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CANNON BONES

SOME DIMENSIONS, HERITABILITIES

AND

RELATIONSHIPS TO CARCASS QUALITY

IN

ROMNEY WETHER LAMBS

A Thesis

Presented in Partial Fulfillment of the

Requirements for the Degree of

M. Agr. Sc.

by

A.H. Hughes

1957
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ACKNOWLEDGMENTS

This study was prompted by Professor A.L. Rae to whom the author is sincerely grateful for, without his advice, help and continued enthusiasm, this thesis would not have been written.

Thanks are also due to Mr. R.A. Barton for advice on carcass quality aspects, also to Miss M.G. Campbell and the Library Staff, Massey Agricultural College for their help in obtaining references from interloan sources.

Finally the author wishes to acknowledge his gratitude to Mrs A.W. Warren for typing this thesis.
INTRODUCTION

In the past and to a certain extent at the present time sheep breeders have paid considerable attention to the dimensions of the cannon bones of their animals in the belief that this bone serves as a good indicator of the quality of the conformation and constitution of their animals. Scientific workers interested in meat and carcass quality have also attached considerable importance to the cannon bone as an index of carcass composition and hence of carcass quality.

The origin of the sheep breeders beliefs is no doubt due to years of farmer observation supported to some extent by the findings of the scientific workers, who of necessity, using relatively small numbers of animals, have established relationships between the dimensions of the cannon bone and other characters of economic importance.

The existence at Massey Agricultural College of complete records, concerning cannon bone dimensions and carcass quality, collected from a relatively large number of animals, prompted this present study which was intended to yield more accurate results than those previously reported. At the same time this study was designed to yield estimates of the heritability of cannon bone dimensions and their relationship to carcass quality thus providing a basis on which breeders might decide whether or not they would continue to place the present amount of emphasis on the cannon bone in their selection practices.
CHAPTER 1

REVIEW OF LITERATURE

This review will be divided into three main sections. The first section will deal with the available literature describing development of bone, particularly the cannon bone in sheep. The second section will deal with carcass quality, its evaluation and the use of the cannon bone as an index of carcass quality. The third section will review estimates of heritability so far developed for conformation and composition characteristics in sheep.

(a) Development of the Long Bones

In typical internal structures such as the long bones of the limbs of tetrapods, cartilage, in the embryo, tends to take the definitive form of the adult bone at an early minute stage. The cartilage begins to undergo modification and degeneration, especially near the middle of its length; cartilage cells begin to multiply and arrange themselves in longitudinal columns and the material between the columns calcifies. Blood vessels break through into the cartilage from the surface and destruction of cartilage in this area takes place making way for the bone marrow. Osteoblasts entering with the blood vessels lay down bone in place of cartilage. Ossification proceeds from the centre towards either end of the element. At the same time cartilage at the extremities continues to grow longitudinally so that the
process of ossification does not catch up with cartilagenous formation until relatively late in the foetal life. In the cannon bone an accessory ossification centre - the epiphysis - develops at the distal end of the shaft. This new centre may ossify the articular region before growth in the shaft region is complete and thus allow the element to function despite its incomplete ossification. Between the epiphysis and the shaft is a band of cartilage which can continue to grow thus allowing increase in the length of the bone. Once ossification replaces this band of cartilage the epiphysis is said to have fused, growth in length is over and the bone has reached its adult definitive length.

Growth in width or thickness is achieved by the direct formation of perichondral bone in concentric layers on the surface of the cartilage. This process may continue after the underlying shaft region has ossified, when additional bone is regarded as perosteal rather than perichondral bone formation. (Romer 1950).

Hammond (1932) quoted Godin (1902) as having formulated the law that "long bones grow in length and thickness alternately and not simultaneously, the intervals between growth in length being occupied by growth in thickness."

Working with the rabbit, Sissons (1953) gives the
development of an individual "long" bone in the growing region as follows:-

"An initial period of approximately thirty six hours when predominantly osteoblastic activity occurs, then progressive remodelling involving balanced osteoblastic and osteoclastic activity continuing for eight to nine days; finally abrupt osteoclastic destruction attaining completion in less than twenty four hours."

Hammond (1932) maintained that since both length and thickness growth affect this weight, it would follow that a study of the combined length and weight growth at different ages would add to knowledge concerning the periodicity of length and thickness growth. Later Hammond (1937) states that the two different forms of bone growth are independent, that to some extent one can be affected without the other, and that it is fairly certain that in the improvement of breeds for mutton qualities thickness growth has been effected to a much greater extent than has length growth.

Palsson (1939) using the formula \[ \frac{\text{weight in g} \times 100}{\text{length in mm}} \]
for the left front\(a\) cannon bone found a correlation to exist between this expression and total weight of bone in a carcass. However for lambs of four and a half months of age and dressed carcass weight of forty pounds this correlation was only significant at the five per cent level whilst

* The term "front" has been used in this report in place of the word "fore" in order to avoid confusion between the words "fore" and "four."
for hoggets thirteen months of age and dressed carcass weight of sixty pounds it was significant at the one per cent level. Palsson explained this difference as being a direct result of the fact that thickness growth in the front cannon bones is a relatively late developing character as compared with length growth. This latter suggestion agreed with Hammond’s (1932) finding that thickness growth of bones in general was inhibited in semi-wild breeds as compared with improved mutton breeds.

(b) Factors Affecting Development of the Cannon Bone

(i) Sex

In the majority of adult mammals and birds the male is larger and heavier than the female; the rabbit and the guinea pig being two of the few exceptions. Hammond (1932) has shown that at all ages there is greater relative thickness of all cannon bones in the rams than in the ewe. In the wether at the age of five months the proportions of the cannon bone approached those of the ewe rather than those of the ram. Palsson and Verges (1952) have shown that in both length and thickness growth of all four of the cannon bones in the ewe exhibited smaller increments than those in the
wether. At the same time these authors noted that males had significantly heavier cannon bones than females.

(ii) Breed

Nathusius (1880) found great breed differences in the relative length to depth of cannon bones in sheep. For the Southdown the length was twelve times the diameter whereas in Heath Sheep it was seventeen times the diameter. Hammond (1932) found that in five month old wethers the early maturing breeds had relatively thicker bones than had the late maturing ones. In adult rams Hammond (1932) found that thickness growth was inhibited in the semi-wild breeds as compared with the improved mutton breeds whilst wool-type sheep were intermediate between the two.

Palsson (1939) found great breed differences in the length of the left front cannon bones in wethers. In some breeds he found much less difference between the thickness of the middle of the shaft of the front cannon bone and its extremities than in others. He also stated that weight per unit length was the best, easily measured, indication of cannon bone thickness.

From the results given by Bonsma (1939) it
appeared that crossing the Merino with various mutton breeds resulted in a reduction in length of the cannon bone in the half bred lambs.

(iii) Plane of Nutrition

Hammond (1932) found that different parts of the body and different tissues of the carcass grow at different rates as the animal grows from birth to maturity.

McMeekan (1940) studied growth in relation to nutrition by making pigs grow along predetermined growth curves from birth to bacon weight by controlling their food intake. He found that the mean weight of the front cannon bones of sixteen week old pigs on a high plane of nutrition to be slightly over double the mean weights of the front cannon bones of pigs on a low plane of nutrition.

Pelasson and Verges (1952) applied the same approach to sheep as McMeekan had done with the pig. They found, in accord with Wallace (1948) that at birth, the weight of the four cannon bones was more affected by a low plane of nutrition in utero than either its length or minimum circumference the latter being the least affected, indicating that growth in length at birth contributed more to its weight than did growth in
thickness. Thus because at this stage the cannon bones possessed greater natural intensity for growth in length than in thickness, its length growth being more affected by limited nutrition. Post-natally, however, thickness growth was more retarded than length growth by limited nutrition. From birth to nine weeks the thickness development of the shaft was more affected than that at the extremities. At nine weeks the low plane animal's cannon bones resembled those of the newborn in thickness though they had increased considerably in length. In contrast to this the high plane animal's cannon bones at nine weeks had assumed the thick relatively short form typical of those in early maturing breeds of even greater age and body weight. At forty one weeks the low plane lambs possessed cannon bones ten per cent shorter as an absolute figure than those on a high plane but relative to their thickness the low plane lamb's bones were very much longer having a thirty six per cent lower weight/length ratio. Both in absolute and relative terms the thickness of the cannon bones of the low plane lambs at forty one weeks was less developed than in the high plane lambs at nine weeks.
When studying the effect of plane of nutrition on lambs of thirty pounds carcass weight Palsson and Verges found that the high-high and low-high plane wether lambs had longer cannon bones than ewe lambs in these groups, whereas the low-low and high-low plane wether lambs had shorter cannon bones than the females of the same plane of nutrition groups. This latter fact was probably due to the greater retarding effect of poor nutrition on wethers compared to females.

Wallace (1948) has shown that by far the greater increment in weight growth of four cannon bones takes place pre-natally and in the first sixty two days after birth. The mean increment in the weight growth of the cannon bones of his experimental lambs being 33.4g from birth to sixty two days; 8.8g from sixty two to 112 days and 7.4g from 112 to 200 days.

Wallace (1948) reported that there was a considerable influence due to the number of young being suckled upon the milk production of the ewe. Over sixteen weeks Suffolk ewes with twins produced 351.6lb of milk or 125.8lb per lamb whereas ewes with singles produced 239.6lb of milk. He found that 96 per cent of the variation in the weight gains made by lambs between birth and 112 days could be accounted for by
the differences between them in respect to their consumption of milk and supplements.

(iv) Age of Dam

Bonsma (1939) working with Merinos crossed with various mutton breeds found the lambs from second and subsequent parturitions were comparatively heavier than first born lambs at both twelve and eighteen weeks of age. Nelson and Venkatachalam (1949) found that lambs from mature ewes were ten per cent heavier at birth than those from two year old ewes. This agrees with Donald and McLean (1935) who found that in New Zealand English Leicester lambs those from two tooth ewes were lighter than those from older ewes. This did not hold for Southdown lambs where there was no real difference due to age of dam. It would be expected that a small part of the birth weight differences might be a reflection of weight differences in the cannon bones.

(v) Time of Lambing

Hammond (1932) reported that the weight of lambs at one week of age increased markedly in singles but to a smaller degree in twins as the lambing season progressed. Only a small number of singles was available but the results indicated that there was very little difference in the rate of growth from one week
onwards between early and late born lambs. If anything, Hammond noted that there was a slightly greater rate of growth in the late born but not as much as the difference in birth weight led him to expect.

Bonsma (1939) found no significant differences in the gains made by lambs born at different times of the lambing season. However this picture was confused since elsewhere he reported that there were significant differences between breed of the ram and gestation period of the resulting lamb; differences in birth weight between early and late lambs in favour of the former; and that there was a highly significant correlation between birth weight and subsequent weight differences.

(vi) State of Fatness

Riney (1955) found that in red deer the first fat depot to respond to favourable metabolic change was the bone marrow. This is in accord with the findings of Hammond (1940), McMeekan (1940), Palsson and Verges (1952) and Pomeroy (1941) who have described how fat deposition and mobilisation starts at different times in the different depots.

(vii) Age

Palsson (1939) found that left front cannon bone
length was slightly shorter in lambs than in hoggets at constant body weight. With increase in age from lambs to hoggets at constant body weight it was found that most breeds of lambs at 41-48lb showed a greater minimum left front cannon bone circumference than hoggets; at 49-59lb both lambs and hoggets were practically alike; whilst at 57-64lb the hoggets possessed the greater minimum circumference. The left front cannon bone length/weight ratio was higher in lambs than in hoggets at the same weight. Palsson stated that the absolutely shorter but heavier left front cannon bone of the lambs at the same weight as the hoggets demonstrated how a late developing character such as bone thickness can be pushed forward in development relative to an earlier developing one, such as bone length by a high level of nutrition in early life compared with a long period at a low level.

(viii) Birth Rank

At birth Hammond (1932) found that singles were 29 per cent heavier than twins and that triplets were nine per cent lighter than twins, this being due he suggested to competition for nourishment in the uterus. During the first month of life the birth weight differences were found to be further increased between
singles, twins and triplets—probably due to competition for the available milk supply. Although the twins and triplets appeared to catch up in body weight to singles later in life they never quite did so. By rearing twins as singles Hammond suggested that the ratios between the weights of singles, twins and triplets were a result of not only the uterine nutrition, but also post-natal conditions governed by the milk supply of the dams. When the foregoing is associated with the findings of Palsson (1939), Palsson and Verges (1952) and Wallace (1948) concerning the effect of nutrition on the cannon bone dimensions it would be expected that birth rank would have an appreciable affect on the weight and length of the cannon bone. Nelson and Venkatachalam (1949) reported that in the five breeds studied single lambs were on the average 22 per cent heavier than twins. Bogart et al (1957) reported birth weights of single lambs to be from 1.92lb to 2.40lb heavier than twins. These authors also found year differences between birth weights to be apparent.

(ix) Sire

Hammond (1932) found it difficult to estimate to what extent a ram can influence the birth weight of the lamb due to the in utero effects exerted on the
foetus. However he believed that the sire had at least some effect. Bonsma on the other hand found significant differences between the breed of ram and the gestation period. Further, half-bred lambs were significantly heavier at birth than Merinos i.e. size of ram influenced birth weight. Berton Phillips and Clarke (1949) have shown that the means of the left front cannon bone lengths of the progeny of "poor quality" sires were significantly longer than those of "good quality" sires. Bogart et al (1957) reported heritability estimates of birth weights obtained by Nelson and Venkatachalam (1949) and Blackwell and Henderson (1955) to vary from 0.25 to 0.33.

(c) Carcass Quality

(i) Definition

The Shorter Oxford Dictionary defines quality as "the degree or grade of excellence possessed by an article." Since meat is eventually consumed by the retail purchaser, i.e. the public, then meat quality or its degree of excellence will ultimately be judged by the public. Thus McMeekan (1939) defined quality in fat lambs as "what the public likes best." However, what the public likes best will depend upon
the taste of the particular public being considered at any given time. This has led McMeekan (1944) to a less general and more fundamental definition. "The quality of any meat animal in any market is dependent fundamentally upon the relative proportions of the body and its relative composition in terms of bone, muscle, fat and offals." Hirzel (1939) has stated that quality is closely linked with and dependent upon conformation, finish and carcass weight which are the chief determinants of the sales value of the carcass or its parts.

Now Hammond (1932, Palsson (1939), McMeekan (1940-41), Hirzel (1939), Wallace (1948), Palsson and Verges (1952) have shown, when their work is reviewed as a whole, that the differences in growth rate, order of growth, development of regions and particular tissues within regions, together with the environmental and hereditary influences which control this growth and development, are responsible for the differences in conformation and histological and chemical composition of meat animals of different weights, ages, breeds, sexes and species.

(11) Assessing Carcass Quality

As has been mentioned earlier the ultimate judge of meat quality is the consuming public. New Zealand
meat interests have recognised this for some considerable time as is evidenced by the grading of carcasses at the freezing works and in the organisation of fat lamb and chiller beef competitions here in New Zealand with subsequent re-judging at Smithfield.

Judging both in New Zealand and at the Smithfield Market is based on visual judgment of conformation and fat finish of the un-cut lamb carcass. For this reason it is liable to variations dependent upon the efficiency, skill and personal preferences of the judges together with the fact that differences of internal composition may not necessarily be apparent to eye appraisal.

Hammond (1940) in a general text book has stated the weight and quality requirements of the market as

".... the consumers' demand today is mainly for lambs from 28-36lb carcass weight and price per lb drops progressively for weights heavier than this. Within each weight class better prices are given for good quality carcasses, but a second quality carcass if it is light (30lb) will bring more per pound than a heavy (40lb) first quality carcass......................

.....The main requirements for good quality are:
1. Short-boned and well filled legs which are U-shaped rather than V-shaped, with a covering of fat carried right down to the hocks ...... such a joint does not dry out in cooking.
2. A wide well filled loin with deep longissimus dorsi, or eye muscle, and with just the right
amount of fat (5mm) over it, for this is the most valuable part of the body.

3. A small depth of rib, with not much weight there or in the neck, for they are both low-priced joints."

The possibility of using carcass measurements for objectively describing differences in form and in some cases estimating the composition of carcasses in terms of bone, muscle and fat have been investigated by Hammond, Palsson and Verges, Hirzel, Wallace, McMeekan and Walker in sheep, by Hirzel, McMeekan and Walker and by Yeates in beef cattle; and by Davidson et al, McMeekan and by Donald in pigs.

Davidson (et al 1937) working with pigs, Hirzel (1939) working with lambs, McMeekan (1939) working with lambs and Kneebone, McMeekan, Marks and Walker (1950) working with beef cattle evolved systems of quality evaluation by point scoring based upon comparison of the carcass being examined with that of an ideal type established by determining the requirements of the Smithfield market.

In some cases high correlation coefficients have been obtained by the workers quoted above between certain "external and internal" carcass requirements and the total weight of bone, muscle and fat in the carcass. In some cases regression equations have been
developed permitting estimation of the weights and proportions of the major tissues in the carcass.

The "external" measures have proved useful in describing the shape and conformation of the carcass whilst the "internal" measures have been employed with more or less success to describe the composition of the carcass in terms of bone, muscle and fat.

The length and weight of the cannon bone have been used by the majority of the workers quoted above as an index for measuring the remainder of the long bones in the skeleton and in a few cases for estimating muscle in the carcass. The correlation coefficients, regression coefficients and regression equations for some of these estimates are summarised in Table 1 whilst a weighting factor for cannon bone weight used to estimate the weight of total bone in the carcass is given in Table 2.

One of the points scoring systems "The Cambridge Block Test for Lambs" (described fully later) has been described by McMeekan (1939) and has been used for evaluation purposes in work carried out at Massey Agricultural College. The "Block Test" for lambs is still dependent in part upon eye judgment, however it has the advantage over the older, purely subjective systems, in that it is based on a standard pointing system. Carcasses are cut at the last rib
### Table 1: Relationship between Cannon Bone Dimensions and some Carcass Measurements

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Palsson 1939</td>
<td>Lambs</td>
<td>9 pairs</td>
<td>Cannon length x skeleton weight</td>
<td>0.754</td>
<td>0.02</td>
<td>19.02</td>
<td>Y = 19.02X + 48.6</td>
</tr>
<tr>
<td>Palsson 1939</td>
<td>Lambs</td>
<td>9 pairs</td>
<td>Cannon weight x skeleton weight</td>
<td>0.543</td>
<td>0.01</td>
<td>46.64</td>
<td>Y = 46.64X + 333</td>
</tr>
<tr>
<td>Palsson 1939</td>
<td>Lambs</td>
<td>9 pairs</td>
<td>Weight x 100 x skeleton weight</td>
<td>0.746</td>
<td>0.05</td>
<td>74.83</td>
<td></td>
</tr>
<tr>
<td>Palsson 1939</td>
<td>Lambs 33-40lb Southdown x Bl. Chev.</td>
<td>23 pairs</td>
<td>Length eye muscle x 100 cannon length</td>
<td>-0.159</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palsson 1939</td>
<td>Lambs 33-40lb Mixed breeds</td>
<td>57 pairs</td>
<td>Length eye muscle x 100 cannon length</td>
<td>-0.579</td>
<td>0.01</td>
<td>-0.58</td>
<td>Y = 118.5 - 0.583X</td>
</tr>
<tr>
<td>Walker &amp; McMeeken 1944</td>
<td>Lambs</td>
<td>18 pairs</td>
<td>Total weight bone x total weight muscle</td>
<td>0.930</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rae 1947</td>
<td>Lambs</td>
<td>169</td>
<td>Length leg (subjective grading) x length cannon bone</td>
<td>0.640</td>
<td>0.01</td>
<td></td>
<td>X = 0.640 + 2003Y</td>
</tr>
<tr>
<td>Rae 1947</td>
<td>Lambs</td>
<td>169</td>
<td>Length cannon bone x height withers</td>
<td>0.772</td>
<td>0.01</td>
<td></td>
<td>X = 0.772 - 2025Y</td>
</tr>
<tr>
<td>Hirzel 1939</td>
<td>Hoggets</td>
<td>169</td>
<td>Increase in cannon length (mm) for 1lb increase in carcass weight</td>
<td>0.07</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walker &amp; McMeeken 1944</td>
<td>Lambs</td>
<td>28 pairs</td>
<td>Length tibia + tarsus x total weight of bone</td>
<td>0.799</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walker &amp; McMeeken 1944</td>
<td>Lambs</td>
<td>28 pairs</td>
<td>(Length tibia + tarsus) x width gigot x total weight of bone</td>
<td>0.913</td>
<td>0.01</td>
<td></td>
<td>X = 0.913Y - 525</td>
</tr>
</tbody>
</table>
TABLE 2

Estimation of total weight of bone in carcass (i.e. number of times cannon bone weight should be multiplied to find total bone weight in carcass.
Hammond (1932)

<table>
<thead>
<tr>
<th>Breed</th>
<th>Suffolk</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ewes</td>
<td>Rams</td>
</tr>
<tr>
<td>Sex</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>Birth</td>
<td>3 mths</td>
</tr>
<tr>
<td></td>
<td>4 yrs</td>
<td>5 yrs</td>
</tr>
<tr>
<td></td>
<td>5 mths</td>
<td>11 mths</td>
</tr>
<tr>
<td>No. from which calculated</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total bones of carcass</td>
<td>39.5</td>
<td>53.0</td>
</tr>
<tr>
<td>One cannon bone</td>
<td>58.9</td>
<td>59.7</td>
</tr>
<tr>
<td></td>
<td>55.3</td>
<td>63.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Breed</th>
<th>Southdown</th>
<th>Welsh</th>
<th>Lincoln</th>
<th>Hampshire</th>
<th>Soay</th>
<th>Shetland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td></td>
<td>Wethers</td>
<td></td>
<td>Rams</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>5 months</td>
<td>11 months</td>
<td>1-2 yrs</td>
<td>5 years</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. from which calculated</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total bones carcass</td>
<td>53.6</td>
<td>53.6</td>
<td>50.6</td>
<td>68.5</td>
<td>51.6</td>
<td>66.7</td>
</tr>
<tr>
<td>One cannon bone</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
and points are awarded for internal composition, and only major characters which influence price determination receive attention. Cutting at the last rib shows internal composition in the most expensive loin region which since it is one of the latest developing parts of the animal is most likely to be the weakest part, any such weakness being shown up by cutting at this point.

(iii) The Cannon Bone as an Index of Carcass Quality

Tables 1 and 2 summarise the estimates which have been evolved using the cannon bones as an index of bone muscle and fat in the carcass. The bones are particularly useful for study since they are normally removed with the pelt at the freezing works and are thus obtained without damage to the dressed carcass. The cannon bones are relatively large and are easy to measure because of their shape.

Palsson (1939) using the weight of the left front cannon bone expressed as a percentage of its length demonstrated that a relatively short cannon bone with a thick shaft but relatively fine, light extremities was associated with early maturity and desirable carcass quality. Further he demonstrated that a cannon bone with a relatively thin shaft and coarse extremities
was associated with inferior carcass quality. This finding has since been supported by Walker and McMeekan (1944) in their comparative study of fat lambs of four different breeds and crosses. They found it to apply both within and between breeds. Palsson (1939) found that short left front cannon boned animals had a higher shape index of eye muscle than long-boned animals. This suggested the possibility of the existence of a relationship between length of the cannon bone and eye muscle shape index. In all cases studied by Palsson a negative correlation was found between this shape index and cannon bone length.

Hirzel (1939) in constructing a points scoring system for evaluating carcass quality in lambs recommends the allotment of marks as given in Table 3.

**Table 3**

**Carcass Points**

*(suggested scale of points-quality evaluation (Hirzel 1939))*

<table>
<thead>
<tr>
<th>Marks for measurement</th>
<th>Max. points</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thickness of flesh (depth eye muscle)</td>
<td>35</td>
</tr>
<tr>
<td>Thickness of fat (over eye muscle)</td>
<td>30</td>
</tr>
<tr>
<td>Shortness of cannon bone</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td><strong>75</strong></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Marks for inspection</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Shape of leg</td>
<td>10</td>
</tr>
<tr>
<td>Colour of meat</td>
<td>10</td>
</tr>
<tr>
<td>Meat on ribs</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td><strong>25</strong></td>
</tr>
<tr>
<td></td>
<td><strong>100</strong></td>
</tr>
</tbody>
</table>
From Table 3 it will be seen that a maximum of ten per cent of the total points scored by this system have been directly awarded to the cannon bone as an index of carcass quality. There could well be a further contribution from the cannon bone since undoubtedly some of the marks for the shape of leg will be a reflection of cannon bone dimensions on the associated dimensions of other long bones.

Whilst the Cambridge Block Test makes no direct allowance for the award of points on cannon bone dimensions, it does so indirectly, in that there are a total of thirty points awarded for blockiness of leg which is dependent upon the lengths of the bones in the leg, which in turn, as has been shown earlier, are highly correlated to cannon bone length.

(d) **Heritability of Body Characters**

Considering the amount of work that has been carried out on the growth and development of the body characters of sheep, both between and within breeds, surprisingly little has been directed towards the investigation of the mode and extent of the inheritance of these characters.

Rae (1956) has summarised the majority of this work and has quoted estimates obtained for body weight, body conformation, degree of fatness or condition score of the
the animal and the various component parts of the body. Table 4 summarises the range of estimates obtained for these various characters.

The only reference which could be found to estimates of heritability of the dimensions of the cannon bone were those reported by Rae (1946). By dam-offspring correlation between Romney ewes and their Down cross offspring he found estimates of heritability of 0.84 for length of cannon bone and 0.84 for its weight. When these two estimates are considered together with the estimates for quality of bone from Table 4 it may be assumed that the heritability of these two dimensions of the cannon bone is high.

(e) Conclusions

From the foregoing review it would be expected that the dimensions of the cannon bone of the sheep would be influenced by:

1. The sex of the animal.
2. The breed of the animal
3. The plane of nutrition upon which the animal was reared both pre- and post-natally.
4. The year in which the animal was born.
5. The age of the dam
6. The birth rank of the animal - i.e. whether it was single, twin or a twin reared as a single
<table>
<thead>
<tr>
<th>TABLE 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimates of Heritability of Body Characters in Sheep (partly from Rae (1956))</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Size and Breed of sample</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Birth Weight</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.34 - 0.40</td>
<td>107 dam offspring pairs Southdown</td>
<td>Ensminger et al 1943</td>
</tr>
<tr>
<td>0.72</td>
<td>504 dam offspring pairs Mixed Breeds</td>
<td>Nelson &amp; Venkatachalam, 1949</td>
</tr>
<tr>
<td><strong>Weaning Weight</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.04 - 0.06</td>
<td>77 dam offspring pairs Southdown</td>
<td>Ensminger et al, 1943</td>
</tr>
<tr>
<td>0.29 - 0.42</td>
<td>348+ dam offspring Mixed Breeds</td>
<td>Nelson &amp; Venkatachalam 1949</td>
</tr>
<tr>
<td><strong>Body Conformation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) Weaning Score 0.07</td>
<td>798 dam offspring pairs Mixed Breeds</td>
<td>Hazel &amp; Terrill 1946</td>
</tr>
<tr>
<td>&quot; 0.22-0.40</td>
<td>62 dam offspring pairs Southdown</td>
<td>Ensminger et al 1943</td>
</tr>
<tr>
<td>(b) Yearling Score 0.15</td>
<td>Extensive data N.Z. Romney</td>
<td>McMahon 1943</td>
</tr>
<tr>
<td>0.12</td>
<td>200 dam offspring pairs N.Z. Romney</td>
<td>Rae 1948</td>
</tr>
<tr>
<td>0.14</td>
<td>640 degrees of freedom N.Z. Romney</td>
<td>Rae 1950</td>
</tr>
<tr>
<td><strong>Body Components</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body as a whole</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td>Breed type</td>
<td>0.41</td>
<td></td>
</tr>
<tr>
<td>Length of leg</td>
<td>0.80</td>
<td>182 degrees of freedom N.Z. Romney</td>
</tr>
<tr>
<td>Bone quality</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td>Shoulders</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>Back</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Loin</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td><strong>Cannon Bone</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>0.84</td>
<td>Extensive data N.Z. Romney</td>
</tr>
<tr>
<td>Weight</td>
<td>0.84</td>
<td></td>
</tr>
</tbody>
</table>
7. The age of the animal when it was slaughtered.

8. The carcass weight within an age group which makes allowance for the possible existence of early or late maturing animals.

9. Hereditary factors dependent upon the genetic make up of the sire, dam, constitution, resistance to disease etc.

10. A residual factor composed of sources of individual variation not already mentioned.

The usefulness of the cannon bone as an index of carcass quality would depend upon the relationship which this bone bears to the relative proportions of the carcass and to the composition of the carcass in terms of bone, muscle and fat. To determine the order of these relationships it would appear necessary to correlate the dimensions of the cannon bone with carcass quality as determined by some overall numerically expressed standard of market suitability. The Cambridge Block Test which describes carcass quality on a reasonably objective points scoring system would appear to be suitable for this purpose.
CHAPTER 2

MATERIALS AND METHODS

The data used in this study were collected during the 1944-45, 1945-46 and 1946-47 seasons from the wether lambs of a flock set up at Massey Agricultural College to study techniques of progeny testing. Collection of data was undertaken by the then members of the Sheep Husbandry Department, Massey Agricultural College.

(a) Experimental Animals

(1) Dams

In the 1944-45 season, the experimental ewe flock was composed of typical hill country Romney Marsh cross-bred ewes originating from three different sources:

- 150 College bred, 5½ year old ewes
- 100 bought in, 5½ year old ewes
- 150 bought in, 2 year old ewes.

In the 1945-46 season the flock was composed entirely of 5½ year old ewes that had been bought in.

In the 1946-47 season, the flock consisted of those ewes of the 1945-46 flock which were still available for breeding together with the two year old ewe progeny of the 1944-45 flock.

Over the period of this experiment the flock as
a whole had been described as one of good average commercial quality. In order to eliminate any complications arising from assortive mating and in-breeding the ewes were assigned at random to their mating groups. The efficiency of this randomisation was shown by the small variation in the mean differences between the sire groups reported by Rae (1946).

(2) Sires

During the 1944-45 season ten, mixed age, pure-bred Romney Marsh rams used in the flock, were procured from widely different sources. They were chosen to be as phenotypically variable as possible with the hope that they would show a wide range of genetic variation. A full description of each ram used is given by Rae (1946). In the 1945-46 season, eight rams were used - seven of the original ten together with one new animal. In 1946-47, six of the original rams, the animal introduced first in the 1945-46 season and an entirely new animal were used. Thus over the three seasons twelve sires were used as is shown in Table 5.

(3) Management of the Flock

The flock was grazed for the whole period on the "Pahiatua" block of the College farm. A description of this area was reported by Peren et al (1938). The
### TABLE 5

**Rams used in 1944, 1945 and 1946 Mating Seasons**

<table>
<thead>
<tr>
<th>Sire</th>
<th>1944</th>
<th>1945</th>
<th>1946</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>No.1</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>South Wairarapa</td>
</tr>
<tr>
<td>2</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>North Manawatu</td>
</tr>
<tr>
<td>3</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>South Wairarapa</td>
</tr>
<tr>
<td>4</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>South Wairarapa</td>
</tr>
<tr>
<td>5</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Central Manawatu</td>
</tr>
<tr>
<td>6</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Central Manawatu</td>
</tr>
<tr>
<td>7</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Rangitikei</td>
</tr>
<tr>
<td>8</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Central Manawatu</td>
</tr>
<tr>
<td>9</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>South Wairarapa</td>
</tr>
<tr>
<td>10</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Rangitikei</td>
</tr>
<tr>
<td>11</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>Central Manawatu</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>0</td>
<td>+</td>
<td>Central Manawatu</td>
</tr>
</tbody>
</table>
Rams were joined with their respective groups of ewes on the 25th March 1944 and were removed on May 19th. From this date throughout the winter the ewe flock was run as one mob on a rotational grazing basis. Just prior to lambing the mob was split into early and late lambing groups according to the date of final service. The first lamb was born on 19th August and within six weeks of this date 97 per cent of the total lambs had been born. Docking was carried out when the lambs were approximately three weeks of age. Those wether lambs which had not been slaughtered by 8th January were weaned and placed on fresh pasture. Management in the 1945-46 and 1946-47 seasons was essentially the same as that described for the 1944-45 season.

(4) Wether Lambs

In this present study data collected only from wether lambs were used. The experimental procedure adopted with these lambs was reported by Rae (1946) as follows:

"Body weight was recorded at intervals until they reached a live weight, in the paddock of 75lb. Lambs attaining this weight were then picked out and transported to the woolshed. They were then shorn and the fleece weight recorded. The lambs were kept overnight in the woolshed and the following morning were slaughtered and graded under the export system of grading. The carcasses were stored overnight in a cooler at 42°F and on the next day the Cambridge Block Test points awarded. The aim in selecting the lambs for slaughter was to have them killing out at a hot dressed carcass weight of about 34lb."
During the slaughtering process the left fore cannon bone was retained from each animal. The bone was scraped to remove skin, flesh and tendons and its green weight (to the nearest 0.1g) recorded on its label. Each bone was subsequently measured for length by the technique described by Palsson (1939) where the length of the front cannon bone was taken as the distance between the cleft of the knuckle of the distal end to the extremity of the proximal end. After these measurements had been taken the cannon bones were put into storage and were readily available for the determination of the additional measurements mentioned in section (c) of this chapter.

(b) The Cambridge Block Test

In this system of points judging of carcass quality, three "external features" and four "internal features" were taken into account. Of the maximum of fifty points awarded for "external features" :-

**Blockiness of Leg received a maximum of thirty points**

"...The leg must be short in the bone, well filled out and fleshed. The space between must be U- and not V-shaped. In a good leg the width across is greater than the length of bone as measured from the crutch to the end of the bone. The latter should not exceed eight inches in a 30lb carcass...." McMeekan (1939)

**Fat Covering received a maximum of ten points**

"...Fat covering in a carcass is invariably thickest
along the back and sides, and thinnest over the extremities.... In judging fat cover, the cover over the legs is examined since it is invariably weakest here. The layer should be well down and evenly distributed.... a good guide is that cover should be just sufficient to prevent the red colour of the underlying muscle being reflected through.... McMeekan (1939)

Fullness of loin received a maximum of ten points

".... the loin must be wide and well filled up in proportion to the rest of the carcass.... The point is assessed by seeing how far it fills up the spread between the thumb and the second finger when grasped by the hand.... McMeekan (1939)

Of the total of fifty points awarded for internal characters depth of fat and depth of eye muscle received the greatest emphasis:—

Depth of Fat over Loin (twenty points)

".... The amount of fat over the chop must be just right. Too little and the meat dries out on cooking — too much and it has to be trimmed.... The optimum of fat over the eye muscle is 4-5mm in a 30lb carcass...." McMeekan (1939)

Size and Shape of Eye Muscle (fifteen points)

".... This indicates the total amount of lean meat in the carcass. The depth is most important.... The muscle should stand out above the line of the spine.... In poor lambs the spine stands out above the muscle.... A good eye muscle measures 30-35mm in a 30lb carcass. McMeekan (1939)

Colour of Lean Meat (5 points)

".... The colour of the muscle should be bright and pink. Darkness is a defect...." McMeekan (1939)

Ribs and Fleshing (ten points)

".... the rib cuts must not be too heavy. The ribs..."
require to be light and well sprung.... To sell this part it should have a cover of thick streaks of lean meat with not too much fat. The quality in this area is readily judged on cross section...." McMeekan (1939)

The Block Test in addition allowed for a maximum of 100 points for market weight suitability but this extrapointing was omitted in this study since the design of the original progeny testing experiment was such that the lambs were slaughtered to yield as near as possible a constant dressed carcass weight. The Block Test score card is shown in Appendix 1 whilst the external and internal features judged are shown in Diagram 3.

It will be noted that in order to make the Block Test more objective in nature some of the original subjective estimates reported by McMeekan were replaced by objective linear measurements - these are also shown in Diagram 3.

(c) Data Used in this Study

Data from 460 wether lambs was provided by the Sheep Husbandry Department and consisted of:-

Length of the left front cannon bone
Green weight of the left front cannon bone
Cambridge Block Test points
Sire of the lamb
Year of birth of the lamb
Birth rank of the lamb
Age of the dam of the lamb
Age at slaughter of the lamb
Hot carcass weight of the lamb.

The stored data listed above was augmented by the determination of the minimum circumference and the volume (as measured by water displacement) of each bone. The development of techniques for obtaining the cross-sectional area of each cannon bone in ten millimetre steps from one extremity to the other was attempted.

The work was carried out in three stages:—

(1) The statistical analysis of the data made available by the Sheep Husbandry Department with a view to obtaining estimates for the effect of sire, year of birth, birth rank, age of dam, age at slaughter and carcass weight on the length and weight of the cannon bones and on the Cambridge Block Test score for the carcasses. In addition the heritability of each of the three characters together with their phenotypic and genetic correlations were calculated at this stage.

(2) The measurement of the cannon bones in order to determine their minimum circumference, volume and cross-sectional area in ten millimetre steps from one extremity to the other.

(3) The statistical analysis of the additional data obtained from (2) above by the same methods as used for stage 1.
As will be seen from Chapter 3, the analytical methods employed in stage 1 above could be directly employed for the determination of heritability, phenotypic and genetic correlations of the additional characters thus accomplishing saving in computational work.

Due to time limitations imposed on this study, only stage 1 was fully completed. Stage 2 proceeded as far as obtaining the raw data for minimum circumference and volume, with some initial attempts at developing techniques for determining cross-sectional areas.

It is intended only to report results from stage 1 in this present work.
CHAPTER 3

METHODS OF ANALYSIS

Records were available for cannon bone length, cannon bone weight and block test carcass score for 460 wether lambs collected in the years of 1944 to 1947 inclusive. Lambs with incomplete records (eight in number) were eliminated in order to simplify the analysis. The wether lambs were the offspring of the twelve sires used in the flock described in the preceding Chapter.

The analysis of the data was carried out in two stages:—

(a) The estimation of the effects of sire, year of birth, birth rank, age of dam, age at slaughter and carcass weight was carried out.

(b) The variance and covariance between sires were analysed in order to find the heritability of each trait and the genetic correlation between each pair of traits.

The observations were classified according to the following factors:—

(a) The sire of the lamb

(b) The year in which the lamb was born

(c) The birth rank of the lamb (whether single, twin, or twin reared as single).

(d) The age of the dam of the lamb.
In addition the age of the lamb at slaughter and carcass weight were included as independent variates. The number of lambs occurring in the various classifications for the years 1944 to 1946 are shown in Table 6.

The number of lambs in each classification are markedly disproportionate, a problem which is frequently encountered in this type of data. Consequently, in the analysis, a method is required which takes into account this disproportion in the subclass numbers and eliminates from the estimates any inequalities due to other factors. The method of fitting constants by least squares as described by Yetes (1934), Hazel (1946) and Kempthorne (1952) is the appropriate procedure in these circumstances.

(a) The Mathematical Model

The first step in the analysis of the data was to choose a mathematical model to describe the various genetic and environmental factors known to influence the observations. The model in effect defines a population of which the observations are considered to be a sample. The problem is then to estimate from the data the unknown parameters which are part of the definition of that population.

The model considered most appropriate for the present data was:
<table>
<thead>
<tr>
<th>Sire</th>
<th>1944</th>
<th>1945</th>
<th>1946</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>14</td>
<td>17</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>21</td>
<td>24</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>16</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>21</td>
<td>23</td>
<td>21</td>
</tr>
<tr>
<td>6</td>
<td>19</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td>7</td>
<td>18</td>
<td>22</td>
<td>16</td>
</tr>
<tr>
<td>8</td>
<td>17</td>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>9</td>
<td>17</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>22</td>
<td>25</td>
</tr>
<tr>
<td>11</td>
<td>-</td>
<td>20</td>
<td>15</td>
</tr>
<tr>
<td>12</td>
<td>-</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td>Singles</td>
<td>67</td>
<td>63</td>
<td>46</td>
</tr>
<tr>
<td>Twins</td>
<td>20</td>
<td>17</td>
<td>16</td>
</tr>
<tr>
<td>Twins as singles</td>
<td>73</td>
<td>87</td>
<td>63</td>
</tr>
<tr>
<td>Two year ewes</td>
<td>43</td>
<td>-</td>
<td>26</td>
</tr>
<tr>
<td>Five year ewes</td>
<td>117</td>
<td>167</td>
<td>99</td>
</tr>
</tbody>
</table>
\[ y_{ijklm} = \mu + s_1 + t_j + b_k + a_l + c (x_{ijklm} - \bar{x}) \\
+ d(z_{ijklm} - \bar{z}) + e_{ijklm} \]

\[ i = 1 \ldots \ldots p \quad j = 1 \ldots \ldots r \]
\[ k = 1 \ldots \ldots q \quad l = 1 \ldots \ldots v \]
\[ m = 1 \ldots \ldots n_{ijkl} \]

In this model \( y_{ijklm} \) is the observation on the \( m \)th animal in the \( i \)th sire group in the \( j \)th year and in the \( k \)th birth rank and the \( l \)th age of dam class.

At this stage it is necessary to define more exactly the population from which the data are considered a sample. The sires used were chosen with no conscious selection for the characters considered in this study from Romney Marsh stud flocks in the Rangitikei, Manawatu and Wairarapa areas. Thus it is not unreasonable to consider the population as being the offspring of sires sold for use in the commercial flocks in this region where environmental conditions are similar to those existing in the flock used for this study.

The constant \( \mu \) in the model is an effect common to all the wether lambs in the population. It was caused by factors which were alike for all lambs, such as being of the same breed and having certain morphological and physiological features in common. When the appropriate conditions are imposed on the other parameters in the model, \( \mu \) can be taken
as a population mean.

The constant $s_1$ is an effect common to all the progeny of the $i^{th}$ sire. For estimating the size of the environmental effects no assumptions are required as to the properties of $s_1$.

The constant $t_j$ is an effect common to all lambs born in the $j^{th}$ year. This effect includes differences caused by the environmental conditions peculiar to that year. Such conditions may be variations in annual climatic conditions which may effect the growth of the lamb either directly or indirectly through effects on the feed supply, presence of parasites or other un definable factors. The year effect may contain a genetic component because average genetic differences are confounded with year effects.

The $b_k$ constant is the effect which the $k^{th}$ classification for birth rank and rearing has on the observations. The types of birth and rearing present in the data are represented by the symbols: $b_1$ for singles, $b_2$ for twins reared as singles and $b_3$ for twins reared as twins.

The $a_1$ constant includes any effects which the age of the dam may have on the measurements of her offspring.

The ages of dam represented are $a_1$ for two-year old ewes and $a_2$ for five-year old ewes.

The age of the lamb at slaughter is represented by $x_{ijklm}$ whilst $\bar{x}$ is the mean age at slaughter for all lambs
considered. Since computational difficulties were encountered as a result of the large variation of the age at slaughter when measured in days, it was found convenient to code this variate by dividing it by ten. The regression coefficient $\beta$ thus measured the average change in the dependent variate resulting from an increase of ten days in the age at slaughter.

The independent variate, carcass weight, is represented by $x_{ijklm}$, whilst $\beta$ is the regression coefficient measuring the average change in the dependent variate for an increase of one pound of carcass weight.

The constant $\epsilon_{ijklm}$ is the error or residual peculiar to each observation. It may be caused by numerous environmental factors not included in the model, the effects that the dam may have on her offspring, effects due to chance at Mendelian sampling and possibly to dominance and epistatic effects.

In the above model, the effects of the dam in determining the measurements of her offspring have been ignored, mainly because the dam effects are almost completely confounded with year effects. This results from the fact that only a small number of ewes appeared in the flock for more than one year. In addition, interaction between the various classifications have been omitted because their inclusion would have increased the complexity of the model beyond the
limit imposed by the facilities available for computation. Variance due to these interactions will be largely included in the error term.

Estimation of the effects in the model was carried out by the method of least squares as described by Kempthorne (1952). The expression

\[ \sum_{ijkl} e_{ijkl}^2 \sum_{ijkl} \left( x_{ijkl} - \mu - \alpha_i - t_j - b_k - a_l \right)^2 \]

was differentiated with respect to each parameter, the derivatives being placed equal to zero to give the following set of equations:

\[ \alpha_i : \Delta \alpha_i + \sum_{j} \alpha_i \alpha_j + \sum_{k} \beta_i \beta_j \alpha_k + \sum_{l} \gamma_i \gamma_j \alpha_k \beta_l = 0 \]

\[ \beta_j : \Delta \beta_j + \sum_{i} \alpha_i \beta_j + \sum_{k} \beta_i \beta_j \alpha_k + \sum_{l} \gamma_i \gamma_j \beta_k \beta_l = 0 \]

\[ \gamma_k : \Delta \gamma_k + \sum_{i} \alpha_i \gamma_k + \sum_{j} \beta_j \gamma_k \alpha_j + \sum_{l} \gamma_i \gamma_j \beta_k \gamma_l = 0 \]
\[ \begin{align*}
\mathbf{a}_1 &= n .. 1 \mathbf{a} + \sum_{i} n_{i..} s_i + \sum_{j} n_{j..} t_j + \sum_{k} n_{..k} b_k + n \ldots \mathbf{l} \\
&+ (x \ldots l \ldots n \ldots l \mathbf{x}) c + (z \ldots l \ldots n \ldots l \mathbf{z}) d = y \ldots l \\
\mathbf{c} &= (x \ldots -N \mathbf{x}) a + \sum_{i} (x_{i..} \ldots -n_{i..} \mathbf{x}) s_i + \sum_{j} (x_{j..} \ldots -n_{j..} \mathbf{x}) t_j \\
&+ \sum_{k} (x_{..k} \ldots -n_{..k} \mathbf{x}) b_k + \sum_{l} (x \ldots l \ldots -n \ldots l \mathbf{x}) a_l \\
&+ \sum_{ijklm} \left( x_{ijklm} - \bar{x} \right)^2 c + \sum_{ijklm} \left( x_{ijklm} - \bar{x} \right) (z_{ijklm} - \bar{z}) d \\
&= \sum_{ijklm} \left( x_{ijklm} - \bar{x} \right) (y_{ijklm} - \bar{y}) \\
\mathbf{d} &= (z \ldots -N \mathbf{z}) a + \sum_{i} (z_{i..} \ldots -n_{i..} \mathbf{z}) s_i + \sum_{j} (z_{j..} \ldots -n_{j..} \mathbf{z}) t_j \\
&+ \sum_{k} (z_{..k} \ldots -n_{..k} \mathbf{z}) b_k + \sum_{l} (z \ldots l \ldots -n \ldots l \mathbf{z}) a_l \\
&+ \sum_{ijklm} \left( z_{ijklm} - \bar{z} \right)^2 c + \sum_{ijklm} \left( z_{ijklm} - \bar{z} \right) (x_{ijklm} - \bar{x}) d \\
&= \sum_{ijklm} \left( z_{ijklm} - \bar{z} \right) (y_{ijklm} - \bar{y})
\end{align*} \]

In these equations, \( n_{ijkl} \) is the number of observations in the \( ijk \)th subclass while a dot (·) implies summation over the classification represented by the subclass it replaces. \( N \) is used to represent the total number of observations.

The equations as they stand are not independent since the sum of the equations for any set of parameters equals the \( a \) equation. In order to obtain unique solutions the last parameter of each set was placed equal to zero, (i.e. \( t_3 = b_3 = a_2 = 0 \)).
(b) **Estimates of Heritability (Paternal $\frac{1}{2}$-sib Method)**

In determining the paternal $\frac{1}{2}$-sib correlation the sire effects ($s_1$) in the model described above are considered to be randomly drawn items from a population having a variance $\sigma^2_s$, this variance to be estimated from the data. A specification of this population has been given in the previous section.

In a population mating at random $4\sigma^2_s$ is equal to the genic variance of the population for the trait under consideration. Heritability is therefore estimated as the ratio:

$$
\frac{4\sigma^2_s}{\sigma^2_s + \sigma^2_e}
$$

To estimate $\sigma^2_s$, the sum of squares between sires and the error sum of squares are required. The analysis of variance is outlined below.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>d.f.</th>
<th>Sum of Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between Sires</td>
<td>$p-1$</td>
<td>$R(\mu,t,b,a,c,d) - R(\mu,t,b,a,c,d)$</td>
</tr>
<tr>
<td>Error</td>
<td>$N-p-r-q-v-1$</td>
<td>$R(T) - R(\mu,s,t,b,a,c,d)$</td>
</tr>
</tbody>
</table>

In this description $R(......)$ denotes the reduction in sums of squares due to fitting the constants included in
the brackets and \( R(T) \) is equal to \( \sum_{ijklm} x^2_{ijklm} \)

To calculate \( R(\mu, s, t, b, a, e, c, d) \) it is necessary to solve the equations given in Section (a) for \( \hat{\mu}, \hat{s}, \hat{t}, \hat{b}, \hat{a}, \hat{e}, \hat{c} \) and \( \hat{d} \), the \( \hat{\cdot} \) being used to indicate the estimates of these parameters.

Since the three characters considered in this study include exactly the same animals in each classification, time was saved in the solving of the equations by inverting the matrix of coefficients. The method used was to associate the constant \( \mu \) with \( s_1 \) and then to eliminate the \( (\mu + s_1) \) equations using the method described by Kempthorne (1952). The resulting matrix was of the order of 7x7. An approximate inverse of this matrix was obtained by using the abbreviated Doolittle method (Dwyer 1951). This approximate inverse was then iterated to give greater accuracy using the method described by Fraser et al (1947).

Because of the particularly large coefficient on the diagonal of the equation \( \sum_{ijklm} (x_{ijklm} - \bar{x})^2 \), a considerable number of iterations had to be carried out in order to obtain eight figure accuracy in the inverse. (see App. III)

Having obtained the inverse, it was used in calculating the estimates of the parameters by the operation of matrix multiplication on the quantities specified in the right-hand sides (see App. IV) of the set of equations given earlier. The reduction due to fitting all constants was
then calculated according to the following relation:

\[
R (\mu, t, b, a, c, d) = \sum_{i} (\mu + s_i) y_{i..} + \sum_{j} (\mu + t_j) y_{j..} + \sum_{k} b_{k..} y_{..k} + \sum_{l} a_{l..} y_{..l} + \sum_{ijklm} \hat{y}_{ijklm} (x_{ijklm} - \bar{x}) + \sum_{ijklm} \hat{y}_{ijklm} (z_{ijklm} - \bar{z})
\]

In computing \(R(\mu, t, b, a, c, d)\) the equations for \(s_i\) were deleted and the remaining equations solved for \(\mu, \tilde{t}_j, \tilde{b}_k, \tilde{a}_l, \tilde{c}\) and \(\tilde{d}\) where the \(\tilde{\ldots}\) indicates the estimates under the hypothesis that \(s_i = 0\). Matrix inversion was again employed in solving these equations. (See App. III for this inverse).

The reduction \(R(\mu, t, b, a, c, d)\) was computed as follows:

\[
\sum_{j} (\mu + t_j) y_{j..} + \sum_{k} b_{k..} y_{..k} + \sum_{l} a_{l..} y_{..l} + \sum_{ijklm} \hat{y}_{ijklm} (x_{ijklm} - \bar{x}) + \sum_{ijklm} \hat{y}_{ijklm} (z_{ijklm} - \bar{z})
\]

The expected values of the total sum of squares and the reductions were obtained by the rules given by Henderson (1953). They are:

\[
E R (T) = S + N (\sigma^2_s + \sigma^2_t)
\]

\[
E R (\mu, s, t, b, a, c, d,) = S + \sigma^2_s + (p+q+r+v-1) \sigma^2_t
\]

\[
E R (a, t, b, a, c, d,) = S + N \sigma^2_a + (q+r+v) \sigma^2_t
\]

where \(S\) is the expectation of the various square and
crossproduct terms involving $\mu, t_j, a_1, c$ and $d$, while $E$ indicates the operation of taking the expectation of the quantity which it precedes. The evaluation of the coefficient $K$ necessitates inverting the matrix of the coefficients of the equations used in finding $R(u, t, b, a, c, d)$.

Then $K$ is computed by summing the products of the elements of the inverse matrix with the coefficients of $\sigma_s^2$ in the $E(Y_iY_j)$ where $Y_i$ and $Y_j$ are the sums associated with the row and column of the element of the inverse matrix (Henderson 1953).

Hence $\sigma_e^2$ is estimated by the error mean square while the formula for estimating $\sigma_s^2$ is:

$$\hat{\sigma}_s^2 = \frac{\text{S.S. between sires} - (p-1) \hat{\sigma}_e^2}{N - K}$$

Heritability is then computed using $\hat{\sigma}_s^2$ and $\hat{\sigma}_e^2$.

(c) Estimation of Genetic Correlations

The estimation of covariance components in multiple classifications with disproportionate subclass numbers has been discussed by Henderson (1953).

If the two variates are represented by $Y$ and $Y'$ then the analysis of the covariation can be presented as follows:
Now \( R'(T) = \sum_{ijklm} Y'_{ijklm} \)

The reductions in the sum of crossproducts were computed by multiplying the estimated constants for one of the variables by the appropriate sum or right-hand side for the other variable, i.e.

\[
R'(\mu+s, t, b, a, c, d) = \left( \sum_{i} (\hat{\mu} + s_{i}) \right) Y_{i}^{1} \ldots + \left( \sum_{j} t_{j} \right) Y_{j}^{2} \ldots + \left( \sum_{k} b_{k} \right) Y_{k}^{3} \ldots
\]

\[
+ \sum_{l} a_{l} Y_{l}^{4} \ldots + \sum_{ijklm} c Y_{ijklm} (x_{ijklm} - \bar{x})
\]

\[
+ \sum_{ijklm} d Y_{ijklm} (z_{ijklm} - \bar{z})
\]

The expected values of these reductions in sums of crossproducts are given below

\[
E R'(T) = P + N (\text{Cov ss' + Cov ee'})
\]

\[
E R'(\mu, s, t, b, a, c, d) = P + N \text{ Cov ss'} + (p + q + r + v - 1) \text{ Cov ee'}
\]

\[
E R'(\mu, t, b, a, c, d) = P + K \text{ Cov ss'} + (q + r + v) \text{ Cov ee'}
\]

From these equations Cov ss' and Cov ee' can be estimated.

In a population mating at random, Cov ss' is equal to \( 1/4 \) Cov GG', the covariance between the additive deviations caused by genes in the two characters. The genetic correlation
between the two characters was therefore estimated by

\[ R_{GG} = \frac{\text{cov} \, GG'}{\text{cov} \, G'G} = \frac{\text{cov} \, ss'}{\text{cov} \, s's'} \]

(d) Estimation of Effects of Environmental Factors

In the process of calculating the reduction \( R(\mu, t, b, a, c, d) \) required for the paternal half-sib correlation, estimates of the effects of the environmental factors included in the model were obtained. They are:

- Single lamb versus twin lamb \( b_1 \)
- Twin reared as single versus twin \( b_2 \)
- Mature dam versus two year old dam \( a_1 \)
- Regression on age at slaughter \( a' \)
- Regression on carcass weight \( d \)
- Deviations from average for each year \( t_j \)

Since the inverse matrix for the equations used in estimating these effects was available, their sampling errors were easily computed. The inverse matrix has the property that the variance of \( b_k = b_{kk} \sigma_e^2 \), where \( b_{kk} \) is the element occurring in the \( k^{th} \) row of the \( k^{th} \) column of the inverse matrix and \( \sigma_e^2 \) is the estimated error variance.
CHAPTER 4

The data from the 452 Romney Marsh wether lambs were analysed by the methods described in Chapter 3. Because the results fall into reasonably discreet sections they will be presented in the following order:

(a) Estimates of Environmental Effects
(b) Estimates of Heritability
(c) Phenotypic Correlations between the Characters
(d) Genetic Correlations between the Characters

(a) Estimates of Environmental Effects

As was shown in Chapter 3, Section (d), estimates of the environmental effects of the environmental factors included in the model together with their standard errors were readily derived from the inverse matrix obtained from the computation of the reduction \( R(u,t,b,a,c,d) \). These effects are presented in Table 7.

An indication of the statistical significance of these estimates of the differences caused by the environmental effects has been shown in Table 7. Significance at the five per cent level has been shown by marking the statistic with an asterisk (*) while significance at the one per cent level has been shown by marking with a double asterisk (**).

In deciding these levels of significance, the procedure
# TABLE 7

Estimates of the Effects of Year, Birth Rank, Age of Dam, Age at Slaughter and Carcass Weight on Cannon Bone Length, Cannon Bone Weight, and Carcass Block Test

<table>
<thead>
<tr>
<th>Effect</th>
<th>Cannon Bone Length (cms)</th>
<th>Cannon Bone Weight (gms)</th>
<th>Carcass Block Test (points)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>11.58</td>
<td>36.33</td>
<td>50.87</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>0.433</td>
<td>2.577</td>
<td>8.456</td>
</tr>
<tr>
<td><strong>Year Effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1944 minus 1946</td>
<td>+0.133 ± 0.55*</td>
<td>-1.059 ± 0.372*</td>
<td>+5.024 ± 1.230**</td>
</tr>
<tr>
<td>1945 minus 1946</td>
<td>+0.968 ± 0.57*</td>
<td>-0.679 ± 0.340*</td>
<td>-4.488 ± 1.116**</td>
</tr>
<tr>
<td><strong>Birth Rank Effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Singles minus Twins</td>
<td>+0.038 ± 0.052</td>
<td>+0.797 ± 0.310*</td>
<td>+8.930 ± 1.020**</td>
</tr>
<tr>
<td>Twins as Singles minus Twins</td>
<td>-0.057 ± 0.067</td>
<td>+0.086 ± 0.400</td>
<td>+4.848 ± 1.315**</td>
</tr>
<tr>
<td><strong>Age of Dam Effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Two year ewes minus Five year ewes</td>
<td>-0.120 ± 0.020**</td>
<td>+1.103 ± 0.378*</td>
<td>-3.121 ± 1.241*</td>
</tr>
<tr>
<td><strong>Regressions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regression on Age at Slaughter (10 days)</td>
<td>+0.0001 ± 0.005</td>
<td>-0.290 ± 0.035**</td>
<td>+0.845 ± 0.011**</td>
</tr>
<tr>
<td>Regression on Carcass Weight (lb)</td>
<td>+0.004 ± 0.010</td>
<td>+0.232 ± 0.060**</td>
<td>+3.022 ± 0.198**</td>
</tr>
</tbody>
</table>

* indicates significance at five per cent
** indicates significance at one per cent
used was as follows:

If the estimate of the difference was greater than twice its standard error, it was considered to be significantly different from zero at the five per cent level. If the estimate of the difference exceeded three times its standard error it was considered significantly different at the one per cent level. While this procedure is only approximate it was considered to be sufficiently accurate as an indicator of the importance of the environmental effects.

1. Year Effects

From the Table it will be seen that the cannon bones from lambs born in 1944 and 1945 were significantly longer than from those born in 1946. The cannon bone weights from lambs born in 1944 and 1945 were significantly less than from those born in 1946 but the weights of the cannon bones from lambs born in 1944 were not significantly different from those born in 1945. The carcass block test score was significantly higher for lambs born in 1944 when compared with those born in 1946 whilst it was significantly lower for those born in 1945 when compared with those born in 1946. Lambs born in 1944 had a higher block test score than those born in 1945. Several factors could have contributed to these differences between years. Firstly differences
in the overall environment from year to year are included in the estimates. Such factors as differences between seasons in the quantity and quality of pasture available, differences in the degree of infestation of internal parasites and other effects peculiar to each year would contribute to the differences in the year effects. Secondly, differences in the average genetic merit of the sires used in the different years are included in the year effects. For example some of the sires used in 1944 were not used in the years 1945 and 1946 (i.e. sire numbers 3, 4 and 9). Comparison of the present year effects with those obtained when the sire effects were taken into account in the model shows them to be similar; thus it appears that the genetic merit of the sires used in the different years is not an important factor in contributing to year differences. Thirdly, average genetic differences between the dams used in different years are involved in the year effects since the same dams were not used in each of the three years. Unfortunately no indication of the genetic differences between the ewes can be obtained from the data.

2. Birth Rank Effects

There were no significant differences found between the lengths of the cannon bones of lambs born as singles
when compared with the lengths of those born as twins, nor were there any significant differences in the lengths of the cannon bones of lambs born as twins and subsequently reared as singles when compared with the lengths of the cannon bones on lambs born and reared as twins. Single lambs showed a significant difference from twins when the cannon bone weights were compared but the difference between the cannon bone weights of twins reared as singles when compared with differences in the cannon bone weights of twins born and reared as twins were not significant. The carcass block test scores however differed in a highly significant manner when both single lambs and lambs born as twins but reared as singles were compared with the block test scores of twins born and reared as twins.

The effects of birth rank on the various characters would be expected to result from the different level of nutrition that the twin lamb receives both pre- and post-natally from its dam in comparison with that received by the single lamb. For example, as shown in the review of literature, a number of workers have found quite large differences in the birth weights between lambs of different birth rank. In addition Barnicost et al (1949) and Wallace (1948) have shown that on average a ewe with twin lambs produces about 1/3rd greater total milk
production than the ewe with a single lamb. Thus effectively a twin lamb receives only 2/3rds of the milk obtained by a single lamb. These authors have also stressed the very important part which milk supply plays in the growth rate of the lamb. However it is necessary to seek an explanation for the fact that the effects of birth rank are not similar in magnitude for the three characters under consideration. It is reasonable to explain this fact on the basis of the evidence obtained by the Hammond school that growth occurs at different rates in different regions of the body and that development is earliest at the extremities. In this connection, it is noted that the development of cannon bone length occurs earlier than the development of cannon bone weight. Reference to the block test score card (App. I) shows that over sixty per cent of the total points are awarded for relatively late maturing characters. Thus it would appear from the results reported above that birth rank has no significant effect on the very early developing character of cannon bone length because it has passed the stage of maximum growth rate before the milk supply of the dam becomes limiting factor. Any effect birth rank may have on the cannon bone weight is significant only in the two extremes of birth rank (singles versus twins) and it is only in
the relatively late maturing characters that the environmental advantages enjoyed by single lambs appears. This explanation is not complete since it disregards the differences in size and weight of single lambs at birth.

3. Age of Dam Effects

The lengths of the cannon bones of lambs from two year old ewes were shown to differ in a highly significant manner from the lengths of the cannon bones from five year old ewes, the bones of lambs from two year old ewes being shorter than those from the five year old ewes. The weights of the cannon bones of lambs from two year old ewes were significantly heavier than those from the five year old ewes, whilst the block test score on carcasses from lambs whose dams were two years old were significantly lower than the block test scores from lambs whose dams were five years old. From reports of other workers cited in the review of literature it would be expected that the cannon bones of lambs from two year old ewes would be shorter and lighter whilst the block test score would be lower than those from lambs having five year old dams. This supposition in this present work holds for cannon bone length (significant at the one per cent level) and for
block test score (significant at the five per cent level) but does not hold for cannon bone weight. In fact, cannon bone weight, as shown by these results, was significantly heavier in lambs from two year old dams than in lambs from five year old dams. No definite explanation of this result can be advanced but it must be noted that the two year old ewes in 1944 were not obtained from the same flock as the five year old ewes. Thus the difference between the two ages will include any difference in the genetic level for the characters analysed.

4. Age at Slaughter Effects

Increments of ten days in the age at slaughter had no significant effect on the cannon bone length of lambs used in this study. On the other hand there was a highly significant decrease in cannon bone weight for each ten days increase in age at slaughter and a highly significant increase in block test score for each increment of ten days in age at slaughter. Since age at slaughter is virtually in this study a measure of growth rate (all lambs being killed at approximately constant live weight) the decrease in cannon bone weight would be explained in terms of Hammond's and Palsson's theory of increasing rate of maturation in improved
mutton breeds. However this argument is untenable in the present case since for their theory to hold, the carcass block test would need to decrease for increases in age instead of which it has shown a significant increase.

5. Carcass Weight

There was no significant increase in cannon bone length with increase in carcass weight in the lambs. Cannon bone weight however increased significantly with increases in carcass weight as did also block test score. Since the animals were slaughtered at a live body weight to give as near as possible a constant carcass weight, differences in carcass weight were small. It is a reasonable assumption that differences in carcass weight were a reflection of differences of fat in the carcass. If this were true then the significant increase in cannon bone weight with increasing carcass weight could have been caused by increases in the fat content of the cannon bones taken from the heavier weight carcasses. This hypothesis tends to be confirmed by unpublished data obtained from Shorland (1957) who has shown with a small number of cannon bones that there is considerable variability in the fat content of the cannon bone with a tendency for fat content to increase with increasing carcass weight.
The highly significant increase in block test with increasing carcass weight can also be explained in terms of increasing fat with increases in carcass weight. From the block test score card it will be seen that of the total possible score awarded to a carcass a maximum of thirty per cent of the points can be awarded directly on state of fatness of various regions and a further ten per cent can be awarded indirectly for state of fatness.

6. The Proportion of the Total Variation Controlled by the Environmental Factors

An analysis was carried out to find the proportion of the total variation in the three characters, cannon bone length, cannon bone weight, and block test points which is determined by the environmental factors taken into account in the present study. The analysis showed that the combined effects of year, birth rank, age of dam, age at slaughter and carcass weight accounted for three per cent of the total variation in cannon bone length, twenty one per cent of the variation in cannon bone weight and forty two per cent of the variation in block test carcass total. As suggested earlier, these results can be interpreted in terms of the earliness of development of the three characters and indicates that the earlier a character develops the smaller the
opportunity the environment has to affect its development.

(b) Estimates of Heritability

As was described in Chapter 3, Section (b), in order to obtain estimates of the heritability of the characters cannon bone length, cannon bone weight, and carcass block test score, the variance of the sire effects together with the error variance of the population are required. The analysis of variance for these characters are presented in Table 8.

**TABLE 8**

Analyses of Variance Required for Estimating the Heritability of the Characters Considered

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>d.f.</th>
<th>SS</th>
<th>Mean Square</th>
<th>Sig</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cannon length</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Sires</td>
<td>11</td>
<td>21.98</td>
<td>1.9163</td>
<td>**</td>
</tr>
<tr>
<td>Error</td>
<td>433</td>
<td>81.18</td>
<td>0.187</td>
<td></td>
</tr>
<tr>
<td><strong>Cannon Weight</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Sires</td>
<td>11</td>
<td>230.66</td>
<td>20.9689</td>
<td>**</td>
</tr>
<tr>
<td>Error</td>
<td>433</td>
<td>2875.82</td>
<td>6.641</td>
<td></td>
</tr>
<tr>
<td><strong>Block Test</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Sires</td>
<td>11</td>
<td>2153.47</td>
<td>195.7700</td>
<td>**</td>
</tr>
<tr>
<td>Error</td>
<td>433</td>
<td>30963.49</td>
<td>71.509</td>
<td></td>
</tr>
</tbody>
</table>
As shown in Chapter 3, Section (b), the error mean square is an estimate of the error variance $\hat{\sigma}_e^2$ while $\hat{\sigma}_s^2$ is obtained from the formula:

$$\hat{\sigma}_s^2 = \frac{\text{SS between sires} - (p-1)\hat{\sigma}_e^2}{N - K}$$

In the present analysis $(p-1)$ is equal to the degrees of freedom between sires (11); $N$ is the total number of observations and $K$ was found to be equal to 67.68. From this information, $\hat{\sigma}_e^2$, $\hat{\sigma}_s^2$ and consequently the heritability of each character, were calculated.

The results of these calculations are presented in Table 9.

<table>
<thead>
<tr>
<th>Character</th>
<th>$\hat{\sigma}_e^2$</th>
<th>$\hat{\sigma}_s^2$</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cannon Length</td>
<td>0.1875</td>
<td>0.0518</td>
<td>0.866</td>
</tr>
<tr>
<td>Cannon Weight</td>
<td>6.6416</td>
<td>3.0121</td>
<td>1.248</td>
</tr>
<tr>
<td>Block Test</td>
<td>71.5092</td>
<td>3.5565</td>
<td>0.189</td>
</tr>
</tbody>
</table>

In general the accuracy of the estimates of heritability derived from the paternal half-sib correlation depends upon the number of sires used in the analysis. In the present analysis, since only twelve sires were used, the accuracy of the estimates is not great. The figure of
eighty seven per cent for the heritability of cannon bone length agrees well with the figure given by Rae (1946) and quoted in the review of literature. The figure of nineteen per cent for carcass block test score is in line with estimates of heritability of body conformation scored on the live animal, which, as would be expected, are low. It is likely that the carcass block test score would be much more affected by environmental factors than heredity factors since block test score measures characters which are late in their relative development. The figure 1.248 per cent is to a certain extent meaningless. However this unduly high figure is probably caused by high sampling errors resulting from the fact that such a small number of sires were used in the comparison. As is often the case data such as were used here when the heritability of the character under review is high, a not very large sampling error is sufficient to swing the estimate of heritability above 1.0. In this particular case a relatively small increase in the sums of squares due to the sires would have brought the estimate of heritability of cannon bone weight below 1.0.

(c) Phenotypic Correlations between Characters

The phenotypic correlations between the three characters were estimated by the use of the normal computational procedure given by Snedecor (1946). In order to eliminate
any known environmental effects the calculations were carried out within groups which were the same for year, birth rank, age of dam and sire. The correlations are given in Table 10.

**TABLE 10**

Phenotypic Correlations between the Characters (based on 433 degrees of freedom)

<table>
<thead>
<tr>
<th>Character</th>
<th>Cannon Weight</th>
<th>Block Test Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cannon Length</td>
<td>+0.681</td>
<td>-0.454</td>
</tr>
<tr>
<td>Cannon Weight</td>
<td></td>
<td>-0.139</td>
</tr>
</tbody>
</table>

The figure of +0.681 for the correlation between cannon bone length and weight indicates a strong positive association between the two characters. To what extent this correlation is automatically the consequence of the fact that weight can be regarded as the product of length multiplied by average weight per unit length cannot be decided from the present analysis of the data. Other information which has been collected, but not analysed, on the volume and circumference of the cannon bones should assist in deciding this issue.

The correlation between cannon bone length and carcass block test score is significantly higher than that between cannon bone weight and carcass block test score. However neither of these correlations are sufficiently high
for predictive purposes. Since it is likely that the lengths of all of the bones in the carcass and particularly the bones of the leg are fairly highly correlated with the length of the cannon bone it would be expected that cannon bone length would be directly related to carcass block test score. Such a relationship is probable because, of the total possible points that could be awarded for block test at least twenty per cent can be awarded on length of leg alone. (See block test score card—appendix I). On the other hand cannon bone weight would appear to have no direct relationship with carcass block test score and this is confirmed by the lower correlation coefficient found between these two characters in this study.

(d) Genetic Correlations between Characters

The method used for the estimation of the genetic correlation between the characters has been described in Chapter 3 section (c). In the analysis, estimates of the covariance between sires and the error covariances are required. The analyses of covariance are presented in Table 11.
TABLE 11

<table>
<thead>
<tr>
<th>Source of Covariation</th>
<th>d.f.</th>
<th>C.P.</th>
<th>Covariance</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cannon Length x Cannon Weight</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Sires</td>
<td>11</td>
<td>134.07</td>
<td>12.1882</td>
</tr>
<tr>
<td>Error</td>
<td>433</td>
<td>328.95</td>
<td>0.7597</td>
</tr>
<tr>
<td><strong>Cannon Length x Block Test</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Sires</td>
<td>11</td>
<td>-234.80</td>
<td>-21.3455</td>
</tr>
<tr>
<td>Error</td>
<td>433</td>
<td>-719.70</td>
<td>-1.6621</td>
</tr>
<tr>
<td><strong>Cannon Weight x Block Test</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Sires</td>
<td>11</td>
<td>-1331.9</td>
<td>-121.082</td>
</tr>
<tr>
<td>Error</td>
<td>433</td>
<td>-6360.5</td>
<td>-14.689</td>
</tr>
</tbody>
</table>

As was shown in Chapter 3 section (c) the error covariance is an estimate of cov ee' and that an estimate of cov ss' can be obtained from the equation:

\[
\text{cov ss'} = \frac{\text{Sum of cross-products between sires} - (p-1) \text{ cov ee'}}{N - K}
\]

In the present analysis (p-1) is equal to the degree of freedom between the sires (11); N represents the total number of observations and K was found to be 67.68 by calculation. From this information estimates of cov ss' were made for
each pair of characters and are presented in Table 12 together with estimates of $\sigma_s^2$ from Table 9.

### TABLE 12

**Estimates of the Covariances between Sires and Genetic Correlations**

<table>
<thead>
<tr>
<th>Characters</th>
<th>$\text{cov ss}'$</th>
<th>$\hat{\sigma}_s^2$</th>
<th>$\hat{\sigma}_g^2$</th>
<th>Genetic Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cannon Length x</td>
<td>+ 0.3269</td>
<td>0.0518</td>
<td>3.0121</td>
<td>+ 0.828</td>
</tr>
<tr>
<td>Cannon Weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cannon Length x</td>
<td>- 0.5633</td>
<td>0.0518</td>
<td>3.5565</td>
<td>- 1.312</td>
</tr>
<tr>
<td>Block Test</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cannon Weight x</td>
<td>- 3.0380</td>
<td>3.0121</td>
<td>3.5565</td>
<td>- 0.928</td>
</tr>
<tr>
<td>Block Test</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

As with the estimation of heritabilities the use of the paternal half-sib method to calculate the correlations means that efficiency of estimation is dependent more on the number of sires than on the total number of observations. In the present case the estimate of the genetic correlation between cannon bone length and block test score is greater than one. It is obviously impossible for this to be true of the genetic correlation for the whole population and its occurrence in the present instance is probably due to sampling errors involved in the particular group of sires used. In the present data, the genetic correlations have
the same sign as the corresponding phenotypic correlations indicating that the gene effects are acting in the same direction as the environmental effects. Unfortunately the degree of accuracy of the estimates does not allow any more detailed interpretation of the genetic correlations or their relationship to the phenotypic correlations.
CHAPTER 5

DISCUSSION

Discussion of the results will be presented in the same order as the results themselves were presented.

(a) The Effects of Environmental Factors

In discussing the effects of environmental factors on cannon bone length and weight and on carcass block test score, it should be emphasised that the statistical significance of the results is not necessarily a sound indication of the importance of the effects in controlling variability in the population being considered. Thus although year and age of dam effects have statistically significant effects on cannon bone length these effects are not of great importance since they control only three per cent. On the other hand both in cannon bone weight and in block test score the environmental effects are statistically significant and also important since it has been shown in the present study that they control twenty one per cent of the variation in cannon bone weight and forty two per cent of the variation in block test score. Consequently for these two characters control of the environmental effects can give a worthwhile increase in precision.

Knowledge of the effects of year, birth rank, age of dam, and of the regressions on age at slaughter and carcass weight is of use in two sets of circumstances:
(1) In increasing the accuracy of selection
(2) In improving the accuracy of experimental comparisons and as an aid in the planning of efficient experiments.

With regard to the problem of increasing the accuracy of selection the present results are only of limited value since they apply to lambs whilst selection is normally done at a later age. It is probable that in selecting for cannon bone length no attention need be paid to adjusting for environmental effects. As far as cannon bone weight is concerned, it is not clear to what extent breeders select for this particular character. The present results indicate that if cannon bone weight and the breeders estimate of "weight" of bone are one and the same thing, then their efforts will be confused, particularly by the effects of birth rank, age of dam and size of the animal. The same difficulty would exist with selection for carcass quality as measured by the block test.

The information on the effects of environment are of much greater importance in considering the methods of improving the accuracy of comparisons in experiments where measurements of cannon weight and carcass block test score are included. The present results suggest that in experimental comparisons where cannon bone weight and block test score are taken into account allowance should be made for
the effects of birth rank, age of dam, age at slaughter and, depending on the purpose of the experiment carcass weight. This could be done in two ways; either by eliminating the variance due to these factors by the techniques of analysis of variance and covariance or by making the experimental comparisons within groups of animals that are the same for the factors mentioned.

It is to be noted that in most of the work done on cannon bone weight in connection with problems of growth and development, little attention has been paid to methods of control over extraneous sources of variation such as birth rank and age of dam. In the work of Hammond (1932) McMeekan and Walker (1944), Palsson and Verges (1952), it would appear that these effects have been disregarded. In the work of Wallace (1948) control was achieved by making comparisons within similar groups of animals. The present results suggest that a worthwhile increase in precision can be achieved by this method.

The information on environmental effects can be useful in the planning of experiments since in some cases experimental control to increase precision can be achieved. For example, restricting experimental animals to single lambs born from five year old ewes and slaughtering at constant age would give control over effects due to birth rank, age of dam and age at slaughter.
(b) Genetic Variation in the Characters

In general, the method of estimating the heritability from the paternal half-sib correlation is the only one available for characters which can only be determined by slaughtering the animal.

Apart from the discussion of the statistical accuracy of this method which has been given earlier, it is also necessary to take into account the contributions which dominance deviations, epistatic variations and interactions between heredity and environment can make to the estimates. Lush (1949) has shown that multiplying the paternal half-sib correlation by four yields an estimate of heritability that includes all of the additively genetic variance, none of the dominance deviations and a small portion of the epistatic variations. The estimates of course give no indication of the size of this contribution from the epistatic variance.

The extent to which possible heredity-environmental interactions may be included in the estimates is not known. It is possible that an indication of the presence of heredity-environment interaction could have been obtained by studying the interaction between sires and years in the present analysis. As was pointed out in Chapter 3 including the sire - year interaction would have increased the computational work beyond the present facilities.
Correlations between the environments of the paternal half-sibs, if present, would have contributed to the paternal half-sib correlation and would result in the estimate in heritability being increased above their true values. Since in the management of the flock no attempt was made to treat the progeny of any sire differently from the progeny of any other sires there it is reasonable to assume that the environmental correlation between half-sibs will be zero. Hence the environmental differences between paternal half-sibs in the present data are unlikely to be either larger or smaller than those between non-sibs. Hence the estimates of heritability are unlikely to be biased by any environmental contribution.

The heritability estimate of a character applies to a particular population and may, in theory, vary from one population to another because of factors or effects that may cause differences in either the genetic or environmental variances. The population of which the sires used in the present data are considered to be a sample, have been defined as that of the Romney Marsh sires sold for commercial use in the Rangitikei, Manawatu, and Wairarapa districts. There is some suggestion that as a result of the analysis, particularly the high value of the estimate of heritability of cannon bone weight, that the actual sample of sires used is genetically more variable than is in fact true of the
population. This could be due to the fact that a small sample is more likely than a large sample to deviate from what is representative of the population. Possibly too there could have been unconscious selection which resulted in choosing a sample of sires showing more than average variation. Whatever the reason the high result shows that it would be unwise to attempt any wide generalisation based on the heritabilities reported in this study.

Present results taken in conjunction with earlier estimates given in Table 4 indicate that cannon bone length and weight are highly heritable whilst carcass quality as measured by the block test score is lowly heritable. In discussing the heritability of block test score, it is to be noted that the block test total is made up of a number of scores which are not necessarily linear. For example, the score for "Depth of Fat on the Loin" is based on the measurement of the fat cover over the eye muscle. The relationship between the score and the measurement of fat cover is such that the highest score is given for a carcass having 5mm of fat over the eye muscle those having either greater or lesser fat cover are given a progressively lower score.

Thus a fat cover of 5mm is regarded as an optimum and the score for this character is based on departures from this optimum. It is to be noted also that this optimum
is an intermediate in that both greater and smaller measurements than 5mm in depth of fat cover occur. The genetic effects of this type of score have been investigated by Wright (1935) and more recently by Rae (1950). In general for a score expressed as a deviation from an optimum many of the genes will act epistatically on the score even though they act additively on the measurement upon which the score is based. Thus hereditability of the block test score may be relatively low because much of the genetic variation in this character is epistatic in nature.

(c) Genetic Covariation among the Characters

The underlying causes of genetic correlations between characters have been reviewed by Rae (1951). In general genetic correlations are produced if some genes effect more than one character. In addition if a gene alters a particular developmental process then even though the gene has only one primary effect it will have some influence on any character or organ which is affected by the developmental process. Also genetic correlations just as with phenotypic correlations, can arise because the characters being correlated are related to each other as a part to a whole. For example, in the present case, if a gene has the effect of increasing cannon bone length without inducing any other alteration in the cannon bone, then
that gene must automatically produce an increase in cannon bone weight. Similarly a gene which produces a shortening of the cannon bone is likely to increase block test scores because of the importance of length of leg in contributing to that score. It would seem wise however to leave further analyses of the interrelationships between the characters until the data on volumes and circumferences of the cannon bone are available.

In the present data, signs of the genetic and phenotypic correlations are the same, but the absolute values of the genetic correlations are not sufficiently reliable to justify any further interpretation. The implication however is that selection for shorter length of cannon bone will lead to a correlated response in the direction of higher block test score and lighter cannon bone weights. On the other hand, selection for heavier cannon bone weight would result in a reduction of block test score and longer cannon bone length.

(d) Conclusion

In the past and to a certain extent at the present time sheep breeders have paid a considerable amount of attention to bone when appraising the quality of their livestock. Such terms as "light" and "heavy" bone appear in the general literature on the subject whilst when discussing the
merits and demerits of their stock, breeders commonly refer to the "length" and "weight" of bone (often the cannon bone). Over the years, there has in the mutton breeds been a conscious selection towards animals which possess short relatively thick bones and the cannon bone region has most often been used as a focal point for such selection. In the 1947 edition of the New Zealand Romney Marsh Flock Book there is a description of the typical New Zealand Romney which states *inter alia* "....The legs should be short, with big bones and large shapely feet..."

Again in the 1955 Flock Book in a similar section there is the statement ".....the cannon bone should be reasonably short with heavy bone of the very best quality." The attention paid to "length" and "weight" of bone would appear to have arisen for two different reasons. The breeder is interested in length of bone because of its relationship to carcass quality whilst "weight" of bone is commonly regarded as being an indicator of "constitution". To what extent the breeder's concept of "weight" of bone is related to the true test of constitution - the ability of the animal to thrive and produce under the conditions or environment in which it is kept - is not known.

From the results quoted in Chapter 4 it would appear that there is good reason for the breeders to associate cannon length with carcass quality particularly since it is not
greatly affected by environmental factors yet has a high heritability. However a certain amount of speculation is allowable as to how much of the association of the length of the cannon bone with carcass quality is due to automatic favouritism because of the method of judging carcass quality and how much of it is real and absolute.

As far as bone "weight" is concerned the association between the "heavy" or "big" bone referred to by breeders and the actual absolute weight of the cannon bone must be decided before any conclusions can be reached. The question that must be answered before any conclusions based on the results presented here can be drawn is:-- When breeders speak of "heavy" bone do they mean its weight in absolute terms or do they refer to the weight/unit length or relative thickness? There is of course no definite answer available to this question but since in the live animal there is no possible way of estimating the absolute weight of bone it must be assumed that breeders are referring to the apparent "weight" or the thickness of the bone. This conclusion is supported by the statement from the 1947 Romney Marsh Flock Book under the heading Instructions to Inspectors which reads "..... a decided Leicester face or bones is to be discouraged .... Good constitution must be apparent and freedom from extremely weak bone."

The results presented in this study show that the
weight of the cannon bone bears a negative relationship with carcass quality but a strong positive relationship with cannon bone length. Thus whilst a short cannon bone on average would be expected to produce a high block test score it would also be expected on average that the cannon bone would be relatively light. On average, the heavier the cannon bone, the poorer the block test. If, then, the breeder's subjective estimate of "weight" of bone is closely related to its true measured weight, it would appear that the objective of combining short bone with heavy weight of bone and good carcass quality is not likely to be achieved because of the structure of the correlations between the three characters.
SUMMARY

1. Data concerning the cannon bone length, cannon bone weight, and carcass block test score collected from 452 Romney wether lambs, was analysed with a view to obtaining the effects of some environmental factors, the heritability, and phenotypic and genetic correlations between these three characters.

2. Environmental factors - year of birth, birth rank, age of dam, age at slaughter and carcass weight - were found to be responsible for three per cent of the total variation in cannon bone length, twenty one per cent of the total variation in cannon bone weight and forty two per cent of the variation in carcass block test score.

3. The heritability of cannon bone length was found to be high (0.866), cannon bone weight high (1.248) and carcass block test score low (0.189). The unduly high figure for the heritability of cannon bone weight was considered to have been due to sampling errors caused by the relatively small number of sires (12) used as a sample of the population.

4. A positive relationship was found to exist both phenotypically and genetically between cannon bone length and cannon bone weight. A negative relationship was found
to exist both phenotypically and genetically between cannon length and carcass block test score as well as between cannon weight and block test score. The absolute values of the correlations were not considered to be accurate enough for predictive purposes.

5. From the results presented it was considered that environmental effects play a considerable part in the determination of cannon bone weight and block test score and that control of the factors of birth rank, age of dam and age at slaughter would lead to a worthwhile increase in precision of experiments concerned with these characters.

It was also considered that selection on the basis of cannon bone length is sound but that selection based on estimated cannon bone weight and block test score is unlikely to give the desired result. Further it is considered that the breeders objective of combining short bones with heavy weight of bone and good carcass quality is unlikely to be achieved.
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APPENDIX I

BLOCK TEST SCORE CARD

A. External Points

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<th>Max. Points</th>
<th>Points Awarded</th>
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</thead>
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<tr>
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<td>30</td>
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</tr>
<tr>
<td>(2) Fat Cover</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>(3) Loin</td>
<td>10</td>
<td></td>
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B. Internal Points

<table>
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<tr>
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<tbody>
<tr>
<td>(4) Depth of Loin Fat</td>
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</tr>
<tr>
<td>(5) Eye Muscle</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>(6) Ribs</td>
<td>10</td>
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</tr>
<tr>
<td>(7) Colour and Texture of Flesh</td>
<td>5</td>
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Carcass Total 100

APPENDIX II (a)

Scale of Points for Legs
(Difference between G & F measurements)

<table>
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<th>Difference</th>
<th>Points Awarded</th>
</tr>
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<tbody>
<tr>
<td>2.1cms and over</td>
<td>30 pts</td>
</tr>
<tr>
<td>1.8cms</td>
<td>29</td>
</tr>
<tr>
<td>1.5</td>
<td>28</td>
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<td>26</td>
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APPENDIX II (b)

Scale of Points for Legs
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<tbody>
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<td>30 pts</td>
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<td>1.8cms</td>
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APPENDIX II (c)

Scale of Points for Legs
(Difference between G & F measurements)

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<td>0.3</td>
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<td>17</td>
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<td>16</td>
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</table>
### APPENDIX II (b)

**Scale for Depth of Fat over Loin**

**Carcass Weight (lb)**

<table>
<thead>
<tr>
<th>Points</th>
<th>28 a/u</th>
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## APPENDIX II (c)

### Scale of Points for Eye Muscle

Carcass Weight (lb)

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**APPENDIX II (a)**

**Scale of Points for Ribs**

(Measurement X)

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### APPENDIX III

#### INVERSE MATRIX I

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## APPENDIX IV

### RIGHT HAND SIDES

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