use of the length, weight and weight : length ratio of the fore cannon as predictors of total bone weight in the carcass. He found that the length of the fore cannon was not as good an index as the length of tibia in lambs while the relationship was reversed in hoggets. Weight of a fore cannon bone, when carefully prepared, was almost as good as weight of all four cannon bones for predicting weight of bone in the carcass, thereby justifying the use of a single fore cannon. As expected, weight of a fore cannon afforded a better measure of total carcass bone than length. Khandekar, et al. (1965), on the other hand, found length of a fore cannon to be more strongly correlated ($r = 0.98$) than its weight ($r = 0.85$) with total weight of bone in the half-carcass. The weight : length ratio in Pálsson's work was correlated with weight of bone in the carcass only at the 5% level of significance in lambs while the correlation was significant at the 1% level in hoggets. Pálsson interpreted this as being due to the fact that thickness growth of bones contributed more to the weight of skeleton at the hogget stage than at the lamb stage when length growth was more important.

C. Carcass measurements as indices of the amount of muscle

As stated by Pálsson (1939), external carcass measurements are more indicative of skeletal development rather than development of muscle or fat. In his work on sheep, he was not able to find a relationship between any external measurement and the total weight of muscle in the carcass close enough for predictive purposes. However, when he used total muscle weight as a percentage of total bone weight (i.e., muscle : bone ratio), some useful relationships were found. Pálsson considered that the difference between the leg length and the length of tibia + tarsus (F - T) gave a very good indication of the muscle development in the leg area; the smaller the difference, the better would be the muscle content of the legs. Indeed, he found a strong negative correlation ($r = -0.93$) between F - T and the weight of muscle as a percentage of total bone weight in lambs. He used the width of gigot (G) expressed as a percentage of leg length (F), ($\frac{G}{F} \times 100$), as a measure of the compactness of the hindquarters and showed this to be highly correlated ($r = 0.87$) with the weight of muscle as a percentage of total bone weight in lambs. Using F - T also as an index of muscle development in the leg area, Khandekar et al. (1965) obtained results similar to those in the work of Pálsson although in their investigations the weight of muscle in the half-carcass was used. In contrast, Walker and McMeekan (1944) reported that F - T was poorly correlated with total muscle weight as a percentage of total bone weight in Canterbury lamb. The measurement T X G was found to be the most satisfactory index of total muscle weight while measurements F, T, F X T and G showed significant correlations of a lower order.

Although Kemp, Lambuth and Barton (1970) were unable to form any positive conclusion, the outcome of their work appears to show that certain width measurements were strongly negatively correlated with percent protein in the side of the carcass. These included width of gigot (G), maximum width of rib (WR), maximum width of forequarter (WF) and minimum width behind the scapulae (WTh).

The value of a carcass depends on its conformation as well as on its composition. In the past, carcass conformation has always been given priority by the meat trade as an indicator of carcass quality possibly due to the influence of the Hammond school. In this respect, carcasses that are short in the leg and blocky are believed to yield more high-priced cuts and edible meat than carcasses that are longer in the leg. Pálsson (1939) insisted upon the fact that for meat production the legs of sheep should be as short as possible. The report by Khandekar et al. (1965) that they obtained a high negative correlation (r = -0.82) between leg length and total weight of muscle in the half-carcass was in direct support of Hammond's and Pálsson's views.

While it is true that the length of leg is of importance in being related to the shape of the hindquarters, the more blocky carcasses yielding larger cuts than the leggy ones, the strong relationship (r = 0.75) between leg length and muscle weight in the carcass reported by Walker and McMeekan (1944) appears to suggest that in Canterbury lamb the leggy carcasses carried more muscle than the blocky carcasses. Kirton and Pickering (1967), from their work on 85 pairs of lambs, half of which had been selected for blocky conformation and half leggy conformation, reached the conclusion that the blocky carcasses had no superiority in terms of meat content or proportion of high-priced cuts. Palatability studies also did not support the commonly-held belief that roasts of leggy carcasses dry out excessively during cooking. On the basis of muscle-by-muscle dissection of a large number of lamb carcasses of the Southdown and Romney breeds and their cross, Fourie (1965) also concluded that the blocky carcass had no advantage over the leggy carcass in muscle content.

A lot of time and effort must have been spent in an attempt to establish the relationship between internal measurements on the cut surface usually made at the level of the last rib and total muscle in the carcass. The measurements most commonly used as indices are the cross-sectional length (A) and depth (B) of the l. dorsi muscle. Pálsson (1939) used these as indices of carcass muscle weight and showed that A was the better index in lambs while B was the better in hoggets. He attributed this difference to the early-developing nature of the "length" of the eye muscle and the late maturity of the depth measurement. Using different combinations of internal measurements alone, he found that A + B and 2A + B gave the most satisfactory correlations with muscle weight in lambs. $^{L}/10$ + A + B, in which L measures body length, was a good index provided by a combination of internal and external measurements in both lambs and hoggets. Walker and McMeekan (1944) anticipated measurement A to provide a better indication of muscle content in the carcass and, indeed, found this to be the case. Khandekar _et al_. (1965) concluded that measurement B was an excellent index of total muscle in the carcass after finding a coefficient of correlation ($r = 0.99$, $p < 0.001$) which approaches unity. However, the true relationship as implied by the extremely high correlation is open to question. Kemp _et al_. (1970) found that measurement B was negatively correlated ($r = -0.47$) with percent protein in the side of the carcass while measurement A was poorly so correlated. In contrast, results provided by Barton (1976, unpublished data) indicate that measurement A was positively, though not strongly, correlated with percent protein ($r = 0.39$) and percent lean ($r = 0.55$) in the half carcass while measurement B was poorly correlated with these.

The relationship between measurements A and B on the eye muscle and the total weight of muscle were first investigated in pigs by McMeekan (1941). In the carcasses he studied, weight of muscle varied from 22.5 to 33.0 kg and although A and B were both significantly correlated to this, neither relationship was sufficiently high to warrant the use of the measurements singly in predicting weight of muscle. The best relationship was provided by a combination of the measurements, 2A + B.

The cross-sectional area of eye muscle is the more commonly used index of carcass muscling than the linear measurements A and B. It may be measured by means of several methods. A tracing of the boundary of the cross-sectional surface of the eye muscle may be made and the area within it measured with a planimeter. If a planimeter is not available, the area may be estimated by superimposing a grid on the tracing and counting the squares. Otherwise, the product of the linear measurements A and B (A X B) may be taken as an estimate of the true area. Bodwell, Harrington and Pomeroy (1959), in an investigation comparing the accuracy of the three methods in beef carcasses, found the planimeter method the most accurate. The grid method, although some 25% less accurate than the planimeter method, was sufficiently repeatable for experimental use. The true area estimated by the product A X B was insufficiently accurate for experimental use.

Branaman (1940) measured the area of eye muscle in the half carcasses of Hampshire and Southdown lambs by means of the planimeter and reported that this measurement was a good indicator of lean weight. However, he did not provide correlation coefficients to support his claim. Working on lambs, Timon and Bichard (1965) found that the area of eye muscle as obtained by the planimeter method was no better an index of carcass muscle weight than the area estimated by A X B although correlations were positive in both. According to Judge, Martin and Outhouse (1966) area of eye muscle was a poor indicator ($r = 0.07$) of percentage of edible portion.

McMeekan (1941) used A X B as an approximation of the area of eye muscle to show that a fairly strong relationship existed between this measurement and total weight of muscle in bacon pigs. In lambs, Walker and McMeekan (1944) found the relationship to be non-significant. Zobrisky, Brady, Lasley and Weaver (1959) reported that in their investigation the cross-sectional area of the loin eye was the single variable most highly correlated (r = 0.60) with the yield of total lean in the carcass. According to Weniger (1966) in his review on carcass value and meat quality, the following workers have reported similar correlations: Whiteman (1953), 0.68; Haring _et al_. (1957), 0.60; Sieburg (1957), 0.63; Kielanowski _et al_. (1954), 0.62.

As shown by Kropf (1962) the area of eye muscle is not constant along the length of the body and as such varies with respect to the location of the perpendicular cut made on the carcass. In fact, in Kropf's work on pig carcasses, the area increased from the third to the tenth thoracic vertebra and was larger at the first lumbar than at the third lumbar vertebra. In a study of the relative value of the eye muscle area at eight different locations on the pork carcass, Kline and Goll (1964) reported that the loin eye muscle area increased posteriorly from the fifth thoracic to the first lumbar vertebra, but remained constant from the first to the sixth lumbar vertebrae. However, they could find no evidence of any differences among the eight positions studied in the relationship between loin eye area and percent ham and loin. This, together with the high correlation of l. dorsi areas at different positions on the same carcass, prompted them to conclude that there was little to be gained in accuracy of predicting ham and loin from measuring loin eye area in more than one location. Kline and Hazel (1955) had arrived at a similar conclusion when comparing the area of eye muscle at the tenth and last ribs as predictors of percent lean cuts.

A review on the findings of many workers relating to correlations between eye muscle area and various measures of carcass leanness in beef cattle has been presented by Preston and Willis (1970). There was little consistency among the findings cited, but in general the correlations were low, particularly with respect to important parameters such as the percentage of first quality edible meat. Adjustment of eye muscle area for carcass weight tended to lower those parameters couched in terms of weight and to increase those expressed as a percentage. In view of the obviously low value of eye muscle area as a predictor of edible or total lean meat, Preston and Willis expressed surprise that this measurement should still feature in indices of carcass merit. However, they realized that eye muscle area should be as large as possible for consumer purchasing decisions. This view is apparently supported by Carpenter (1966) in the case of lambs.

D. Carcass measurements as indices of fat content

The relationships one would expect to find between linear carcass measurements and total fat in the carcass are best expressed by Walker and McMeekan (1944) in their statement: "Since fat deposits are largely independent of skeletal development, and since the primary dimension in regard to fat depots is that of depth, it would be unreasonable to expect any close association between linear carcass measurements and the total amount of fat in the carcass. Any such correlations as might exist would necessarily be purely fortuitous." By "linear" measurements they meant external carcass measurements.

Pálsson (1939), although generally agreeing with the fact that no external measurements were directly correlated with the weight of fat in the carcass, found a highly significant negative correlation, in both lambs and hoggets, when the weight of fat was expressed as a percentage of the weight of bones in the carcass and the length of leg (F) was used as an index. Khandekar, Goldstone and McManus (1965) reported a negative, but non-significant correlation ($r = -0.31$) between leg length and the weight of fat in the half-carcass. If significant, they pointed out, it would have indicated that the blockier the leg the better the fat cover of the carcass would be.

Of the many external measurements studied by Kemp, Lambuth and Barton (1970), the following were related to percent fat in the side of carcass : gigot width, G ($r = 0.57$); maximum width of rib, WR ($r = 0.63$); maximum width of forequarter, WF ($r = 0.66$); minimum width behind scapulae, WTh ($r = 0.76$); depth of thorax, Th ($r = 0.44$) and body length from pubic symphysis to the first rib, L ($r = 0.40$).

Development of fat on the transverse section of the last rib has been extensively used as a measure of the fatness of the carcass. Linear measurements of fat depth are made here and these include measurements C, D, J and Y. (The specifications for these measurements are given in detail in another section.) Pálsson (1939) found most of them to be good indices of the weight of fat in sheep carcasses. In his work, measurement C, which is fat depth over the eye muscle, was more strongly correlated with weight of fat in hoggets ($r = 0.94$) than in lambs ($r = 0.70$). According to him, this confirmed the fact that a measure of a late-developing character was not as good a guide to the composition of the body early in life as later. In bacon pigs, McMeekan (1941) showed that measurement C was the single measurement most closely related ($r = 0.97$) to total fat. In Pálsson's work, the sum of the three fat measurements ($C + J + Y$) was better related to carcass fat weight than measurement C in both lambs and hoggets. When various combinations of internal and external measurements were tried, he found $^{L}/10 \times (C + J + Y)$ to be the most satisfactory index, L in this case denoting carcass length. Timon and Bichard (1965) reported that measurements C and J individually, and their sum ($C + J$), were best related to carcass fat weight and carcass fat percentage. Other studies have used carcass fat percentage as the sole measure of carcass fatness. Latham, Moody and Kemp

(1966), for instance, found that fat thickness over the eye muscle at the 12th rib was indicative (r = 0.67) of the percentage of fat in the carcass while in the work of Kemp, Lambuth and Barton (1970), of all the measurements listed, fat depth measurements C, D, J and Y, also taken at the 12th rib, had the highest correlations with carcass chemical composition, including fat.

Backfat thickness has also featured prominently as a measure of the fatness of cattle. In 133 steers representing eight breeds, Ramsey, Cole and Hobbs (1962) were able to show that a single fat thickness measurement, or an average of three measurements, over the rib eye muscle was a good estimator of percent carcass fat. The correlations in their study were 0.82 and 0.80, respectively. The work of Field, Schoonover and Nelms (1966) on bull carcasses and, Powell, Huffman and Patterson (1968) confirmed the strong relationship between these two parameters. In the investigation of Allen, Merkel, Magee and Nelson (1968), fat thickness measured at the 12th rib ranged between 0.64 and 3.18 cm. in their carcasses. They found that the average of three measurements was slightly superior to a single measurement and gave correlations of 0.50 and 0.78 with carcass fat weight and percentage, respectively, and, 0.59 and 0.71 with excess fat weight and percentage, respectively.

"Measurements of the thickness of the subcutaneous fat layer at various points on the surface revealed when the carcass is split into two halves have long been taken as indicators of the general level of fatness of the pig", according to Harrington (1958).

Hankins and Ellis (1934) stated that the thickness of backfat was usually considered when forming an opinion on the fatness of a hog carcass and was generally regarded as a dependable, practical guide. In their study on 60 centre-split hog carcasses, thickness of backfat was measured at five different points. The average of these five measurements, designated the "average thickness of backfat", was found to have a correlation of 0.84 with the percentage of fat in the total edible portion of the carcass. Results in the literature confirm the fairly strong relationship which exists between backfat thickness and carcass measures of fatness, according to Weniger (1966).

On a pig carcass split into two halves, a cross-section of the m.gluteus medius (rump muscle), which encroaches slightly into the backfat layer at about the level of the femur, is revealed. This muscle serves as a reference point for three backfat measurements known as the "rump fat" measurements. McMeekan (1941) showed that the average of these three measurements was better correlated with total carcass fat than either the shoulder fat or the loin fat. Harrington (1958) quoted the findings of Kielanowski and Osinska (1954) which confirmed the fact that the shoulder and mid-back fat measurements were less closely related to carcass fatness than were the various rump fat measurements.

Measurement of backfat thickness using the common ruler and measuring tape can only be made in carcasses which are split longitudinally or cut transversely. In unsplit carcasses, the determination of such measurements poses some problems and other methods have to be used. Three instruments which deserve mention in this regard are the ruler probe, the "Lean Meter" and ultrasonics. Of these, the first to come into use is the ruler probe developed by Hazel and Kline (1952). It involves making an incision with a scalpel on the skin and pushing a narrow metal ruler with a blunt end through the soft fat to the firm tissue underneath. Sufficient resistance is encountered when the ruler reaches the juncture of the fat and firm tissue to indicate that the ruler has passed through the fat layer. The "Lean Meter" developed by Andrews and Whaley (1955) works on the principle that the electrical resistances of muscle and fat are different when detecting the change from fat to muscle as the probe is pushed into the body. Probing devices were employed satisfactorily on live pigs by Holland and Hazel (1958), and Walker-Love, Cormack and Laird (1958a, 1958b). Pearson, Price, Hoefer, Bratzler and Magee (1957) found little difference in the usefulness of the ruler probe or "Lean Meter" in estimating backfat thickness in live pigs. Gottsch, Merkel and Mackintosh (1961), and Brungardt and Bray (1963) reported using probing devices of some kind for measuring subcutaneous fat thickness of beef carcasses.

Temple (1957) was probably the first person to apply the principles of ultrasonics for measuring fat thickness in live animals, in this case cattle. According to Stouffer (1966), it was European workers, however, who adopted this technique for application on live hogs. With ultrasonic measurement of fat thickness in live animals becoming increasingly common, it is surprising to find that its use on carcasses has been minimal. This could be attributed to the fact that the velocity of ultrasonic impulses and, therefore, the accuracy of the measurement is affected by temperature as shown in the investigations of Muller-Haye (1965) and Horst (1963), quoted by Weniger (1966). The effect of temperature implies that measurement of backfat thickness on chilled carcasses are meaningless unless some kind of standardization is made. However, ultrasonic measurement of carcasses 15 to 20 minutes after slaughter at the slaughter house offers a very plausible alternative and is technically possible.

II. HERITABILITY OF CARCASS TRAITS

In a study made by Taneja (1958) involving a total of 557 Australian Merino ewe lambs, heritability estimates were determined for several characters of the live animals. The estimates, obtained by paternal half-sib correlation were: body depth, 0.01; body length, 0.00; body width, 0.27; cannon length, 0.24 and mutton score, 0.13. Although only live animal measurements were analysed in this study, the results would be expected to have some bearing on the heritability of carcass measurement data. This is so because measurements such as cannon length and body length taken on the live animal are indicative, to a certain extent, of similar measurements made on the carcass. The very low estimates obtained in that study were attributed to the fact that the sires and dams were highly selected and some sires were used in more than one selection group. These factors were thought to have reduced the additive genetic variance for the characters.

The heritability of skeletal measurements made on the lamb carcass are known to be high, usually in the range of 0.40 to 0.80. In a study reported by Bichard and Yalçin (1964), where Suffolk rams were mated to crossbred Border Leicester X Cheviot ewes and carcass measurements were recorded on the progeny, heritabilities of 0.40, 0.83 and 0.78 were found for cannon bone length, length of tibia + tarsus (T) and leg length (F), respectively. Although the last of the measurements is not a direct measure of bone length, it is a close enough estimate for most practical purposes. Rae (1946), however, produced estimates for leg length (F) and length of tibia + tarsus (T) which were much lower than those of Bichard and Yalçin (1964). His estimate for measurement F was 0.38 and for T, a negative value. He expressed surprise at the low values obtained for these two measurements which, from all available information, were expected to be strongly inherited. The low values were attributed to the small number of observations and, consequently, the large error likely to be present in the estimates. A further explanation given was that the leg length measurement (F) could not be taken very accurately because it was affected by the development of fat and muscle in the leg region while there was some doubt also on the accuracy of the T measurement. The heritability of 0.07 for cannon bone weight reported by Bichard and Yalçin (1964) was much lower than the value of 0.35 obtained by Munson (1966). However, Munson's work involved different breeds of lambs and he cautioned that his estimates of heritability should be considered as preliminary because they were based on a small number of observations and therefore subject to rather large sampling errors. Length of leg of the pig is a highly heritable character as suggested by the findings of many workers. The heritability estimates for this character have been consistently high, ranging from 0.46 in the study of Smith and Ross (1965) to 0.61 reported by King (1957). All evidence on pigs and sheep, therefore, point to the fact that skeletal measurements in livestock are from moderately to highly heritable while measurements indicating width and depth of the carcass are only moderately heritable. This implies that selection may be effective in bringing about genetic change in carcass conformation.

Carcass weight is apparently a trait of low to moderate heritability. Al-Barhawe (1966) and Dynes were reported by Carpenter (1968) to have obtained estimates of 0.30 and 0.25, respectively, for this trait. However, the reliability of the results from these studies was to be regarded with caution because in Carpenter's words they were "preliminary in nature". In analysing data obtained from crossbred progeny of 73 rams of Suffolk, Dorset Down, Hampshire and Southdown breeds, Bowman, Marshall and Broadbent (1968) obtained a value of 0.02 for this trait. The method used by the workers was paternal half-sib analysis and the low heritability of carcass weight is emphasized by the fact that the estimates were probably overestimates because no allowance was made for full-sibs included in the half-sib analysis. Four of the 10 traits in the study appeared to have a large amount of additive genetic variation. These were percentage leg, percentage best end, age at slaughter and eye muscle area with heritabilities of 0.23, 0.49, 0.28 and 0.53, respectively. The large amount of additive genetic variation in these traits suggested that worthwhile response may be expected from selection.

There is reason to believe that the heritability of carcass weight in pigs is either low or moderate. The estimate of 0.30 for pedigree pigs of the Large White breed presented by King (1957) was much higher than the values reported for sheep. The heritability of hot carcass weight estimated at 0.14 by Buxadé (1972) for the

Angeln Saddleback pigs was more in line with the values for sheep.

A low estimate of heritability for carcass weight ($h^2 = 0.11$) was also reported by Bowman and Hendy (1972) in a study involving the carcasses of 118 pedigree Poll Dorset Horn wether lambs. There is a close agreement in the estimates of heritability for the various traits obtained in this study and those reported by Bowman, Marshall and Broadbent (1968) even though different breeds were used and also the latter study included data on "rejected" carcasses while Bowman and Hendy (1972) excluded such data in their study. The heritabilities obtained by Bowman and Hendy (1972) for the different proportions of the carcass were as follows: percent shoulder, 0.01; percent leg, 0.16; percent best end, 0.35; percent loin, 0.32 and percent remainder, 0.03. From the relatively large heritabilities for percent best end, loin and, to a lesser extent, leg, they inferred that selection in an effort to change carcass proportions would be effective. However, the coefficients of variation for all the carcass proportions were very small, implying that there would not be any effective selection differential for these traits. On the other hand, selection for eye muscle area would be effective because the heritability is at least 0.14 and the coefficient of variation is also comparatively large (about 0.10).

Botkin, Field, Riley, Nolan and Roehrkasse (1969) collected data on 802 offspring of 58 ram lambs consisting of 435 ewe and 367 wether lambs of the Rambouillet, Columbia and Corriedale breeds and all possible crosses between them. Estimates of heritability for carcass traits were determined from these data by paternal half-sib correlation as well as by regression of offspring on sire. In general, they found that estimates of heritability obtained by paternal half-sib correlation were higher and had lower standard errors than those derived by the regression method. The different estimates by the two methods could have been due to several factors. First, there was more variation in weight between sires than between offspring because offspring were slaughtered at a relatively constant weight, whereas sires were slaughtered at a relatively constant age. Secondly, all lambs were contemporaries, which was not true when comparing sire and offspring in the regression method. Finally, the design of the experiment was such that estimates obtained by paternal half-sib correlation were the most reliable. According to Dickerson (1960), the regression method is likely to give estimates which are biased downward. The estimates of heritability obtained by Botkin _et al_. (1969) for the weights and percentages of the various cuts and tissues were as follows: trimmed loin weight, 0.28; trimmed rack weight, 0.19; trimmed shoulder weight, 0.42; trimmed leg weight, 0.51; retail cut weight, 0.40; lean weight, 0.39; bone weight, 0.28; percent fat, 0.54; percent bone, 0.23; percent lean, 0.40 and percent retail cuts, 0.39. Heritabilities of 0.17, 0.17 and 0.64 for percent carcass lean, percent carcass fat and percent carcass bone reported by Munson (1966), coupled with values given by Botkin _et al_. (1969) suggest that measures of carcass composition, in terms of the major tissues, are moderately heritable.

In beef cattle, the indications are that the heritabilities of percentage edible and first quality meat are moderately high, but slightly lower than those for fat thickness. The heritabilities of percent round, chuck, loin and rib reported by Christians, Chambers, Walters, Whiteman and Stephens (1962) for the Angus breed were 0.30, 0.46, 0.60 and 0.46, respectively.

Area of eye muscle and backfat thickness appear to be moderately to highly heritable in sheep. For eye muscle area, except for the values of 0.14 reported by Bowman and Hendy (1972) and 0.12 reported by Smith *et al*. (1968), all other estimates were larger than 0.3: Botkin *et al*. (1969), 0.34; Hillman, Menzies, Wheat, Mackintosh and Merkel (1962), 0.39; Carpenter (1963), 0.40; Timon (1965), 0.23 for *l. dorsi* area at the 12th rib and 0.55 for *l. dorsi* area at the 6th rib; Munson (1966), 0.51; Bowman, Marshall and Broadbent (1968), 0.53; Ray, Bell and Holland (1972), 0.53, 0.86, 0.38 and 0.61 for four different breeding groups; Al-Barhawe (1966), 0.90 and Borton (1961), 0.93.

The most common measure of fat depth in the sheep carcass is one made over the *l. dorsi* muscle, *i.e.*, measurement C, on the cut surface of the rib or loin. The heritability of this trait has been determined by various workers and their estimates were: Borton (1961), 0.04; Hillman *et al*. (1962), 0.21; Smith, Kemp, Moody and Cundiff (1968), 0.27; Timon (1965), 0.31 for rib fat depth and 0.44 for loin fat depth; Bowman and Hendy (1972), 0.40; Botkin *et al*. (1969), 0.51 and Ray *et al*. (1972), from 0.59 to 1.10 in four estimates. The reliability of the estimates of Ray and co-workers are open to question since the standard errors of the estimates in their study were large. The lowest standard errors for the estimates were in the "D" breeding group, where the average number of progeny per sire group was 3.7, whereas the largest standard errors were obtained for the "S" group, where the average progeny per sire was 2.5.

Backfat thickness and carcass length are perhaps the two most commonly studied traits in pigs as far as genetic parameters are concerned. King attributed this to the great importance placed upon measurements of backfat thickness made at the shoulder, mid-back and loin and on carcass length in the assessment of the carcass quality of pigs in commerce. Moreover, it is well-known that backfat thickness is a reliable indicator of the fat content of the carcass and, to a lesser extent,of the other components. The high values for the heritabilities of these two traits are widely known and well-documented in the literature. In an account of the Danish system of progeny testing of swine, Lush (1936) presented a value of 0.47 for backfat thickness. Dickerson (1947) put the value at 0.54 in pigs of Poland China, Danish Landrace and Landrace-Poland China crossbreds while Stothart (1947) found a value of 0.37 in Canadian bacon hogs. At this point, it is perhaps worthwhile to mention in passing that most of the estimates of genetic parameters in pigs are made in conjunction with progeny testing work.

King (1957) used the average of three measurements made on the shoulder, mid-back and rump as a measure of backfat thickness and showed that the heritability of this trait in British bacon pigs was 0.46. Smith, King and Gilbert (1962) found high heritabilities for measurements of backfat thickness over the shoulder ($h^2 = 0.62$), the mid-back ($h^2 = 0.73$) and the average of two measurements over the loin ($h^2 = 0.70$). When the average of two backfat measurements only were used, one made over the shoulder and the other over the loin, Smith and Ross (1965) obtained an estimate of heritability of 0.74.

It would be anticipated from the high heritability of backfat thickness measurements made on the centre-split carcass of the pig that the heritability of fat depth measurements taken on the cross-sectional surface of the transversely cut carcass would also be high. This is evidently so as results from the studies of Smith, King and Gilbert (1962) and Smith and Ross (1965) indicate. The estimates reported by Smith, King and Gilbert were: fat depth C, 0.65; fat depth J, 0.64, and fat depth K, 0.73. Those found by Smith and Ross (1965) were: fat depth C, 0.62 and fat depth K, 0.42.

Available information suggests that the heritability of the area of eye muscle in pigs is fairly similar to that in sheep; i.e., in the medium to high range. The various estimates that have been made are: Enfield and Whatley (1961), 0.79; Smith, King and Gilbert (1962), 0.35; Smith and Ross (1965), 0.49 and Buxadé (1972), 0.38. In their review on genetic parameters of carcass traits of beef cattle, Preston and Willis (1970) stated that "... The longissimus dorsi area is apparently a highly heritable trait with a median value of 0.60 - 0.70."

The only available estimates of heritability for the width measurement (A) and depth measurement (B) of the eye muscle are those made on the pig. King's estimate put the value at 0.29 for measurement B and Smith _et al_. (1962) put the heritabilities for measurements A and B at about equal, namely, 0.46 and 0.48, respectively. On the other hand, Smith and Ross (1965) presented a value of 0.65 for measurement A, which was almost twice the value of 0.38 they gave for measurement B.

Estimates of heritability of carcass length in sheep have been inconsistent. Low values of 0.0 and 0.09 were reported by Ray (1967) and Borton (1961), respectively. Higher values of 0.38 and 0.50 were found by Field, Botkin, Schoonover and Parker (1967) and Botkin _et al_. (1969), respectively. As stated earlier, carcass length plays a more important part in the assessment of the pig carcass and consequently it has featured more prominently in that species than in either sheep or cattle. Most of the heritability estimates for this character have been larger than 0.4, putting it in the moderately to highly heritable category. The following are some of the published estimates made by various workers: Lush (1936), 0.54; Dickerson (1947), 0.73; Stothart (1947), 0.42; Johansson and Korkman (1950), 0.62; Osterhoof (1956), 0.66; Fredeen and Jonsson (1957), 0.48; King (1957), 0.54; Enfield and Whatley (1961), 0.50; Jonsson and King (1962), 0.45; Smith, King and Gilbert (1962), 0.60 for carcass length to first rib and 0.78 for carcass length to atlas; Smith and Ross (1965), 0.87 and Buxadé (1972), 0.45.

The subjective nature of carcass grading, coupled with the fact that it is a composite character made up of many components, could account for the inconsistent estimates of heritability obtained in various analyses. This is strongly evident in beef cattle where estimates range from 0.00 (Magee *et al.*, 1958) to 0.84 (Knapp and Nordskog, 1946). In lambs, it appears that carcass grade is of low heritability, Botkin *et al.* (1969) obtained a value of 0.06 while Ray *et al.* (1972) obtained an estimate of 0.24 in one breeding group and 0.00 in each of three other groups.

The dearth of information on measures of depth and width of the carcass is quite apparent and no definite inference can be made regarding their heritabilities. However, Bichard and Yalçin (1964) reported heritabilities for width of gigot (G), circumference of gigot (G_c) and circumference of rump (R_c) of 0.02, 0.29 and 0.40, respectively, and from these estimates reached the conclusion that measurements assessing fleshing of the carcass were less heritable than skeletal measurements. Ray *et al.* (1972) obtained zero estimates of heritability for width of loin in two breeding groups and 0.20 and 0.09 for the other groups. The heritability for width of leg reported by Botkin *et al.* (1969) was 0.36; the estimates given by Ray *et al.* (1972) were 0.20, 0.09, 0.00 and 0.00. Smith, King and Gilbert (1962) and Smith and Ross (1965) used the maximum depth from sternum to the top of the vertebral column as a measure of carcass depth in the pig and found estimates of 0.34 and 0.56, respectively, for this measurement.

The estimates of heritability of carcass traits in sheep reported by various workers are summarized in Table 2.1.

TABLE 2.1 Published estimates of heritability of carcass traits in sheep.

TRAIT	HERITABILITY	AUTHORS
Length of tibia + tarsus (T)	0.83	Bichard and Yalçin (1964)
Length of leg (F)	0.38	Rae (1946)
	0.78	Bichard and Yalçin (1964)
Cannon bone length	0.40	Bichard and Yalçin (1964)
	0.84	Rae (1946)
Cannon bone weight	0.07	Bichard and Yalçin (1964)
	0.35	Munson (1966)
	0.84	Rae (1946)
Width of leg	0.20	Ray *et al.* (1972)
	0.09	
	0.00	
	0.00	
	0.36	Botkin *et al.* (1969)
Width of gigot (G)	0.02	Bichard and Yalçin (1964)
	0.33	Rae (1946)
Width of loin	0.00	Ray *et al.* (1972)
	0.00	
	0.20	
	0.09	

TABLE 2.1 (Continued)

TRAIT	HERITABILITY	AUTHORS
Circumference of gigot	0.29	Bichard and Yalçin (1964)
Circumference of rump	0.40	Bichard and Yalçin (1964)
Eye muscle area	0.14	Bowman and Hendy (1972)
	0.34	Botkin *et al*. (1969)
	0.39	Hillman *et al*. (1962)
	0.23	Timon (1965)
	0.55	
	0.51	Munson (1966)
	0.53	Bowman *et al*. (1968)
	0.53	Ray *et al*. (1972)
	0.86	
	0.38	
	0.61	
	0.90	Al-Barhawe (1966)
	0.93	Borton (1961)
Fat depth C	0.04	Borton (1961)
	0.21	Hillman *et al*. (1962)
	0.27	Smith *et al*. (1968)
	0.31	Timon (1965)
	0.44	
	0.40	Bowman and Hendy (1972)
	0.51	Botkin *et al*. (1969)
	0.59	Ray *et al*. (1972)
	1.04	
	1.09	
	1.10	
Carcass length	0.00	Ray (1967)
	0.09	Borton (1961)
	0.38	Field *et al*. (1967)
	0.50	Botkin *et al*. (1969)

TABLE 2.1 (Continued)

TRAIT	HERITABILITY	AUTHORS
Carcass weight	0.02	Bowman *et al*. (1968)
	0.11	Bowman and Hendy (1972)
	0.30	Al-Barhawe (1966)
	0.33	Botkin *et al*. (1969)
Carcass grade	0.06	Botkin *et al*. (1969)
	0.24 0.00 0.00 0.00	Ray *et al*. (1972)
Shoulder (%)	0.01	Bowman and Hendy (1972)
	0.05	Bowman *et al*. (1968)
Shoulder (wt.)	0.42	Botkin *et al*. (1969)
Leg (%)	0.16	Bowman and Hendy (1972)
	0.23	Bowman *et al*. (1968)
Leg (wt.)	0.51	Botkin *et al*. (1969)
Best end (%)	0.35	Bowman and Hendy (1972)
	0.49	Bowman *et al*. (1968)
Loin (%)	0.07	Bowman *et al*. (1968)
	0.32	Bowman and Hendy (1972)
Loin (wt.)	0.28	Botkin *et al*. (1969)
Carcass fat (%)	0.17	Munson (1966)
	0.54	Botkin *et al*. (1969)
Carcass bone (%)	0.23	Botkin *et al*. (1969)
	0.64	Munson (1966)
Carcass lean (%)	0.17	Munson (1966)
	0.40	Botkin *et al*. (1969)
Trimmed wholesale cuts (%)	0.11	Munson (1966)
Retail cut (%)	0.39	Botkin *et al*. (1969)
Retail cut (wt.)	0.40	Botkin *et al*. (1969)

III. GENETIC AND PHENOTYPIC CORRELATIONS AMONG CARCASS TRAITS

There is a general lack of information on genetic and phenotypic correlations among carcass traits in sheep and particularly for those traits being analysed in the present study. More work has been done on pigs.

It appears that "length", depth and area of the eye muscle are negatively correlated, phenotypically and genetically, to measurements of carcass fatness. In the work of Ray, Bell and Holland (1972) area of the loin eye muscle was negatively correlated, phenotypically, to fat trim and fat thickness in three out of four breeding groups of lambs. The genetic correlations were highly negative in three breeding groups (D, -0.28 and -0.87; L, -0.65 and -0.73; R, -1.24 and -0.85), but was highly positive in the other group (S, 0.33 and 1.01). Inconsistencies in the magnitude and sign of the estimated correlations between the breeding groups are very apparent in their study. They attributed this variation to either sampling errors associated with the sources of variance and covariance components or to real differences in gene frequencies among the groups. The standard errors of the genetic correlations were, in general, large because of small numbers of offspring per sire group and many of the genetic correlations were calculated to have absolute values greater than unity.

Bowman and Hendy (1972) estimated the phenotypic correlation between eye muscle area and backfat thickness at -0.05. Although they did not estimate the genetic correlation between these two traits, the knowledge that, in general, the genetic correlation between two traits is of the same sign as but greater in absolute value than the corresponding phenotypic correlation leads one to expect a negative genetic correlation between eye muscle area and backfat thickness.

Bradford and Spurlock (1972) reported a phenotypic correlation between area of the eye muscle and fat depth over the eye muscle of -0.26 and a genetic correlation of-0.32.

In pigs, King (1957) found that the phenotypic correlations between depth of eye muscle and the three backfat thickness measurements were close to zero. In addition, he found that the genetic correlation between depth of eye muscle and width of body was large (0.69) while those with thickness of backfat and belly were consistently negative, indicating that improvement towards a greater depth of eye muscle might be made by selecting pigs wide in the shoulder and thin in the streak and some progress might possibly be made by selecting pigs with a thin layer of backfat. Since the first two changes are undesirable, he concluded that the prospects of improving the eye muscle by indirect means appeared to be slight. Smith, King and Gilbert (1962) reported that the phenotypic correlations between backfat thickness and fat depth over the eye muscle and, measurements A, B and area of the eye muscle, were all negative, except for one positive value which was close to zero. The corresponding genetic correlations between these traits were also negative but again the absolute values were greater.

Negative phenotypic and genetic correlations between area of the eye muscle and backfat thickness in pigs have also been reported by Enfield and Whatley (1961), Smith and Ross (1965) and, Isler and Swiger (1969). In contrast, Jensen, Craig and Robison (1967) provided evidence which suggested that there was no relationship between the two traits at the genetic as well as phenotypic levels.

The antagonistic relationships between area of the eye muscle and backfat thickness has important implications. At the phenotypic level, the negative values indicate that backfat thickness may be used to predict roughly the area of the eye muscle, i.e., the carcass endowed with a thin layer of backfat would be expected to have a larger eye muscle. At the genetic level, the antagonism implies that selection for less fat in the carcass would result in a desirable correlated increase in the area of the eye muscle.

Available evidence indicates that area of the eye muscle is positively associated with measures of carcass cutability in lambs. Ray, Bell and Holland (1972) reported that their estimates of the phenotypic correlations between eye muscle area and retail meat per day of age ranged from -0.15 to 0.24 in the four breeding groups. The genetic correlations they found were 0.54, 0.25 and -0.01 in three breeding groups. Bradford and Spurlock (1972) reported a phenotypic correlation of 0.45 between area of the eye muscle and percent trimmed cuts and a genetic correlation of 0.47. Bowman and Hendy (1972) found that area of the eye muscle was positively correlated with the proportions of the more expensive joints, namely the leg, best end and loin and negatively correlated with the proportions of the cheaper joints, namely shoulder and the remainder although all the estimates were low in magnitude. The phenotypic correlations they provided indicated that carcasses of higher total value (£) tended to produce larger areas of eye muscle. In pigs, Jensen, Craig and Robison (1967) obtained estimates of 0.37 and 0.49 for the phenotypic and genetic correlations, respectively, between area of the eye muscle and percent lean cuts. A genetic correlation of 0.79 between these traits was reported by Isler and Swiger (1969).

A negative relationship exists between measures of carcass fatness and measures of cutability. This must largely be due to the negative relationship known to exist between carcass fatness and carcass lean content. In lambs, Ray, Bell and Holland (1972) found highly negative phenotypic correlations between fat thickness and carcass fat trim and, retail meat per day of age. The phenotypic and genetic correlations between fat depth over the eye muscle and percent trimmed cuts found by Bradford and Spurlock (1972) were -0.52 and -0.91. The phenotypic correlations between backfat thickness and the proportions of the various joints reported by Bowman and Hendy (1972) were: shoulder (%), 0.08; leg (%), -0.54; best end (%), 0.51; loin (%), 0.32 and remainder (%), -0.01. The positive correlations with shoulder (%), best end (%) and loin (%) are expected as an increase in the amount of fat in the animal would result in greater deposition in these joints relative to the rest. The negative correlation with leg (%) is also expected following the same line of argument. In pigs, highly negative phenotypic and genetic correlations between backfat thickness and percent lean cuts were reported by Jensen, Craig and Robison (1967) and, Isler and Swiger (1969).

There is a definite lack of information on the relationship between measurements of carcass width or depth and internal measurements made on the cross-sectional surface of the cut rib. Ray, Bell and Holland (1972) produced estimates of phenotypic correlations between width of legs of live lambs and, fat trim and fat thickness which were negative in the L and R breeding groups. The corresponding estimates at the genetic level were also negative with the exception of that between width of legs of live lambs and fat thickness in the S breeding group. Width of loin was positively related, phenotypically, to fat trim and fat thickness in all groups except the S breeding group. At the genetic level, estimates were available in two groups only. In the D breeding group, the correlations between width of loin and fat trim and fat thickness were positive (1.96 and 1.36, respectively) while in the L group the correlations were both negative (-0.32 and -0.41, respectively). In the same study, width of legs of live lambs was positively correlated while width of loin was negatively correlated with eye muscle area.

According to King (1957), a small positive phenotypic correlation exists between width of body and depth of eye muscle of pigs. The corresponding genetic correlation is in the same direction but of a greater magnitude. He found that length of body and length of leg were apparently not associated with depth of eye muscle and from these findings he came to the conclusion that none of the external carcass measurements was of any value for predicting depth of eye muscle, the highest correlation being only 0.19.

Estimates of phenotypic correlations between width of body and measurements of backfat thickness reported by King (1957) were small but positive. He argued that since the thickness of fat in the shoulder region will be included in the measurement of body width, a positive correlation was to be expected although why this was apparent only in the genetic correlations and not in the phenotypic correlations was not clear. Depth of carcass would similarly be expected to be affected by fat deposition in the thorax region. This appears to be the case from the positive phenotypic and genetic correlations between backfat thickness and fat depth measurements and, depth of carcass reported by Smith, King and Gilbert (1962).

Estimates of phenotypic and genetic correlations involving the eye muscle and backfat thickness and, other carcass traits in sheep are presented in Table 2.2.

In the work of Bowman, Marshall and Broadbent (1968) carcass weight was found to be positively correlated with percentage loin (0.14) and percentage "remainder" (0.23), but negatively correlated with percentage leg (-0.31) at the phenotypic level. In the opinion of these authors, the latter finding can be explained by the fact that the extremities of the lamb are the earliest parts to develop and this rate of development declines relative to that of other parts as the weight of the lamb increases. The proportions of the various

TABLE 2.2 Published estimates of phenotypic and genetic correlations between eye muscle area and backfat thickness and, other carcass traits in sheep.

	EYE MUSCLE AREA		FAT DEPTH OVER EYE MUSCLE		
TRAIT	PHENOTYPIC	GENETIC	PHENOTYPIC	GENETIC	AUTHOR
Fat depth over eye muscle	-0.05	-			Bowman and Hendy (1972)
	-0.26	-0.32			Bradford and Spurlock (1972)
	-0.41	-0.85			Ray, Bell and Holland (1972)
	-0.32	-0.87			
	-0.23	-0.73			
	0.11	1.01			
Fat trim	-0.17	-1.24	0.53	0.62	Ray, Bell and Holland (1972)
	-0.16	-0.65	0.56	1.18	
	-0.41	-0.28	0.62	1.33	
	-0.17	0.33	0.56	1.54	
Percent trimmed cuts	0.45	0.47	-0.52	-0.91	Bradford and Spurlock (1972)
Retail meat per day of age	-0.15	-	-0.26	-	Ray, Bell and Holland (1972)
	-0.03	0.54	-0.54	-0.98	
	0.03	0.25	-0.46	-0.79	
	0.24	-0.01	-0.40	-1.14	

TABLE 2.2 (Contimued)

TRAIT	EYE MUSCLE AREA		FAT DEPTH OVER EYE MUSCLE		AUTHOR
	PHENOTYPIC	GENETIC	PHENOTYPIC	GENETIC	
Shoulder (%)	-0.25	-	0.08	-	Bowman and Hendy (1972)
Leg (%)	0.12	-	-0.54	-	
Best end (%)	0.09	-	0.51	-	
Loin (%)	0.17	-	0.32	-	
Remainder (%)	-0.16	-	-0.01	-	
Total value (£)	0.37	-	0.35	-	
Width of legs	0.07	-	-0.11	-	Ray, Bell and Holland (1972)
	-0.02	0.61	-0.11	-0.07	
	0.09	0.04	-0.09	-0.28	
	0.03	1.87	-0.07	0.43	
Width of loin	0.06	-	-0.02	-	Ray, Bell and Holland (1972)
	0.14	-	0.09	-	
	-0.05	0.09	0.11	-0.41	
	-0.10	-1.48	0.16	1.36	
Carcass weight	0.32	-	0.36	-	Bowman and Hendy (1972)

joints were found to be mainly negatively correlated with each other. Similar findings were reported by Bowman and Hendy (1972). This is to be expected since an increase in the proportions of one or more joints must be accompanied by a decrease in the proportions of the other joints, assuming that carcass weight remains constant. Bowman, Marshall and Broadbent (1968) also reported that the value of the carcass in terms of pence yield per lb. of carcass weight was highly positively correlated, phenotypically, with the high-priced joints. For example, with percentage leg the correlation was 0.52. It is highly negatively correlated with the cheapest joints. Thus with percentage "remainder" the correlation was -0.91.

Positive phenotypic correlations between carcass weight and, internal measurements of backfat thickness and eye muscle area in lambs have been reported by Bowman, Marshall and Broadbent (1968) and Bowman and Hendy (1972). Their findings imply that an increase in the dressing-out % of the carcass is associated with a desirable increase in the area of the eye muscle and an antagonistic increase in the thickness of backfat.

Published relationships between carcass length and internal measurements appear to be non-existent in sheep. We have to rely, therefore, on work carried out with pigs for this purpose. In this species, estimates of the relationship between carcass length and measurements of carcass backfat have consistently been negative. According to Fredeen and Jonsson (1957) the negative phenotypic correlations may reflect, in part, the "automaticity" introduced by slaughtering at constant weight, i.e., when slaughter occurs at a constant weight, any change in the carcass dimension of length must be compensated by an opposite change in one or more of the other carcass dimensions. Length of carcass in the pig is a poor indicator of measurements and area of the eye muscle as implied by the low phenotypic correlations (King, 1957; Enfield and Whatley, 1961; Smith, King and Gilbert, 1962; Smith and Ross, 1965). From the low correlations, Enfield and Whatley (1961) concluded that: "Although carcass length appears to be quite highly heritable it has only a moderate relationship to measures of carcass leanness. On this basis there seems to be little value in including carcass length in a selection program if the improvement in the meatiness of the carcass is the main objective." Table 2.3 presents the phenotypic and genetic correlations between carcass length and, backfat thickness and eye muscle measurements in pigs.

TABLE 2.3 Published estimates of phenotypic and genetic correlations between carcass length and, backfat thickness and eye muscle measurements in pigs.

TRAIT	PHENOTYPIC	GENETIC	AUTHOR
Backfat thickness:			
Average	-0.19	-0.22	Smith and Ross (1965)
	-0.24 (males)	-0.47 (males)	Fredeen and Jonsson (1957)
	-0.24 (females)	-0.32 (females)	
Shoulder	-0.27	-0.50	King (1957)
	-0.18	-0.32	Smith, King and Gilbert (1962)
Mid-back	-0.32	-0.51	King (1957)
	-0.22	-0.29	Smith, King and Gilbert (1972)
Rump	-0.19	-0.24	King (1957)
Loin	-0.18	-0.42	Smith, King and Gilbert (1972)
Not specified	-0.36	-0.19	Enfield and Whatley (1961)
Eye muscle A	-0.05	0.11	Smith, King and Gilbert (1972)
	-0.07	0.03	Smith and Ross (1965)
Eye muscle B	-0.04	0.02	Smith, King and Gilbert (1972)
	-0.03	0.07	Smith and Ross (1965)
	0.06	-0.16	King (1957)
Eye muscle area	-0.04	0.08	Smith, King and Gilbert (1972)
	-0.09	-0.05	Smith and Ross (1965)
	0.10	-0.14	Enfield and Whatley (1961)

CHAPTER 3

DATA

I. SOURCE OF DATA

The data used in the present study were obtained from the wether lambs of a flock of Romney sheep started at Massey Agricultural College, Palmerston North, in 1944. The wether lambs, totalling 474 in number, were the progeny of twelve mixed-age rams over a period of three years from 1944 to 1947. Table 3.1 presents the number of lambs classified according to sire, year and birth rank.

Experimental animals

The management of the experimental animals has been discussed in detail by Rae (1946, 1957). The wether lambs in the present study were the progeny of five-year-old ewes only, which in 1944 numbered 250. In 1945, the whole flock was completely replaced by the purchase of 450 five-year-old ewes. The following year, 160 of these ewes from the previous year were culled.

The sires were procured from several sources in the Manawatu-Wairarapa area. In the first year, ten sires were used. Seven of these sires were used in the 1945 mating season and six of them

TABLE 3.1. Number of wether lambs according to sire, year and birth rank.

Year / Sire No.	Year 1 (1944/45)			Year 2 (1945/46)			Year 3 (1946/47)			
	Singles	Multiples as twins	Multiples as singles	Singles	Multiples as twins	Multiples as singles	Singles	Multiples as twins	Multiples as singles	Total
1	5	9	1	8	8	2	1	2	0	36
2	5	10	6	6	17	3	-	-	-	47
3	5	2	2	-	-	-	-	-	-	9
4	9	7	0	-	-	-	-	-	-	16
5	7	14	3	9	14	1	7	12	2	69
6	14	5	0	15	8	3	9	9	2	65
7	4	13	3	6	11	4	6	9	2	58
8	8	6	4	5	8	2	7	5	2	47
9	7	8	2	-	-	-	-	-	-	17
10	3	5	2	7	12	6	5	15	5	60
11	-	-	-	8	13	1	5	10	1	38
12	-	-	-	-	-	-	7	3	2	12
Total	67	79	23	64	91	22	47	65	16	474

again in the 1946 season. In 1945, a new sire was added, this sire being used again in 1946. In 1946, another new sire was brought into service.

The mating season started between March 15 and 25 in each year and the rams remained with the ewes for eight weeks. Allotment of the ewes to each sire was at random. After the removal of the rams, the ewes were run in one mob and wintered on pasture alone with no supplementary feeding. The lambs were born in August and September and remained with their dams until weaning in January.

The body weight of the wether lambs was recorded at intervals until they reached a live weight in the paddock of about 74 lb. (33 kg.). Lambs which attained this weight were shorn and then slaughtered the following morning. The carcasses were then graded under the export system of grading (Barton, 1947) and then stored in a cooler overnight at 42°F. The next day, cold carcass weight was recorded and various carcass measurements made.

The killing of the lambs usually took place once a week, but at the height of the season in January, it was necessary to kill twice weekly. Selection of lambs for slaughter was such that their dressed carcasses weighed about 34 lb. (15 kg.). However, lambs killed later in the season had to be picked at a slightly higher live weight in the paddock in order to take into account the increase in weight of wool as the lambs became older.

In general, the system of management was typical of a flock run in the Manawatu area except that no preferential treatment was given to any group of ewes or lambs.

II. DESCRIPTION OF CARCASS DATA

A. Cannon bone measurements

The left fore cannon bone was collected from each carcass as it was dressed. Following removal of all soft tissue, the weight was recorded to the nearest 0.1g. Each bone was labelled with the lamb's eartag number and the length measurement taken.

B. Carcass grading

Within a few hours after slaughter, each carcass was evaluated for the points quoted below and graded according to the export lamb system of grading as described by Barton (1947).

i. Hindquarter

a. Conformation: An estimate of the length of leg, fullness of crutch and depth of meat in the hindquarter.

b. Finish: An estimate of the fat cover over the leg. An even covering of fat sufficiently deep so that the underlying muscles do not show through was highly desirable at that time.

ii. Loin

a. Conformation: Width, flatness and fullness of loin.

b. Finish: Referring to the development of fat cover over the loin.

iii. Forequarter

a. Conformation: General conformation of the forequarter with particular reference to width and fullness of shoulder.

b. Finish: Referring to the fat cover of the forequarter region.

iv. Colour

a. Muscle: The colour of the lean meat should be a bright pink. Darkness was considered a defect.

b. Fat: Yellow fat colour, or departure from the ideal whitish, light cream colour, were undesirable and carcasses were graded down for this.

v. Grade

Each carcass was alloted into one of the following grades: Prime Down Crossbred, Prime Crossbred and Second Quality (Y).

C. Carcass Weight

After slaughter, each carcass was hung overnight on a gambrel of standard width in a cooling chamber. The next morning each carcass was weighed to determine its cold carcass weight.

D. Carcass measurements

External and internal measurements as detailed below were made on each carcass. The technique employed was similar to that described by Pálsson (1939). The measurements described here are shown in Figure 1.

i. External measurements

F = length of leg

G = width of gigots

WR = maximum width of ribs

WF = maximum width of forequarter in line with the shoulders.

WTh = minimum width behind the scapulae.

Th = depth of thorax. This is the maximum depth of chest behind the shoulders.

T = length of tibia + tarsus from the tubercle on the proximal end of the tibia to the anterior edge of the distal end of the tarsal.

R = length of radius-ulna from the olecranon process to the styloid process.

K = length of body from the tail head to the base of the neck.

L = length of body from the symphysis pubis to the anterior edge of the middle of the first rib.

H = length from the symphysis pubis to the posterior edge of the last rib, at the junction with the vertebra.

P = length of leg from the symphysis pubis to the anterior edge of the distal end of the tarsal.

ii. Internal measurements

The carcasses were divided into two portions by a cut vertically through the flank to the anterior edge of the last rib on each side. Then the curve of the ribs was followed to the vertebral column where the latter was severed at the junction of the last and second to last thoracic vertebrae. The last thoracic vertebra was therefore left on the hindquarter.

The following measurements were then made on this section.

A = "length" of the "eye muscle". The maximum distance across the cross-section surface of the longissimus dorsi from the end of the spinal process outwards along the rib.

B = depth of "eye muscle". The greatest distance at right angles to A on the same surface.

C = thickness of backfat over the deepest part of the "eye muscle".

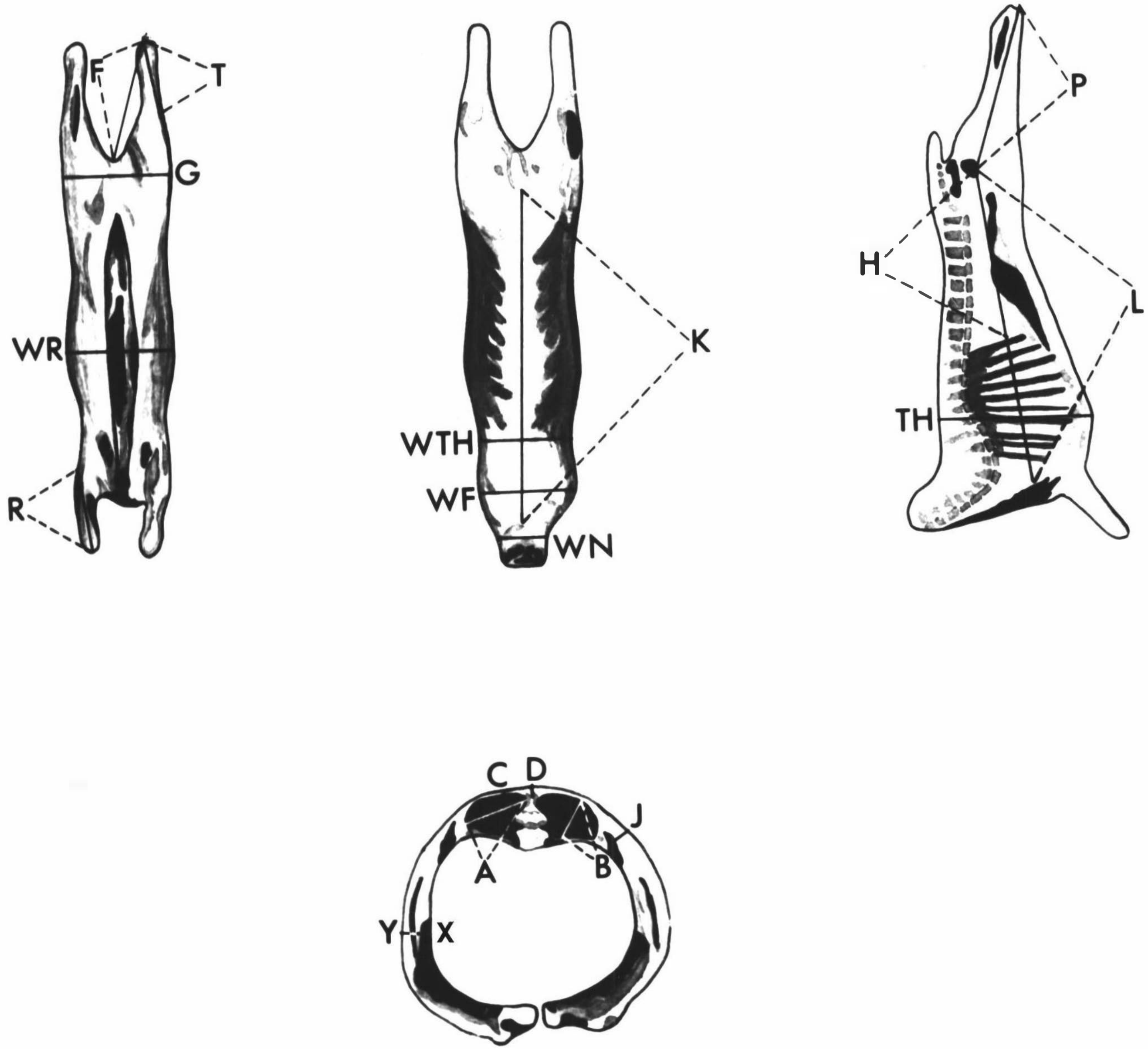
D = thickness of fat over the spinous process.

X = thickness of muscle layer (mixed with fat, plus rib) on lower half of rib at the point illustrated.

Y = thickness of subcutaneous fat layer over X.

J = thickest layer of fat over rib at the point illustrated.

Fig. 1 Carcass Measurements



E. Carcass total

The "Cambridge" Block Test for lambs was performed on each carcass using the technique described by McMeekan (1939). The characteristics on which each carcass were evaluated are given in Table 3.2.

TABLE 3.2 The "Cambridge" Block Test Judging Scale.

	Maximum points
External	
Blockiness of leg	30
Fat covering over leg	10
Fullness of loin	10
Internal	
Depth of fat over loin	20
Size and shape of eye muscle	15
Colour of lean meat	5
Lightness of rib and proportion of lean over rib	10
Total	100

Some of the carcass measurements described previously were used for the Block Test. Fat cover of legs and fullness of loin were subjective scores.

F. FQ/HQ

This is the ratio of the weights of the forequarter and the hindquarter.

CHAPTER 4

STATISTICAL METHODS

Data in this study were classified into subclasses as shown in Table 3.1. The subclass numbers are unequal and several cells had no observation in them. Methods of analysing data with equal subclass frequencies are well known and simple; the different kinds of effects and sums of squares for tests of significance can be obtained directly from the class or subclass totals. Unequal subclass frequencies with a few or many missing subclasses are typical of most animal breeding data. Such data are more complex and, consequently, their analysis more difficult.

I. LEAST-SQUARES ANALYSIS

In this section, the statistical model chosen to fit these data will be presented and the procedures involved in least-squares analysis described.

Model

A linear mathematical model of the following form was adopted:

$$Y_{ijkl} = \mu + s_i + t_j + b_k + (st)_{ij} + C\,(X_{ijkl} - \bar{X}_{...}) + e_{ijkl} \qquad \ldots (1)$$

$i = 1,\ldots,12$

$j = 1,2,3$

$k = 1,2,3$

$l = 1,\ldots, n_{ijk}$, where n_{ijk} varies due to unequal subclass frequencies.

The different components of model (1) are defined as follows:

Y_{ijkl} = the observation made on the l^{th} wether lamb belonging to the k^{th} birth and rearing rank in the j^{th} year by the i^{th} sire,

μ = the overall mean with equal subclass frequencies,

s_i = the effect of the i^{th} sire,

t_j = the effect of the j^{th} year of birth,

b_k = the effect of the k^{th} birth and rearing rank,

$(st)_{ij}$ = the interaction effect between the i^{th} sire and the j^{th} year,

c = the partial regression coefficient of the dependent variable Y on age of lamb at slaughter,

X_{ijkl} = the age at slaughter of the l^{th} lamb belonging to the k^{th} birth and rearing rank in the j^{th} year by the i^{th} sire,

$\bar{X}_{...}$ = the arithmetic mean of the X_{ijkl}, and

e_{ijkl} = random errors, assumed to be independent. For tests of significance it was essential to make the further assumption that the e_{ijkl} were normally distributed with mean zero and variance σ_e^2.

The overall mean, μ, the year effect, the birth and rearing rank effect and the regression term in the above model are "fixed" effects. The sire effect and the error term are considered as "random" effects since they are assumed to have been obtained from a population, respectively, of sires and error terms. The $(st)_{ij}$ interaction term is also random since it involves the sire effect, which is a random effect. Thus (1) is a model containing a mixture of fixed and random effects. Such a model is called a mixed model.

Model (1) may be represented in matrix form by

$$y = Xb + e \qquad \ldots (2)$$

where y is an N x 1 vector of observations, X is an N x p design matrix consisting of 0's and 1's, b is a p x 1 vector of parameters to be estimated and e is a vector of random error terms. The distributional properties of e are defined as before with its mean zero and variance σ_e^2,

<u>i.e.</u>, $E(e) = 0$

and $\text{var}(e) = E(ee') = \sigma^2 I_N$

Derivation of the least-squares estimator of b involves minimization of the sum of squares of the observations from their expected values. This sum of squares is

$$\begin{aligned} e'e &= [y - E(y)]'[y - E(y)] \\ &= (y - Xb)'(y - Xb) \\ &= y'y - 2b'X'y + b'X'Xb. \end{aligned}$$

Taking the estimate of b that value which minimizes e'e involves differentiating e'e with respect to each element of b. Equating $\partial(e'e)/\partial b$ to zero, the resulting equations, in terms of $\hat{b}$, may be shown to be of the form:

$$X'X\,\hat{b} = X'y \qquad \ldots (3)$$

Equations derived in this manner are called least-squares or normal equations. If X'X is of full rank, then $(X'X)^{-1}$ exists and a unique solution for $\hat{b}$ can be obtained as

$$\hat{b} = (X'X)^{-1}\,X'y \qquad \ldots (4)$$

However, the X'X matrix of model (1) is not of full rank so that $(X'X)^{-1}$ does not exist. Therefore, no unique solution to the normal equations can be obtained until they are reduced in number to the number of degrees of freedom (Harvey, 1960). Many different types of restrictions may be imposed to accomplish this. In the present study the restrictions adopted were such that the constants for the main effects sum to zero within a set and that the constants for the $(st)_{ij}$ sum to zero over each row and over each column,

i.e., $\sum_i \hat{s}_i = \sum_j \hat{t}j = \sum_k \hat{b}_k = \sum_i (\widehat{st})ij = \sum_j (\widehat{st})ij = 0$

The linear mathematical model of (1) itself suggests this set of restrictions since the effects of s_i, t_j, b_k, regression term and e_{ijkl} are expressed as deviations of the mean μ.

If $(X'X)_R$, $\hat{b}_R$ and $(X'y)_R$ represent X'X matrix and, $\hat{b}$ and X'y vectors of equation (3) after the appropriate restrictions have been imposed, then

$$(X'X)_R\,\hat{b}_R = (X'y)_R \qquad \ldots (5)$$

This leads to the solution for $\hat{b}_R$, which is:

$$\hat{b}_R = (X'X)_R^{-1}\,(X'y)_R \qquad \ldots (6)$$

In the present study, the interaction term for each trait was first estimated following the procedure to be discussed in Section II of this Chapter. For those traits in which the interaction term was found to be significant, the interaction effects for each of the sire-year subclass were computed as shown in Section II also. For traits in which the interaction term was not significant, the main effects and the regression term were estimated from the model without interaction, which in this case is:

$$Y_{ijkl} = \mu + s_i + t_j + b_k + C\,(X_{ijkl} - \bar{X}\ldots) + e_{ijkl} \qquad \ldots (7)$$

Suppose that under this model the solution for the estimates, after the appropriate restrictions have been imposed, is given by:

$$\hat{b}_r = (X'X)_r^{-1}\,(X'y)_r \qquad \ldots (8)$$

where the subscript r is used to distinguish the $\hat{b}$, $(X'X)^{-1}$ and $(X'y)$ obtained from this model from those of model (1). The necessary restrictions imposed using model (7) were such that:

$$\sum_i s_i = \sum_j t_j = \widehat{\sum_k b_k} = 0$$

The reduction in sum of squares due to fitting all constants of this model was computed as:

$$\begin{aligned} R[\hat{b}_r] &= \hat{b}_r'\,(X'y)_r \\ &= (y'X)_r (X'X)_r^{-1}\,(X'y)_r \qquad \ldots (9) \end{aligned}$$

The error sum of squares was computed from $y'y - R[\hat{b}_r]$

where $y'y = \sum_{ijkl} Y^2_{ijkl}$

= total uncorrected sum of squares of observations.

The sum of squares for the different main effects and the regression term were computed as follows:

Sire sum of squares

$$= R[u,s_i,t_j,b_k,c] - R[u,t_j,b_k,c]$$

where $R[u,t_j,b_k,c]$ was computed from the sub-model:

$$Y_{jkl} = u + t_j + b_k + C(X_{jkl} - \bar{X}...) + e_{jkl} \qquad ... (10)$$

Year sum of squares

$$= R[u,s_i,t_j,b_k,c] - R[u,s_i,b_k,c]$$

where $R[u,s_i,b_k,c]$ was computed from the sub-model:

$$Y_{ikl} = u + s_i + b_k + C(X_{ikl} - \bar{X}...) + e_{ikl} \qquad ... (11)$$

Birth and rearing rank sum of squares

$$= R[u,s_i,t_j,b_k,c] - R[u,s_i,t_j,c]$$

where $R[\mu,s_i,t_j,c]$ was obtained from the sub-model:

$$Y_{ijl} = \mu + s_i + t_j + C(X_{ijl} - \bar{X}...) + e_{ijl} \qquad ... (12)$$

Regression sum of squares

$$= R[u,s_i,t_j,b_k,c] - R[u,s_i,t_j,b_k]$$

where $R[u,s_i,t_j,b_k]$ was computed from the sub-model:

$$Y_{ijkl} = \mu + s_i + t_j + b_k + e_{ijkl} \qquad ... (13)$$

II. ESTIMATION OF SIRE-YEAR INTERACTION

The sire-year interaction sum of squares may be obtained from the difference in the reduction in sum of squares due to fitting all constants of model (1) and the reduction in sum of squares due to fitting all constants except the interaction,

i.e., sire-year interaction sum of squares

$$= R[u,s_i,t_j,b_k,(st)_{ij},c] - R[u,s_i,t_j,b_k,c]$$

The reduction in sum of squares due to fitting all constants was computed as $R[(\widetilde{st})_{ij},b_k,c]$ from a simplified model:

$$Y_{ijkl} = \widetilde{(st)}_{ij} + b_k + C(X_{ijkl} - \bar{X}_{...}) + e_{ijkl} \quad \dots (14)$$

where $\widetilde{(st)}_{ij} = \mu + s_i + t_j + (st)_{ij}$.

In other words, the compound parameter $\widetilde{(st)}_{ij}$ represents the mean of the $(st)_{ij}$ interaction subclass. With this model, the sum of squares for the interaction is, therefore:

$$R[\widetilde{(st)}_{ij}, b_k, C] - R[u, s_i, t_j, b_k, C]$$

In the computation of $R[\widetilde{(st)}_{ij}, b_k, C]$, the matrix of normal equations obtained when using model (14) was not of full rank and required the restriction that $\sum_k b_k = 0$ before an inverse could be obtained.

The error sum of squares for testing the significance of the interaction

$$= y'y - R[\widetilde{(st)}_{ij}, b_k, C].$$

The interaction effects for each of the sire-year subclass were computed from the following relationship:

$$(st)_{ij} = \widetilde{(st)}_{ij} - (\mu + s_i) - t_j.$$

$(\mu + s_i)$ and t_j were estimated from the following equations:

$$\begin{bmatrix}
3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \\
 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 \\
 & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
 & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
 & & & & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \\
 & & & & & 3 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \\
 & & & & & & 3 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \\
 & & & & & & & 3 & 0 & 0 & 0 & 0 & 1 & 1 & 1 \\
 & & & & & & & & 1 & 0 & 0 & 0 & 1 & 0 & 0 \\
 & & & & & & & & & 3 & 0 & 0 & 1 & 1 & 1 \\
 & & & & & & & & & & 2 & 0 & 0 & 1 & 1 \\
 & & & & & & & & & & & 1 & 0 & 0 & 1 \\
 & & & & & & & & & & & & 10 & 0 & 0 \\
 & & & & & & & & & & & & & 8 & 0 \\
 & & & & & & & & & & & & & & 8
\end{bmatrix}
\begin{bmatrix}
\widehat{\mu + s_1} \\
\widehat{\mu + s_2} \\
\widehat{\mu + s_3} \\
\widehat{\mu + s_4} \\
\widehat{\mu + s_5} \\
\widehat{\mu + s_6} \\
\widehat{\mu + s_7} \\
\widehat{\mu + s_8} \\
\widehat{\mu + s_9} \\
\widehat{\mu + s_{10}} \\
\widehat{\mu + s_{11}} \\
\widehat{\mu + s_{12}} \\
\hat{t}_1 \\
\hat{t}_2 \\
\hat{t}_3
\end{bmatrix}
=
\begin{bmatrix}
\sum_j (\widetilde{st})_{1j} \\
\sum_j (\widetilde{st})_{2j} \\
\sum_j (\widetilde{st})_{3j} \\
\sum_j (\widetilde{st})_{4j} \\
\sum_j (\widetilde{st})_{5j} \\
\sum_j (\widetilde{st})_{6j} \\
\sum_j (\widetilde{st})_{7j} \\
\sum_j (\widetilde{st})_{8j} \\
\sum_j (\widetilde{st})_{9j} \\
\sum_j (\widetilde{st})_{10j} \\
\sum_j (\widetilde{st})_{11j} \\
\sum_j (\widetilde{st})_{12j} \\
\sum_i (\widetilde{st})_{i1} \\
\sum_i (\widetilde{st})_{i2} \\
\sum_i (\widetilde{st})_{i3}
\end{bmatrix}
\qquad \ldots (15)$$

The right hand members in the above equations were derived as follows:

$$\sum_j \widetilde{(st)}_{1j} = \widetilde{(st)}_{11} + \widetilde{(st)}_{12} + \widetilde{(st)}_{13},$$

$$\sum_j \widetilde{(st)}_{2j} = \widetilde{(st)}_{21} + \widetilde{(st)}_{22},$$

$$\begin{array}{c} \cdot \\ \cdot \\ \cdot \\ \underline{\text{etc}}. \end{array}$$

Equation (15) may be written in a more concise form as:

$$\begin{bmatrix} (A)_{12 \times 12} & (B)_{12 \times 3} \\ & \\ & \\ & \\ & \\ (B)'_{3 \times 12} & (D)_{3 \times 3} \end{bmatrix} \begin{bmatrix} \widehat{\mu + s_1} \\ \cdot \\ \cdot \\ \cdot \\ \widehat{\mu + s_{12}} \\ \hat{t}_1 \\ \hat{t}_2 \\ \hat{t}_3 \end{bmatrix} = \begin{bmatrix} \sum_j \widetilde{(st)}_{1j} \\ \cdot \\ \cdot \\ \cdot \\ \sum_j \widetilde{(st)}_{12j} \\ \sum_i \widetilde{(st)}_{i1} \\ \sum_i \widetilde{(st)}_{i2} \\ \sum_i \widetilde{(st)}_{i3} \end{bmatrix}$$

where A is a diagonal matrix of order 12 x 12 of the number of years in which the sires are included,

B is a matrix of order 12 x 3 consisting of 1's and 0's denoting the years in which the sires are included, and

D is a diagonal matrix of order 3 x 3 of the number of sires occuring in each year.

III. ESTIMATION OF VARIANCE COMPONENTS

The estimation of variance components from balanced data depends almost entirely on one method, namely, the analysis of variance method. For a random (or mixed) model, this method involves the computation of the mean squares of the analysis of variance as though the effects were fixed. Then, the expected values of the mean squares under the random (or mixed) model are derived. Equating the calculated mean squares to their expected values leads to linear equations, the solutions to which may be taken as the estimates of the variance components.

For unbalanced data, there are several methods available for estimating variance components. Henderson (1953) described three such methods which subsequently became known as Henderson's Methods 1, 2 and 3. Method 1 is perhaps the most widely used of the three because of its relative simplicity. Basically, it involves calculating uncorrected sums of squares analogous to those used for analyses of variance of balanced data and equating these to their expected values. However, this method is only appropriate for the random model. Searle (1968) has shown that if there are fixed effects in the model, they cannot be eliminated from the expectations used in Method 1, so that the estimates obtained would be biased. The bias in the estimates of variance components obtained by using Method 1 on a mixed model can, under certain conditions, be removed by first estimating the fixed effects by least-squares, then correcting the data according to these estimates, and finally using Method 1 on the corrected data.

This is the basis of Henderson's Method 2. Although this method yields unbiased estimates, it suffers from the limitation that it cannot be used in a model which contains interactions between fixed and random effects. A variant of this method which Searle (1968) described as the Generalized Method 2 has limited value as a useful procedure because it contains elements of arbitrariness and is not uniquely specified for any set of data. Method 3 involves the use of reductions in sums of squares due to fitting constants. It is the most suitable method for obtaining unbiased estimates of variance components in mixed models and models where covariances between random effects are known to exist. The main disadvantages of Method 3 are that it can involve matrices of very large order and difficulties may arise in deriving the expectations of reductions in sums of squares. Method 3 was used in the present study because of its appropriateness for the mixed model.

Henderson's Method 3

Method 3 was formulated by Henderson (1953), and Searle (1968, 1971) made it more readily accessible by reformulating it in matrix terminology. The presentation given here follows closely those of Searle.

The general model $y = Xb + e$ may be rewritten as

$$y = X_1 b_1 + X_2 b_2 + e \qquad \ldots (16)$$

where the b has been partitioned into b_1 and b_2 with no assumption at this moment whether they represent fixed or random effects. The reduction in sum of squares due to fitting the above model is $R(b_1, b_2)$ and that due to fitting the sub-model

$$y = X_1 b_1 + e \qquad \text{... (17)}$$

is $R(b_1)$. The expectations of $R(b_1, b_2)$ and $R(b_1)$ will be taken under the full model. Finding the expectations of the reduction in sum of squares involves finding the expectations of the quadratic form $y'Qy$. For the full model this is:

$$E(y'Qy) = tr[Q\ var(y)] + E(y')\ QE(y)$$

If $E(b_i) = b_i$ for fixed effects, then $E(b)$ is defined whatever the nature of b. Then,

$$E(y'Qy) = tr[Q\left\{ Xvar(b)X' + \sigma_e^2\ I\right\}] + E(b')X'QXE(b)$$

$$= tr[X'QXE(bb')] + \sigma_e^2\ tr(Q) \qquad \text{... (18)}$$

For the model $y = Xb + e$ with normal equations $X'X\widehat{b} = X'y$, the reduction in sum of squares is $y'X(X'X)^{-}X'y$ where $(X'X)^{-}$ represents the generalized inverse of $X'X$. Therefore,

$$R(b_1, b_2) = y'X(X'X)^{-}X'y \qquad \text{... (19)}$$

whereby

$$ER(b_1, b_2) = tr\left\{ (X'X)E(bb')\right\} + \sigma_e^2\ r(X)$$

$$= tr\left\{ \begin{bmatrix} X_1'X & X_1'X_2 \\ X_2'X & X_2'X_2 \end{bmatrix} E(bb') \right\} + \sigma_e^2\ r\ (X) \qquad \text{... (20)}$$

Similarly,

$$R\ (b_1) = y'X_1(X_1'X_1)^{-}X_1'y \qquad \text{... (21)}$$

$$\text{with } ER(b_1) = tr\left\{ X'X_1(X_1'X_1)^-X_1'XE(bb') \right\} + \sigma_e^2\, r(X)$$

$$= tr\left\{ \begin{bmatrix} X_1'X_1 \\ \\ X_2'X_1 \end{bmatrix} (X_1'X_1)^- \left[X_1'X_1 \quad X_1'X_2\right] \; E(bb') \right\}$$

$$+ \sigma_e^2\, r(X_1)$$

$$= tr\left\{ \begin{bmatrix} X_1'X_1 & X_1'X_2 \\ X_2'X_1 & X_2'X_1(X_1'X_1)^-X_1'X_2 \end{bmatrix} \quad E(bb') \right\}$$

$$+ \sigma_e^2\, r(X_1) \qquad \ldots (22)$$

Hence,

$$E[R(b_1,b_2) - R(b_1)]$$

$$= tr\left\{ X_2' \,[I - X_1(X_1'X_1)^-X_1']X_2E(b_2b_2') \right\}$$

$$+ \sigma_e^2\,[r(X) - r(X_1)] \qquad \ldots (23)$$

The importance of Henderson's Method 3 lies in the fact that $E[R(b_1,b_2) - R(b_1)]$ is a function of only $E(b_2b_2')$ and σ_e^2. It does not involve either $E(b_1b_1')$ or $E(b_1b_2')$. Thus, if b_1 of model (16) represents only fixed effects and b_2 only random effects, $E[R(b_1,b_2) - R(b_1)]$ contains no terms at all due to the fixed effects. Also, since $E(b_1b_2')$ is not involved, Method 3 yields unbiased estimates even if terms in b_1 are correlated with terms in b_2.

The error sum of squares due to fitting model $y = Xb + e$ is $y'y - R(b_1,b_2)$. The expectation of $y'y$ can be derived from (18).

When $Q = I_N$,

$$\begin{aligned} E(y'Qy) &= E(y'y) \\ &= \mathrm{tr}\,[X'XE(bb')] + N\sigma_e^2 \\ &= \mathrm{tr}\left(\begin{bmatrix} X_1'X & X_1'X_2 \\ X_2'X_1 & X_2'X_2 \end{bmatrix} E(bb') \right) + N\sigma_e^2 \end{aligned} \qquad \ldots (24)$$

Therefore,

$$E[y'y - R(b_1,b_2)] = [N - r(X)]\,\sigma_e^2 \qquad \ldots (25)$$

Considering now the main effects in the present study, the mean μ, the year and birth-rearing rank effects, and the regression term are fixed effects. They are the b_1 effects of model (16). The sire effect, being the only random effect in a no-interaction model, then falls into the b_2 classification. The sire sum of squares given by $R(\mu, s_i, t_j, b_k, C) - R(\mu, t_j, b_k, C)$ has expectation similar to (23) with no terms in $E(b_1 b_1')$ and $E(b_1 b_2')$ involving the fixed effects.

The procedures for estimating the variance components for traits which showed no interaction of sires and years will be presented first followed by the procedures for traits which showed significant interaction.

A. Model without interaction

In traits which showed no interaction between sires and years, the analysis of variance table for estimating the variance components contained lines only for the sire and error terms. The sire sum of squares was computed as:

$$R(\mu, s_i, t_j, b_k, C) - R(\mu, t_j, b_k, C),$$

and the error sum of squares as

$$\sum_{ijkl} Y_{ijkl}^2 - R(\mu, s_i, t_j, b_k, C).$$

The expectations of the above terms are as follows:

$$E\left[\sum_{ijkl} Y_{ijkl}^2\right] = n...\mu^2 + n...\sigma_s^2 + n...\sigma_e^2$$

$$ER(\mu, s_i, t_j, b_k, C) = n...\mu^2 + n...\sigma_s^2 + (p + q + r - 1)\sigma_e^2$$

$$ER(\mu, t_j, b_k, C) = n...\mu^2 + k_1\sigma_s^2 + (q + r)\sigma_e^2$$

From these, the expectations in the sums of squares for the sire and error terms can be worked out.

$$E[\text{Sire S.S.}] = ER(\mu, s_i, t_j, b_k, C) - ER(\mu, t_j, b_k, C)$$
$$= (n...-k_1)\sigma_s^2 + (p - 1)\sigma_e^2,$$

$$\text{and } E[\text{Error S.S.}] = E\left[\sum_{ijkl} Y_{ijkl}^2\right] - ER(\mu, s_i, t_j, b_k, C)$$
$$= (n...-p - q - r + 1)\sigma_e^2.$$

The analysis of variance table for the sire and error terms may be set up as in Table 4.1.

The coefficient for σ_s^2 in the E(M.S.) for the sire term,

$$k_1' = \frac{n... - k_1}{(p - 1)}$$

$$= \frac{n... - tr\,[N_1' R_1^{-1} N_1]}{(p - 1)}$$

where N_1 is the segment of the matrix of least-squares equations obtained from the model (7) which contains the coefficients associating the sire effects with all others in the model and R_1^{-1} is the inverse of the matrix of least-squares equations for the model:

TABLE 4.1 Analysis of variance table for the estimation of variance components in the case of no interaction.

Source of variation	d.f.	S.S.	E(S.S.)	E(M.S.)
Sire	$p - 1$	$R(u,s_i,t_j,b_k,c)$ $-R(\mu,t_j,b_k,c)$	$(p - 1)\,\sigma_e^2$ $+(n... -k_1)\sigma_s^2$	$\sigma_e^2 + k_1'\sigma_s^2$
Error	$n... -p - q - r + 1$	$\sum_{ijkl} Y_{ijkl}^2$ $-R(\mu,s_i,t_j,b_k,c)$	$(n... -p - q - r + 1)\sigma_e^2$	σ_e^2

$$Y_{jkl} = \mu + t_j + b_k + C(X_{jkl} - \bar{X}_{...}) + e_{jkl}.$$

B. Model with interaction

In cases where the sire-year interaction were present, the analysis of variance table for estimating the variance components contained a line for the interaction term in addition to those for the sire and error terms. The sums of squares for these terms were computed from the following:

Sire sum of squares

$$= R(\mu, s_i, t_j, b_k, C) - R(\mu, t_j, b_k, C)$$

Note that it was not computed from

$$R[\mu, s_i, t_j, b_k, (st)_{ij}, C] - R[\mu, t_j, b_k, (st)_{ij}, C].$$

Interaction sum of squares

$$= R[\mu, s_i, t_j, b_k, (st)_{ij}, C] - R(\mu, s_i, t_j, b_k, C).$$

Error sum of squares

$$= \sum_{ijkl} Y^2_{ijkl} - R[\mu, s_i, t_j, b_k, (st)_{ij}, C].$$

The expectations for the above terms are:

$$E[\sum_{ijkl} Y^2_{ijkl}] = n_{...}\mu^2 + n_{...}\sigma^2_s + n_{...}\sigma^2_{st} + n_{...}\sigma^2_e.$$

$$ER[\mu, s_i, t_j, b_k, (st)_{ij}, C] = n_{...}\mu^2 + n_{...}\sigma^2_s + n_{...}\sigma^2_{st} + (pq + r - m)\sigma^2_e.$$

$$ER(\mu, s_i, t_j, b_k, C) = n_{...}\mu^2 + n_{...}\sigma^2_s + k_3\sigma^2_{st} + (p + q + r - 1)\sigma^2_e.$$

$$ER(\mu, t_j, b_k, C) = n_{...}\mu^2 + k_1\sigma^2_s + k_2\sigma^2_{st} + (q + r)\ \sigma^2_e.$$

The expectations in the sums of squares for the sire, interaction and error terms were then derived from the expectations of the above terms.

$$E[\text{Sire S.S.}] = ER(\mu, s_i, t_j, b_k, C) - ER(\mu, t_j, b_k, C)$$
$$= (n... - k_1)\,\sigma_s^2 + (k_3 - k_2)\,\sigma_{st}^2 + (p - 1)\,\sigma_e^2 .$$

$E[\text{Interaction S.S.}]$

$$= ER[\mu, s_i, t_j, b_k, (st)_{ij}, C] - ER(\mu, s_i, t_j, b_k, C)$$
$$= (n... - k_3)\,\sigma_{st}^2 + [(p - 1)(q - 1) - m]\,\sigma_e^2$$

$E[\text{Error S.S.}]$

$$= E[\Sigma_{ijkl} Y_{ijkl}^2] - R[\mu, s_i, t_j, b_k, (st)_{ij}, C]$$
$$= (n... - pq - r + m)\,\sigma_e^2 .$$

The analysis of variance may then be set up as in Table 4.2.

The coefficient k_1' is the same as that computed for the case without interaction. The computation of the coefficients k_2' and k_3' is given below.

$$k_3' = \frac{n... - k_3}{[(p-1)(q-1) - m]}$$
$$= \frac{n... - tr[N_3' R_3^{-1} N_3]}{[(p-1)(q-1) - m]}$$

where N_3 is the segment of the matrix of least-squares equations obtained from the model (1) which contains the coefficients associating the interaction effects with all the other effects in the model. R_3^{-1} is the inverse of the matrix of least-squares equations for the model:

$$Y_{ijkl} = \mu + s_i + t_j + b_k + C(X_{ijkl} - \bar{\bar{X}}...) + e_{ijkl} .$$

$$k_2' = \frac{k_3 - k_2}{(p-1)}$$

where $k_2 = tr\,[N_2' R_2^{-1} N_2]$. In this case, N_2 is the matrix of least-squares equations obtained from the model (1) which contains the coefficients associating the interaction effects with other

TABLE 4.2 Analysis of variance table for the estimation of variance components in the presence of sire-year interaction.

Source of variation	d.f.	S.S.	E(S.S.)	E(M.S.)
Sire	$p - 1$	$R(u,s_i,t_j,b_k,c)$ $-R(\mu,t_j,b_k,c)$	$(p-1)\sigma_e^2$ $+ (k_3 - k_2)\sigma_{st}^2$ $+ (n\ldots-k_1)\sigma_s^2$	$\sigma_e^2 + k_2'\sigma_{st}^2$ $+ k_1'\sigma_s^2$
Interaction	$[(p-1)(q-1) -m]$	$R[u,s_i,t_j,b_k,(st)_{ij},c]$ $-R(u,s_i,t_j,b_k,c)$	$[(p-1)(q-1)-m]\sigma_e^2$ $+(n\ldots-k_3)\sigma_{st}^2$	$\sigma_e^2 + k_3'\sigma_{st}^2$
Error	$n\ldots-pq-r+m$	$\sum_{ijkl} Y_{ijkl}^2$ $-R[u,s_i,t_j,b_k,(st)_{ij},c]$	$(n\ldots-pq-r+m)\sigma_e^2$	σ_e^2

effects, but not including the sire effects. R_2^{-1} is the inverse of the matrix of least-squares equations for the model:

$$Y_{jkl} = \mu + t_j + b_k + C\,(X_{jkl} - \bar{X}_{...}) + e_{jkl}.$$

IV. ESTIMATION OF HERITABILITY

The heritability of a trait may be estimated by several methods. Falconer (1960) presented four methods, namely the regression of offspring on one parent, the regression of offspring on mid-parent, the half-sib correlation and the full-sib correlation, and discussed the relative merits of each of them. The most reliable method is the one in which the covariance between relatives is least likely to be augmented by an environmental component. In this respect, the half-sib correlation and the regression of offspring on father are the most reliable, and the full-sib correlation the least reliable due to the presence of an environmental variance as well as a dominance variance. The regression of offspring on mother is liable to give a biased estimate on account of the maternal effects. In the present study heritability was estimated by the paternal half-sib correlation method.

The heritability of a trait may be defined as the ratio of additive genetic variance (σ^2_A) to phenotypic variance (σ^2_P).

Thus, $$h^2 = \frac{\sigma^2_A}{\sigma^2_P} \qquad \ldots (26)$$

In a population mating at random, the between-sire variance, σ^2_S, is the variance between the means of half-sib families and it estimates the phenotypic covariance of half-sibs, cov(H.S.), which is $\frac{1}{4}\,\sigma^2_A$. Thus $\sigma^2_S = \text{cov(H.S.)} = \frac{1}{4}\,\sigma^2_A$. From this, the additive genetic variance is

$$\sigma^2_A = 4\sigma^2_S \; .$$

When the sire-year interaction was found to be non-significant, the estimate of the phenotypic variance was taken as the sum of the error variance and the between-sire variance,

<u>i.e.</u>, $\sigma^2_p = \sigma^2_e + \sigma^2_s$.

In this case, heritability was computed as:

$$h^2 = \frac{4\sigma^2_s}{\sigma^2_e + \sigma^2_s} \qquad \ldots (27)$$

When the sire-year interaction was significant, the phenotypic variance also contained a component due to the interaction. Thus $\sigma^2_p = \sigma^2_e + \sigma^2_{st} + \sigma^2_s$, and heritability was then estimated as:

$$h^2 = \frac{4\sigma^2_s}{\sigma^2_e + \sigma^2_{st} + \sigma^2_s} \qquad \ldots (28)$$

The precision of an estimate of heritability depends on its sampling variance, the smaller the sampling variance the greater the precision; the standard error is the square root of the sampling variance. The sampling variance of estimates of heritability derived from an intra-class correlation coefficient has been discussed by Robertson (1959) for the situation where the number of half-sibs are the same in all groups.

In the case where there are N groups each of n half-sibs, the sampling variance of the intra-class correlation t is given by:

$$\sigma^2_t = \frac{2[1 + (n-1)t]^2(1-t)^2}{n(n-1)(N-1)} \qquad \ldots (29)$$

When the restriction is imposed that the total number of half-sibs, T(=Nn), is fixed, then in the case of n being large, the sampling variance is simplified to:

$$\sigma^2_t \doteq \frac{2(1-t)^2(1+nt)^2}{nT} \qquad \ldots (30)$$

Considered as a function of n, this has a minimum value when $nt = 1$, i.e., $n = \frac{1}{t}$. The optimum group size is then the reciprocal of the intra-class correlation. Thus at the optimum,

$$\sigma^2_{\hat{t}} \doteq \frac{8(1-t)^2 t}{T}$$

$$\doteq \frac{8t}{T} \qquad \ldots (31)$$

In the case of half-sib families, $h^2 = 4t$, so that in the most efficient design the half-sib family size, $n = \frac{4}{h^2}$.

Therefore under the condition of optimum group size, the sampling variance of estimates of heritability is:

$$\sigma^2_{\hat{h}^2} \doteq 16\, \sigma^2_{\hat{t}} \doteq \frac{32\, h^2}{T} \qquad \ldots (32)$$

The standard error of this sampling variance is:

$$\sigma_{\hat{h}^2} = \sqrt{\frac{32h^2}{T}} \qquad \ldots (33)$$

In order to use the above equation to compute the standard errors of the heritability estimates, the conditions required are that the number of progeny per sire group, n, is the same between sires and that it is at the optimum value. However, in the present study these conditions were not fulfilled because the number of progeny varied between sire groups. Nevertheless, it was considered that the use of equation (33) in the present study would not cause too much departure from accuracy.

V. ESTIMATION OF COVARIANCE COMPONENTS

The procedures involved in the estimation of covariance components are, in many ways, similar to those used in the analysis of variance components. That the former is but an extension of variance component analysis was first demonstrated for data with equal subclass numbers by Hazel, Baker and Reinmiller (1943). Henderson (1953) described briefly the procedures to carry out the analysis with non-orthogonal data. In a more recent paper, Grossman and Gall (1968) discussed them in greater detail.

As an example, consider two traits Y_1 and Y_2 with observations represented by Y_{1ijkl} and Y_{2ijkl}. In the estimation of variance components using Method 3, the sums of squares for the appropriate effects were computed from the difference between two reductions in sums of squares. The procedures in covariance component estimation are in many ways analogous to Method 3 in that the sums of crossproducts for the appropriate effects are computed from the difference between two reductions in sums of crossproducts. In Section I of Chapter 4 reductions in sums of squares were computed from:

$$R[\hat{b}_r] = \hat{b}_r'(X'y)_r$$

$$= (y'X)_r(X'X)_r^{-1}(X'y)_r$$

i.e., by summing the products of each of the constant estimates for a particular trait with the corresponding right-hand members of that trait. Reductions in sums of crossproducts were, however, obtained by summing the products of each of the constant estimates for trait Y_1, say, with the corresponding right-hand members for trait Y_2,

$$\underline{\text{i.e.}}, \quad C[\hat{b}_r] = \hat{b}'_{1r}(X'y)_{2r}$$

$$= (y'X)_{1r}(X'X)^{-1}_{1r}(X'y)_{2r} \qquad \ldots (34)$$

Unlike variance component estimation, where the interaction term is either included in or excluded from a model depending on its level of significance for a given trait, three different situations have to be considered in covariance component analysis. The first case for consideration is one in which the interaction term is non-significant in both traits, in which the model for the covariance analysis may be called the "no interaction model". In the second case, both traits show significant interaction terms, in which the model may be termed the "interaction model". The third case is one in which the interaction term is significant in only one of the two traits. The three cases are discussed separately below.

A. No interaction term in both traits

For the estimation of covariance components in the case where the interaction term is non-significant in both traits, the analysis of covariance table contained lines only for the sire and error terms. In this case, the sire sum of crossproducts was computed as:

$$C\,[u,s_i,t_j,b_k,c] \;-\; C\,[u,t_j,b_k,c]$$

and the error sum of crossproducts as:

$$\sum_{ijkl} Y_{1ijkl}Y_{2ijkl} - C\,[u,s_i,t_j,b_k,c]$$

where $\sum\limits_{ijkl} Y_{1ijkl}Y_{2ijkl}$ is the total uncorrected sum of crossproducts of observations for traits Y_1 and Y_2. The expectations of each of the above terms are:

$$E\,[\sum_{ijkl} Y_{1ijkl}Y_{2ijkl}] = n\ldots u_1u_2 + n\ldots \mathrm{cov}\; s_1s_2 + n\ldots\; \mathrm{cov}\; e_1e_2$$

$$EC\,[u,s_i,t_j,b_k,c] = n\ldots u_1u_2 + n\ldots\; \mathrm{cov}\; s_1s_2 + (p + q + r - 1)\; \mathrm{cov}\; e_1e_2$$

$$EC\,[u,t_j,b_k,c] = n\ldots u_1u_2 + k_1\; \mathrm{cov}\; s_1s_2 + (q + r)\; \mathrm{cov}\; e_1e_2$$

Hence, the expectations in the sums of crossproducts for the sire and error terms are:

$$\begin{aligned} E\,[\text{Sire S.C.P.}] &= EC\,[u,s_i,t_j,b_k,c] - EC\,[u,t_j,b_k,c] \\ &= (n\ldots - k_1)\; \mathrm{cov}\; s_1s_2 + (p - 1)\; \mathrm{cov}\; e_1e_2 \end{aligned}$$

$$\text{and } E[\text{Error S.C.P.}] = E[\sum_{ijkl} Y_{1ijkl} Y_{2ijkl}]$$

$$- EC[u, s_i, t_j, b_k, c]$$

$$= (n... - p - q - r + 1) \text{ cov } e_1 e_2$$

Thus, the coefficients of the covariance components in the expectations in the sums of crossproducts in the analysis of covariance are the same as the coefficients of the variance components in the sums of squares in the analysis of variance. Two further assumptions that have to be introduced here are that:

$$E(s_{1i} s_{2i}) = \text{cov } s_1 s_2 \quad \text{and}$$

$$E(e_{1ijkl} e_{2ijkl}) = \text{cov } e_1 e_2$$

The analysis of covariance is presented in Table 4.3.

TABLE 4.3 Analysis of covariance for the case where there is no interaction term in both traits

Source of covariation	d.f.	S.C.P.	E(S.C.P.)	E(M.C.P.)
Sire	$p - 1$	$C[u, s_i, t_j, b_k, c]$ $- C[u, t_j, b_k, c]$	$(p-1) \text{cov } e_1 e_2$ $+ (n... - k_1)$ $\text{cov } s_1 s_2$	$\text{cov } e_1 e_2$ $+ k'_1 \text{ cov}$ $s_1 s_2$
Error	$(n...$ $-p-q$ $-r+1)$	$\sum_{ijkl} Y_{1ijkl} Y_{2ijkl}$ $- C[u, s_i, t_j, b_k, c]$	$(n...-p-q-r+1)$ $\text{cov } e_1 e_2$	$\text{cov } e_1 e_2$

The coefficient, k_1', for cov s_1s_2 in the E(M.C.P.) for the sire term is the same as that computed in the estimation of variance components.

B. Interaction term significant in both traits

In this case, the analysis of covariance table contained a line for the interaction term in addition to the sire and error terms. The sums of crossproducts were computed as follows:

Sire sum of crossproducts

$$= C[u, s_i, t_j, b_k, c] - C[u, t_j, b_k, c].$$

Interaction sum of crossproducts

$$= C[u, s_i, t_j, b_k, (st)_{ij}, c]$$

$$- C[u, s_i, t_j, b_k, c]$$

Error sum of crossproducts

$$= \sum_{ijkl} Y_{1ijkl}Y_{2ijkl} - C[u, s_i, t_j, b_k, (st)_{ij}, c]$$

The expectations for the above terms are:

$$E[\sum_{ijkl} Y_{1ijkl}Y_{2ijkl}] = n_{\cdots}u_1u_2 + n_{\cdots} \text{ cov } s_1s_2$$

$$+ n_{\cdots}\text{cov}(st)_1(st)_2$$

$$+ n_{\cdots}\text{cov } e_1e_2$$

$$EC[u, s_i, t_j, b_k, (st)_{ij}, c]$$

$$= n_{\cdots}u_1u_2 + n_{\cdots} \text{ cov } s_1s_2$$

$$+ n_{\cdots}\text{cov}(st)_1(st)_2 + (pq+r-m)\text{cov } e_1e_2$$

$$\begin{aligned} EC[u, s_i, t_j, b_k, c] &= n\ldots u_1 u_2 + n\ldots \operatorname{cov} s_1 s_2 \\ &\quad + k_3 \operatorname{cov}(st)_1 (st)_2 \\ &\quad + (p + q + r - 1) \operatorname{cov} e_1 e_2 \end{aligned}$$

$$\begin{aligned} EC[u, t_j, b_k, c] &= n\ldots u_1 u_2 + k_1 \operatorname{cov} s_1 s_2 \\ &\quad + k_2 \operatorname{cov}(st)_1 (st)_2 \\ &\quad + (q + r) \operatorname{cov} e_1 e_2 \end{aligned}$$

The expectations of the sire, interaction and error sums of crossproducts are then:

$$\begin{aligned} E[\text{ Sire S.C.P. }] &= (n\ldots - k_1) \operatorname{cov} s_1 s_2 \\ &\quad + (k_3 - k_2) \operatorname{cov}(st)_1 (st)_2 \\ &\quad + (p - 1) \operatorname{cov} e_1 e_2 \end{aligned}$$

$$\begin{aligned} E[\text{Interaction S.C.P. }] &= (n\ldots - k_3) \operatorname{cov} (st)_1 (st)_2 \\ &\quad + [(p - 1)(q - 1) - m] \operatorname{cov} e_1 e_2 \end{aligned}$$

$$E[\text{Error S.C.P. }] = (n\ldots - pq - r + m) \operatorname{cov} e_1 e_2$$

In deriving the above expectations, it is necessary to assume that:

$$E[(st)_1 (st)_2] = \operatorname{cov}(st)_1 (st)_2$$

The analysis of covariance is presented in Table 4.4.

The coefficients k_1', k_2' and k_3' of the covariance components in the expectations of means of crossproducts are the same as those computed for the estimation of variance components.

TABLE 4.4 Analysis of covariance table for the case where the interaction terms are significant in both traits

Source of covariance	d.f.	S.C.P.	E(S.C.P.)	E(M.C.P.)
Sire	$p - 1$	$C[u, s_i, t_j, b_k, c]$ $- C[u, t_j, b_k, c]$	$(p-1)\text{cov } e_1 e_2$ $+ (k_3 - k_2)$ $\text{cov}(st)_1(st)_2$ $+ (n... - k_1)$ $\text{cov } s_1 s_2$	$\text{cov } e_1 e_2$ $+ k_2' \text{ cov}(st)_1(st)_2$ $+ k_1' \text{ cov } s_1 s_2$
Interaction	$[(p - 1)$ $(q - 1) - m]$	$C[u, s_i, t_j,$ $(st)_{ij}, b_k, c]$ $- C[u, s_i, t_j, b_k, c]$	$[(p - 1)(q - 1) - m]$ $\text{cov } e_1 e_2$ $+ (n... - k_3)$ $\text{cov}(st)_1(st)_2$	$\text{cov } e_1 e_2$ $+ k_3' \text{ cov } (st)_1(st)_2$
Error	$(n... - pq$ $- r + m)$	$\sum_{ijkl} Y_{1ijkl} Y_{2ijkl}$ $- C[u, s_i, t_j,$ $(st)_{ij}, b_k, c]$	$(n... - pq$ $- r + m) \text{ cov } e_1 e_2$	$\text{cov } e_1 e_2$

C. Interaction term significant in only one trait

For this case the procedures for A may be used.

In the present study, the covariance components for all traits were estimated under the assumption of no interaction in both traits, i.e., by the procedures given in A.

VI. ESTIMATION OF GENETIC AND PHENOTYPIC CORRELATIONS

The additive genetic covariance (cov A_1A_2) describes the covaration of the breeding values for the traits Y_1 and Y_2. The phenotypic covariance is the sum of the covariances arising from genetic and environmental causes.

The expected composition of the covariance components cov s_1s_2 and cov e_1e_2 for autosomal inheritance is shown in Table 4.5.

The additive genetic covariance estimated from the sire component of covariance is:

$$\widehat{\text{cov}}\ A_1A_2 = 4\ \widehat{\text{cov}}\ s_1s_2$$

For this to be true, the necessary assumptions are that epistatic effects and effects of genotype by environment interaction are absent.

The phenotypic covariance is estimated as the sum of the sire covariance and the error covariance in the model without interaction,

i.e., $\widehat{\text{cov}}\ P_1P_2 = \widehat{\text{cov}}\ e_1e_2 + \widehat{\text{cov}}\ s_1s_2$

TABLE 4.5 Expected composition of covariance components

Covariance components	cov A_1A_2	cov D_1D_2	cov $A_1A_1A_2A_2$	cov $A_1D_1A_2D_2$	cov $D_1D_1D_2D_2$	cov $G_1E_1G_2E_2$	cov E_1E_2
cov s_1s_2	$\frac{1}{4}$	0	1/16	0	0	$\frac{1}{4}$	0
cov e_1e_2	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{7}{8}$	15/16	$\frac{1}{2}$	1

cov A_1A_2 = covariance from additive effects of genes.

cov D_1D_2 = covariance from dominance deviations from additive gene effects.

cov $A_1A_1A_2A_2$ = covariance from two-loci interactions of additive gene effects.

cov $A_1D_1A_2D_2$ = covariance from two-loci interactions of additive effects with dominance deviations.

cov $D_1D_1D_2D_2$ = covariance from two-loci interactions of dominance deviations.

cov $G_1E_1G_2E_2$ = covariance from interaction of genotypes with environments.

cov E_1E_2 = covariance from environments differing for different progeny groups.

The genetic correlation, r_g, between two traits Y_1 and Y_2 may be defined as the correlation between an animal's genetic value for one trait and its genetic value for the other trait. It is estimated as:

$$r_g = \frac{\widehat{\text{cov}}\, A_1A_2}{\sqrt{\hat{\sigma}^2_{A_1}\ \hat{\sigma}^2_{A_2}}}$$

where $\hat{\sigma}_{A_1}^2$ and $\hat{\sigma}_{A_2}^2$ are the estimates of the additive genetic variances for traits Y_1 and Y_2 obtained from the sire components of variance.

The phenotypic correlation, r_p, between two traits Y_1 and Y_2 is the correlation between records of the traits on the same animal. It is estimated as:

$$r_p = \frac{\widehat{\text{cov}}\, P_1P_2}{\sqrt{\hat{\sigma}^2_{P_1}\ \hat{\sigma}^2_{P_2}}}$$

where $\hat{\sigma}_{P_1}^2$ and $\hat{\sigma}_{P_1}^2$ are the estimates of the phenotypic variances for traits Y_1 and Y_2.

The sampling variances of the genetic correlation coefficients were computed using the formula given by Tallis (1959),

<u>i.e.</u>, Est. var $(\hat{r}_g)$

$$= \frac{32\ \hat{r}_g^{\,2}}{k^2} \left[\frac{V_{11}^2/d_s + v_{11}^2/d_i}{4\ \hat{G}_{11}^{\,2}} \right.$$

$$
+ \frac{V_{22}{}^{2}/d_s + v_{11}{}^{2}/d_i}{4\,\hat{G}_{22}{}^{2}}
$$

$$
+ \frac{(V_{11}V_{22} + V_{12}{}^{2})/d_s + (v_{11}v_{22} + v_{12}{}^{2})/d_i}{2\,\hat{G}_{12}{}^{2}}
$$

$$
- \frac{V_{11}V_{12}/d_s + v_{11}v_{12}/d_i}{\hat{G}_{11}\,\hat{G}_{12}}
$$

$$
- \frac{V_{22}V_{12}/d_s + v_{22}v_{12}/d_i}{\hat{G}_{22}\,\hat{G}_{12}}
$$

$$
+ \frac{V_{12}{}^{2}/d_s + v_{12}{}^{2}/d_i}{2\,\hat{G}_{11}\,\hat{G}_{22}} \Bigg]
$$

where $\hat{r}_g$ = estimate of genetic correlation,

k = number of offspring per sire group. In the present study this is not constant so the estimate of k_1' in Table 4.3 is used.

V_{11} = mean squares (M.S.) for between sires component,

V_{12} = mean crossproducts (M.C.P.) for between sires component,

v_{11} = mean squares (M.S.) for within sires (error) component,

v_{12} = mean crossproducts (M.C.P.) for within sires (error) component,

d_s = degrees of freedom for sires,

d_i = degrees of freedom for error,

$\hat{G}_{11}$ = estimate of additive genetic variance, and

$\hat{G}_{12}$ = estimate of additive genetic covariance.

CHAPTER 5

RESULTS AND DISCUSSION

I. SAMPLE MEANS AND STANDARD DEVIATIONS

The sample means and standard deviations for the traits analysed in this study are shown in Table 5.1. The standard deviations are in the original units of measurement and their values indicate the variability of the observations about the mean values for the traits presented.

II. THE INTERACTION OF SIRES AND YEARS

The sire-year interaction sums of squares and the reductions in sums of squares used in their computation are given for each trait in Appendix I. The error sums of squares for testing the significance of the sire-year interaction are given in Appendix II. The mean squares for the interaction term and the error term in the analysis of variance are presented in Table 5.2. Of the 25 traits studied, only four showed significant sire-year interaction. These were width of gigot (G) and the ratio of the weight of the forequarter to the hindquarter (FQ/HQ) at the 1% level of probability and, carcass grade and cannon bone weight at the 5% level of probability.

TABLE 5.1 Means and standard deviations for the various carcass traits.

Trait	Mean ± S.D.	Trait	Mean ± S.D.
A (mm)	52.31 ± 3.51	Th (cm)	25.77 ± 0.73
B (mm)	27.13 ± 2.26	T (cm)	19.16 ± 0.64
C (mm)	2.71 ± 1.44	Carcass grade	2.39 ± 0.49
D (mm)	2.39 ± 1.61	R (cm)	18.13 ± 0.62
X (mm)	14.65 ± 2.37	K (cm)	57.45 ± 1.99
Y (mm)	2.52 ± 1.35	L (cm)	56.39 ± 1.78
J (mm)	7.59 ± 3.03	H (cm)	29.84 ± 1.93
Carcass total (points)	54.42 ± 11.09	P (cm)	35.26 ± 1.16
F (cm)	25.27 ± 1.03	Carcass weight (kg)	15.06 ± 1.01
G (cm)	21.88 ± 0.61	Cannon bone weight (g)	36.75 ± 3.37
WR (cm)	21.82 ± 1.02	Cannon bone length (cm)	11.58 ± 0.48
WF (cm)	17.55 ± 0.74	FQ/HQ	1.15 ± 0.05
WTh (cm)	15.68 ± 0.82	Age at slaughter (days)	151.09 ± 40.75

TABLE 5.2 Test of significance of the sire-year interaction

	Mean Squares		
Trait	Interaction (d.f. = 12)	Error (d.f. = 445)	F value
A	10.000	7.962	1.26 n.s.
B	6.167	4.416	1.39 n.s.
C	2.575	1.730	1.49 n.s.
D	1.756	2.198	0.79 n.s.
X	4.500	5.099	0.88 n.s.
Y	2.343	1.669	1.40 n.s.
J	9.225	7.792	1.18 n.s.
Carcass total	125.833	101.616	1.24 n.s.
F	1.333	0.863	1.55 n.s.
G	0.667	0.292	2.28 **
WR	0.833	0.825	1.01 n.s.
WF	0.250	0.487	0.51 n.s.
WTh	0.250	0.563	0.44 n.s.
Th	0.583	0.414	1.41 n.s.
T	0.333	0.337	0.99 n.s.
Carcass grade	0.423	0.214	1.98 *
R	0.417	0.313	1.33 n.s.
K	5.000	3.418	1.46 n.s.
L	4.167	2.590	1.61 n.s.
H	1.917	2.826	0.68 n.s.
P	0.917	1.125	0.81 n.s.
Carcass weight	3.667	4.421	0.83 n.s.
Cannon bone weight	12.833	7.026	1.83 *
Cannon bone length	0.133	0.188	0.71 n.s.
FQ/HQ	0.006	0.002	3.05 **

n.s. = not significant

** = $P < 0.01$

* = $0.01 < P < 0.05$

The presence of the sire-year interaction implies that the merit of the sires with respect to each other in terms of the means of their progeny was not the same from year to year. Rae (1958) in a study of fleece characters of hoggets from the same sires used in this study, found that fleece quality was the only character which showed a significant sire-year interaction. He suggested three possible causes which might have given rise to the interaction and these were:

(i) Genuine non-linear interaction between the transmitting ability of the sires and the environmental conditions peculiar to each year. This could have been the possible cause of the interaction terms in width of gigot (G), the ratio of the weights of the forequarter to the hindquarter (FQ/HQ) and cannon bone weight. The sires could have differed in the genes they transmitted to their offspring controlling the response of these traits to changing environmental factors from year to year. One such environmental factor is different feed levels between years. If the progeny of a sire responded to a condition of high feed level in one year with a favourable growth in bone tissue, for example, then cannon bone weight would be higher in that year than in a year in which the feed level was low.

(ii) The fact that the sires were mated to different groups of ewes each year could have contributed to the interaction component. For instance, if the ewes mated to a sire were well above average in their genetic merit in one year, the progeny of that sire in that particular year would be expected to show above average performance. If in the next year a different group of ewes with average genetic merit far below the average for the year was mated to the same sire, then the difference in the means of the progeny in the two years would be included in the interaction component. This, as a factor, is considered as unlikely to contribute much to the interaction component since, in the present study, the ewes were mated to each sire at random.

(iii) Yearly variations in the standards of grading may have contributed to the interaction component for carcass grade. Carcass grade is a composite character determined by several factors. The grader may have emphasized one of these factors in some years while he may have emphasized a different factor in other years and if the sires differed in the genes they transmitted for the two factors, then this source of variation could have contributed to the sire-year interaction for carcass grade.

The interaction effects for the traits showing significant sire-year interaction were computed and presented in Tables 5.3 to 5.6. The size of the interaction effects were based on their deviations from additivity. In general, sires 1 and 11 showed the largest interaction effects for most of the traits with the exception of carcass grade and the ratio of the weights of the forequarter to the hindquarter (FQ/HQ) which showed small interaction effects for all the sires. The other sires on the whole showed small interaction effects with all measurements except cannon bone weight in which all sires produced large interaction effects. The character showing the smallest interaction effects for all sires was the ratio of the weights of the forequarter to the hindquarter (FQ/HQ). Although Tables 5.3 to 5.6 provide information as to the distribution of interaction effects between sires and between years for the four traits, they do not provide any evidence as to the possible causes of the interaction.

TABLE 5.3 Sire-year interaction effects for width of Gigots (G).

Sire*	1944/45	Year 1945/46	1946/47
1	-0.44	0.43	0.01
2	-0.09	0.09	-
5	0.04	-0.29	0.25
6	0.07	-0.15	0.08
7	0.04	-0.32	0.28
8	-0.06	-0.14	0.20
10	-0.41	0.02	0.39
11	-	-0.49	0.49

* Sires 3, 4, 9 and 12 are not included in Tables 5.3 to 5.6 because they were represented in one year only.

TABLE 5.4 Sire-year interaction effects for carcass grade.

Sire	1944/45	Year 1945/46	1946/47
1	-0.04	0.23	-0.19
2	0.06	-0.06	-
5	-0.11	0.14	-0.03
6	-0.01	0.19	-0.18
7	0.11	-0.12	0.01
8	0.07	-0.13	0.06
10	-0.07	-0.12	0.19
11	-	-0.14	0.14

TABLE 5.5 Sire-year interaction effects for cannon bone weight.

Sire	1944/45	Year 1945/46	1946/47
1	-0.78	0.10	0.68
2	0.48	-0.48	-
5	-0.32	0.44	-0.12
6	0.18	0.47	-0.65
7	0.97	-1.00	0.03
8	0.54	-0.32	-0.22
10	-1.09	-0.06	1.15
11	-	0.85	-0.85

TABLE 5.6 Sire-year interaction effects for the ratio of the weights of the forequarter to the hindquarter (FQ/HQ)

Sire	1944/45	Year 1945/46	1946/47
1	-0.01	0.00	0.01
2	0.00	-0.00	-
5	0.00	0.00	-0.00
6	-0.01	-0.00	0.01
7	-0.01	0.01	-0.00
8	0.02	-0.01	-0.01
10	0.00	-0.00	-0.00
11	-	0.00	-0.00

III. THE MAIN EFFECTS AND REGRESSION TERM

The main effects and regression term for traits where the sire-year interaction was found to be significant were not individually estimable without entanglement with the interaction term. Therefore, in this section only the estimates for those traits where the sire-year interaction was shown to be non-significant will be presented.

The reductions in sums of squares due to fitting different models for estimating the main effects and regression term are shown in Appendix III. The total sums of squares and the reductions in sums of squares $R[\mu, s_i, t_j, b_k, C]$ for these are the same as given in Appendix I and II. The sums of squares and mean squares for the main effects and regression term, which are required for testing their significance, are given in Appendix IV and V. The significance of the main effects and regression term for each trait are presented in Table 5.7.

Differences due to sires were significant in all traits except carcass weight. This implies that there were no real differences between sires in terms of the means of carcass weight of their progeny. This is to be expected since all lambs were chosen for slaughter on the basis of liveweight. If there were no sire differences for dressing-out % (carcass weight as a percentage of liveweight) one would not expect to

TABLE 5.7 F-Values for testing the significance of the main effects and the regression term for traits where sire-year interaction is non-significant.

Trait	Sire[a]	Year[b]	B. Rank[c]	Regression[d]
A	15.19 **	4.99**	1.87 n.s.	91.08 **
B	2.95 **	5.27**	0.56 n.s.	30.93 **
C	4.09 **	25.53**	9.11 **	14.64 **
D	3.68 **	19.81**	9.20 **	3.54 n.s.
X	1.89 *	10.13**	5.02 **	5.11 *
Y	3.84 **	2.80 n.s.	3.59 *	1.96 n.s.
J	4.53 **	9.59**	18.87 **	9.59 **
Carcass total	4.48 **	26.55**	5.43 **	1.76 n.s.
F	9.25 **	4.57 *	1.71 n.s.	4.57 *
WR	2.31 **	29.08**	1.21 n.s.	48.46 **
WF	1.89 *	11.43**	11.43 **	0.00 n.s.
WTh	4.75 **	11.71**	11.71 **	18.02 **
Th	8.47 **	0.00 n.s.	1.19 n.s.	26.28 **
T	7.82 **	2.97 n.s.	2.97 n.s.	5.93 *
R	6.92 **	9.51**	1.59 n.s.	3.17 n.s.
K	4.47 **	7.23**	1.45 n.s.	2.89 n.s.
L	6.91 **	1.89 n.s.	0.00 n.s.	7.59 **
H	2.95 **	41.75**	0.36 n.s.	1.43 n.s.
P	8.93 **	0.89 n.s.	0.89 n.s.	2.68 n.s.
Carcass weight	1.24 n.s.	16.25**	10.22 **	1.36 n.s.
Cannon bone length	10.23**	4.82**	0.27 n.s.	0.55 n.s.

a = 11 degrees of freedom for sire effects

b = 2 degrees of freedom for year effects

c = 2 degrees of freedom for birth and rearing rank effects

d = 1 degree of freedom for regression term

** $P < 0.01$

* $0.01 < P < 0.05$

n.s. = not significant

find differences in carcass weight between sires. Dirrerences between years were significant in most of the traits. Those not significantly affected were fat measurement Y, depth of thorax (Th), length of tibia + tarsus (T), carcass length (L) and length of leg (P). The effect of birth and rearing ranks was significant in fat measurements C, D, Y and J, muscle measurement X, carcass total, width of forequarter (WF), width of thorax (WTh) and carcass weight. Width measurements in the forequarter region are known to be affected by fat deposition and various studies have shown that fatty tissue is a major factor influencing carcass weight in sheep. Thus, it appears that the effect of birth and rearing ranks is brought about by differences in the level of fat deposition. The most plausible explanation is that lambs born and reared as singles received better pre- and post-natal maternal environments and, therefore, are heavier at birth, tend to deposit more fat and as a result tend to have heavier carcass weights than lambs born and reared as multiples.

The effect of including the regression on age at slaughter in the statistical model was significant in measurement A and B of the eye muscle, fat depths C and J, muscle measurement X, length of leg (F), width of ribs (WR), width of thorax (WTh), depth of thorax (Th), length of tibia + tarsus (T) and carcass length (L). The inclusion of the regression term has the influence of increasing the efficiency and precision of the tests of significance for the main effects brought about by the reduction of the error variance.

IV. ESTIMATES OF VARIANCE COMPONENTS

Estimates of variance components for the various traits are presented in Table 5.8. For illustratuve purposes, "length" of eye muscle (A) is taken as an example of a trait in which sire-year interaction is non-significant, and the steps involved in the computation of its variance components are shown in Appendix VI. Width of gigot (G) is chosen to represent traits where sire-year interactions are significant, and the steps involved in the computation of the variance components for G are shown in Appendix VII.

V. ESTIMATES OF HERITABILITY OF CARCASS TRAITS IN THE NEW ZEALAND ROMNEY

Table 5.9 presents the additive genetic variance, σ_A^2, computed as 4 X σ_s^2, together with the estimates of heritability of the various carcass traits. The estimates, obtained by paternal half-sib correlation, are of limited reliability since they were based on only 11 degrees of freedom on which to estimate the variance in the genetic values of sires. The small number of sires on which to base the analysis is obviously insufficient since they may not actually be representative of the population from which they came in terms of the variance in genetic values. In Table 5.9 the traits are put

TABLE 5.8 Estimates of variance components for various carcass traits.

Trait	Error Component, σ_e^2	Sire Component, σ_s^2	Interaction Component, σ_{st}^2
A	8.0153	3.0641	
B	4.4617	0.2348	
C	1.7522	0.1458	
D	2.1867	0.1579	
X	5.0832	0.1226	
Y	1.6866	0.1289	
J	7.8291	0.7444	
Carcass total	102.2516	9.5841	
F	0.8748	0.1943	
G	0.2921	0.0362	0.0207
WR	0.8254	0.0292	
WF	0.4812	0.0115	
WTh	0.5549	0.0560	
Th	0.4186	0.0842	
T	0.3370	0.0619	
Carcass grade	0.2139	-0.0023	0.0116
R	0.3154	0.0503	
K	3.4597	0.3229	
L	2.6318	0.4187	
H	2.8024	0.1473	
P	1.1193	0.2391	
Carcass weight	4.4011	0.0284	
Cannon weight	7.0263	2.4861	0.3208
Cannon length	0.1867	0.0464	
FQ/HQ	0.0019	0.0000	0.0002

TABLE 5.9 Additive genetic variance and estimates of heritability of carcass traits.

Trait	Additive genetic variance, σ^2_A	Heritability
A	12.2564	1.11 ± 0.27
B	0.9392	0.20 ± 0.12
C	0.5832	0.31 ± 0.14
D	0.6316	0.27 ± 0.13
X	0.4904	0.09 ± 0.08
Y	0.5156	0.28 ± 0.14
J	2.9776	0.35 ± 0.15
F	0.7772	0.73 ± 0.22
T	0.2476	0.62 ± 0.20
R	0.2012	0.55 ± 0.19
P	0.9564	0.70 ± 0.22
Cannon length	0.1856	0.80 ± 0.23
Cannon weight	9.9444	1.01 ± 0.26
G	0.1448	0.41 ± 0.17
WR	0.1168	0.14 ± 0.10
WF	0.0464	0.09 ± 0.08
WTh	0.2240	0.37 ± 0.16
Th	0.3368	0.67 ± 0.21
K	1.2916	0.34 ± 0.15
L	1.6748	0.55 ± 0.19
H	0.5892	0.20 ± 0.12
Carcass weight	0.1136	0.03 ± 0.04
Carcass grade	-0.0092	-0.04
Carcass total	38.3364	0.34 ± 0.15
FQ/HQ	0.0	0.00

into several groups so that each group can be considered separately for discussion.

A. Internal measurements

As stated in Section II of Chapter 2, all estimates of heritability of eye muscle area in sheep, pigs and cattle have been in the medium to high range. From this information one would expect that the heritabilities of measurements made on the eye muscle would also fall within this range. In fact the estimates of 1.11 for the heritability of the "length" of eye muscle (measurement A) and 0.20 for the depth of eye muscle (measurement B) obtained in the present study lend support to this contention. The value greater than 1.0 for measurement A is due to a large sampling error. In the absence of previous estimates of heritability of measurements A and B in sheep, a worthwhile comparison cannot be made, but estimates for these two measurements in pigs are in general agreement with those in the present study. Table 5.10 presents the estimates of heritability of measurements A and B in pigs for the purpose of comparison.

The relative importance of measurements A and B in determining the shape of the eye muscle is found in the following statement by Pálsson (1939):

"An ideal cutlet has a large deep eye muscle, elliptical to circular in shape, the upper level of which should reach above the point of the spinous process. Such a cutlet is

TABLE 5.10 Estimates of heritability of "length" and depth of eye muscle in pigs.

Measurement	Heritability	Author
"Length" of eye muscle (A)	0.46	Smith, King and Gilbert (1962)
	0.65	Smith and Ross (1965)
Depth of eye muscle (B)	0.29	King (1957)
	0.38	Smith and Ross (1965)
	0.48	Smith, King and Gilbert (1962)

more attractive and has more muscle in proportion to bone than one with an oblong, shallow muscle with the spinous process standing far above its upper level. The latter cutlet is inclined to dry on cooking, while the former will remain juicy ... The greater the depth B in proportion to the length A the better." The presence of a large proportion of additive genetic variance in measurements A and B in sheep found in the present study and in pigs reported by other workers implies that selection in an effort to change the shape of the eye muscle may be effective. However, it would be interesting to know the genetic correlation between these two measurements so that the correlated response in one measurement brought about by selection for the other measurement can then be determined.

From Table 5.9 it can be seen that the heritabilities of measurements of fat depth on the cut surface of the rib fall within the range of 0.25 and 0.35. These compare favourably with the estimates of other workers for fat depth over the eye muscle (C), presented in Table 2.1. In particular, the estimate of 0.31 for fat depth measurement C found in this study is exactly equal to the estimate for the same measurement given by Timon (1965). The heritabilities of fat thickness and fat depth measurements in pigs are, in general, much higher than those of fat depth in sheep. This becomes obvious when estimates for fat depth in sheep obtained in the present study and by other workers are compared with estimates for similar measurements in pigs reported by Smith, King and Gilbert (1962) and, Smith and Ross (1965). The higher values for pigs are not at all surprising when it is realized that the proportion of fatty tissue in the carcass of the pig is much higher than that in sheep and cattle. Moreover, fatty tissue is the most variable of the three major tissues in the body of the pig, namely bone, muscle and fat. The high heritability implies that a high proportion of this variability is due to the additive effects of genes, i.e., additive genetic variance. Thus there is greater scope for progress in selecting for or against fatness in the pig than in either sheep or cattle.

The estimate of heritability of the thickness of muscle layer (measurement X) is low ($h^2 = 0.09$). This muscle is relatively unimportant compared to the eye muscle and has received little attention.

B. Measurements indicative of bone length and weight

The heritabilities of measurements of bone length and weight or those indicative of them obtained in this study are high, all greater than 0.50. These, in general, support the conclusion that skeletal measurements are strongly inherited characters. The estimate of 0.80 for the heritability of cannon bone length is much higher than that of 0.40 reported by Bichard and Yalçin (1964) but is close enough to the estimate of 0.84 given by Rae (1946) although the method used by Rae was dam-offspring regression involving Romney ewes and their Down Cross offspring. The estimate of 1.01 for cannon bone weight found in the present study is perhaps too high; the value greater than unity could be attributed partly to the strong heritability of the character and partly to a large sampling error. The estimate of 0.84 for cannon bone weight reported by Rae (1946) seems to support the contention that weight of bones may be as heritable as measurements of skeletal length. However, the estimates reported by Bichard and Yalçin (1964) of 0.07 and by Munson (1966) of 0.35 are very much in contrast to that in the present study.

The estimates of heritability of length of leg (F) and length of tibia + tarsus (T) are both high. The values of 0.73 for length of leg and 0.62 for length of tibia + tarsus are lower than the estimates of 0.78 and 0.83, respectively, reported by Bichard and Yalçin (1964).

The other two measurements of bone length, the length of radius-ulna (R) and the length of leg from the symphysis pubis to the anterior edge of the distal end of the tarsal (P), were both strongly inherited as indicated by their heritabilities of 0.55 and 0.70, respectively. Unfortunately, there appears to be no published estimates of heritability of these measurements in the literature so that a comparison cannot be made.

C. Measurements indicative of width or depth of body

Measurements which fall into this category are: width of gigot (G), maximum width of rib (WR), maximum width of forequarter in line with the shoulders (WF), minimum width of thorax behind the scapulae (WTh) and depth of thorax (Th).

Estimates of heritability of these measurements presented in Table 5.9 vary from low to moderately high. The value for width of gigot (G) of 0.41 is much higher than the estimate of 0.02 reported by Bichard and Yalçin (1964). Nevertheless, it appears to support the conclusion reached by the latter workers that measurements assessing fleshing were less heritable than skeletal measurements. However, these workers arrived at their conclusion by including estimates of heritability of circumference of gigot (G_c) and circumference of rump (R_c) whereas in the present study no such measurements were analysed.

Heritabilities of measurements of width in the forequarter region, *i.e.*, WR, WF and WTh, are low to moderate with values of 0.14, 0.09 and 0.37, respectively. The lower heritabilities of these measurements compared to the heritability of width of gigot may partly be due to the greater tendency for excess fat to be deposited in this region than in the hindquarter region. Barton (pers. comm.) pointed out that width measurements in the thorax region would be expected to be more affected by fat deposition. Thus it is possible that the variability in fat deposition has added to the environmental and measurement variation in these measurements. Following this argument, the higher estimates of heritability of width of gigot (G) and depth of thorax (Th) may be taken as indicative of the lesser influence of fat deposition on these two measurements.

According to Rae (1946) measurement WR indicates differences in the costal angle in lamb carcasses and is, therefore, of some importance in indicating conformation. The amount of additive genetic variance in this measurement, although small, is probably sufficient to allow selection to alter conformation in the thorax region.

Depth of thorax (Th) is a strongly heritable character ($h^2 = 0.67$). In the absence of any previous estimates for this measurement in sheep no comparison can be made. In pigs, Smith, King and Gilbert (1962) and, Smith and Ross (1965) used the maximum depth from sternum to the top of the vertebral column as a measure of thoracic depth and obtained heritability estimates of 0.34 and 0.56, respectively.

The lack of information on the heritabilities of the width and depth measurements is perhaps due to their relative unimportance in the consideration of the conformation of the carcass. The reason for this is quite obvious: the thorax region produces one of the cheapest cuts of the carcass.

D. Measurements indicative of length of body

The estimates of heritability, shown in Table 5.9, for carcass length, taken either as that measurement from the tail head to the base of the neck (K) or that from the symphysis pubis to the anterior edge of the middle of the first rib (L), indicate that it is moderately to strongly inherited. The value of 0.55 for measurement L agrees well with the estimate of 0.50 reported by Botkin *et al*. (1969). The lower value of 0.34 for measurement K found in the present study is probably due to the fact that it cannot be taken with the same degree of accuracy as measurement L. The lower accuracy associated with measurement K suggests that it should be considered as an alternative measure of carcass length only in cases where L cannot be measured, as in frozen carcasses. The importance of body length in the consideration of the conformation of the carcass lies in the fact that the *l. dorsi* muscle, perhaps one of the most valuable muscles in the body, lies adjacent to the vertebral column on each side from the pelvis to the shoulders. Thus, from this view point, a longer carcass would be considered as highly desirable provided that, at constant carcass weight, increased body length is not accompanied by a reduction in muscle thickness. Perhaps there is an optimum value at which the combination of carcass length and muscle thickness produces the greatest amount of edible meat and increase in length above this value will result in a reduction in muscle thickness. The high estimates of heritability of carcass length found in this study and those of other workers, both in sheep and pigs, suggest that single-trait selection for this character would be highly effective.

The length of the carcass from the symphysis pubis to the posterior edge of the last rib at the junction with the vertebra (H) measures the length of the hindquarter region. Since this is where some of the most expensive cuts of the carcass are found, it is reasonable to suggest that a longer hindquarter should be desirable. Again, increase in length should only be allowed to take place as long as reduction in muscle thickness does not occur. This is the only study which has attempted to estimate the heritability of measurement H. The value of 0.20 suggests that it is fairly responsive to selection.

E. The "other" carcass traits

The heritability estimate of 0.03 for carcass weight found in the present study is very close to that of 0.02 reported by Bowman, Marshall and Broadbent (1968). Coupled with the values of 0.11 given by Bowman and Hendy (1972) in sheep and 0.14 by Buxadé (1972) and, 0.30 by King (1957) in pigs, it appears confirmed that carcass weight is a trait of low to moderate heritability, perhaps more on the low side. This is to be expected since, in most studies, animals were selected for slaughter on a constant liveweight basis. For instance, in the present study, the wether lambs were chosen for slaughter when they reached a liveweight in the paddock of about 33 kg. Selection for slaughter at about the same liveweight is expected to reduce the variability of carcass weight and hence the genetic variance for this trait in the selected lambs.

The subjective nature of carcass grading and the inconsistency in the estimates of heritability of this trait have been discussed in Section II of Chapter 2. The estimate of heritability of this trait in the present study is -0.04, the negative value indicating either a zero or a low heritability. Previous estimates for this trait in sheep have been low, Botkin _et al_. (1969) giving a value of 0.06 and Ray _et al_. (1972) reporting zero estimates in three breeding groups.

The "Cambridge" Block Test for lambs was proposed by John Hammond (McMeekan, 1939) as a means of evaluating a carcass on a points system, paying particular attention to its conformation in the loin and leg regions, which are considered to be the most important parts of the carcass. Points are given for the various external and internal characters as shown in Table 3.2. Thus the term carcass total refers to the total number of points, out of a possible 100, scored by a carcass. Like carcass grading it suffers from being subjective with regard to the scores given to the external parts of the carcass such as blockiness of leg, fat covering over leg and fullness of loin. Likewise the heritability estimates for carcass total would be expected to be variable following the knowledge that the estimates for carcass grade have been inconsistent. However, carcass total, or to be more precise the "Cambridge" Block Test for lambs, have not been used as extensively as perhaps anticipated by Hammond, and estimates of heritability of this character are non-existent. The estimate of 0.34 in this study suggests that it is a character of moderate heritability.

The ratio of the weights of the forequarter and the hindquarter (FQ/HQ) of each wether lamb carcass was included when the data were being collected because at that time it was thought that there was a possibility of transferring some of the weight of the animal in the forequarter region, where the cheap cuts are, to the hindquarter region, where the more expensive cuts are. This opinion was largely the influence of the Hammond school and was shared by many people at that time. However, recent research investigations have proven that this is not possible to achieve so that at present the ratio FQ/HQ no longer features in studies aimed at improving carcass merit. The estimate of heritability of 0.00 for FQ/HQ found in the present study shows that there is no additive genetic variance for this trait so that attempts at increasing the weight of the hindquarter region through selection will not give any response. Therefore, it is recommended that the ratio FQ/HQ should be excluded from any investigation involving carcass traits in the future on the grounds that it is a poor indicator of carcass merit.

VI. ESTIMATES OF GENETIC AND PHENOTYPIC CORRELATIONS AMONG CARCASS TRAITS IN THE NEW ZEALAND ROMNEY

Steps involved in the computation of covariance components and phenotypic and genetic correlations between measurements A and B of the eye muscle are shown, for illustrative purposes, in Appendix VIII.

Estimates of genetic and phenotypic correlations among carcass traits in the New Zealand Romney are presented in Tables 5.11 to 5.25. For convenience in discussion, the traits are divided into groups as in Section V of this Chapter and the relationships between them discussed separately.

A. Among internal measurements

The genetic and phenotypic correlations among internal carcass measurements are presented in Table 5.11.

As expected, there is a positive correlation between "length" (A) and depth (B) of the eye muscle at the phenotypic and genetic levels. At the phenotypic level, this implies that in New Zealand Romney lambs the "longer" eye muscle is associated with having greater depth and, therefore, a larger cross-sectional area. The high positive genetic correlation (0.60) indicates that selection to increase the "length" of eye muscle, for example, would be effective in bringing about a correlated increase in the depth measurement and, therefore,

Table 5.11 Estimates of phenotypic[a] and genetic correlations among internal carcass measurements

Trait	B	C	D	X	Y	J
A	0.24 **[b] 0.60±0.27	-0.28** -0.45±0.29	-0.17** -0.44±0.31	-0.01 n.s. -0.07±0.45	-0.09 * 0.03±0.36	-0.29** -0.64±0.22
B		0.19** -0.12±0.43	0.34** -0.38±0.42	0.28 ** 0.31±0.49	0.17 ** 0.00	0.20** -0.28±0.41
C			0.68 * 0.61±0.25	0.26 ** 0.34±0.46	0.52 ** 0.54±0.29	0.64** 0.93±0.08
D				0.31 ** 0.60±0.38	0.40 ** 0.43±0.34	0.54** 0.62±0.25
X					0.14 ** -0.01±0.51	0.33** 0.24±0.47
Y						0.47** 0.28±0.36

[a] Phenotypic correlations on the upper line, genetic correlations on the lower line

** P < 0.01

* 0.01 < P < 0.05

n.s. not significant

the area of the eye muscle.

The phenotypic correlations between "length" of eye muscle and fat measurements C, D, Y and J are negative while those involving depth of eye muscle are positive. These imply that lambs with a thicker layer of backfat tend to have a "short", but deep eye muscle. The corresponding genetic correlations are negative except for those with fat measurement Y. The antagonostic relationships indicate that improvement in the "length" and depth of the eye muscle and, therefore, in its area could be made by selection aimed at reducing carcass fatness. The low positive correlations between the eye muscle measurements and fat measurement Y are probably due to the high degree of inaccuracy associated with the measurement of this latter trait.

The strong relationship existing among fat measurements C, D, Y and J at both genetic and phenotypic levels are also as anticipated, since they are closely inter-related and are indicative of the same basic component, namely carcass fatness.

B. Between internal measurements and measurements indicative of bone length and weight

Estimates of genetic and phenotypic correlations between internal measurements and measurements indicative of bone length and weight are presented in Table 5.12.

The phenotypic correlations between "length" of eye muscle and measurements of bone length and weight are positive, but not very large. Depth of eye muscle appears to be weakly related to the skeletal measurements. From these estimates, it can be concluded that skeletal length and weight in the carcass may be used for predicting the "length" of the eye muscle to a limited extent, but are totally unsatisfactory for predicting depth of eye muscle. At the genetic level, "length" of eye muscle is positively correlated with measurements indicative of bone length and weight. On the other hand, depth of eye muscle is negatively correlated with these. Therefore, it appears that selection for shorter skeletal length may lead to a reduction in "length" of eye muscle but to an increase in its depth.

The antagonistic relationships between fat measurements C, D, Y and J and measurements indicative of bone length and weight are very apparent at both levels. At the phenotypic level, the negative estimates serve to confirm the generally found relationship that lambs which are blocky tend to have a greater level of fat deposition than leggy lambs. This is to be expected since the lambs in the present study were slaughtered at about the same liveweight and lambs with smaller skeletal dimensions would be compensated by having a relatively greater level of fatness.

Relationships existing between internal measurements and measurements indicative of skeletal length and weight, at the genetic level, are of particular interest to the sheep industry. It is generally agreed that, with regard to consumer preference, an ideal cutlet is one with a large deep eye muscle, elliptical

TABLE 5.12 Estimates of phenotypic[a] and genetic correlations between internal measurements and measurements indicative of bone length and weight.

Trait	F	T	R	P	Cannon bone length	Cannon bone weight
A	0.10*[b] 0.04±0.33	0.19** 0.10±0.33	0.24** 0.34±0.30	0.18** 0.17±0.32	0.20** 0.24±0.31	0.29** 0.24±0.30
B	-0.20** -0.50±0.31	-0.02 n.s. -0.10±0.39	0.00 n.s. -0.07±0.40	-0.05 n.s. -0.21±0.38	-0.03 n.s. -0.04±0.39	- 0.02 n.s. -0.23±0.37
C	-0.36** -0.29±0.33	-0.23** -0.10±0.37	-0.27** -0.27±0.35	-0.23** -0.31±0.34	-0.29** -0.31±0.33	-0.38** -0.66±0.22
D	-0.35** -0.51±0.28	-0.20** -0.42±0.32	-0.25** -0.56±0.28	-0.25** -0.56±0.28	-0.23** -0.52±0.29	-0.32** -0.63±0.24
X	-0.29** -1.23±0.23	-0.20** -1.06±0.25	-0.19** -1.03±0.26	-0.26** -1.14±0.22	-0.19** -0.81±0.30	-0.18** -1.00±0.24
Y	-0.26** -0.33±0.33	-0.20** -0.41±0.32	-0.17** -0.49±0.30	-0.17** -0.53±0.29	-0.26** -0.61±0.25	-0.30** -0.69±0.22
J	-0.30** -0.11±0.36	-0.18** 0.04±0.37	-0.21** -0.29±0.34	-0.17** -0.17±0.35	-0.17** -0.03±0.36	-0.29** -0.41±0.30

[a, b] See footnote of Table 5.11

to circular in shape and with as little excess fat as possible. The estimates of genetic correlations found in the present study suggest that selection for blockiness of leg and shortness in the bones would, in general, have the effect of reducing the "length" and increasing the depth of the eye muscle and would favour greater deposition of fat in the carcass. With regard to improving the cutlet, only the increase in depth of eye muscle can be considered desirable, the other two changes would be detrimental.

The relationships between muscle layer X and measurements indicative of skeletal length and weight are of less importance. All correlations are negative, being highly so at the genetic level. In fact, four of the genetic correlations have absolute values greater than unity. This could be attributed partly to the strong relationships existing between these measurements and partly to large sampling errors.

C. Between internal measurements and measurements indicative of width or depth of body

The relationships between internal measurements and measurements indicative of width or depth of body are given in Table 5.13.

Most of the measurements indicative of body width or depth are weakly correlated, phenotypically, to "length" of eye muscle except for width of gigot (G) at 0.29. They are positively correlated to depth of eye muscle. The relationships existing

TABLE 5.13 Estimates of phenotypic[a] and genetic correlations between internal measurements and measurements indicative of width or depth of body

Trait	G	WR	WF	WTh	Th
A	0.29** [b] 0.52±0.27	-0.04 n.s. -0.13±0.41	0.12** 0.52±0.50	-0.04 n.s. 0.10±0.35	0.10 * -0.07±0.33
B	0.23** 0.04±0.40	0.22 ** 0.40±0.43	0.46** 0.60±0.43	0.32 ** -0.07±0.42	0.14 ** 0.37±0.35
C	-0.07 n.s. -0.95±0.13	0.22 ** 0.27±0.43	0.27** -0.51±0.50	0.45 ** 0.45±0.31	0.16 ** 0.46±0.30
D	0.04 n.s. -0.72±0.25	0.25 ** 0.44±0.40	0.35** -0.41±0.53	0.49 ** 0.69±0.23	0.08 n.s. 0.17±0.37
X	0.10* -0.08±0.48	0.21 ** 1.60±0.55	0.35** 0.59±0.53	0.31 ** 0.63±0.36	0.05 n.s. -0.40±0.44
Y	-0.09* -0.83±0.19	0.08 n.s. 0.03±0.47	0.25** -0.07±0.52	0.39 ** 0.93±0.12	0.12** 0.26±0.35
J	-0.08 n.s. -0.90±0.20	0.15 ** 0.21±0.44	0.30** -0.98±0.71	0.50 ** 0.28±0.35	0.23** 0.62±0.25

[a, b] See footnote of Table 5.11

between width of gigot and the eye muscle measurements at the phenotypic level suggest that the former may be used to a limited extent to predict the area of the eye muscle in the carcass, i.e., the greater the width of gigot, the "longer" and deeper the eye muscle would be and, therefore, the larger its area.

The relationships at the genetic level between measurements indicative of width or depth of body, and the eye muscle measurements imply that increase in the "length" of eye muscle could be made by selecting for greater width of gigot, width of forequarter in line with the shoulder (WF) and also possibly width of thorax behind the scapulae (WTh). Improvement in the depth of eye muscle, which is perhaps more important than that in its "length", can possibly be made by selecting for greater width of ribs (WR), width of forequarter in line with the shoulders (WF) and depth of thorax (Th).

In general, the phenotypic correlations between fat measurements C, D, Y and J and width measurements in the forequarter region (WR, WF and WTh) are positive and moderately large. The relationships between the fat measurements and width of gigot and depth of thorax are much weaker.

These findings confirm the fact that measurements of body width in the forequarter region are affected to a greater extent by deposition of fat than measurement of width in the hindquarter region (gigot) and depth of thorax. In particular, width of thorax (WTh) is known to be affected to a large extent by fat deposition. The fact that this measurement showed the strongest correlations with the fat measurements support this contention. At the genetic level, the estimates found in the present study imply that reduction in the thickness of backfat could be made by selecting animals wider in the gigots (G) and forequarters (WF), narrower in the ribs (WR) and thorax (WTh) and shallower in the thorax (Th).

D. Between internal measurements and measurements indicative of length of body

Estimates of phenotypic and genetic correlations between internal measurements and measurements indicative of body length are presented in Table 5.14.

Measurements of length of carcass (K and L) are poor indicators of "length" and depth of eye muscle as suggested by the low phenotypic correlations. Similar findings have been reported in pigs by King (1957), Enfield and Whatley (1961), Smith, King and Gilbert (1962) and Smith and Ross (1965). The phenotypic correlations between carcass length (K and L) and fat measurements C, D, Y and J are generally low and consistently negative. The antagonistic relationships are also reported in pigs although in this species the correlations are much larger in magnitude. The weaker relationships in sheep could be attributed to the lesser variability of fat deposition in this species than in pigs.

Estimates of genetic correlations between eye muscle

TABLE 5.14 Estimates of phenotypic[a] and genetice correlations between internal measurements and measurements indicative of body length

Trait	K	L	H
A	0.07 n.s.[b] 0.01±0.35	0.07 n.s. -0.10±0.33	-0.01 n.s. -0.08±0.38
B	-0.09* -0.56±0.33	-0.05 n.s. -0.55±0.31	0.05 n.s. -0.12±0.45
C	-0.19** -0.14±0.39	-0.11 * -0.13±0.37	0.02 n.s. 0.53±0.35
D	-0.15** -0.13±0.40	-0.09 * -0.28±0.36	0.04 n.s. 0.23±0.42
X	-0.07 n.s. -0.56±0.42	-0.06 n.s. -1.17±0.26	-0.08 n.s. -0.40±0.49
Y	-0.04 n.s. -0.05±0.40	-0.03 n.s. -0.06±0.38	0.05 n.s. 0.31±0.40
J	-0.11* -0.04±0.39	-0.08 n.s. 0.06±0.37	0.06 n.s. 0.70±0.29

[a, b] See footnote of Table 5.11

measurements A and B and carcass length (K and L) imply that selection to increase carcass length may have little effect on "length" of eye muscle, but may result in a substantial reduction in its depth.

The genetic correlations between the fat measurements and carcass length (K and L) are negative except for one estimate. Although the magnitude of the correlations found in the present study are not as high as those in pigs, a similar reason may be given for the antagonistic relationships, i.e., when lambs are selected for slaughter on a constant liveweight basis, any change in carcass length must be compensated for by an opposite change in one or more of the other carcass dimensions which in this case is backfat thickness.

E. Between internal measurements and the "other" carcass traits

Estimates of genetic and phenotypic correlations between internal measurements and the "other" carcass traits are presented in Table 5.15.

At the phenotypic level, carcass weight is positively correlated with all the internal measurements indicating that carcasses with higher dressing-out percentages have "longer" and deeper eye muscles and greater deposition of backfat. The relationships between carcass weight and the backfat measurements are not at all unexpected since it is knownthat an increase in carcass fatness contributes to a marked extent to an increase in dressing-out percentages. At the genetic level, the correlations

TABLE 5.15 Estimates of phenotypic[a] and genetic correlations between internal measurements and the "other" carcass traits, namely carcass weight, carcass grade and carcass total.

Trait	Carcass Weight	Carcass Grade	Carcass Total
A	0.13**[b] 0.82±0.84	-0.10* 0.24±0.71	-0.11* -0.18±0.34
B	0.43** 0.96±0.73	0.28** 1.01±1.23	0.46** 0.34±0.37
C	0.42** 0.04±0.79	0.49** 0.66±0.48	0.72** 0.61±0.24
D	0.44** -0.21±0.90	0.39** 0.22±0.56	0.63** 0.56±0.27
X	0.43** -0.20±1.15	0.28** 1.07±1.49	0.54** 1.14±0.17
Y	0.32** -0.39±0.92	0.34** 0.44±0.52	0.38** 0.30±0.36
J	0.49** -0.23±0.88	0.43** 0.21±0.68	0.54** 0.43±0.31

[a, b] See footnote of Table 5.11

between carcass weight and "length" and depth of eye muscle are highly positive, implying that selection for higher dressing-out percentages may be a highly effective means of enlarging the eye muscle. The genetic correlations between carcass weight and the fat measurements indicate that, in general, aiming for higher dressing-out percentages may also result in a reduction in carcass fatness. This is difficult to interpret in view of the existing positive relationships between carcass weight and the fat measurements at the phenotypic level.

There is a low negative phenotypic correlation between carcass grade and "length" of eye muscle and a positive phenotypic correlation of moderate size between carcass grade and depth of eye muscle. The genetic correlations between carcass grade and these two measurements indicate that improvement in the eye muscle can be made by selecting for better grade. All the correlations, at both levels, between carcass grade and fat depth measurements are positive. At the phenotypic level, they imply that carcasses with a thicker layer of backfat tend to grade better. This is to be expected since the system of grading used placed a great deal of emphasis upon the level of fatness in the carcass. These results also point to the need for a change in emphasis on the factors affecting carcass grade; that, in the future, systems of grading should take more into consideration those factors indicative of carcass leanness and cutability.

It is interesting to note that, in general, the relationships between carcass total and the internal measurements follow the same trend as those between carcass grade and the latter. This is not surprising since most of the characteristics used in carcass grading are also employed in the "Cambridge" Block Test. The phenotypic correlations between carcass total and "length" and depth of eye muscle are in line with the emphasis placed upon these measurements in the Block Test. In this respect, the deeper eye muscle scored more points than the "longer" eye muscle. Improvement in terms of Block Test performance can be made by selecting for greater depth of eye muscle, as implied by the genetic correlations.

The same basic factors which influence the relationships between carcass grade and the fat measurements, as described previously, probably affect the relationships between carcass total and these measurements at the genetic as well as the phenotypic level.

F. Among measurements indicative of bone length and weight

The relationships among measurements indicative of bone length and weight are strong, the lowest correlation being 0.57 (Table 5.16). It is worth noting that all the genetic correlations are larger in magnitude than the phenotypic correlations. The highly positive relationships at both levels are as expected since the measurements are closely inter-related with each other. At the phenotypic level, the correlations indicate that the length of any of the long bones may be used to

TABLE 5.16 Estimates of phenotypic[a] and genetic correlations among measurements indicative of bone length and weight

Trait	T	R	P	Cannon bone length	Cannon bone weight
F	0.76**[b] 0.86±0.09	0.75** 0.86±0.10	0.78** 0.94±0.05	0.62** 0.73±0.16	0.61** 0.82±0.11
T		0.82** 0.93±0.06	0.78** 0.99±0.02	0.66** 0.79±0.13	0.57** 0.71±0.17
R			0.73** 0.97±0.03	0.63** 0.69±0.18	0.63** 0.70±0.18
P				0.63** 0.86±0.10	0.60** 0.87±0.09
Cannon bone length					0.70** 0.91±0.14

[a, b] See footnote of Table 5.11

predict the length of the other bones to quite a high degree of accuracy. In particular, the measurements which may be useful for predictive purposes are length of leg (F and P) and cannon bone length, all of which can be measured without the inconvenience of having to cut the carcass. The relationships between cannon bone weight and the other measurements show that length of bones is an important factor determining their weight.

The genetic correlations imply that the skeletal dimensions of length and weight can be changed by selecting for a change in any one of the measurements in Table 5.16.

G. Between measurements indicative of bone length and weight and those indicative of width or depth of body

Estimates of phenotypic and genetic correlations between measurements indicative of bone length and weight and those indicative of width or depth of body are presented in Table 5.17.

At the phenotypic level, the estimates indicate that leggier carcasses, *i.e.*, those with long legs and long bones, are slightly wider at the gigots (G), deeper in the thorax (Th) and narrower in the forequarter region (WR, WF and WTh).

At the genetic level, the correlations between the skeletal measurements and the measurements indicative of width of depth of body are in the same direction as the corresponding phenotypic correlations, but in general greater in magnitude. This is particularly so in the case of the correlations involving the three width measurements in the forequarter region, *i.e.*, WR,

TABLE 5.17 Estimates of phenotypic[a] and genetic correlations between measurements indicative of bone length and weight and those indicative of width or depth of body.

Trait	G	WR	WF	WTh	Th
F	0.07 n.s.[b] 0.28±0.32	-0.22** -1.19±0.16	-0.33** -0.92±0.25	-0.31** -0.54±0.27	0.16** 0.15±0.33
T	0.11* 0.07±0.35	-0.16** -1.06±0.17	-0.14** -0.97±0.27	-0.14** -0.61±0.25	0.31** 0.33±0.31
R	0.19** 0.38±0.31	-0.13** -1.13±0.17	-0.08 n.s. -0.69±0.36	-0.10* -0.64±0.25	0.28** 0.10±0.34
P	0.15** 0.26±0.33	-0.16** -1.06±0.17	-0.16** -0.79±0.31	-0.16** -0.73±0.20	0.27** 0.19±0.33
Cannon bone length	0.14** 0.25±0.32	-0.14** -0.77±0.26	-0.20** -0.71±0.33	-0.20** -0.75±0.19	0.26** 0.44±0.28
Cannon bone weight	0.25** 0.56±0.24	-0.09* -0.82±0.24	-0.05 n.s. -0.56±0.38	-0.24** -0.81±0.15	0.19** 0.12±0.33

[a, b] See footnote of Table 5.11

WF and WTh. The implications are that selection for a blocky conformation ("blockiness" in this case referring to shortness of leg and the bones) would result in a decrease in the width of gigot and the depth of thorax, but at the same time would also cause a substantial widening of the forequarter region.

H. Between measurements indicative of bone length and weight and those indicative of body length

The positive genetic and phenotypic correlations shown in Table 5.18 are to be expected. Measurements indicative of body length (K, L and H) are largely influenced by the length of the vertebral column and, therefore, at the phenotypic level, would be expected to be related to measurements indicative of skeletal length. Also any increase in skeletal length due to selection would automatically result in the elongation of the vertebral column and, therefore, of the body. The estimates of genetic correlations involving the length of body from the symphysis pubis to the posterior edge of the last rib at the junction with the vertebra (H) and measurements indicative of skeletal length show that an increase in the former can be obtained by selection aimed at increasing the latter. Measurement H represents the length of the loin region from which expensive cuts are derived. An increase in the length of this region should, therefore, be desirable.

TABLE 5.18 Estimates of phenotypic[a] and genetic correlations between measurements indicative of bone length and weight and those indicative of length of body.

Trait	K	L	H
F	0.30**[b] 0.45±0.29	0.39** 0.75±0.17	0.23** 0.26±0.37
T	0.24** 0.03±0.37	0.34** 0.45±0.28	0.18** 0.21±0.38
R	0.32** 0.15±0.36	0.37** 0.38±0.30	0.24** 0.01±0.40
P	0.25** 0.21±0.35	0.36** 0.60±0.23	0.24** 0.18±0.38
Cannon bone length	0.21** 0.22±0.34	0.29** 0.64±0.22	0.23** 0.42±0.33
Cannon bone weight	0.35** 0.43±0.29	0.43** 0.73±0.17	0.20** 0.24±0.36

[a, b] See footnote of Table 5.11

I. Between measurements indicative of bone length and weight and the "other" carcass traits, namely carcass weight, carcass grade and carcass total

Estimates of phenotypic correlations between carcass weight and measurements indicative of skeletal length (Table 5.19) show that the former is little, if at all, related to the latter. At the genetic level, it is difficult to understand why carcass weight should be negatively correlated to length of leg (F and P), length of tibia + tarsus (T) and length of radius-ulna (R), but positively correlated to cannon bone length. The relationships between carcass grade and carcass total and measurements indicative of bone length and weight are distinctly antagonistic. The phenotypic correlations are to be expected since greater length of leg and of the bones were considered undesirable by the grader at that time. According to Barton (1947), "... He (the grader) looks for shortness of leg, shape and meatiness, and for width, flatness, and fullness in the loin...". The same characteristics are also looked for in the "Cambridge" Block Test. It is, therefore, obvious, that improvement in carcass grade and Block Test performance could be made by selecting for animals with shortness of the leg and the long bones generally. This contention is supported by the estimates of genetic correlations shown in Table 5.19.

J. Among measurements indicative of width or depth or body

Table 5.20 presents the estimates of genetic and phenotypic correlations among measurements indicative of width or depth of body. The phenotypic correlations indicate that animals wider in

TABLE 5.19 Estimates of phenotypic[a] and genetic correlations between measurements indicative of bone length and weight and the "other" carcass traits, namely carcass weight, carcass grade and carcass total.

Trait	Carcass weight	Carcass grade	Carcass total
F	-0.12 **[b] -0.58±0.76	-0.39 ** -1.05±0.39	-0.66 ** -0.91±0.43
T	0.08 n.s. -0.31±0.77	-0.25 ** -0.62±0.42	-0.45 ** -0.73±1.09
R	0.14 ** -0.27±0.78	-0.24 ** -0.59±0.43	-0.45 ** -0.71±1.31
P	0.11 * -0.33±0.77	-0.23 ** -0.90±0.36	-0.47 ** -0.87±0.35
Cannon bone length	0.01 n.s. 0.33±0.74	-0.25 ** -0.68±0.40	-0.41 ** -0.72±1.43
Cannon bone weight	0.12 ** -0.02±0.71	-0.30 ** -1.06±0.33	-0.45 ** -0.92±0.10

[a], [b] See footnote of Table 5.11

TABLE 5.20 Estimates of phenotypic[a] and genetic correlations among measurements indicative of width or depth of body.

Trait	WR	WF	WTh	Th
G	0.30 ** [b] -0.19±0.44	0.32 ** 0.39±0.42	0.15** -0.54±0.30	0.05 n.s. -0.54±0.27
WR		0.37 ** 1.01±0.27	0.44** 0.28±0.41	0.07 n.s. -0.48±0.37
WF			0.63** -0.18±0.53	0.07 n.s. -0.76±0.36
WTh				0.13 ** -0.03±0.36

[a, b] See footnote of Table 5.11

the hindquarter region, as measured by their gigot width (G), tend to be wider also in the forequarter region, as measured by their width of ribs (WR), width of forequarter (WF) and width of thorax (WTh).

At the genetic level, the relationships are less easy to interpret. An explanation cannot be found for the fact that selection for animals with wider gigots would lead to an increase in the width of forequarter (WF) but at the same time to a decrease in the width of ribs (WR) and width of thorax (WTh). It is also not known why an increase in the width of thorax (WTh) would be accompanied by an increase in the width of ribs (WR) but a decrease in the width of forequarter (WF). The genetic correlations between depth of thorax (Th) and the width measurements imply that increase in body width would be followed by a reduction in its depth.

K. Between measurements indicative of width or depth of body and those indicative of length of body

The phenotypic correlations given in Table 5.21 show that the length of a carcass, represented by any of the measurements K, L or H, bear little or no relationship to its width. There is a positive relationship between carcass length and depth of thorax (Th) indicating that the longer carcass is also one that is deeper in the thorax.

Estimates of genetic correlations between measurements indicative of width or depth of body and those indicative of length of body are also presented in Table 5.21. Those between carcass

TABLE 5.21 Estimates of phenotypic[a] and genetic correlations between measurements indicative of width or depth of body and those indicative of length of body.

Trait	K	L	H
G	0.11*[b] 0.45±0.31	0.11* 0.11±0.35	0.04 n.s. -0.29±0.38
WR	-0.12** -0.38±0.25	0.01 n.s. -0.87±0.46	-0.03 n.s. -0.32±0.17
WF	-0.02 n.s. -0.32±0.47	0.00 n.s. -0.76±0.35	0.04 n.s. -0.70±0.45
WTh	-0.10* -0.14±0.38	-0.09* -0.47±0.30	0.10* -0.01±0.42
Th	0.15** 0.07±0.36	0.27** 0.41±0.29	0.24** 0.92±0.15

[a, b] See footnote of Table 5.11

length (K and L) and width of gigot (G) show that increase in carcass length will be accompanied by a correlated increase in the width of gigot. However, an increase in the length of the hindquarter region, i.e., in measurement H would result in a decrease in gigot width. There is an antagonistic relationship between measurements indicative of body length and those indicative of width in the forequarter region (WR, WF and WTh) implying that a change in the carcass dimension of length would be compensated by an opposite change in the dimension of width. In contrast, a change in carcass length would result in a change in carcass depth in the same direction.

L. Between measurements indicative of width or depth of body and the "other" carcass traits, namely carcass weight, carcass grade and carcass total

Table 5.22 presents estimates of genetic and phenotypic correlations between measurements indicative of width or depth of body and the "other" carcass traits, namely carcass weight, carcass grade and carcass total.

The phenotypic correlations between carcass weight and the width and depth measurements are indicative of the fact that carcasses of higher dressing-out percentages tend to be wider and deeper in the body. It has been shown that an increase in carcass fatness contributes to a large extent to an increase in dressing-out percentages and, to a lesser extent, affects the width and depth measurements, particularly width of thorax (WTh). Therefore, it is possible that the relationships between carcass

TABLE 5.22 Estimates of phenotypic[a] and genetic correlations between measurements indicative of width or depth of body and the "other" carcass traits, namely carcass weight, carcass grade and carcass total.

Trait	Carcass weight	Carcass grade	Carcass total
G	0.36**[b] 0.08±0.74	0.13** -0.72±0.48	0.22** -0.46±0.96
WR	0.34** 0.24±0.85	0.22** 0.88±0.48	0.35** 1.07±3.33
WF	0.69** -0.44±1.43	0.38** 0.42±0.60	0.48** 0.43±3.43
WTh	0.61** -0.69±1.11	0.43** 0.40±0.47	0.49** 0.54±0.91
Th	0.48** 0.78±0.68	0.14** 0.34±0.49	0.07 n.s. 0.02±0.37

[a], [b] See footnote of Table 5.11

weight and the width and depth measurements are partly influenced by carcass fatness.

It appears that there is little prospect of improving dressing-out percentage by means of selection for width of gigot (G), based on the estimate of genetic correlation between width of gigot and carcass weight. More rapid progress could possibly be made by selection for greater width of ribs (WR) or depth of thorax (Th). The antagonistic relationships between carcass weight and width of forequarter (WF) and width of thorax (WTh), at the genetic level, are difficult to interpret. Estimates of genetic correlations between these traits show large sampling errors.

Carcass grade and carcass total show the same trend of relationships with the width and depth measurements. In general, the phenotypic correlations indicate that carcasses which are wider and deeper tend to be graded better and perform better in the Block Test. This is not unexpected in view of the fact that carcass grading at the time these data were collected and the Block Test paid particular attention to the width conformation of the carcass. The genetic correlations seem to imply that improvement in carcass grading and Block Test performance could be made by selecting for animals which are wider in the forequarter region.

M. <u>Among measurements indicative of length of body</u>

The high values of the estimates of genetic and phenotypic correlations among measurements indicative of length of body are apparent in Table 5.23. The strong relationships are to be expected in view of the fact that the measurements are closely inter-related.

TABLE 5.23 Estimates of phenotypic[a] and genetic correlations among measurements indicative of length of body.

Trait	L	H
K	0.67** [b] 0.86±0.11	0.33** 0.83±0.20
L		0.45** 0.87±0.15

[a, b] See footnote of Table 5.11

N. Between measurements indicative of length of body and the "other" carcass traits, namely carcass weight, carcass grade and carcass total

Estimates of genetic and phenotypic correlations between measurements indicative of body length and the "other" carcass traits, namely carcass weight, carcass grade and carcass total are presented in Table 5.24. At the phenotypic level, the estimates show that longer carcasses tend to have higher dressing-out percentages, grade lower and score less in the "Cambridge" Block Test. The relationships between carcass length and carcass grade and carcass total are expected since the longer carcasses generally give the appearance of lack of blockiness in the leg and loin regions and it has already been mentioned that these two factors were important in the grading of carcasses and the allocation of points in the Block Test. At the genetic level, the estimates imply that selection for increased body length would result in an increase in dressing-out percentages, a lowering of carcass grade and poorer performance in the Block Test.

O. Among the "other" carcass traits, namely carcass weight, carcass grade and carcass total

The relationships existing among the "other" carcass traits are given in Table 5.25.

Carcass weight is positively correlated to carcass grade and carcass total at the phenotypic level. These relationships could have resulted through the intermediate influence of carcass fatness. It is known that increased fatness contributes markedly to an increase in dressing-out percentages, and as

TABLE 5.24 Estimates of phenotypic[a] and genetic correlations between measurements indicative of body length and the "other" carcass traits, namely carcass weight, carcass grade and carcass total.

Trait	Carcass weight	Carcass grade	Carcass total
K	0.19**[b] 0.62±0.77	-0.22** -0.96±0.37	-0.26** -0.43±0.35
L	0.27** 0.23±0.72	-0.16** -1.10±0.36	-0.24** -0.75±0.25
H	0.25** 1.40±1.08	-0.04 n.s. -0.24±0.59	-0.13** -0.05±0.42

[a, b] See footnote of Table 5.11

TABLE 5.25 Estimates of phenotypic[a] and genetic correlations among the "other" carcass traits, namely carcass weight, carcass grade and carcass total.

Trait	Carcass grade	Carcass total
Carcass weight	0.45**[b] 0.01±1.17	0.49** 0.32±1.25
Carcass grade		0.63** 1.12[c]

[a], [b] See footnote of Table 5.11

[c] The standard error of this genetic correlation has been omitted because it is extremely large.

stated earlier, much emphasis was placed upon fatness in the grading of lamb carcasses and in the Block Test. Estimates of genetic correlations in Table 5.25 cannot be regarded as reliable as they show very large sampling errors. However, the values imply that there is little to be gained in carcass grade by selecting for higher dressing-out percentages, although improvement in Block Test performance may be made by doing so. The strong relationship between carcass grade and carcass total, at both levels, is to be expected since many of the characteristics of the carcass taken into account in grading are also considered in the Block Test.

CHAPTER 6

CONCLUSION

Sire-year interaction were found to be significant in only four of the 25 traits analysed in the present study. These were width of gigot (G), the ratio of the weight of the forequarter to the hindquarter (FQ/HQ), cannon bone weight and carcass grade. For the first three traits, genuine non-linear interaction between the transmitting ability of the sires and the environmental conditions peculiar to each year, could have been the possible cause of the interaction terms. Carcass grade is a composite trait determined by several characteristics. Yearly variations in the emphasis placed on the different characteristics could have contributed to the interaction term found in carcass grade.

Estimates of phenotypic correlations between traits are important for predictive purposes. Under normal circumstances, carcasses are seldom cut to expose the internal development at the 12th rib. In such cases, therefore, it would be useful if external measurements on the intact carcass could be found which were related in some way to the development of the more important internal measurements.

Fat development at the level of the 12th rib is perhaps the best indicator of carcass leanness. In general, as fat deposition increased, carcass leanness and cutability decreased. With regard to the eye muscle, the results of the present study suggest that carcasses with thicker backfat have "short", deep eye muscles. For fat thickness to become useful for predicting leanness in the intact carcass or in the live animal, a suitable method must be developed for its measurement. In this respect, ultrasonic measurement, which has been satisfactorily applied in pigs, appears promising.

Measurements indicative of skeletal length and weight were found to be unsuitable for predicting "length" and depth of eye muscle, but were related to the fat measurements at the 12th rib such that lambs which were short in the leg and blocky, were generally fatter than those which were leggy. The antagonistic relationship between skeletal length and fat thickness can be attributed to the fact that the lambs were slaughtered at approximately the same liveweight. Those with smaller skeletal dimensions would be compensated by having a greater fat deposition.

Carcass length was found to be a poor indicator of eye muscle development and fat thickness at the 12th rib. In contrast, carcass weight appeared to be a satisfactory indicator. In general, with liveweight at slaughter being constant, area of eye muscle increased as also did fat deposition with an increase in carcass weight. The relationships between carcass weight and the other carcass traits indicated that an increase in carcass weight in lambs slaughtered at a similar liveweight was associated with an increase in carcass backfat thickness and also with increases in width and length of body. Skeletal length was little affected.

The estimates of phenotypic correlations also indicated that carcasses that were short in the leg and body and had more fat graded better and scored more points in the Block Test than those which were long and leggy in conformation and had less fat. This is not unexpected in view of the fact that the system of grading used until recent times and the Block Test favoured carcasses of the former characteristics.

It is generally agreed that leanness is a very important consideration to the consumer when exercising purchasing decisions. In this respect, high quality lamb may be defined as that which has a high percentage of lean meat especially in the preferred cuts. It is difficult to decide whether selection should be aimed at increasing total edible meat or for some combination of this and the cross-sectional area of the more important muscles, such as the l. dorsi. In terms of efficient meat production by a single animal, total edible meat is probably more important, but in relation to consumer preference, an increase in muscle size is likely to be also important.

"Length" and depth of eye muscle were the only direct measures of leanness in the present study and, obviously, they did not adequately represent carcass leanness as a whole. Therefore, it is suggested that future studies similar to the present one should include other measures of carcass leanness and cutability such as total lean content and the proportions of the various joints.

The eye muscle measurements, particularly that of "length" showed large heritabilities, indicating that the shape of the eye muscle could be effectively changed by selection. In this regard, the aim should be to select for a large deep eye muscle, elliptical to circular in shape. The genetic correlation between these measurements imply that selection to increase either the "length" or depth of eye muscle would result in an increase in the other measurement and, therefore, in eye muscle area.

Fat thickness at the level of the 12th rib is probably the most informative single measure for predicting carcass cutability. In general, as fat deposition increases, carcass cutability decreases. However, more information is required concerning an acceptable minimum depth of the fat layer needed on lamb carcasses, not only in terms of consumer preference, but also taking into consideration such factors as preservation of quality in storage and in transportation. In this respect, a fat covering of perhaps 3 mm is probably sufficient to prevent dehydration and to produce an attractive cut at the point of ultimate sale at retail.

The fat measurements were found to be of moderate heritabilities, with estimates ranging from 0.25 to 0.35. Therefore, indications are that direct selection to change backfat thickness in lambs will be effective.

Antagonistic relationships were found between the fat measurements (except Y) and "length" and depth of eye muscle at the genetic level. These imply that selection aimed at reducing carcass fatness would be an effective means of increasing the "length" as well as the depth of eye muscle. Similar antagonistic relationships are known to exist between carcass fatness and measures of carcass leanness.

The strongly-inherited nature of the skeletal dimensions of length and weight is well-documented in the literature and the estimates of heritabilities for these in the present study support this finding.

There has been a lot of controversy in the past regarding the type of conformation which indicated good carcass merit. The Hammond School believed that carcasses which were short in the leg and blocky yielded more high-priced cuts and edible meat than carcasses of leggy conformation. However, the findings of some workers provided evidence which challenged this belief. Walker and McMeekan (1944) found evidence to suggest that in Canterbury lamb the leggy carcass, in fact, carried more muscle than the blocky carcass. Kemp and Barton (1965), Fourie (1965), and Kirton and Pickering (1967) were able to show that carcasses of blocky conformation or those in the higher grades had no advantage over those of leggy conformation in terms of meat content or proportion of high-priced cuts.

The correlated changes in the carcass brought about by long-term selection favouring a short and blocky conformation are, therefore, of considerable importance to the sheep industry. The genetic correlations between leg length and the other measurements of skeletal length and, the internal measurements indicate that long-term selection for a blocky conformation is likely to have the following effects: a reduction in "length" of eye muscle, an increase in its depth and an increase in carcass backfat. From the standpoint of consumer preference for lamb cutlets, only the increase in depth of eye muscle can be considered as desirable, the other two changes being undesirable. The changes which take place in the eye muscle cannot be taken as indicating that changes in a similar direction will occur in other measures of carcass leanness. Thus there is an obvious need for more research in this connection.

As stated in Section V of Chapter 5, the importance of carcass length in a consideration of carcass quality is because the l. dorsi muscle lies adjacent to the vertebral column on each side from the sacrum anterior to the shoulders. From this standpoint, it was considered that an increase in carcass length would be desirable, provided that this is not accompanied by a reduction in muscle thickness. The estimates of heritabilities of measurements K and L found in the present study indicated that carcass length could be changed by selection.

An antagonistic relationship was found between carcass length (measurements K and L) and depth of eye muscle at the genetic level.

This is in accordance with the belief that selection for increased carcass length would result in a subsequent reduction in muscle thickness. Also, the genetic correlations between carcass length (measurements K and L) and the fat measurements imply that a change in the former would bring about an opposite change in carcass fatness. Thus from the evidence gained in the present study, it can be concluded that an increase in carcass length in lambs is not to be encouraged since the undesirability of a reduction in muscle thickness outweighs the desirable reduction in carcass fatness. It can only be suggested that further research is required to determine the "optimum" carcass length which would yield acceptable levels of both muscle thickness and carcass fatness.

The very low estimate of heritability ($h^2 = 0.03$) for carcass weight found in the present study could only be attributed to selection of the lambs for slaughter on a constant liveweight basis. This is thought to have reduced variability in carcass weight and, therefore, the additive genetic variance for this character in the selected lambs.

High carcass yields are certainly desirable provided that the factors contributing to them do not detract from those related to the quality of the carcass. Available information points to the fact that increased dressing-out percentages contribute little to carcass desirability and are largely due to increased fatness. High dressing-out percentages for overfat or incorrectly-finished lambs are, therefore, to be avoided from the point of carcass desirability. Evidence from the present study indicates that selection aimed at getting higher dressing-out percentages would not only result in the enlargement of the eye muscle, but also in a reduction of carcass fatness. The latter change is difficult to interpret in view of the relationships found at the phenotypic level between carcass weight and the fat measurements. This suggested that heavier carcasses, i.e., those with higher dressing-out percentages, were generally fatter.

Due to the subjective nature of carcass grading and carcass total, estimates of their heritabilities are less important than their relationships with the other carcass traits, at the genetic and phenotypic levels. The heritability of the ratio of the weights of the forequarter and the hindquarter (FQ/HQ) was 0.0. The absence of additive genetic variance for this character suggested that selection cannot increase the weight of the hindquarter relative to that of the forequarter. It is recommended that, since FQ/HQ is a poor indicator of carcass merit and the heritability is zero, it should not be included as a trait to be measured in future research.

The grade standard and the "Cambridge" Block Test favoured carcasses of blocky conformation, i.e., those factors which were usually associated with carcass fatness. Therefore, it was not unexpected to find that carcasses which graded better and scored more points in the Block Test were heavier, fatter and had shorter legs and bodies. These carcasses also had short, deep eye muscles.

The genetic correlations implied that improvement in carcass grade and Block Test performance could be made by selecting for a blocky conformation and higher fat content. It is interesting to note that, generally, the relationships between carcass total and the other carcass traits followed the same trend as the relationships between carcass grade and these traits. This could be due to the fact that the characteristics taken into account in carcass grading and in the Block Test were similar in most cases.

The results of the present study support the fact that too much emphasis was previously given to carcass fatness in grading and, since it is known that fatter carcasses have proportionately less lean content, it is only logical to suggest that in future systems of grading or classifying carcasses emphasis should be more on factors indicative of carcass leanness and cutability.

The thorax region of the carcass is perhaps the least important; the cheapest cuts are found here. As such the correlated changes in the conformation of this region brought about when selecting for other traits are of no great importance. The estimates of heritabilities for the width and depth measurements in the forequarter region, particularly WR, WTh and Th, however, indicate that changes in this region could be made by direct selection.

APPENDIX I

Table showing sire-year interaction sum of squares

Trait	$R[(\widetilde{st})_{ij}, b_k, c]$ (1)	$R[u, s_i, t_j, b_k, c]$ (2)	Interaction S.S. [(1) - (2)]
A	1299320.00	1299200.00	120.00
B	349343.00	349269.00	74.00
C	3685.13	3654.23	30.90
D	2958.76	2937.69	21.07
X	102148.00	102094.00	54.00
Y	3129.36	3101.24	28.12
J	28181.80	28071.10	110.70
Carcass total	1416930.00	1415420.00	1510.00
F	302881.00	302865.00	16.00
G	226863.00	226855.00	8.00
WR	225757.00	225747.00	10.00
WF	146080.00	146077.00	3.00
WTh	116651.00	116648.00	3.00
Th	314936.00	314929.00	7.00
T	174018.00	174014.00	4.00
Carcass grade	2735.80	2730.72	5.08
R	155801.00	155796.00	5.00
K	1564980.00	1564920.00	60.00
L	1507830.00	1507780.00	50.00
H	422578.00	422555.00	23.00
P	589450.00	589439.00	11.00
Carcass weight	531039.00	530995.00	44.00
Cannon weight	642542.00	642388.00	154.00
Cannon length	63564.80	63563.20	1.60
FQ/HQ	626.11	626.04	0.07

APPENDIX II

Table showing the error sum of squares for testing the significance of the interaction effects.

Trait	$\sum_{ijkl} Y^2_{ijkl}$ (1)	$R[(\widetilde{st})_{ij}, b_k, c]$ (2)	Error S.S. [(1) - (2)]
A	1302863.00	1299320.00	3543.00
B	351308.00	349343.00	1965.00
C	4455.00	3685.13	769.87
D	3937.00	2958.76	978.24
X	104417.00	102148.00	2269.00
Y	3872.00	3129.36	742.64
J	31649.00	28181.80	3467.20
Carcass total	1462149.00	1416930.00	45219.00
F	303264.80	302881.00	383.80
G	226993.00	226863.00	130.00
WR	226124.20	225757.00	367.20
WF	146296.90	146080.00	216.90
WTh	116901.60	116651.00	250.60
Th	315120.30	314936.00	184.30
T	174168.00	174018.00	150.00
Carcass grade	2831.00	2735.80	95.20
R	155940.12	155801.00	139.12
K	1566501.06	1564980.00	1521.06
L	1508982.74	1507830.00	1152.74
H	423835.71	422578.00	1257.71
P	589950.53	589450.00	500.53
Carcass weight	533006.31	531039.00	1967.31
Cannon weight	645668.72	642542.00	3126.72
Cannon length	63648.52	63564.80	83.72
FQ/HQ	626.97	626.12	0.85

APPENDIX III

Reductions in sums of squares due to fitting different models for traits where sire-year interaction are non-significant.

Trait	$R[u,t_j,b_k,c]$	$R[u,s_i,b_k,c]$	$R[u,s_i,t_j,c]$	$R[u,s_i,t_j,b_k]$
A	1297860.0	1299120.0	1299170.0	1298470.0
B	349124.0	349222.0	349264.0	349131.0
C	3575.41	3564.77	3622.32	3628.58
D	2849.11	2851.03	2897.41	2929.96
X	101988.0	101991.00	102043.0	102068.0
Y	3029.99	3091.78	3089.12	3097.93
J	27680.9	27920.8	27775.6	27996.0
Carcass total	1410380.0	1409990.0	1414310.0	1415240.0
F	302776.0	302857.0	302862.0	302861.0
WR	225726.0	225699.0	225745.0	225707.0
WF	146067.0	146066.0	146066.0	146077.0
WTh	116619.0	116635.0	116635.0	116638.0
Th	314890.0	314929.0	314928.0	314918.0
T	173985.0	174012.0	174012.0	174012.0
R	155772.0	155790.0	155795.0	155795.0
K	1564750.0	1564870.0	1564910.0	1564910.0
L	1507580.0	1507770.0	1507780.0	1507760.0
H	422464.0	422321.0	422553.0	422551.0
P	589329.0	589437.0	589437.0	589436.0
Carcass weight	530935.0	530852.0	530905.0	530989.0
Cannon bone length	63542.2	63561.4	63563.1	63563.1

APPENDIX IV

Sums of squares for the main effects and regression term for traits where sire-year interaction are non-significant.

Trait	Sire S.S. (d.f. = 11)	Year S.S. (d.f. = 2)	B. Rank S.S. (d.f. = 2)	Regression S.S. (d.f. = 1)
A	1340.00	80.00	30.00	730.00
B	145.00	47.00	5.00	138.00
C	78.82	89.46	31.91	25.65
D	88.58	86.66	40.28	7.73
X	106.00	103.00	51.00	26.00
Y	71.25	9.46	12.11	3.31
J	390.20	150.30	295.50	75.10
Carcass total	5040.00	5430.00	1110.00	180.00
F	89.00	8.00	3.00	4.00
WR	21.00	48.00	2.00	40.00
WF	10.00	11.00	11.00	0.00
WTh	29.00	13.00	13.00	10.00
Th	39.00	0.00	1.00	11.00
T	29.00	2.00	2.00	2.00
R	24.00	6.00	1.00	1.00
K	170.00	50.00	10.00	10.00
L	200.00	10.00	0.00	20.00
H	91.00	234.00	2.00	4.00
P	110.00	2.00	2.00	3.00
Carcass weight	60.00	143.00	90.00	6.00
Cannon bone length	21.00	1.80	0.10	0.10

APPENDIX V

Mean squares for the main effects and regression term for traits where sire-year interaction are non-significant.

Trait	Sire M.S.	Year M.S.	B.Rank M.S.	Regression M.S.
A	121.81	40.00	15.00	730.00
B	13.18	23.50	2.50	138.00
C	7.17	44.73	15.96	26.65
D	8.05	43.33	20.14	7.73
X	9.64	51.50	25.50	26.00
Y	6.48	4.73	6.06	3.31
J	35.47	75.15	147.75	75.10
Carcass total	458.18	2715.00	555.00	180.00
F	8.09	4.00	1.50	4.00
WR	1.91	24.00	1.00	40.00
WF	0.91	5.50	5.50	0.00
WTh	2.64	6.50	6.50	10.00
Th	3.55	0.00	0.50	11.00
T	2.64	1.00	1.00	2.00
R	2.18	3.00	0.50	1.00
K	15.45	25.00	5.00	10.00
L	18.18	5.00	0.00	20.00
H	8.27	117.00	1.00	4.00
P	10.00	1.00	1.00	3.00
Carcass weight	5.45	71.50	45.00	6.00
Cannon bone length	1.91	0.90	0.05	0.10

APPENDIX VI

Example to show steps involved in the computation of variance components in a measurement (A) in which sire-year interaction is non-significant.

Source of variation	d.f.	S.S.	M.S.	E(M.S.)
Sire	11	1340.00	121.81	$\sigma_e^2 + k_1' \sigma_s^2$
Error	457	3663.00	8.0153	σ_e^2

$$k_1' = \frac{n_{...} - \mathrm{tr}[N'R^{-1}N]}{\text{degrees of freedom}}$$

$$\mathrm{tr}[N'R^{-1}N] = 65.4857$$

$$\therefore\ k_1 = \frac{474 - 65.4857}{11}$$

$$= 37.1377$$

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

$$= 8.0153$$

$$\text{Sire M.S.} = \text{E(Sire M.S.)},$$

$$\underline{\text{i.e.}},\ 121.81 = 8.0153 + 37.1377\ \sigma_s^2$$

$$\therefore\ \sigma_s^2 = \frac{121.81 - 8.0153}{37.1377}$$

$$= 3.0641$$

Therefore the general formula for computing σ_s^2 is:

$$\sigma_s^2 = \frac{\text{Sire M.S. - Error M.S.}}{k_1}$$

APPENDIX VII

Example to show steps involved in the computation of variance components in a measurement (G) in which sire-year interaction is significant.

Source of variation	d.f.	S.S.	M.S.	E(M.S.)
Sire	11	22.0	2.0	$\sigma_e^2 + k_2'\sigma_{st}^2 + k_1'\sigma_s^2$
Interaction	12	8.0	0.6667	$\sigma_e^2 + k_3'\sigma_{st}^2$
Error	445	130.0	0.2921	σ_e^2

$$k_1' = 37.1377$$

$$k_3' = \frac{n_{\cdots} - k_3}{[(p-1)(q-1)-m]}$$

$$= \frac{474 - 256.7677}{12}$$

$$= 18.1027$$

$$k_2' = \frac{k_3 - k_2}{(p-1)}$$

$$= \frac{256.7677 - 63.1155}{11}$$

$$= 17.6047$$

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

$$= 0.2921$$

$$\text{Interaction M.S.} = \text{E(Interaction M.S.)},$$

<u>i.e.</u>, $0.6667 = 0.2921 + 18.1027\ \sigma^2_{st}$

$$\therefore \sigma^2_{st} = \frac{0.6667 - 0.2921}{18.1027}$$

$$= 0.0207$$

Therefore, the general formula for computing σ^2_{st} is given by:

$$\sigma^2_{st} = \frac{\text{Interaction M.S. - Error M.S.}}{k'_3}$$

$$\text{Sire M.S.} = \text{E(Sire M.S.)},$$

<u>i.e.</u>, $2.0 = 0.2921 + (17.6047)(0.0207) + 37.1377\ \sigma^2_s$

$$= 0.2921 + 0.3644 + 37.1377\ \sigma^2_s$$

$$\therefore \sigma^2_s = \frac{2.0 - 0.2921 - 0.3644}{37.1377}$$

$$= 0.0362$$

Therefore, the general formula for computing σ^2_s is:

$$\sigma^2_s = \frac{\text{Sire M.S. - Error M.S. - } k'_s\sigma^2_{st}}{k'_1}$$

APPENDIX VIII

Example to show steps involved in the computation of covariance components and genetic and phenotypic correlations between "length" (A) and depth (B) of the eye muscle.

Source of covariation	d.f.	S.C.P.	M.C.P.	E(M.C.P.)
Sire	11	220.0	20.1818	$\text{cov } e_1e_2$ $+ k_1' \text{ cov } s_1s_2$
Error	457	542.0	1.1859	$\text{cov } e_1e_2$

$$k'_1 = 37.1377$$

$$\text{cov } e_1e_2 = E(\text{Error M.C.P.})$$

$$= 1.1859$$

$$\text{Sire M.C.P.} = E(\text{Sire M.C.P.}),$$

$$\underline{\text{i.e.}},\ 20.1818 = 1.1859 + 37.1377 \text{ cov } s_1s_2$$

$$\therefore \text{ cov } s_1s_2 = \frac{20.1818 - 1.1859}{37.1377}$$

$$= 0.5115$$

Additive genetic covariance,

$$\text{cov } A_1A_2 = 4 \text{ X cov } s_1s_2$$

$$= 4 \text{ X } 0.5115$$

$$= 2.0460$$

Additive genetic variances for traits A and B, $\sigma^2_{A_1}$ and $\sigma^2_{A_2}$, are 12.2564 and 0.9392.

Therefore, genetic correlation between traits A and B of the eye muscle,

$$r_g = \frac{\text{cov } A_1A_2}{\sqrt{\sigma^2_{A_1} . \sigma^2_{A_2}}}$$

$$= \frac{2.0460}{\sqrt{(12.2564)(0.9392)}}$$

$$= 0.60$$

Phenotypic covariance,

$$\text{cov } P_1P_2 = \text{cov } e_1e_2 + \text{cov } s_1s_2$$

$$= 1.1859 + 0.5115$$

$$= 1.6974$$

Phenotypic variance for trait A,

$$\sigma^2_{P_1} = \sigma^2_{e_1} + \sigma^2_{s_1}$$

$$= 8.0153 + 3.0641$$

$$= 11.0794$$

Phenotypic variance for trait B,

$$\sigma^2_{P_2} = \sigma^2_{e_2} + \sigma^2_{s_2}$$

$$= 4.4617 + 0.2348$$

$$= 4.6965$$

Therefore, phenotypic correlation between traits A and B of the eye muscle,

$$r_P = \frac{\text{cov } P_1P_2}{\sqrt{\sigma^2_{P_1} . \sigma^2_{P_2}}}$$

$$= \frac{1.6974}{\sqrt{(11.0794)(4.6965)}}$$

$$= 0.24.$$

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