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A STUDY OF THE PLEIOTROPIC EFFECTS OF THE
DOMINANT GENE N
IN THE NEW ZEALAND ROMNEY SHEEP

being a thesis
presented for the degree
of Doctor of Philosophy in the
University of New Zealand

F.R.M. COCKREM
Massey Agricultural College
University of New Zealand

1956

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IN THE NEW ZEALAND ROMNEY SHEEP.

Summary

Research on the causes of medullation of the fibres from the New Zealand Romney sheep by Dry (1940), lead to the description of a dominant gene, N, causing a high abundance of halo-hairs in the birth coat of the lamb. Sheep showing this characteristic were called N-type sheep.

This thesis has been concerned with the possible pleiotropic effects of this gene and with their relationships, both to the economic potentialities of N-type sheep and to their possible use in research on genetic and phenotypic correlations.

The investigation involved lambs from matings made in two consecutive years. Those from the first year were used primarily for a study of lamb's growth and a general survey of the problem, while the second year's lambs were used to examine hypotheses which arose from the first year's results and which concerned the relationships between birthcoat type, body growth and the hogget fleece characteristics.

The results, which are based on statistical analysis, can be summarised as follows:

1. The hypothesis of a single dominant gene was not disproved.
2. Growth in the first year showed
 - (a) There were no differences of weight or body size at birth attributable to the presence of N in the genotype.
 - (b) Differences in body weight occurred at 30 days of age, N-type sheep being lighter than the ordinary Romney. These differences were proportional in the sub-groups of sex and birth rank (single or twin lamb)
 - (c) These differences were confirmed at the mean ages of 67, 100 and 144 days. For these ages the differences were greater between the groups of single lambs than between the groups of twin lambs, being of the order of ten or more pounds for single lambs at the final age.

- (d) These later differences were probably to a large extent the result of those already present at 30 days and this initial effect was found to be the more important when the data was analysed in terms of relative growth.
 - (e) Differences of weight could not be attributed to differences in the skeletal size of the animals.
 - (f) Effects may have been present, associated with the homozygous animals (NN) that were not the sole result of the gene N but were also the result of possible inbreeding and selection associated with the development of these animals for the production of carpet wool.
3. Examination of the carcasses of ram lambs from this experiment indicated no differences not associated with those of weight corrected for age.
 4. These results were not confirmed in the second year when no effect of the gene N on growth was detected in a comparison of heterozygous (N+) and ordinary (++) lambs.
 5. The major difference between the two years' experiments being one of environment, it is suggested that there is an interaction between the genotypes containing N and the environment. Comparison of the growth curves of the ordinary lambs for the two years and consideration of the different conditions suggests that this interaction may well be one of climate conditions and birthcoat type.
 6. The long dorsal spines of the thoracic vertebrae of N-type sheep appeared to be associated with the presence of horns, although further information is required on the early development of both the horns and these spines.

Fleece Characters:

7. When corrected for body weight, the greasy fleece weight of N-type lambs and hoggets was greater than that of ordinary animals. The difference was greater for twin than for single lambs.

In the first year:

8. Wool from ewe hogget twins had a greater staple length and more 'hairiness' (benzol test) than single lambs (70 lambs)
9. There was a negative association between body weight at 30 days of age and the percentage of coarse continuously medullated fibres in the hogget fleece. In heterozygous animals a greater density of halo-hairs at birth was associated with more coarse fibres in the hogget fleece.
10. Medulla diameter at constant fibre diameter was found to decrease with greater body weight (or faster growth) in both years.
11. Results in the first year suggested penalisation of the secondary follicle population in N-type sheep following the poor growth of the lamb with the resulting coarse fleece of low density. This was shown, for instance, in the coarser fleece with longer staple length of twin animals. This hypothesis formed the basis for the major part of the second year's work.

The second year's work: *

12. Ordinary lambs had more fibres per unit area (density) at birth and at 25 weeks of age.
13. The lower fibre density of N-types at birth was interpreted as the result of the higher density of halo-hairs, as a high proportion of halo-hairs was found to be associated with a low birthcoat density of all fibres.
14. N-type twins had a higher halo-hair density than N-type single lambs, and larger animals (measured by the height at withers) had a lower total density. These results were assumed to follow from the different skin expansions in the last few weeks of pre-natal life. This, with a suppressing effect of large primary follicles on the formation of (or production of fibre from) new secondary follicles, could account for the observed density differences and associations at birth.
15. The variance amongst N-type lambs of halo-hair density was not fully accounted for and it is suggested that other unknown factors, genetic or otherwise, may affect the number of primary follicles which are originally of sufficient size to produce halo-hairs.
16. The fleece density at six weeks of post-natal age would depend on the density at birth, the skin expansion and the number of new fibres added. The results for different relative skin expansions were:
 - (a) Skin expansion less than two (times birth area): the number of new fibres were penalised by high birth fleece density or by many halo-hairs.
 - (b) Skin expansion greater than two for N-types and 2.5 for ordinary lambs: fibre numbers added were independent of initial densities and, in addition, at expansions greater than 2.5, the N-types added more fibres per unit area than did the ordinary lambs.
 - (c) Skin expansion greater than four for N-types and three for ordinary lambs: a maximum of about 6000 fibres added to an initial square centimetre for N-types and of about 3000 fibres for ordinary lambs, is reached.
17. The results under section 16 above are similar (with additions) to those obtained by other authors and suggest penalisation of secondary follicle formation or of fibre growth from these follicles (no actual follicle counts were available) under the circumstances detailed.

* Note: The wool samples were from ^{the} standard loin position, being carried out in duplicate for the determination of sampling and other errors.

18. The density of the hogget fleece, sampled at about 25 weeks of age, after shearing, depended on that at six weeks and the intervening skin expansion. Only a small proportion of new fibres were added to the fleece over this period.
19. Weighted mean fibre diameters were inversely proportional to the fleece density at each sampling time except for the ordinary lambs at birth. N-types showed a greater diameter for a given density and in addition, for both types of hogget, the diameter at constant density was greater for a faster growing animal.
20. At birth higher halo-hair density was associated with a smaller mean diameter of the unmedullated fibres.
21. When the component fibre types (A,B & O; after Burns 1953) from which the overall mean weighted diameters were calculated were examined, it was found that there was a large increase after birth, this being proportional to the maximum diameter, which was attained at six weeks. It should be emphasised that the mean diameter frequently used in work on fleece characteristics may be based on a trimodal skewed distribution and this does not reflect the true pattern of diameters.
22. There was a tendency for the fibre diameter mean and variance to be reduced in the N-types at 25 weeks of age and the means of the N-type and ordinary lambs tended to converge at this age.
23. Unmedullated fibres (O types) from N-type hoggets were smaller than those from ordinary hoggets.
24. It was reasonable to suppose that halo-hairs were generally followed by coarse medullated fibres and the importance of these in the hogget fleece depended on the original halo-hair density and the number of other fibres added to the fleece. Consequently the hogget fleece characters depended in turn on the early growth of the lamb.
25. An examination of fibre diameters at the thinnest pre-natal portion and at six weeks for both N-type and ordinary sheep and the various fibre types from them, indicated that the proportional reduction in diameter was similar in both types of sheep. Fibres had a reduction in pre-natal diameter which was proportional to the diameter at six weeks.
26. It was suggested that the 'pre-natal check' and the fibre type array phenomena are in part the morphological end point of the different pre-natal and post-natal fleece densities, the lambs' growth at the two periods and the distribution of potential fibre sizes which can be produced by the follicles. Consequently further investigation in these terms and in terms of follicle ratios and measurements are likely to be profitable.
27. The relationships between medulla diameter, fibre diameter and body weights were similar for the hoggets from both years' work. There was a greater medulla diameter for

a given fibre diameter at birth and at six weeks than at the hogget stage. Differences in 'Hairiness' observed in the fibre type arrays would be the result of the fibre diameters which in turn would depend on the factors in sect. 25 above.

From these results a suggested plan of the pleiotropic effects of the gene N has been constructed.

If the initial action is one producing large primary follicles, then it is possible to account for the results obtained above. Some confirmation is naturally required on various points by repeated or more detailed work, but the general plan seems clear. These large follicles will produce the halo-hairs and in addition affect the formation of secondary follicles or the growth of fibres from them. The effects which follow this show considerable variation as a result of interactions with other genetic effects or with the environment. The environmental interactions are shown markedly by the differences between twin and single lambs in the various characteristics and also by the different results of the growth experiments in the two years. The various factors affecting the fleece density at six weeks will also be dependent to a considerable extent on the environment, and on other genetic factors. These interactions are included in this plan of pleiotropy which can thus follow various paths. These paths are not, however, discrete/and separate, but form the pattern of continuous variation observed in the hogget fleeces. Thus by establishing connections between the growth of the lambs and the fleece characteristics, much of the variation in the N-type hogget fleece can be accounted for. In addition, some overlapping between the characteristics of N-type and ordinary

hogget fleeces found in particular in the first year is explained although there is a gene difference with marked phenotypic manifestation at birth.

The thesis concludes with a discussion on the possible research uses of N-type sheep and suggests various investigations in which they could be of use. The important research use lies in the possibility of producing two groups of lambs of very different wool types from one group of ewes, it being known that this difference is a genetic one and that all maternal and similar effects are randomised amongst the two groups. Some suggestions for an N-type experimental flock and for its part in sheep and wool research are made.

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Dry, F.W. (1940) Nature 145: 390

Burns, M. (1953) J. Agric. Sci. 43: 422

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INTRODUCTION

In dealing with problems of inheritance in domestic animals the emphasis tends to be placed on those factors which are of economic importance. Such factors are likely to be the result of many interacting and related causes, both genetic and environmental. This has resulted in the use of an approach based on the concepts of multifactorial and population genetics of Fisher, Wright and other workers. Using these concepts, the existence of certain genetic and phenotypic correlations can be shown and the results of certain selection policies predicted. However it is of considerable interest to know the mechanisms whereby these correlations arise. One such mechanism is pleiotropy, and it is proposed in this thesis to show how N-type Romney sheep (Dry and Fraser 1947) can, by a study of the pleiotropy of the gene N, be used to investigate the chain of events leading to various genetic and environmental correlations amongst fleece and body characters of the sheep.

The first part of the thesis is concerned with preliminary investigations of the growth of the N-type sheep, which were initiated as part of a study of the carcass quality of lambs from these sheep. It was as a result of this study that the potentialities for the second year's work were realised. The second part is concerned with realising these potentialities in a study of the relationship of the body growth of the lamb and the development of the fleece.

The history of the N-type sheep has been described by Dry and Fraser (1947); briefly they are New Zealand Romney sheep*, either heterozygous or homozygous for a dominant gene with the symbol N or homozygous at a different locus for a recessive gene, nr. The dominant gene N only is considered in these investigations. The phenotype of these animals is simply recognised from the birthcoat of the new-born lamb, which has a high abundance of coarse fibres known as halo-hairs (Dry 1935⁴). The adult fleece type is considered extremely useful for the production of wool for the manufacture of carpets and the use of N-type sheep for this purpose was being considered.

Before commercial exploitation could be attempted, it was necessary to examine the sheep on which this wool was grown, for the system of farming in this country requires a sheep suitable for the production of lambs as well as of wool. Alternatively, a sheep suitable for difficult hill country conditions is required, and in either case the 'thrift' of the sheep is of paramount importance. Doubts had been expressed on both the body conformation and the thrift of these sheep and investigation was required before the use of these sheep as a new carpet wool 'breed' could be considered.

This was the initial problem although Rae(1952a) had pointed out the possible uses of these sheep as outlined in the opening paragraphs. Thus it also seemed desirable to

* All the sheep used in these experiments were of the New Zealand Romney breed and will be referred to as 'sheep' or 'lambs'. Sheep of other breeds referred to in discussion will be given their full title. 'Ordinary sheep' means those carrying the normal alleles +/+

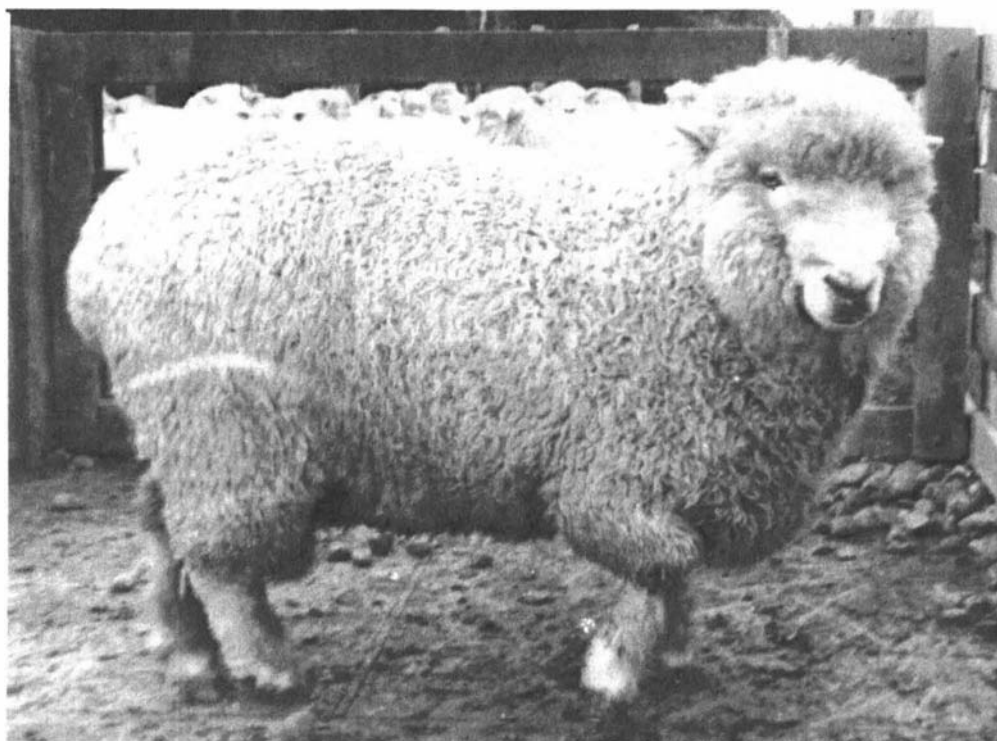
examine and open up what appeared to be a profitable field of research.

Thus this thesis is divided into two parts, representing the two years' work:

- (1) A general investigation of possible pleiotropic effects of N on the growth and carcass of the lamb.
- (2) A more detailed investigation into the effects of different birthcoat types and different rates of body growth on the development of the fleece.

PLATE I

An Ordinary Romney Ram



A Heterozygous N-type Ram

PART ONE

A GENERAL INVESTIGATION OF POSSIBLE PLEIOTROPIC EFFECTS OF N ON THE GROWTH AND CARCASS OF THE LAMB

I. INTRODUCTION

The occurrence of multiple effects of a single gene have been shown in particular by Grüneberg (1938) in his investigation of a lethal cartilage anomaly in the rat. In other work on mutants in the mouse he has shown that an apparent diversity of characters can be traced back through developmental sequences to an original single developmental fault. As a result he assumes that pleiotropy is a result of various branching developmental sequences which depend on an original single event effected by the locus concerned. Whether true pleiotropy, multiple action of the gene itself, exists or not, this wider definition is a convenient one and will be adopted throughout this thesis.

When this investigation started, previous work had shown that the pleiotropic effects of the gene N were high halo-hair abundance with brown pigmented fibres at the base of the neck at birth. In addition, horns were grown by homozygous and heterozygous rams and with a few exceptions by homozygous ewes (Dry and Fraser 1947). General observation had also suggested that N-type sheep were 'unthrifty' and had poor body conformation; i.e., they had body proportions unsuitable for the production of good quality meat carcasses. A particular example was the 'pointed withers' usually associated with long dorsal thoracic

spines. Thus a syndrome was suggested involving both fleece and body characters. Previous investigations have tended to separate these two main economic products under the general headings of fleece biology and carcass quality studies, and it is therefore convenient to divide reviews of past work into these two main classes. These reviews will^{be} presented at the beginning of this part of the thesis although they cover the field of both parts.

II. REVIEW OF LITERATURE

A. Wool Biology

1. Papers published prior to 1939.

The review can be conveniently divided into two parts determined by the papers in which Carter (1939a and b) described a standardised method for treating skin samples and analysing follicle populations. Except for Wildman (1932), Tanzer (1926) and Teodoranu (1934), most work prior to Carter's had been carried out on the wool fibre rather than on the follicle.

Much early work was concerned with classification and description of the fibres of the fleece of the various breeds of sheep. A publication by the Research Association of the Woollen and Worsted Industries (1926) contains a summary by various authors of knowledge of kemp at that time. The medullation of the fibres was shown to be caused by air spaces in the centre of the fibres which reached a maximum in kemp fibres of which a description is given. The birthcoats of Welsh mountain sheep were described and the abundance of halo-hairs (birthcoat kemps) was correlated with the amount of kemp in the adult fleece.

This type of work was extended in a classification of fibre types of the Merino fleece by Duerden and Seale (1927). They divided the fibres into kemp, hair, wool (non-medullated) and heterotype fibres which were partially medullated. These long partially medullated heterotype fibres were found to be

the characteristic long fibres of carpet wool and of some long-woolled sheep by Duerden (1929). This primary classification of fibre types was used for work on the fleece by Lockner (1931) and Darling (1932). They both found that new fibres were formed after birth but no fibre measurements were given. Lockner described the birthcoat of the Blackface lamb, which was very similar to that of the N-type lamb, and Darling also noted that the wool was 'exceptionally fine' when the hair was well developed. Bryant (1936) described the distribution of kemp over the body of the Scottish Blackface ewe and concluded that the occurrence of kemp is inherited on a multifactorial basis.

Descriptive work on the lambs' fleece has been carried out by many authors, but few have seen the necessity for measurement. Of these Crew and Blyth (1922) divided fibres from the skins of Scottish Blackface lambs into three groups A, B, and C, corresponding to kemp, hair, and wool, of which the proportions, densities, and mean diameters were determined. Duerden and Boyd (1930) described the birthcoat fibres of the Persian Blackhead lamb and of the Merino, defining in particular the sickle fibre, so named after the shape of its tip. This tip shape was attributed to the mechanical effect of the fibre forcing its way out of the skin when it was first formed and was dependent on the fibre diameter at the time. Rudall (1934) found a similar effect in fibres regenerating after epilation. Duerden and Boyd (1930) also described the thinning of the fibres at or about the time of birth, and they attributed this to the environmental effects involved in a lamb's being born.

No evidence is offered as to the exact birthpoint but mean measurements of pre- and post-natal fibre diameters are given.

A classification method, similar to that of Crew and Blyth above, was also used but with a different terminology. Barker (1933) pointed out that the classification of fibres macroscopically can be deceptive and suggested that the thinning of sickle-fibres can be an illusion due to their twisting. He confirms an increase of diameter post-natally.

The major development of work of this type has been due to Dry (1935) working on the New Zealand Romney lamb. He first described various fibre types: the halo-hair or birth-coat kemp, sickle-fibres (after Duerden and Blyth) and fibres with curly tips. These last were further sub-divided according to presence or absence of medulla in the different regions. Fibres without any definite tip structure are called histero-trichs. By placing these fibre types on a black background in order of probable appearance in the fleece, various classifications can be obtained according to the presence or absence of different fibre types and their individual characteristics. These are called arrays, which fall into five groups which have been given the names of topographical features. These arrays are described by Stephenson (1955) and their form is attributed by Dry to the pre-natal check, 'a restricting or checking force' which is 'manifold in its effects upon the development of the coat.' The thinning of the neck of the sickle-fibres is attributed to this force, as is the form of the other fibres, depending on when, relative to the 'check', the follicle was first laid down. By assuming variations in the time of onset of the check, the intensity of the check, the decline of the check and the vigour of the follicle, the fibre types could be explained. In addition these factors are then assumed to have a permanent effect on the follicle.

The shedding or decrease in diameter ('crisis thinning') of some fibres in the first few months of post-natal life was also described. Medullation was held to be a sign of vigorous growth of wool from the follicle. Shedding was also held to be a sign of follicle vigour, for 'if a follicle works extremely hard it is compelled to take a rest'. Galpin (1935) has described the distribution of these fibre type arrays over the body of the New Zealand Romney lamb.

Whereas a fibre type classification system can be useful in the initial stages of work on the fleece, there is a danger of eye artefacts and any detailed work requires the use of objective measurement techniques. The most obvious of these is fibre diameter, and Duerden and Seale (1927) determined the distributions of diameter for three fibre types in the Merino. These distributions increased in both mean and variance as the fibre types became more medullated. Duerden and Bosman (1926) obtained similar results when comparing strong and fine -woolled Merinos, the distribution of fibre diameters tending to become trimodal as the mean and variance increased. Northcroft (1929) working on New Zealand Romney-Lincoln cross sheep, obtained a similar trimodal curve for length measurements. He also described methods for measuring fibre and medulla diameters.

Wilson (1929) described the use of glycerine for measuring the medullation of wool. When immersed in glycerine the cortex is rendered invisible while the medulla shows as a black or white line in transmitted or reflected light respectively. This effect is true for any medium of similar refractive index to the cortical material, and Elphick (1932) developed the method using benzene (commercial benzol) to obtain quantitative estimates of medullation. This was further developed by McMahon (1936)

who used a photo-electric cell to measure the light reflected from a given weight of wool immersed in benzol. This is known as the benzol test, the results being expressed as a percentage on an arbitrary scale. Duerden and Ritchie (1923) commented on a connection between fibre diameter and medulla diameter, while Thommaset (1938) also emphasised the importance of considering frequency distributions of fibre diameters rather than means, if maximum information is to be obtained, because of the trimodal form of the distribution. He also stated that medullated fibres tend to increase in diameter by increase of the diameter of the medulla rather than by increase of the cortex.

The most comprehensive use of the measurement techniques available is that by Bosman (1937) on the fleece of the South African Merino. Fibre diameters, fibre lengths, fibres per unit area and the area occupied by fibre are all determined and the inter-relationships discussed; from these a description of the fleece in biometrical terms is obtained but no detailed analysis of it is attempted. R. Burns (1935) discusses methods of measuring skin area increases in sheep but errors are not determined nor are body weights given so the results cannot be applied for other work.

Summarising at this stage, the gradual placing of wool research on a basis of measurement rather than subjective description is shown, while the dangers of the latter are indicated by the work of Barker (1933). In this biometrical description the occurrence of a trimodal distribution of fibre diameter associated with the higher values of the mean and variance is of importance as a basis for any statistical analysis, an approach which does not seem to have been exploited although powerful techniques were available by

1930. This is probably because of the wide use of purely descriptive techniques and the difficulty of obtaining sufficient measurements to make analysis worthwhile. Sampling techniques have also been discussed by many of the above authors and the use of suitable techniques has emerged as an important aspect of any work on the fleece.

Factors affecting wool production have also been considered by many authors over this period, the emphasis being on nutrition. Many authors have obtained an increased weight of wool from the feeding of additional rations and this has been associated with increased body weight and fibre diameter (Fraser and Nichols 1934, 1935; Wilson 1931; Weber 1932; and others). Fraser and Roberts (1933) found no response to an increase in the protein fraction of the diet nor in this case was there an increase in body weight. A relationship between fleece weight and body weight has been found by many workers, the value of this relationship varying for different breeds. Bosman (1935) examined seasonal factors using three Merino wethers which were left unshorn for three years with constant rations over the whole period but with widely varying seasonal conditions of temperature and humidity. He found no variations in wool production between seasons or over the three years, and concludes that seasonal trends in wool production were the result of correlated effects of changing feed conditions. This appears to be the only experiment on seasonal trends not confounded by the possible shearing effects suggested by Rudall's (1935) experiments in which one side only of a number of sheep was shorn. The shorn side showed an increase of hairiness which could well be correlated with an increase in diameter and amount of wool grown. This effect was also found in areas

as small as eight square inches, and Rudall interpreted the increase as a temperature effect as it could be prevented by covering the clipped area. Rudall (1934) also tried the effect of epilation but obtained no positive results.

Dry (1935~~6~~) in the study of some 'poorly grown' lambs found failure to add the normal number of histerotrichs to the coat and a reduction of fibre diameter and medullation. In addition he suggests that there is no relation between birth weight and halo hair abundance in 'normal' lambs. Galpin (1936) related the fibre type array determined from a wool sample from a particular position on a lamb to the foetal growth. She suggests that follicle size was related to the relative rate of growth of the part of the animal underlying the follicle at the time it was formed. She also suggests that the pre-natal check is the result of crowding of follicles before birth.

Leslie (1935) examined the effect of factors such as birth rank, birth weight and plane of nutrition of the ewe on halo-hair abundance of the lamb estimated on a five point scale. No positive results were obtained but the results for birth rank and ^{for}plane of nutrition of the ewe suggested the need for further investigation.

2. Papers published after 1939.

The work of Carter (1939 a and b) gave a fresh impetus to wool research, in particular with respect to the connection between the development of the sheep and the fleece. These papers described a convenient and accurate histological method for analysis of the follicle population. Follicles can be divided into two major groups, primary and secondary, variable numbers of the latter being associated with a primary central

and two primary lateral follicles. The primary follicles are formed first in developmental order and the determination of their number per unit area and of the number of secondary follicles associated with a primary group, gives a biometrical description of the follicle population. This can then be used to compare breeds, individual sheep, or in particular, the development of the secondary follicle population. The ratio of secondary to primary follicles is commonly used and symbolised as the S/P ratio.

Carter (1943) and Carter and Hardy (1943) developed the technique in an account of the pre-natal development and general histology of the follicle groups of the Merino sheep and clarified some previous misconceptions. Gradients over the body are determined and as a result a standard sampling area suggested.

M. Burns (1949, 1953, 1954a and b) used these methods in the examination of the post-natal development of the follicle population of the Kent Romney Marsh, English Leicester, Scottish Blackface and Suffolk breeds of sheep. Various estimates of skin expansion and some more detailed examinations of individual follicle groups were also made. The results were analysed on a developmental basis but the small numbers of sheep used and the poor growth of lambs in some cases allows only limited induction from the results. Schinckel (1953) reports from studies of the Merino breed, that twins and the progeny of young ewes have a lower S/P ratio than single lambs and the progeny of mature ewes. The results indicate pre-natal and post-natal environmental effects on the development of secondary follicles, these being further confirmed by a significant

correlation between birthweight and S/P ratio. Conversely Henderson (1953) examined the development of the fleece of the Kent Romney Marsh sheep in relation to various nutritional treatments. He finds that the ultimate wool production per unit area corrected for body weight or skin area (as a function of weight) was not affected by the treatments, nor did a low plane of nutrition affect the numbers of new fibres added to the fleece after birth. This latter result, which conflicts with those of other authors, could be attributed to the first sample having been taken when the lambs were four weeks of age. The number of fibres added over these first four weeks was then estimated from the number of histerotrichs or ^{by} use of a fibre type array technique. Goot (1941) and Burns (1954) both report that some fibres classified as histerotrichs appear before birth and this possibility combined with the use of twin lambs for the low plane treatment and single lambs for the high plane treatment may well account for the result observed.

Later work by Schinckel (1955a) has shown that for the Australian Merino the primary follicle population is complete at birth, and subsequent changes in the density of this population merely reflect the skin expansion. This validates the use of the S/P ratio as a measure of the increase in the number of secondary follicles post-natally. Schinckel (1955b) showed further that all follicles were initiated prior to birth but that the number of secondary follicles maturing was dependent on body growth between birth and one month. The number of follicles initiated depended on pre-natal growth and other factors.

These findings have been confirmed by Short (1955a) who also investigated the effect of adverse nutrition of the ewe

on its lamb's fleece development (Short 1955b). He confirmed Henderson's (1953) finding that subsequent fleece production of the lamb was not affected, but found that those lambs which were smaller in the initial stages of growth as a result of poor maternal nutrition, had fewer follicles in the mature fleece with consequent lower density and coarser fibres. From this he deduces that weight of wool per unit area is not determined by the density of the fibre population but is, as suggested by Galpin (1947) a constant value. Further, he suggests that this result supports Fraser's (1953⁴) theory of follicle efficiency which is reviewed below.

Somewhat indirect evidence on the development of fibre populations is presented by Pohle, Keller and Hazel (1945) who examined the fleeces of 'hairy' lambs and compared their yearling fleeces with those of 'non-hairy' lambs. Rambouillet, Targhee, Corriedale and Columbia breeds were used and it was found that visual impression was misleading,^{as} there were only a small proportion of very coarse fibres in the hairy lambs' fleeces. 'Hairiness' and fibre diameter decreased rapidly after birth, leading to similar yearling fleeces in the two groups.

Hardy and Wolf (1947) found that in Shropshire sheep the fleece density at 20 weeks was highly correlated with that at 52 weeks of age. However their indirect method of estimating fleece density involving mean fibre diameter, mean staple length, the specific gravity of wool, clean fleece weight, two body measurements and body weight seems likely to lead to considerable errors.

Grandstaff and Wolf (1947) working on Navajo and 'cross-bred' sheep found a 5.9% reduction in kemp and a 20.7%

reduction in other medullated fibres over the period 28-364 days; the major part of these reductions had occurred by the 84th day.

Burns and Clarkson (1949) made a detailed histological study of a few follicle groups from four Kent Romney sheep of both sexes. Detailed examination of all follicle dimensions and keratinisation regions were made and papilla shapes were classified but no relationship was found between these and fibre diameter and medullation. From 'a general examination of the material' medullation was reported to be independently controlled in primary and secondary follicles and, within the secondary follicles, more medullation was observed in those on the ectal margin (first formed) of the group, this being in accordance with an observation of Carter (1943) for the Merino. They also found that different animals of the same breed with follicles of similar size had fibres with different degrees of medullation. In addition they found that primary follicles are generally deeper in the skin than secondary follicles, this being confirmed by Fraser (1952a)

Auber (1950) made a detailed histo-chemical study of fibre formation in the follicle of Herdwick and Kent Romney sheep. Medulla formation was also examined in detail and the results will be discussed in the text in relation to results obtained on factors affecting medullation.

In the study of the factors affecting the amount of wool grown on adult sheep Galpin (1947, 1948) followed wool growth in the Cambridge experimental Romney flock over a period of four years. A technique of repeated sampling of a tattooed square was used. The square was tattooed on the lamb at one month of age and the weight of wool and subsequent area of

these squares were studied. For a particular region of the sheep and under maximal environmental conditions a constant positive relationship was found between the tattooed area and the weight of wool grown on it. Thus the sheep that increased most in body size also produced the most wool and under ideal environmental conditions weight of wool produced for a particular area would be constant. Under poor conditions the weight of wool produced falls below this maximum constant value by a factor depending on the skin expansion of the region and sheep concerned. The less this skin expansion factor then the greater the falling off in production per unit area.

In Galpin's second paper the argument is extended and lamb growth and seasonal effects are considered. The method used of calculating variables seems unnecessary in some cases where the actual measurements have apparently been taken, particularly where these calculations involve the specific gravity of wool when medullated fibres may be present. Conclusions from this work are that the area covered by fibre increases in proportion to the increase in size of the tattooed square and also that the mean cross-sectional area of fibres is inversely proportional to fleece density. The number of fibres in the square at seven months of age was proportional to the number at one month and the relative skin expansion between the two times of sampling. The mean length of fibre grown per day depends on this initial skin expansion and the conditions at the time.

Marston (1948a,b, and c) carried out detailed metabolic studies of two Merino sheep and followed this with a study of the relations of nitrogen intake and available energy to wool growth. It is concluded from the results that, at low

nitrogen intakes, wool formation competes with the basal metabolism, while at high intakes it competes with the laying down of tissue proteins. The two sheep differed in the utilisation of nitrogen and in efficiency of conversion, the first converting to keratin about 5% and the second 10% of the available protein. He concludes that the substrate in tissue fluids and not the follicles is the limiting factor in normal wool production. Increases of wool production took place by increases in both diameter and length of the fibre, and the frequency distribution of the diameters changed in form as the mean diameter increased. The importance of considering the distribution as well as the mean diameter is emphasised. In the third paper copper deficiency effects are studied and it is concluded that the chemical processes involved in keratinisation depend fundamentally on this element.

Ferguson, Carter and Hardy (1949) in exploratory work to determine a measure of the wool-producing capacity of the sheep for use in genetic work, examined the asymptotic value of the weight of wool in a given square when it is plotted against the nitrogen intake of the animal. Environmental factors likely to affect this curve were also examined. They found a positive correlation between temperature and the weight of wool grown but this is confounded with other seasonal trends and requires experimental verification. They also confirmed the result of Duerden and Bosman (1927) of a reduction in cross-sectional area of the fibre as fleece weight increases, this being attributed by Ferguson et al. to increasing tissue hydrostatic pressure. The temperature effect, it is suggested might be due to induced vasodilation increasing the

blood supply to the follicles, Rudall's (1935) shearing results being quoted. Both these are preliminary hypotheses, 'experimental verification being required'.

However Wodzicka (1954) found a marked increase in skin thickness in Romney ewes for a short period after shearing. In addition, Ferguson (1949) using a technique of unilateral thoracic sympathectomy thus causing vasodilation on one side of five sheep, obtained an increased wool growth on that side for ten weeks. After this period there was an increase in air temperature which possibly counteracted the treatment effect by causing increased vasodilation on the control side. This approach therefore, possibly using shearing as a simple treatment, could yield interesting results.

A general point of interest from the results of Ferguson et al. of detailed studies of wool growth in relation to nitrogen intake is the curved nature of the relationship, which tends to become asymptotic to the wool growth axis, while studies of fleece weight relative to body weight have given straight line relationships.

Further studies of food intake in relation to wool growth by Daly and Carter (1955) showed a gradual decrease in intake until the time the sheep were shorn after which there was a sudden increase. The food intake and wool growth per unit area were found to be related, but it^{is} possible that this was a spurious association of seasonal trends.

Coop (1953) has reviewed and presented results on factors affecting wool growth rate in the New Zealand Romney. He used the tattooed square technique and found that repeated clipping did not have an effect on the weight of wool grown, but also

found that on areas clipped monthly a greater length of wool was grown than on areas clipped annually. Seasonal trends are then examined although the possible effect of the annual shearing of the sheep has not been considered. Using nutritional treatments, and, with Hart, light cycle effects and some temperature treatments, it is concluded that the annual cycle of wool growth cannot be entirely explained by the effects of the annual cycles of temperature, variations in length of day, or of available feed. The results of Ferguson et al. (1949) were not confirmed but a treatment varying the rhythms of light and darkness gave increased wool growth.

The remainder of this section of the review of literature will concern work relevant to New Zealand conditions and N-type Romney sheep.

D. Ross (1950) in a study of the benzol test for hairiness found it unreliable for higher values of hairiness due to effects of uneven lighting. (The apparatus has since been redesigned) In a study of factors leading to a particular benzol test percentage value, he plotted the frequency distributions of fibre diameters in the N-type Romney and obtained multimodal relationships. He also found a relationship between fibre and medulla diameter but did not examine it in any great detail.

Goot (1945) gave an account of variations in hairiness in the New Zealand Romney and discussed biological and genetic concepts. He appears to confuse genetic and phenotypic correlations between 'hairiness' and fleece weight, and also suggests that an observed decrease of hairiness from three months to a year of age 'follows the law of constant growth'.

Rae (1952b) reported negative genetic correlations between count and staple length, count and fleece weight, and also a

positive correlation between hairiness and fleece weight.

The gene N in the New Zealand Romney has been reported by Dry in a series of notes (1940a and b, 1941). The recessive gene nr with similar phenotype was reported by Dry (1944) and results showing that the dominant and recessive genes were not allelic were reported by Dry, Fraser and Wright (1947). These were reports of work in progress and a complete account of the breeding experiments and results obtained has now been published (Dry 1955a,b,c). The interpretation of Olbrycht (1941) based on a system of polygenic modifiers does not appear to have been substantiated.

Dry and Fraser (1947) give a general summary of conclusions from work on N-type sheep, reporting horns as a pleiotropic effect and also giving a method of distinguishing phenotypically between homozygous and heterozygous dominant N-type lambs using the presence or absence of a high density of halo hairs in a small region behind the shoulder.

Schinckel (1951) reports the possible occurrence of a dominant gene causing high halo hair density in Merino sheep. Chapman, Mule and Richards (1954) give a review of three cases reported of mosaics in Merino sheep. These took the form of a small area of coarse fibres in an otherwise normal sheep. If these are considered to be the result of somatic mutation then they offer supporting evidence for a single gene conditioning an abrupt change of fleece type in the Australian Merino sheep.

Fraser and Hamada (1952) correlate birthcoat fibre types with follicle types and report a high correlation between P/S ratios estimated by the two methods. They suggest from the information available that P/S ratios are the same in all

breeds at birth and (from Fraser's data) that N-type lambs and ordinary Romney lambs have the same P/S ratio at birth. It should be noted that the method used for calculating the average ratio gives a biased result unless equal numbers of primary follicles were counted in all sheep. Also, in view of Schinckel's (1953) results, effects of maternal age and birth rank should also be allowed for before this hypothesis can be confirmed.

It is suggested that the difference between 'coarse' and 'fine' birthcoats in different breeds is due to the presence or absence of Dry's pre-natal check and also to another epigenetic system determining the length of the fibres. The difference between longwool and shortwool sheep is attributed to this system and to a different amount of fibre substrate. A third system affecting fleece type is that controlling the density of secondary follicles which is considerably higher in the Merino and associated breeds. On the basis of these three independent systems, a somewhat speculative theory of evolution of the main sheep breeds is suggested.

These ideas are developed by Fraser (1953⁴) into a general theory of fleece structure based on the relative 'efficiency' of a follicle, which is related to its time of initiation. Available substrate is divided amongst the follicles according to their 'efficiency', and if the number of follicles of each 'efficiency' is considered and also their density, four possible ^{variables} are obtained.

By consideration of these variables frequency distributions of follicle 'efficiencies' for different fleece types are obtained. These appear to be closely related to those of fibre diameter, which is to be expected when the relation of fibre

length and diameter is considered and also the relation of follicle size to age of initiation (Carter and Hardy 1943; Burns and Clarkson 1949) An evolutionary scheme rather similar to that of Fraser and Hamada (1952) is suggested based on changes in substrate, P/S ratios and densities of follicles.

Fraser (1952a) used N-type lambs' wool and related the shapes of fibre tips in the fibre type array to the different rates of growth of the fibres. The rapid increase in rate of growth of body weight of lambs after birth is quoted (Winters and Feuffal 1937) and it is suggested that this is correlated with an increased rate of fibre growth. He estimated that a check in growth of fibres from primary central follicles occurs at the time that the fibres from primary lateral follicles enter the fleece and from this deduces the form of the sickle fibre and the cause of the pre-natal check; that is, a check in growth rate of the fibres due to competition by new follicles starting to produce wool.

Fraser (1952b) argued that the primary effect of the gene N is to increase the efficiency of the first formed follicles, i.e. the primary follicles. By assuming similar follicle populations and fleece weights for N-type and ordinary sheep, he demonstrated from fibre length measurements that the efficiency concept is sufficient to explain the difference between N-type and ordinary fleece types. In support of this, the lowering of efficiency of the late formed secondary follicles in N-types to compensate for the increased efficiency in the remainder, is shown by the observation that histerotrich diameter is less in N-type than in ordinary sheep. Von Bergen and Mausberger (1948) and Lang(1947) are quoted as having obtained similar results with other breeds; that is, an increase of diameter in one

group of fibres was compensated by a decrease in the complementary group.

Fraser and Short (1953) gave evidence of competition in terms of follicle diameters, finding a negative correlation between the size of a fibre and the size and distance of adjacent fibres. Maximum distances for this interference effect are given for three sheep of different breeds. Short also reported a negative correlation between P/S ratio and primary follicle size for sheep of two breeds.

B. Body Growth and Carcass Quality

The basis for a scientific study of the meat carcass of an animal has been laid by Hammond and co-workers, starting with a study by Hammond (1932) of how the relative development of the various parts and tissues of the sheep lead to the final product of a good or poor quality carcass. This work, accompanied by an extensive review of the knowledge at the time, laid down certain general principles concerning the time of maximum development of parts of the carcass relative to the whole and the consequent relationships between them.

McMeekan (1940) using the pig, and Wallace (1948) and Palsson and Verges (1952) using sheep, have examined the effect of varying the plane of nutrition of the animals at the time of maximum relative growth of certain parts. From his results McMeekan claimed that the concept of allometric growth (Huxley 1932) was only valid for a particular plane of nutrition. He did not however, analyse the data on a logarithmic scale. Wallace, from his own data and from that of McMeekan, concluded that within a given tissue, for example the skeleton, the

relationship between a part and the remainder was the same regardless of the nutritional plane. Palsson and Verges found differences in the regressions of parts of the skeleton on the remainder of the skeleton, but also used an arithmetical scale. Their main methods of analysis of the effect of the treatment on the different parts of the body make use of a ratio of the high plane weight to the low plane weight, which ratio is then expressed as a percentage of a similar ratio for a 'standard part'. This 'standard part' is one shown to be unaffected by the treatment. This type of analysis is difficult to interpret in biological terms.

Whatever the final biological explanation of these results, it is clear that in an experiment to determine differences in carcass quality between two groups of lambs, growth must be a primary consideration. If one group of lambs reaches slaughter weight before another then differences may be expected and the mere demonstration of such differences is of very little use in the solution of the problem.

Weight gains are not in themselves sufficient for this purpose, partly because of errors involved in weighing animals under field conditions (Walker and McMeekan 1944). These, however, can be minimised, but a large thin animal can have the same weight as a small fat one and this type of difference will not be reflected in the data. The use of other body measurements is therefore desirable.⁴ Such measurements should meet certain requirements; they should be sufficiently accurate to detect differences between sheep in relation to the errors involved and also, if differences are found they must be capable of interpretation either biologically or in terms of prediction. The remainder of this review will therefore deal with live

animal measurements and their meanings, methods of assessment of carcass quality, and general aspects of growth and its measurement.

Although live animal measurements have been very extensively used there have been few systematic studies of the errors involved, nor have there always been estimates of the errors for the particular conditions under which the measurements were finally taken for experimental purposes. One of the more comprehensive studies using sheep was that of Phillips and Stoehr (1945) who compared direct measurement with a photographic technique. They found the former the more accurate and of the measurements taken, 'height at withers' was the most accurate while width of shoulder, length, depth of chest, heart girth and various other measurements were of 'sufficient accuracy'. They used freshly shorn sheep and the standard errors and coefficients of variation are given for all the measurements tried. In contrast, with cattle, Smith, Hobbs, Warwick and Whitaker (1950) found a photographic technique slightly better than direct measurement. They give the repeatability for various measurements.

Lamont (1934) carried out a large number of measurements on shorn sheep to determine the correlations between them. Where repeated measurements were taken he gives the average error as being about 4%. Rae (1946) also measured shorn sheep and analysed the errors in some detail and concludes that height at withers was the most accurate of those measurements tried. He also correlated the live animal measurements with certain carcass measurements and found that height at withers was likely to be of the most use, being correlated with the lengths of the cannon bone and radius ulna. There was also a negative correlation

between this measurement and points awarded the carcass on the Cambridge Block Test (McMeekan 1939b), but the errors of estimate from the regression equations were too high for practical use.

Bonsma (1939) made extensive use of live animal measurements for studying the growth of various sheep breed crosses for producing fat lambs. Their meanings are discussed and are expressed in terms of measurements of the carcass. He concludes that heart girth is 'essentially an index of constitutional development' but that height at withers conveys little information apart from comparative size. Many of the measurements taken appear only to serve the purpose of confirming results already obtained. He also concludes that there is an effect of plane of nutrition on skeletal dimensions but this is of doubtful validity because of the wide variation due to the many breeds and crosses used.

Ritzman and Davenport (1920) used live animal measurements for a genetical investigation and conclude that the proportions of the head are a dominant characteristic. This was followed by further work on the Southdown and Rambouillet breeds by Ritzman (1923) who discusses body measurements in relation to the anatomy of the carcass. He analyses the heart girth measurement in relation to a cross section of the carcass at the point where this measurement is taken and from his analysis decides that the thickness of flesh and broadness of the back are not determined by the 'spring of rib' but by the length of the spinous process and the length of costal cartilage relative to the length of the rib. Various other conclusions are drawn, it being emphasised that external measurements should be

based on definite skeletal units.

Von Borstal (1952) found that the sharpness of withers in the Cheviot ewe was associated with heavier fleshing on the shoulder. It was the result of longer thoracic spinous processes and the apparently poor conformation of the live sheep in the shoulder region was not reflected in the carcass.

More work has been done on the measurement of cattle than of sheep but the two are sufficiently similar to make the former results worth considering. Moulton, Trowbridge and Haigh (1921) found that a low plane of nutrition from birth affected heart girth measurements in the adult steer, but did not affect those measurements concerned with the length of skeletal parts.

Brody (1945) discusses measurements on cattle and concludes that height at withers is little affected by plane of nutrition or environment and is therefore the best estimate of genetic size of an animal.

Black, Knapp and Cook (1938) found that the ratio of weight to height at withers gave the best estimate of 'performance' in beef cattle, and also that 50% of the increase in the height at withers took place pre-natally.

Pontecorvo (1939) using Chianina cows, found simple allometry between height at withers and length of trunk. Using data on other breeds, he found a similar value for the growth constant for six different breeds; as Huxley (1932) had pointed out that the value of the growth constant for grazing mammals must be greater before than after birth to account for the long limbs, it is suggested that differences in conformation could arise through the timing of the change of this growth constant value. He considers that height at withers

is a sufficiently reliable measure of the growth of forelimb length in cattle, quoting a paper of Engelters (1935) to show that the two principal angles in the limb do not change very much with age.

Kidwell, Gregory and Guilbert (1952) using Hereford cattle, took measurements at intervals of four months starting at birth. Using heart girth as a standard, they calculated allometric equations for various other measurements and using the half-sib method, calculated the heritability of the growth constants. They concluded that in the equation $Y = bX^a$ (where X is the heart girth, Y the measurement under consideration and a and b are constants) b and a cannot be modified by selection but that the 'a-b complex' can be so modified.

An approach that might well be repeated for carcass measurements and live sheep measurements, is that of Tanner and Burt (1954) who showed by the use of factor analysis that many of the measurements being widely used on cattle are contained in a few simple measurements, height at withers being one of the most important from this point of view. As well as considerable saving of labour in the future there are also biological conclusions to be drawn from this type of approach.

Work on carcass quality has mainly come from the original work of Hammond (1932) and has been developed by Hirzel (1936) and Palsson (1939) for sheep and McMeekan (1939a) for pigs. The carcass can be assessed by certain standard measurements and its composition estimated by means of the dissection of sample joints. From the measurements, in particular those of the cannon bone, indices of quality can be calculated. However, Walker and McMeekan (1944) disagree with some of Palsson's (1939) results on suitable indices. McMeekan (1939b) suggests a points system known as the Cambridge Block Test for large

scale carcass assessment. This is based on measurement and eye judgement and its use is illustrated in the work of Clarke, Barton and Wilson (1953). The various techniques available in meat production studies are summarised by McMeekan (1942).

The work of Huxley (1932) and D'Arcy Thompson (1942) is too well known to require discussion here and methods used to measure growth will be discussed later in justification of the method of analysis used in the first part of this thesis. The many difficulties and pitfalls have been discussed and methods of overcoming them suggested in a recent symposium of the Royal Society led by Zuckerman (1950). This symposium and the reviews of Brody (1945) cover most of the important mathematical aspects of the huge amount of literature on growth which it is outside the scope of this thesis to summarise. Biological aspects will also be discussed in the text where they are relevant, and two quotations on this aspect will complete this review. The first (J.Z.Young 1950) is from the symposium mentioned above:

'Nevertheless, today, although we spend much time on the mathematics of "form" there are few who feel the urgency of the need to link the form with its biochemical determinants.'

The second is from Paul Weiss (1949):

'At any rate, a purely formal treatment of growth, as is often attempted through the interpretation of growth curves, is only a valuable guide to and supplement of, but never a substitute for, a precise analysis of the different forms in which growth manifests itself.'

III. THE COMPARISON OF THE GROWTH AND CARCASS OF N-TYPE AND ORDINARY LAMBS

A. Preliminary Trials on Live Animal Measurements

Before the growth of the lambs was studied, a preliminary investigation was carried out to determine the accuracy of certain body measurements on the live animal. In addition it was necessary to find if there were any difficulties which might prevent their use under field conditions. It should be noted that the effect of the use of a measurement of low accuracy is a failure to detect a real difference that exists between sheep or groups of sheep. Large differences may be detected, however inaccurate the measurement and therefore the size of the difference likely to be present should be considered as well as the size of the errors of measurement.

Eleven shorn N-type lambs aged seven months were used for a trial group of measurements. The measurements finally selected for use in the field were also tested by repeating them on a few lambs during the experiment. All measurements of the experimental animals were taken by the author so it was his accuracy that was of importance. Differences between observers, where taken, were for comparison with the results of other workers.

Various measurements were rejected as unreliable or impracticable for field conditions and only those finally used are discussed here. Further results on the accuracy obtained from lambs under the conditions of the experiment are also included.

Table 1.
Analysis of Variance of the Height at Withers

Source	d.f.	Mean Square	V	Expected Mean Squares	Component	% Component
Sheep	10	12.58	S	E +2F +2G +4S	2.90	60.0
Observers	1	9.38	O	E +11A +2G +22O	0.36	7.5
Repeats	1	6.35	R	E +11A +2G +22R	0.22	4.6
Sheep - Obs.	10	1.33	F	E +2F	0.02	0.5
Sheep - Rep.	10	0.95	G	E +2G	-0.17	-
Rep. - Obs.	1	1.79	A	E +11A	0.05	1.0
Error	10	1.28	E	E	1.28	26.5

V = Variance component symbol
d.f. = Degrees of freedom
Standard deviation 1.13 cms.

1. The height at withers.

This measurement was taken with special calipers designed by Rae (1946) for the work already described. The bottom bar of the instrument rests on the ground and the top bar is then brought down to rest on the back of the sheep, just behind the line of the fore legs. The top bar is then clamped and the distance between the bases of the two bars measured with a metre rule.

The accuracy of a similar instrument had already been analysed by Rae (1946) but a further trial was carried out. The sheep were taken in random order and two observers measured each sheep twice. As the differences between sheep as well as the errors of measurement are of interest, the analysis of variance was divided into its components (Fisher 1948). This analysis is shown in Table 1 with the method of arriving at the components. The standard errors of these components have not been calculated but it should be remembered that they are estimates and are therefore liable to error.

From Table 1 the coefficient of variation calculated from the error term is 2.04% and although rather a high proportion of the variance is attributable to error, there is no interaction and only a small percentage of variance is due to repeated measurements. When considered with other workers' results, it was decided to use this measurement. That this was justified is shown by results obtained in the field, a repeatability trial being carried out on ten lambs at the end of a day's measuring when unusual care would not be taken. The lambs were taken in random order for the second measurements after being measured normally with the remainder of the lambs. In this field trial 81% of the variance was attributable to

differences between lambs and only 1.6% to the repeated measurements. The standard deviation was 1.05 cms.

2. The depth of thorax.

For this measurement the height at withers instrument was used, the measurement being taken directly behind the fore-legs, the instrument being held vertical and the bars being against the upper and lower surfaces of the chest. An initial attempt using large calipers was found to be unsatisfactory when analysed by the method shown in Table 1. However the method with the height at withers instrument showed 81% of the variance attributable to sheep and 15% to repeated measurements. This latter high figure was not found in trials under the field conditions described above, when 88% of the variance was ascribed to differences amongst lambs and the component due to repeated measurements was negligible. The standard deviation in this last trial was 4.0 mms.

3. Conclusions.

Although methods of measurement were also developed for heart girth and head size, it was later found that they did not add sufficient information to justify their use. There were some difficulties (which were eventually overcome) with heart girth because of the length of the fleece. However results presented with the data collected at birth indicate that little additional information would have been added by its use.

Under the field conditions of the experiment only a few measurements could be taken with speed and sufficient accuracy and the height at withers and depth of chest fulfilled these requirements. The interpretation of these has been discussed in the review of literature.

B. The Plan for the 1952 Experiment.

1. General.

This first year's experiment was essentially a survey of possible differences between N-type and ordinary sheep with the main emphasis on the growth of the lambs. The lambs available for study came from matings already decided upon and techniques had to be adjusted to fit in as far as possible with normal farming routine. This was the result of the experiment being started at short notice and the necessity for the sheep to be run on a private farm. The sheep described in sections IV and V were also from the matings to be described, the ewe hoggets being kept after the finish of the experiment on lamb growth in January. The carcasses described were from ram lambs slaughtered at this time.

2. The matings.

These were intended for some other genetical research and for the maintenance of the N-type stocks, as well as for the growth experiment. It was decided to use all the sheep available, however, as the maximum number was required at this survey stage. The available ewes are classified by genotype in Table 2. In addition, homozygous N-type rams were available, but only two heterozygous rams, one of which was anomalous in that it was of the homozygous (NN) phenotype, but known from breeding results to be N+

It is possible from these available sheep to plan matings to compare lambs of different genotypes and also allow for possible effects of the dams' genotype, while at the same time ensuring that there will be sufficient lambs in each sub-class

Table 2
Ewes Available for All Experiments

Genotype	NN	N+	++
	34	43	76

Table 3
Matings and the Numbers of Lambs Expected

Mating number	I	II	III	IV	V
Ram genotype	NN (1)	NN (1)	N+(1)	N+(1)	N+(2)
Ewe genotype	34NN	18N+	25N+	26++	50++
Lambs NN	34	9	6	-	-
N+	-	9	12	13	25
++	-	-	6	13	25

Notes:

The same ram is used in groups I & II and groups III & IV.

The N+(2) ram is the one of homozygous phenotype.

The ewes in groups II & III differed in that the latter group were derived from ordinary ewes and the former from N-type ewes.

The ewes in groups IV & V were from one group divided at random.

The number of lambs is calculated on the assumption of 100% lambing.

for analysis. Such a mating scheme would not have allowed for the other purposes for which the matings were primarily intended, and the actual matings are shown in Table 3.

It can be seen that the lambs are classified in two ways, by their own genotype and by the mating from which they came. The ten possible sub-groups of lambs will therefore be referred to as the genotype-mating groups throughout this thesis. The scheme shown in Table 3 enables some of the comparisons described above to be made, but mating III in particular had sub-class numbers, which when sex and birth rank are allowed for, were liable to be of little use. It was clear that the analysis of such a plan was liable to be somewhat complicated and it was decided to analyse weights and measurements at given points in time rather than attempt analysis of actual growth curves. The practical planning of the taking of weights and measurements was therefore based on this approach; that is, if a difference occurs, then at what point in time can this difference be established as a real effect.

3. Practical details and husbandry.

The farm on which the sheep were run was an flat, undrained country in the Manawatu district and was normally used for the breeding and raising of fat lambs. The N-type ewes arrived on March 19 and were in generally poor condition.

The ordinary (++) ewes were cast-for-age hill country animals in good condition. Their previous history was unknown in detail, but they could be considered a sample of the New Zealand Romney ewe normally used for fat lamb production.

Table 4 shows the distribution of ages by mating groups; the ages of the ordinary animals were estimated from their

Table 4
Numbers of Ewes in Each Age Group

Mating group	I	II	III	IV	V
Age					
Over 6 years	3	nil	nil	18	32
6 yrs.	5	5	1	3	2
5 yrs.	4	1	14	3	6
4 yrs.	9	4	7	nil	5
3 yrs.	13	8	3	2	5
Totals	34	18	25	26	50

Table 5
Mean Weights of Ewe Groups during Pregnancy

Mob number	I		II		III
Ewe group	I	II	III	IV	V
May 19	117	116	136	142	141
June 19	116	115	148	153	149
July 15	132	129	149	154	144
Difference May - July	+14.6	+12.3	+13.0	+12.7	+2.8

teeth and are therefore only approximate, while those of the N-types were available from the records.

It is clear from Table 4 that the N-types had considerably more young animals in the mating groups (I,II and III) and that therefore the age of ewe should be considered if lambing percentages are to be compared.

On arrival at the farm, the mating groups were made up, the ewes for groups IV and V being allotted at random from the 76 ordinary ewes available. The ewes were then run with the appropriate rams which had been raddled so as to mark those ewes served.

The rams were taken out on May 19 and the ewes weighed and returned to the same paddocks. The weighing was repeated on June 19 when considerable paddock differences were apparent; this was counterbalanced by rearranging the ewes amongst the paddocks. They were weighed again on July 15 and all ewes allotted at random to one of the three paddocks, so that nutritional effects over the six weeks prior to lambing can be considered as random effects ^apart from those effects carried over from the previous poor condition of the N-type ewes. Wallace (1948) concluded that this last period was the most important in determining the effect of the ewe's nutrition on the lamb's birth weight and subsequent growth. The randomisation was based on the tables of Fisher and Yates (1949). No weights could be taken after this period due to the wet condition of the paddocks and yards. Those of the last weighing (July 15) were therefore used for any correction purposes. The weights on these three dates are given in Table 5.

The initial differences could be due to a number of causes which will not be considered further. Overall weight

gains were very similar for the two months from May to July except for Group V, but there were considerable differences in the absolute mean weight when the ewes were randomised. The possible effects of this are considered in the interpretation of the results.

During the last two months of pregnancy (July and August) the weather and paddocks were very wet, but from September to early December, when the weather is likely to affect lamb growth, it was generally fine and feed was plentiful.

The first lamb was born on August 11 and the procedure during lambing was as follows: a round was made every day by the author and an assistant and all new lambs were ear-tagged, weighed, and the height at withers and depth of chest and heart girth measured; the lamb was then classified for halo hairs according to the system of Dry (1955^{a,b}) and the ewe was caught, its ear tag read and the udder checked for milk.

The possibility of ewes exchanging lambs was considered and the lambs concerned in the one probable case were rejected from the experiment. An additional check on parentage occurred in the normal lambing rounds of the farmer. The last lamb used for the growth experiment was born on October 2 and there was thus a considerable spread of lambs' ages. Causes of death up to three weeks of age were estimated in the field or by veterinary examination but nothing unusual or consistent was found.

Weights and measurements were taken every three weeks from the birth of the first lamb, only those lambs over a week old being considered. A spring balance and tripod was used in the yards until the lambs were large enough to make the use of a weighing crate practicable. The effect of the lambs

being away from the mothers for different periods is assumed to be random amongst all groups. After the initial stages weights and measurements were taken at longer intervals and a timetable of all events is set out below. It was not possible to take lamb weights at shearing or within a few days owing to difficulties associated with the wet weather at the time. The body weights used to correct fleece weights are discussed in the relevant section. At the end of lambing the animals were randomised over the three paddocks by the simple expedient of leaving the gates between them open so that effectively they were in one paddock.

TIMETABLE

Date	Event
Mar. 19, 1952	Arrival of <u>N</u> -type ewes
Mar. 21	Rams joined with ewes
May 19	Rams removed, ewes weighed
June 19	Ewes weighed
July 15	Ewes weighed and randomised
Aug. 11	Start of lambing
Sept. 3	All lambs over week old weighed and measured
Sept. 24	Weighing
Oct. 15	Lambs weighed and measured
Nov. 5	Lambs weighed and measured
Dec. 8	Lambs weighed and measured
Dec. 30, 31	Ewes and lambs shorn. Greasy fleece weights taken Horns measured. Fleeces graded on 3-point scale.
Jan. 21, 1953	Lambs weighed and measured and marked for drafting.

Table 6

The Coverage Gradings

Reductions on:-	Withers	Shoulder	Shoulder Patch	Grade
	None	None	None	0
	None	None	Slight	1
	None	Slight	Medium	2
	None	Reduction continuous		3
	Slight	"	"	4
	Medium	"	"	5
	Large continuous reduction			6
	<u>N</u> -grade restricted to the back			7
	Grade VI			8

Note: Grade VI is included as animals of this grade are frequently found to be N+

C. Results from Gradings at Birth

1. The grading system.

The system of grading lambs for the abundance of halo-hairs on the back has been fully described by Dry (1955 a and b). In the first of these papers the grades I - VI are illustrated, these being the grades that were originally found in the ordinary Romney lamb. The maximum grade is called N-grade which appears as a complete mat of halo-hairs and lambs showing this grade can be considered to be homozygous or heterozygous for the N-gene.

A second system of grading was also used (Dry 1955b) which makes use of variations in the area over the body of the lamb which is covered with halo-hairs of N-grade abundance. The grading system which is based on that of Dry (1955b) is shown in Table 6.

The homozygous N-type lamb invariably has N-grade abundance of halo-hairs over its entire fleece-bearing area (Dry and Fraser 1947) while the heterozygote has a reduction from this abundance in a region behind the shoulder (the shoulder patch) which may extend over the shoulder and withers. Exceptions to this such as the N+ ram with no shoulder patch used in mating V are fully discussed by Dry (1955b). This grading system is therefore one of reductions from the complete coverage of halo-hairs of the NN phenotype and it is known as the coverage grading (Stephenson 1956)

2. Results.

(i) Genetic differences.

Table 7 shows all the lambs born, dead or alive, divided

Table 7
Number of Lambs Born

Group	I	II	III	IV	V	Total
Ewes	30 NN*	18 N+	25 N+	26 ++	50 ++	149
Sex	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	-
Lambs' NN	17 13	4 3	1 4	- -	- -	42
Pheno- N+	- 1	7 3	5 6	7 12	16 20	77
type ++	- -	- -	1 5	5 11	16 19	57
Totals	31	17	22	35	71	176
Deaths	7	4	4	3	3	21
Live lambs as % of ewes	93	72	80	123	136	108

* 4 ewes were removed during pregnancy for other experimental purposes.

The lamb of heterozygous phenotype included in Group I was at first thought to be anomalous but a check on the records indicated possible doubt as to the ewe parent's genotype.

according to their genotype*and the mating group of the ewe parent. The deaths up to three weeks of age include those lambs born dead.

Reasons for expecting some difference in the lambing percentage have already been given, but the marked contrast between N-type and ordinary ewes indicated the need for further investigation before the N-type animals could be considered for economic purposes.

There were no consistent causes of lamb deaths, but if all causes are included, then the death rate as a percentage of all lambs born was 15% for N-type lambs and 5% for ordinary lambs.

The numbers of lambs of the various genotypes expected in each mating on a hypothesis of a single dominant gene can be estimated from Table 7. In group II 8.5 lambs of each genotype would be expected and in Group III 5.5 of each of the homozygotes and 11.0 of the heterozygotes. It is clear from the table without further testing that there is no significant deviation from these expected numbers. The remaining matings should give equal numbers of heterozygous N-type lambs and ordinary lambs. Table 8 shows these results

* Some lambs in mating group V were of NN phenotype but they must have been heterozygotes from such a mating. These have been regarded as heterozygotes of coverage grade 0 throughout this thesis. The genetic problem is discussed elsewhere (Dry 1955b)

Table 8
Tests of the Ratios of N-type and
Ordinary Lambs

		Number of lambs			χ^2 (1 d.f.)	P
		N+	++	Total		
1952	Mating IV	19	16	35	0.257	0.5-0.7
	Mating V	36	35	71	0.014	0.9
	Mating 1	16	22	38	0.947	0.4
	Mating 2	23	14	37	2.189	0.1-0.2
	Heterogeneity Test (Mather 1949)					
	Source	d.f.		χ^2	P	
	Deviation	1		0.271	0.5 - 0.7	
	Heterogeneity	3		3.137	0.3 - 0.5	
	Total	4		3.408		

Note: 1953 mating 1 was the same as 1952 mating IV.
1953 mating 2 was an ordinary ram X N+ ewes.

Table 9
Tests of Sex Ratio of Lambs by Ram N+(1)

		Number of Lambs			χ^2 (1 d.f.)
		Male	Female	Total	
1952	Mating III	7	15	22	2.909
	Mating IV	12	23	35	3.457
1953	Mating 1	15	23	38	1.684
Totals		34	61		
Heterogeneity Test (Mather 1949)					
	Source	d.f.		χ^2	P
	Deviation	1		7.674	0.01 - 0.001
	Heterogeneity	2		0.377	0.8 - 0.9
	Total	3		8.051	

with the Chi square (χ^2) and the probability of a deviation from this expected result. The results from the matings made in 1953 have been included here for the purpose of the heterogeneity test. The methods used for testing were those of Mather (1949). The analysis shown in Table 8 indicates no reason to doubt that the rams concerned were not heterozygous for a dominant gene causing high halo-hair abundance. The second mating of 1953, that of an ordinary ram with N+ ewes had not been made before and the slight excess of N-type lambs is of interest. The χ^2 for heterogeneity between the two 1953 matings is 3.021 which has a probability of 0.1 - 0.05. This result should be treated with reserve with such small numbers of lambs but it suggests that further matings of this type would be of interest.

A further point of interest was a deficiency of male lambs in the offspring of the heterozygous ram of expected phenotype. This ram was used in both years and Table 9 summarises the numbers of each sex and the appropriate tests for deviations from the expected 1 : 1 ratio.

The test indicates that there was a real deficiency of ram lambs from ewes mated to this particular ram. The cause is not clear but was presumably the result of pre-natal mortality. The results of Rasmusson (1941) suggest that there is a higher pre-natal mortality of twin ram lambs than of other groups, but the data here were not sufficient to test this satisfactorily. No departure from the expected sex ratio was found in any of the other groups and it is therefore possible that this deficiency of males was genetic in origin.

Table 10
Birth Rank and Sex Effects on Halo-Hair Coverage

Grades (Table 6)	Males		Females		Total	
	0 - 3	4- 8	0- 3	4 - 8	0 - 3	4 - 8
Single lambs	6	7	2	11	8	18
Twin lambs	10	4	18	4	28	8
Totals	16	11	20	15	36	26
Analysis of Heterogeneity						
Source	d.f.	χ^2		P		
Birth rank	1	13.701		Less than 0.001		
Sex	1	2.809		0.1		
Total	2	16.510				

(ii) Variations within genotypes.

The variation in coverage of heterozygous lambs has been described in the section on the grading system. Some of this variation could possibly be explained by differences in pre-natal environment which would be expected to show as differences between single and twin lambs. In Table 10 the heterozygous lambs alive at birth (dead lambs were not always graded in detail) have been classified by sex, birth rank and by high or low halo coverage. The χ^2 analysis for heterogeneity between coverage classification shows a marked difference for birth rank but not for sex. This difference is the result of the greater coverage of the twin lambs which shows that there is some effect of pre-natal environment on halo-hair abundance. This will be further discussed in Part II of this thesis where results on halo-hair density at birth are presented.

The final point to be mentioned here, which confirms results from larger numbers of lambs (Dry 1955b), concerns the ordinary Romney lambs from these matings. These have a higher average halo-hair grading (2.5) than those of a sample from ordinary flocks (1.66; Dry 1955b). It will be shown in Part II that such a difference represents an increase of only five halo-hairs in a square centimetre of skin, in a total of 2.500 other fibres. It is not therefore likely to be of importance to the assumption that these animals are, for birthcoat type, ordinary New Zealand Romney lambs.

D. Methods of Analysis of the Growth Data

1. Review and problems.

The problem was one of differentiating between the growth, measured in terms of weight and selected body measurements, of the ten groups of sheep. Each group was divided into four sub-groups, male singles and twins and female singles and twins, twins reared as singles being treated as if they were singles (Hammond 1932). To treat the problem as one of regression as suggested by Brody (1945) was unsatisfactory as any differences might be the result of the irregular growth of one or more groups over certain periods, and if so, the identification of these periods was of major interest. Also Medewar (1950) points out that average growth curves can be different in form from the individual growth curves of which they are made up, particularly if there are abrupt changes which occur at different ages for different individuals. Sholl (1950) indicates various dangers in applying statistical methods to constants obtained from growth formulae, while Yates (1950) at the same symposium also discussed dangers of spurious regularity resulting from the fitting of growth curves.

Further problems to be considered were disproportion in the sub-class numbers, the relationships of weights and body measurements and the necessity for corrections for different birth dates and other variables, all of which pose problems when a method of comparing regressions is used.

The method used, therefore, has been the consideration of weights and measurements at certain points in time, it

being assumed that if a difference was found at, say, the fourth point, but not the third then this was the result of differences of growth during the intervening period. In cases where groups differed at both these points, the second difference may merely be the result of the first and the weight or measurement was therefore corrected for the corresponding previous one. It can be shown (Appendix I) that correction of weight gains over the period for the initial weight would give an identical result. The birth date (coded from August 1) was used as an independent variable throughout and can be interpreted as an environmental correction confounded with one for age.

The problem then, was to develop a suitable computational method for use with a number of variance and covariance analyses with unequal sub-class numbers and at the same time obtain estimates of the genotype-mating group effects (see page 35 and Table 3) and sex-birth rank effects, as a two way classification.

2. Statistical and computational methods.

The final computational method was not arrived at directly and the first analysis carried out was that of the estimated weight of the lambs at 30 days of age. The method was modified for the subsequent analyses of birth weight and of the actual weights at the later weighing times.

Both methods of analysis are computational variations of the solution of sets of equations set up under the general linear hypothesis (Kempthorne 1952).

For the analyses of variance the following model was considered:

$$y_{rij} = \mu + g_r + s_i + e_{rij}$$

where y_{rij} = the individual observations
 μ = the general mean
 g_r = the genotype - mating group effect
 s_i = the sex - birth rank effect
 and r is 1 - 10 and i is from 1 - 4
 e_{rij} is the error term.

The necessary assumptions are:

- (1) That the g and s effects are additive
- (2) That the errors are independent and normally distributed with zero mean and constant variance.

Because of this first assumption it is necessary to test for interaction between the g and s effects before they can be tested for significance. If interaction was present then the results for single and twin lambs were analysed separately and if the first assumption still did not hold, then a simple orthogonal analysis was carried out for each sex and birth rank.

The four sex - birth rank classes for the values of 1 were:

1. Ram singles
2. Ewe singles
3. Ram twins
4. Ewe twins

The methods of computation described below were used for all cases where a linear model has been set up including those cases where different or additional effects have been estimated.

The first computational method used was due to A. Carter (Personal communication) and was used to analyse the weights at 30 days of age. This method has been shown by Rae (Personal communication) to be a computational variation of the direct solution of the above model.

The system is as follows:

The symbols of the above model are used with, in addition n_{ri} being the number observations in the r th class. The notation for summation is that used by Kempthorne (1952) e.g. $y_{r..}$ indicates the values of y summed over i and j .

A system of tabulation is followed:

Table I gives values of n_{ri} and $\bar{y}_{ri}$.

Table II gives values of $w_{ik}^{(r)} = n_{ri} \cdot n_{rk} / n_{r..}$

$$\text{and } \sum_r w_{ik}^{(r)} = W_{ik}$$

Table III gives values of $d_{ik}^{(r)} = \bar{y}_{ri} - \bar{y}_{rk}$.

$$\text{Also } Y_i = \sum_{k \neq i} D_{ik} \text{ where } D_{ik} = \sum_r w_{ik}^{(r)} d_{ik}^{(r)}$$

A check on computation at this point is $\sum_i Y_i = 0$ and $\sum_k W_{ik} = n_{.i}$.

Then if $W_{i0} = \sum_{k \neq i} W_{ik}$ then a matrix can be formed with the W_{i0}

as the leading terms and the W_{ik} forming the remaining terms ($i \neq k$) these being negative.

If the inverse of this matrix is v_{ij} then:

$$\hat{c}_g = \sum_h v_{gh} Y_h \text{ are unbiased estimates of the effects of the } s_1$$

Residual sums of squares (S_2) are then calculated as

$$S_2 = \sum_r \sum_i \sum_j y_{rij}^2 - \sum_r n_r \cdot \bar{y}_r^2 - \sum_h \hat{c}_h Y_h$$

these having $(N - r - 1 + 1)$ degrees of freedom

i.e. $N - (r-1) - (1-1) - 1$.

The second sums of squares required (S_1) is within the sub-sub-classes:

$$\sum_r \sum_i \sum_j y_{rij}^2 - \sum_{ri} n_{ri} \bar{y}_{ri}^2 \text{ with } r1 - 1 \text{ d.f.}$$

The test for interaction is now $(S_2 - S_1)/S_1$ expressed as the appropriate mean squares.

If interaction is not present, then ignoring the first factor, a residual sum of squares S_A is calculated and then the second effect is tested as $(S_A - S_2)/S_2$ in the form of the appropriate mean squares.

These are the usual tests based on the likelihood ratio and will have the F distribution, for the appropriate number of degrees of freedom.

The covariance analysis for this method follows directly by the use of residual sums of squares after the appropriate sums of squares due to the required regression(s) have been subtracted. These residuals are as follows:

(1) Within sub-sub classes (S'_1) obtained in the usual way from the total sums of squares and cross products and those between the sub-sub classes.

(2) Within main classes (S'_2) by subtraction of the sums of

squares and cross products between main classes from the totals. The sums of squares between main classes are those obtained by the method above, being calculated for each independent variable; while the cross products are derived from the appropriate c_g times the Y_h of the corresponding variate.

The tests are then the same as for analysis of variance with these alternative residual sums of squares from the regression analyses being used. If no interaction is present then the residuals for the various effects are obtained in the similar manner. The degrees of freedom will be one less for each independent variate corrected for and the F test is used to test the ratios of mean squares.

This method was not found to be the quickest for computational purposes or the most convenient for obtaining some of the estimates of genotype-mating group effects which were required. The method used for the analysis of all the data apart from the weight at 30 days was therefore modified as follows.

Equations of the linear model for estimation of genotype-mating group and sex - birth rank effects were set up and solved for each variable. These estimates were subject to the usual assumptions and the calculations were arranged so that in the case of interaction then the appropriate sums of squares for analysis by the separate groups were available. As the sub-class numbers were the same throughout one inverse matrix of these could be used for the solution of the equations for all analyses involving this model.

From these estimates sums of squares for the analyses of variance could be obtained in the usual way and the covariance analyses made in the way described for the method above. The cross-products required for these covariance analyses from which the residual sums of squares were obtained were calculated from the estimated constant multiplied by the corresponding total of the required independent variable. It can be shown by direct algebraic manipulation that this gives the same result as the method above and as the result obtained by including the required regression coefficients in the original linear model. Such a method as this has the advantage of giving estimates of all the variables after which analyses of covariance can be carried out on any combination of them which seems desirable.

Where interaction occurred and single and twin lambs were considered separately, the resulting analysis involves a matrix of sub-class numbers of the order 2×10 . In this case when the same matrix of sub-class numbers is to be used for many variables a simple computational method is available to solve for the various effects.

The solutions are obtained by simple algebra from the setting up of the equations and are as follows: (notation as above)

$$\text{Where } W = n_{11}n_{12}/n_{1.} + n_{21}n_{22}/n_{2.} + \&c$$

$$D = \cancel{E}n_{12}\bar{y}_{1.} - y_{.2}$$

$$\text{then } \hat{s} = D/2W \quad (\hat{s}_1 = -\hat{s}_2)$$

$$\text{Where } a_r = (n_{r1} - n_{r2})/n_{r.}$$

$$\text{then } (g_r + \mu) = y_{r.} - a_r \hat{s}$$

W and a will be the same for all variables so these forms lead to a simple computational procedure for large scale computational purposes.

If, in any analysis, a difference is indicated amongst the genotype-mating groups, it is of interest to find which of these groups are likely to differ. It should be remembered that in such a case there will be $9 + 8 + 7 + \dots + 1$ possible comparisons and therefore one or differences at the 5% level amongst these will be expected by chance.

Where covariance analysis was used the regressions corresponding to the S_2 residual (within sub-sub classes) were used to correct the weighted means. The differences between these means were then examined with the above problem in mind.

This problem and that of deciding which groups differ has been discussed by Tukey (1949). The standard errors of individual estimates can be used as a guide in the present case but considerable computation is required for their estimation where a 14×14 inverse matrix is involved. This would not be worth while unless an exact method of comparing the individual estimates was available.

The approach has therefore been to consider the genotype-mating group estimates empirically, bearing in mind the standard deviation from the residual error variance and the sub-class number involved. A second series of analyses has then been carried out ignoring the mating groups and with the classifications of lambs' genotypes and sex - birth rank only. This then helps to confirm analytically the results deduced for the genotype-mating group analysis.

Table 11
Partial Regressions of Birth
Weight

	On Birth Date	On Ewes' Weight
Partial regression	+0.037	- 0.00163
Standard error	0.014	0.00974
t 97 d.f.	2.64	Less than 1
P.	0.01	Non-significant

Table 12
Numbers in the Sub-classes and Mean Birth Weights

Genotype		♂ singles		♀ singles		♂ twins		♀ twins	
Dam	Lamb	n	$\bar{y}$	n	$\bar{y}$	n	$\bar{y}$	n	$\bar{y}$
NN	NN	6	11.6	6	11.2	6	9.4	7	9.3
NN	N+	-	-	4	10.6	2	11.0	2	7.6
N+	N+	7	10.7	6	9.9	3	9.2	2	7.4
N+	++	1	10.7	2	9.3	-	-	3	8.7
++	N+	9	11.3	9	11.0	12	9.5	20	9.1
++	++	6	12.1	7	11.3	13	10.0	19	9.3

The means are in pounds weight.

Table 13
Analysis of Variance of Interaction

Source		d.f.	Sums of squares	m.s.	F
Total	T	151	15,654.83		
Fitted constants	S ₁	7	15,430.82		
Sub-sub-classes	S ₂	23	15,442.55		
Interaction	S ₂ - S ₁	16	11.73	0.733	{less than 1
Residual	T - S ₂	128	212.28		

Table 14
Analysis of Variance of the Sub-groups

Source		d.f.	Sums of squares	m.s.	F
Total	T	151	15,654.83		
Fitted constants	S ₁	7	15,430.82		
Fitting D & S	S _g	5	15,425.21		
Fitting G & S	S _d	5	15,418.41		
Lambs' genotype	S ₁ - S _g	2	5.62	2.806	1.80
Dams' genotype	S ₁ - S _d	2	12.41	6.205	3.99
Residual	T - S ₁	144	224.01	1.556	

F values. 2 & 144 d.f. P = 0.1 is 2.35
P = 0.05 is 3.07

D stands for dams' genotype, G for lambs' genotype, and
S for sex - birth rank.

E. The Results from the Analyses of the Growth Data

1. Data collected at birth.

(i) Birth weight.

As the analysis of the 30 days weight had been carried out before the analysis of birth weight, and as this latter had been used with the ewes' weight and lambs' birth date to calculate inter-relationships, the values of these relationships were used in order to decide the analysis method.

The partial regressions of ewes' weight and of birth date within the genotype-mating groups and sex - birth rank groups are shown in Table 11. There is no effect of the weight of the ewe and re-calculation omitting this variate gave a significant value for the simple regression of birth weight on birth date. This showed that on average for each day later that a lamb was born, the weight increased by 0.029 pounds. As the maximum difference between groups in birth date was only 10 days it was decided to carry out an analysis of variance only and to allow for this small difference in the interpretation of the estimated means.

The analysis of variance was based on a linear model to estimate effects due to genotype of lamb, genotype of dam and sex - birth rank. This classification with the mean weights and number of lambs is shown in Table 12. The analysis of variance to test interaction is shown in Table 13 where it can be seen that it is not significant and therefore the analysis was continued on the assumption that the sub-classification effects were additive.

Estimation of the weighted means and the resulting

Table 15

Estimated Mean Birth Weights and Dates by Lamb and Dam Genotype

Genotype dam	NN	N+	N+	N+	++	++
Genotype lamb	NN	NN	N+	++	N+	++
Mean weight	10.38	10.08	9.30	9.61	10.28	10.59
Mean birth date	25.2	25.4	29.5	28.0	34.6	35.3

Table 16

Estimated Mean Birth Weights by Lambs' Genotype and Mating Group

Mating Group	I	II	III	IV	V
Lambs' Genotype					
NN	10.38	10.70	9.03	-	-
N+	-	9.17	9.55	9.97	10.43
++	-	-	9.41	10.51	10.64

From Table 14 the standard deviation (s.d.) is 1.245

sums of squares gave the analysis of variance shown in Table 14. The additional calculation to test the sex - birth rank effects was not considered worthwhile as the interaction test had shown that these were the same for all groups. It can be seen from this analysis that there is no effect associated with genotype of lamb but that there is a significant effect associated with genotype of the dam. The estimated mean weights under the classification of dam and lamb genotype are shown in Table 15 with the mean birth date of the group. The significant result appears to be due to the lighter birth weights of those lambs from N+ mothers and this difference is not accounted for by the different birth dates. It is possible that the homozygous lambs were heavier and that this has counteracted a general effect of the poorer condition of the N-type ewes. This, however, is not supported by the absence of a relationship between ewes' weight and birth weight or by the absence of a significant lambs' genotype effect.

To obtain further information on the significant differences amongst dams a model involving the classifications of genotype - mating groups and sex - birth rank groups was solved. A significant difference amongst the genotype - mating groups was shown by the analysis of variance and the estimated mean weights from the analysis are shown in Table 16. There was no interaction but this and other analyses are not presented as all the numerous analyses of variance follow the same form and it would not be economic to present them in full.

Table 16 shows a similar picture to that obtained from the first analysis, i.e. the only consistent difference is

Table 17.

Analysis of Differences amongst Groups of the Regressions
of Birth Weight on Body Measurements

Leg Length	Source	d.f.	Mean Square	F
	Pooled regressions	10	9.987	5.36
	Differences	9	2.975	1.60
	Residual	132	1.864	
Depth of thorax	Pooled regressions	10	17.661	13.77
	Differences	9	1.026	Less than 1
	Residual	132	1.283	

For 10 and 132 degrees of freedom the F value at the 0.001 level is 3.3

For 9 and 132 degrees of freedom the F value at the 0.1 level is 1.66

The measurements are in centimetres, the weights in pounds.

that of lower birth weights of lambs from mating group III which was made up of N+ ewes. Further experiments using ewes of different genotypes, which have been reared and grazed together, are required to interpret this result which could have arisen from the different treatments of the ewes prior to this experiment.

(ii) Body measurements.

For this analysis an estimate of 'leglength' was obtained by subtraction of the depth of thorax from the height at withers and the values obtained were then analysed by a similar classification to that in Table 12. The depth of thorax was also analysed in this way and neither measurement showed an effect of interaction, genotype of lamb or of the genotype of the dam.

As differences between the genotype - mating groups were shown for birth weight, it is of interest to know if the relationships of this weight to the measurements are the same for these groups. An analysis of differences amongst the simple regressions of birth weight on each of these two measurements was therefore carried out and is shown in Table 17. The method is that given by Mather (1949). No differences are shown amongst the regressions on either measurement and it was concluded that the relationships with birth weight were similar in all genotype - mating groups, it being remembered that this type of test is not very sensitive.

A separate analysis for the sex - birth rank groups gave a similar result there being no difference in the regressions amongst these groups for either measurement.

Table 18.

Partial Regression Coefficients of Weight
on Certain Measurements

Body Measurement	Heart Girth	Leg Length	Depth of Thorax
Coefficient	+0.245	+0.104	+0.485
Standard error	0.00127	0.00159	. 0.00954

All measurements were in centimetres.

Analysis of Variance

Source	d.f.	Mean Square	F
Due to regressions	3	81.130	96.03
Residual	148	0.847	

For 3 and 148 d.f. the F value at 0.001 level is 5.79

Table 19.

Reductions of Sums of Squares due to
Individual Partial Regression Coefficients

Measurement	Heart Girth	Leg Length	Depth of Thorax
Reduction	43.442	6.315	22.644

In the review of literature and in the account of the preliminary investigation, it was suggested that if body weight was used to measure growth, then the most informative body measurements would be those that were least associated with weight. Three measurements taken at birth, have been examined for their association with birth weight by means of a multiple regression on them of birth weight. This was calculated over all lambs ignoring the sub-groups and the results are shown in Table 18 with an analysis of the variance accounted for by the regressions. Fisher (1948) gives a method whereby the reduction in sum of squares due to a partial regression coefficient can be calculated from the value of the coefficient and the leading terms of the inverse of the variance - covariance matrix. The reductions calculated in this way are shown in Table 19.

If the most informative body measurement is one which reflects body weight the least, then in statistical terms it is the one which accounts for the least variance of body weight. On this criterion leg length is the most satisfactory, then presumably, height at withers, and then depth of chest, with heart girth as the least satisfactory.

Summary of section E.1.

The analysis of birth weight showed no differences resulting from the genotype of the lamb.

A lower birth weight was found in lambs from heterozygous ewes but further experiments are required to explain this.

No differences amongst any groups were found for body measurements or in the relationships of these measurements to body weight.

Table 20

The Number of Lambs in each Sub-class.

Mating Group	Lambs' Genotype	♂ Singles	♀ Singles	♂ Twins	♀ Twins	Total
I	NN	5	8	5	5	23
II	NN	-	3	1	-	4
	N+	4	3	1	-	8
III	NN	-	1	-	2	3
	N+	2	3	2	1	8
	++	1	2	-	3	6
IV	N+	4	5	2	6	17
	++	1	5	2	6	14
V	N+	6	6	6	11	29
	++	3	5	10	9	27
Totals		26	41	29	43	139

Table 21

Analysis of Variance of the Weight at 30 days.

Source	d.f.	m.s.	F
Interaction	27	7.359	Less than 1
Sub-classes residual	99	10.544	
Genotype - mating groups	9	28.125	2.85
Sex - birth rank	3	360.979	36.60
Fitted constants residual	126	9.862	
F values. 9 & 126 d.f. for P = 0.01 is 2.65. For P = 0.001 is 3.42			
3 & 126 d.f. for P = 0.01 is 3.95. For P = 0.001 is 5.79			

Table 22

Estimated Mean Weights of Genotype - Mating Groups at 30 days of Age.

Mating Group	I	II	III	IV	V
Lambs' Genotype					
NN	21.76	20.00*	20.37*	-	-
N+	-	21.72	24.08	23.05	23.21
++	-	-	23.23	23.74	26.17

s.d. 3.140

* indicates groups with less than 5 lambs

2. The lambs' weight at 30 days of age.

The methods for the analysis of this weight have already been described (p.46). The liveweight was estimated for each lamb by proportion from the weighings before and after it was 30 days old.

The classifications and the numbers in each sub-class for this and for subsequent analyses are shown in Table 20, while Table 21 gives the analysis of variance. This gives no evidence of interaction but does show significant differences amongst genotype - mating groups and amongst sex - birth rank groups. The latter is to be expected as twin and female lambs are usually the lighter. The estimates for the weighted means of the former are shown in Table 22 and show a trend in favour of ordinary lambs.

To decide which variables to use for an analysis of covariance to compare these groups on a uniform basis, multiple regression coefficients on ewes' weight, lambs' birth date and birth weight were calculated within the genotype - mating and sex - birth rank groups. These are shown in Table 23 and as there is no significant relationship for ewes' weight it was rejected, and an analysis of covariance carried out for the other two variables. Table 24 shows the analysis of the residuals after allowance for the regressions and again there are significant genotype - mating group effects. These effects, shown in Table 25 show similar relationships to those of the uncorrected weights. These corrected values are the same as gains in weight corrected to the same initial weight, with a constant term added (Appendix I) In addition they are corrected to the same mean birth date.

Table 23

Partial Regressions of Weight at 30 Days of Age

	On Birth Date	On Ewes' Weight	On Birth Weight
Regression	+ 0.0836	+0.0131	+ 1.333
Standard error	0.0235	0.0157	0.164
t 96 d.f.	3.56	less than 1	8.14
P	0.001	Non-significant	0.001

Table 24

Analysis of the Covariance Residuals of 30 Days' Weight

Source	d.f.	m.s.	F
Interaction	27	2.823	{Less than 1
Sub-class residual	97	5.244	
Sex - birth rank	3	129.699	27.50
Genotype - mating groups	9	18.292	3.88
Constants residual	124	4.717	

F. values. 3 & 124 d.f. P = 0.001 is 5.79
 9 & 124 d.f. P = 0.001 is 3.42

Table 25

Estimated Mean Values of 30 days' Weight Corrected for Birth Weight and Birth Date

Mating group	I	II	II	IV	V
Lambs' genotype					
NN	22.28	20.06*	21.89*	-	-
N+	-	22.81	24.76	23.13	22.81
++	-	-	23.81	23.68	25.14

From Table 24 s.d. = 2.172

* indicates groups with less than 5 lambs.

Therefore, bearing in mind those groups where the number of lambs is small, it is possible from Tables 22 and 25, to compare mating groups for a particular lambs' genotype and lambs' genotype for a particular mating group, both for actual weights and for weight gains from a constant initial weight. The only consistent differences are in both cases those of ordinary lambs being heavier than N+ lambs which in turn are heavier than NN lambs. The same is true for weight gains and as, in addition, there were no detectable differences of birth weight, it can be concluded that N is in some way detrimental to lambs' growth over the first few weeks of life. This statement is, of course, only true for the particular environmental conditions prevailing over the time these weights were taken. As there were no interactions it can also be concluded that these effects were proportional for single and twin lambs of both sexes.

Summary of E.2.

Ordinary lambs showed greater weight gains than N-type lambs over the first 30 days from birth.

N+ lambs showed greater weight gains than NN lambs.

These effects were proportional in the sex - birth rank groups.

3. Live weight and body measurements at 67, 100 and 144 days of age.

(1) Differences between genotypes within the mating groups.

This section contains the results of analyses made of the genotype - mating groups and the methods used are those given in Section D.2.

The mean age of the animals, which differed for singles and

Table 26

The Mean Ages of the Lambs at the Different Times of Analysis

Number of analysis	1	2	3	4	5
Age in days	0	30	67	100	144
Age in weeks	0	4.0	9.5	14.0	20.5

Table 27

The Covariance Analyses made in Section 3

Dependent variable	Independent Variables
Body weight	Birth date
	Birth date and previous body weight
	Birth date and height at withers
Height at withers	Birth date
	Birth date and previous height at withers

Table 28
Tests of Interaction

I. Body Weight

Independent Variables	Interaction Mean Square	Residual Mean Square	F
30 days			
B. date and Ht. at Withers	<1	>1	<1
67 days			
Birth date	65.572	24.895	2.63**
B. date & previous Wt.	7.216	7.038	1.03
B. date & Ht. at W.	11.218	20.237	<1
100 days			
Birth date	92.117	42.586	2.16**
B.date & Prev. Wt.	11.317	7.868	1.44
B. date & Ht. at W.	18.967	32.553	<1
144 days			
Birth date	129.936	51.565	2.52**
B.date & Prev.Wt.	11.941	15.413	<1
B.date & Ht. at W.	31.251	42.440	<1

II. Height at Withers

30 days			
Birth date	32.101	4.885	6.57***
67 days			
Birth date	42.625	4.565	9.34***
B. date and Prev.Ht. at W.	10.376	3.174	3.27***
100 days			
Birth date	55.012	3.363	16.36***
B.date & Prev.Ht. at W.	2.33	2.23	1.04
144 days			
Birth date	52.240	3.591	14.55***
B. date & prev. Ht. at W.	8.359	1.806	4.63***

Degrees of freedom:

1 independent variate	27	97
2 independent variates	27	96

Values of F for various probability levels:

P	F	
0.2	1.29	
0.05	1.65	*
0.01	2.04	**
0.001	2.54	***

twins by only 0.6 of a day, is shown in Table 26 according to the five points in time at which they were analysed. The last three of these correspond to the last three weighing dates of the lambs shown in the time-table of events. It is to these mean ages that all lambs' weights and measurements, including those cases where singles and twins have been analysed separately, have been corrected by the appropriate regression on birth date.

The analyses are based on the classification which has been presented with sub-class numbers in Table 20, except that one ewe twin lamb reared as a single, from mating group I, died.

Body weight and height at withers have been analysed at the last three points in time and in addition height at withers has been analysed at 30 days of age. The various covariance analyses made in this section are shown in Table 27.

(a) Tests of interaction.

The results of these tests have been summarised in Table 28 which shows the mean squares and the values of F for all the analyses in this section. For the body weights, interaction is shown at each time of analysis but the interaction disappears when corrections are made for the previous weight or for the height at withers. The reasons for the interactions will be discussed later when further tests involving lambs' genotype only, have been made. The height at withers results all show interaction except for the corrected gain from 67 to 100 days.

As the differences in weight at constant age were to be examined first and as these showed interaction, it was decided to analyse all the results in this section for single lambs and

Table 29.
Tests of the Genotype - Mating Group
Effects for Single Lambs

I. Body Weight

Independent Variables	Effects Mean Square	Residual Mean Square	F
30 days			
B. date and Ht. at withers	29.386	5.711	5.14***
67 days			
Birth date	75.110	26.761	2.81**
B. date & Prev. Wt.	20.443	9.245	2.21*
B. date & Ht. at W.	79.239	19.319	4.10***
100 days			
Birth date	129.183	43.954	2.94**
B. date & Prev. Wt.	9.379	9.719	<1.0
B. date & Ht. at W.	169.823	28.183	6.02***
144 days			
Birth date	140.872	56.125	2.51*
B. date & Prev. Wt.	35.512	14.709	2.41*
B. date & Ht. at W.	164.079	40.012	4.10***

II. Height at Withers

30 days			
Birth date	4.461	6.442	<1.0
67 days			
Birth date	2.325	4.748	<1.0
B. date & Prev. Ht. at W.	3.010	3.831	<1.0
100 days			
Birth date	4.021	3.512	1.14
B. date & prev. Ht. at W.	4.626	2.707	1.71
144 days			
Birth date	5.856	3.943	1.49
B. date & Prev. Ht. at W.	3.360	1.728	1.94

Degrees of freedom:

1 independent variate	9	54
2 independent variates	9	53

Values of F for various probability levels:

P	F	
0.2	1.41	
0.05	2.00	*
0.01	2.66	**
0.001	3.64	***

twin lambs separately. This then leads to a simpler interpretation where ten genotype mating groups are concerned.

No interactions were found, on analysis, between sex and the genotype - mating groups for any of the analyses of singles and twins in this section. The estimates and results of analyses for the two birth rank groups will now, therefore, be considered.

(b) Single lambs.

The method used for analysis was that described in Section D for the case when there are only two groups in one of the classifications. The results of the covariance analyses of the genotype - mating group effects are shown in Table 29.

It can be seen that the differences in weight amongst these groups persisted until 144 days. Differences in corrected gain were also present from 30 - 67 days and from 100 - 144 days. There were no differences in the height at withers except possibly in gains from 100 - 144 days, while the highly significant differences for weight at constant height at withers suggest that growth differences were not ones of skeletal size. In general terms this could mean that the groups showing lower weights were not smaller animals, but either had longer legs for their weight or a lower proportion of fat or muscle to the skeleton. In any case the results presented in the review of literature would suggest that animals with a lower weight for a given height at withers were likely to produce a less desirable carcass.

Before studying the individual differences amongst the genotype - mating groups, it is of interest to see the values of the regression coefficients within the estimated groups at the different points in time. The values for the twin lambs will also be given for comparative purposes and the coefficients

Table 30
Regression Coefficients within Genotype - Mating Groups and Sex, for Single and Twin Lambs

The standard errors are given in parenthesis.

		Mean Age at Analysis		
		67 days	100 days	144 days
Dependent Variate				
Body weight				
Independent Variate(s)*				
<u>Birth date</u>	singles	-0.37 (0.06)	-0.30 (0.08)	-0.20 (0.09)
	twins	-0.47 (0.05)	-0.46 (0.07)	-0.40 (0.08)
Birth date & <u>prev.wt.</u>	singles	+1.29 (0.13)	+1.13 (0.08)	+0.97 (0.08)
	twins	+1.59 (0.10)	+1.17 (0.07)	+0.93 (0.07)
Birth date & <u>Ht. at withers</u>	singles	+1.28 (0.27)	+2.15 (0.39)	+2.06 (0.43)
	twins	+0.82 (0.26)	+1.52 (0.37)	+1.47 (0.42)
Dependent Variate				
Height at withers				
Independent Variate(s)*				
<u>Birth date</u>	singles	-0.08 (0.03)	+0.08 (0.02)	+0.06 (0.02)
	twins	-0.10 (0.03)	-0.10 (0.02)	-0.04 (0.02)
B.date & <u>prev. Ht. at withers</u>	singles	+0.39 (0.10)	+0.42 (0.10)	+0.80 (0.10)
	twins	+0.72 (0.09)	+0.49 (0.09)	+0.68 (0.08)

*Where there is more than one independent variable the coefficients are partial regression ones
 All the coefficients are significantly different from zero. /for the variates underlined.
 The standard errors are based on 53 or 54 degrees of freedom.

with the standard errors are shown in Table 30. All the values given are significantly different from zero by the t test (Fisher 1948).

The regression values for weight on birth date reflect the age of the animal and environmental effects associated with the time the lamb was born. They show a decrease with increased mean weight of the lambs, while the standard errors increase. This reflects the lessening importance of age and time of birth as the animals become older. At all weighing times twin lambs show a greater effect than single lambs.

Those regressions correcting height at withers for birth date show that at the mean ages of 100 days and 144 days, later born single lambs had a slightly greater height at withers, while later born twin lambs had slightly less height. The reason for this is not clear and requires a more detailed experiment, planned with this point in mind. However the effect is a very small one and would have little real importance except over a large range of birth dates.

The partial regression coefficients for weight on previous weight at constant age, are a measure of the weight gain in relation to the initial weight. They showed a steady decrease as the animals became older. Twins showed a greater gain of both weight and height at withers from 30 to 67 days, which was not unexpected as there was a tendency for twins to approach the size of single lambs as they became older.

The regressions showing the correction for weight at constant size indicate that an increase of size led to a greater increase of weight for single lambs than for twin lambs. This could be the result of weight increases with

Table 31
Estimates of Mean Body Weight at Constant Birth Date

Lamb Genotype	Mating Group	Mean Age at Time of Estimation		
		67 Days	100 Days	144 Days
NN	I	48.8	61.9	69.3
	II	41.7	52.0	68.2
	III*	47.1	60.3	71.5
N+	II	49.2	62.1	71.5
	III	52.4	64.6	70.7
	IV	52.2	66.5	73.5
	V	50.1	64.3	71.6
++	III	54.5	71.5	83.8
	IV	54.7	70.5	81.3
	V	55.7	69.0	78.4

* One lamb only in this group.
The weights are in pounds.

Table 32
The Genotype - Mating Group Estimates Corrected for
Birth Date and Previous Weight

Lamb Genotype	Mating Group	Mean Age at Time of Estimation		
		67 Days	100 Days	144 Days
NN	I	50.2	No differences shown by analysis	71.7
	II	44.9		80.2
	III*	50.1		75.4
N+	II	50.1		73.6
	III	50.7		70.3
	IV	51.9		71.3
	V	50.4		71.6
++	III	54.1		76.7
	IV	52.9		75.2
	V	51.0		73.9

* One lamb only.

only small increases in size being an indication that the lamb had reached the fattening or 'finishing' stage. If this is so then twin lambs reach this stage of laying down primarily fat and muscle later than do single lambs.

The regressions can be used to correct the estimates of the genotype - mating group effects obtained from the original equations. These corrected estimates are the same as those which would be obtained if the regression values had been included in these equations. The estimates of mean body weights corrected for birth date are shown in Table 31. Examination of this table shows no consistent mating group differences except for the greater weights in group III than in group II. This would mean that lambs from N+ ewes themselves derived by outcrossing, grew better than those from N+ ewes derived from the N-type stock. This is, however, confounded with ram differences and, in addition, there is only one NN lamb in mating group III.

At 67 days it seems that ++ lambs are heavier than N+ lambs which are in turn heavier than the NN lambs. By 144 days the difference is mainly between the ordinary lambs and the N-type lambs of both genotypes, this difference being of the order of 10 pounds.

Table 32 shows the estimates in Table 31 corrected for the weight at the previous mean age. Those for 100 days have been omitted as no differences were shown by the analysis (Table 29). The mean weights shown here can be interpreted as gains corrected to constant weight at the start of the period. They can be expressed as such by subtraction of the overall mean weight at this time (Appendix I) but the differences between groups would still be the same and it is in these that the interest lies.

Table 33

Genotype - Mating Group Estimates Corrected for Birth
Date and Height at Withers

Lamb Genotype	Mating Group	Mean Age at Analysis			
		30 days	67 days	100 days	144 days
NN	I	27.6	48.0	60.2	66.8
	II	25.4	42.3	51.2	68.6
	III*	27.8	47.2	62.3	69.6
N+	II	28.3	48.3	59.3	70.9
	III	30.6	53.0	66.5	72.3
	IV	30.8	51.2	68.9	76.4
	V	29.6	50.7	63.9	73.8
++	III	29.7	55.9	71.1	81.6
	IV	31.1	54.3	71.1	80.9
	V	33.8	55.4	68.3	79.2

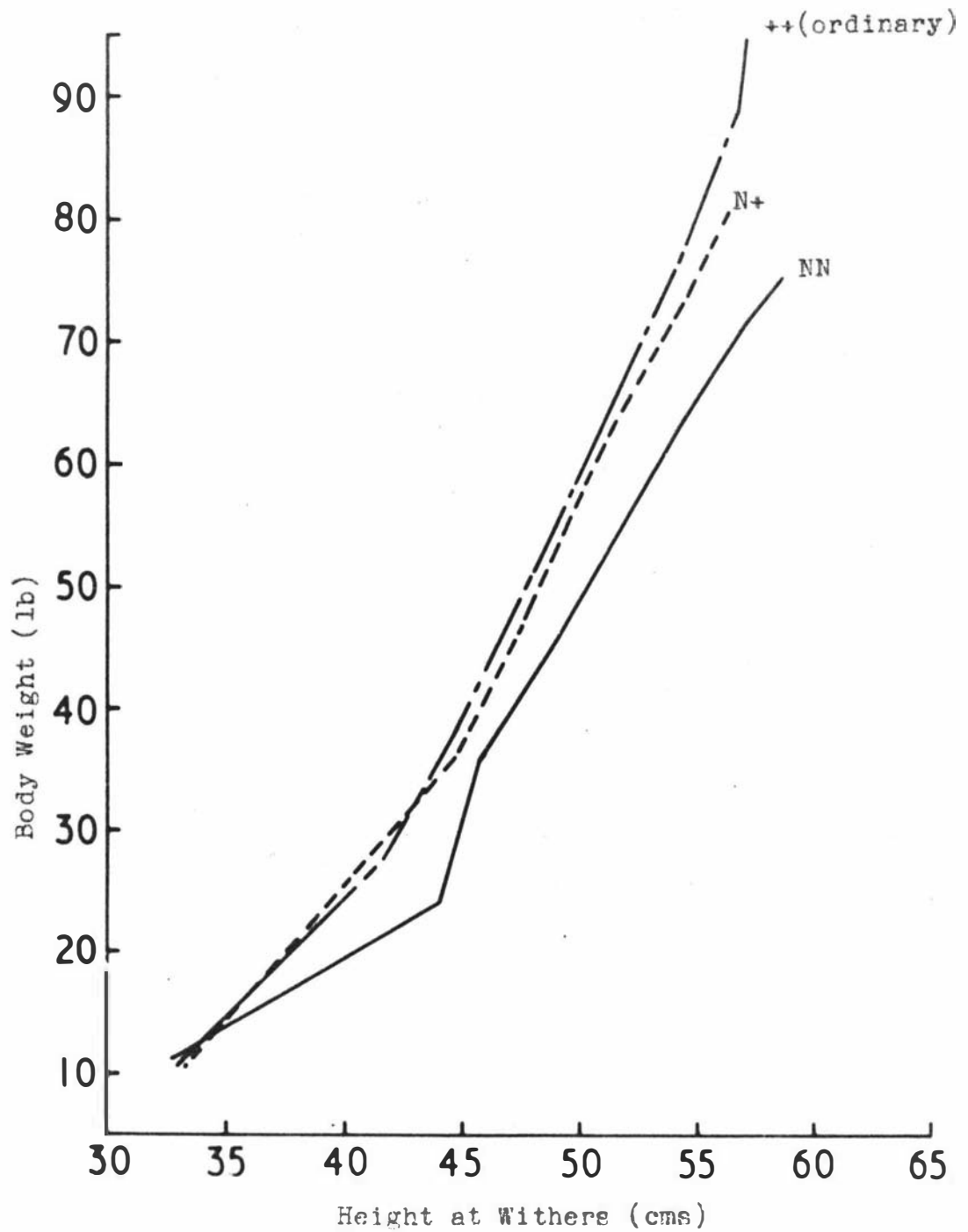
* One lamb only

The differences from 30 to 67 days show a slight superiority of the ordinary lambs, which is emphasised by the low gains of the NN lambs in group II. This group appears to make a recovery over the final period, after weaning, and as there are only three lambs in the group, it is possible that all their dams had a low milk production, and this retarded their growth prior to weaning. A slight increase in the rate of growth was observed for twin lambs in the following year's experiment, which suggests that this type of effect can occur. Apart from this group and the one NN lamb in group III, the results suggest that the ordinary lambs showed greater gains than the N-type lambs over the last period, after they had been weaned and shorn.

Finally the estimated mean weights have been corrected for height at withers and these estimates, including those for 30 days of age are shown in Table 33 and are illustrated in Figure 1 by a graph of weight and height at withers for lamb genotypes. The lower values of body weights for mating group II and also those differences resulting from the lambs' genotype are emphasised when considered at constant size. The low value for mating group I could be associated with this group or it could be an effect of the lambs' genotype. It might also be an additive effect of these two. The former effect could be partially a maternal one, but this is unlikely as it does not show until the time of weaning (100 days) or later. It is, therefore, more likely to be associated with other genetic effects connected with the N-type carpet wool flock which effects emphasise the lower body weight for a given height at withers. The small number of NN lambs in groups II and III makes it impossible to confirm this with a separate analysis comparing

Figure 1

Relationships between Body Weight and
Height at Withers for Single Ewe Lambs



them with group I lambs, but some confirmation is offered by the values for N+ lambs in group II (ewes from N-type stock) which are lower than those of N+ lambs in the other groups (outcross stock).

Thus Table 33 shows that the weight differences shown in Table 31 cannot be explained by differences in the size of the animals. This was confirmed by the direct analyses of height at withers at constant age which showed no differences in this characteristic, nor were differences found in the corrected gains of this measurement over any period.

Summary of conclusions, Section E3 (1) b.

- (1) Differences in mean weight at constant age were found between the various groups at the times weights were taken. These have been interpreted as being the result of the genotypes of the lambs, homozygous N-types being lighter than the heterozygotes which were in turn lighter than the ordinary Romney lambs.
- (2) These differences were not the result of possible variation in the size of the animals as they were still found when the animals were compared at constant size. Confirming this, no differences in absolute size as measured by height at withers, were found.
- (3) It is possible that there were lower weights at constant size associated with the N-type carpet wool flock and resulting from genetic effects other than the gene N.
- (4) The differences in absolute weight were the result of differences in weight gains from birth to 30 days of age, and possibly, to a more limited extent, between 30 - 67 days and 100 - 144 days. The initial effect is considered the more important one as the later effects could be associated with the response of an already 'unthrifty' lamb to its environment.

Table 34

Tests of the Genotype - Mating Group Effects for
Twin Lambs

I. Body Weight			
Independent Variables	Effects Mean Square	Residual Mean Square	F
30 days			
B. date & Ht. at Withers	13.121	4.079	3.22**
67 days			
Birth date	41.401	20.237	2.05*
B. date & Previous Wt.	7.639	4.473	1.71
B. date & Ht. at Withers	32.768	17.913	1.83
100 days			
Birth date	81.216	34.312	2.36*
B. date & Previous Wt.	10.153	6.882	1.48
B. date & Ht. at Withers	83.669	26.840	3.12**
144 days			
Birth date	75.967	42.207	1.80
B. date & Previous Weight	15.620	12.903	1.21
B. date & Ht. at Withers	100.712	32.261	3.12**
II. Height at Withers			
30 days			
Birth date	6.821	3.985	1.71
67 days			
Birth date	3.005	4.530	<1.0
B. date & Prev. Ht. at W.	1.760	2.484	<1.0
100 days			
Birth date	9.046	3.301	2.74*
B. date & Prev. Ht. at W.	5.403	2.273	2.38*
144 days			
Birth date	6.297	3.183	1.98
B. date & Prev. Ht. at W.	1.950	1.674	1.16
Degrees of freedom			
1 independent variate	9	60	
2 independent variates	9	59	

Values of F for various probability levels

P	F
0.2	1.43
0.05	2.08*
0.01	2.74**
0.001	4.07***

(c) Twin lambs.

The method of analysis was the same as that used for the single lambs. The results of the analyses of the genotype - mating groups are shown in Table 34. It can be seen that there are no further weight gain differences amongst these groups and that by 144 days the differences in weight between the genotype - mating groups are of doubtful significance. Significant differences in height at withers occurred at 100 days as a result of differences in gain of this measurement from 67 to 100 days. The presence of the interactions shown earlier in Table 28 appear therefore to be the result of the differences occurring between single lambs not always being found for the twin lambs.

The estimated values of the mean weights and height at withers corrected for birth date are shown in Table 35. Only those times when significant differences occurred are shown, except for weight at 144 days which is given for comparison with the values for single lambs. Group II has been omitted as there was only one lamb of each genotype in it.

NN lambs from both mating groups are lighter than the other lambs. The N+ lambs are lighter than the ordinary lambs by a small amount, except in mating group III where the weights are similar. In general the results follow those for single lambs, the differences between genotypes, however, being considerably smaller and no longer significant at 144 days. For mating groups IV and V the differences between ordinary and N+ lambs are of the order of three pounds compared with ten pounds for the single lambs.

The differences in height at withers at 100 days appear to follow the differences in body weight except for those lambs

Table 35

Estimates of the Genotype - Mating Group Means
Corrected for Birth Date

Mean age		Body Weight			Height at Withers
		67 days	100 days	144 days	100 days
Lamb Genotype	Mating Group				
NN	I	42.36	52.51	62.96	51.86
	III	39.38	51.00	59.16	47.73
N+	III	45.38	59.03	66.90	49.94
	IV	40.36	53.61	62.71	49.07
	V	43.48	55.30	66.37	50.07
++	III	45.65	59.76	64.51	50.87
	IV	44.18	56.79	66.52	49.97
	V	45.96	58.62	68.84	51.72

The body weight is in pounds and the height at withers in cms.

Table 36

Estimates of the Genotype - Mating Group Means of
Body Weight Corrected for Birth Date and for Height
at Withers, and of Height at Withers
Corrected for Birth Date and the
Previous Height at Withers

Mean age		Body Weight			Height at Withers
		30 days	100 days	144 days	100 days
Lamb Genotype	Mating Group				
NN	I	23.79	50.41	61.24	51.54
	III	24.94	54.18	62.91	48.81
N+	III	25.35	59.39	66.43	49.97
	IV	22.99	55.07	63.97	49.57
	V	23.77	55.49	66.20	49.87
++	III	25.23	58.92	65.78	50.84
	IV	24.23	57.13	67.30	49.70
	V	25.47	56.69	67.90	51.28

from mating group I. These show a lower body weight for a given height at withers which is confirmed by the results in Table 36. This table also shows the height at withers at 100 days corrected for that at 67 days, and indicates that the larger size of lambs from mating group I at the former time was the result of their faster growth over this period. It also shows the lower weight for size of the NN lambs, in particular those from group I at 144 days. In addition, a small difference is shown between N+ and ordinary lambs within the mating groups IV and V.

There was only a small difference in size between single and twin lambs and comparison of this difference with the differences in weight showed that twin lambs had a lower weight for a given height at withers. This is presumably an environmental effect and the contrast in these and the body weight results for single and twin lambs suggest an interaction between N and the environment.

Summary of conclusions, Section E3 (1) c.

- (1) Differences in weight between lamb genotypes for twins followed the same pattern as for single lambs.
- (2) These differences were smaller and became non-significant at 144 days.
- (3) These results and the relationships of weight to height at withers, suggest the presence of an interaction between the environment and the genotype of the lamb.
- (4) Results for mating group I confirmed results for the single lambs in that other factors besides N affecting growth were indicated in matings derived from the N-type stock.

Table 37
Sub-class Numbers for the Analysis
of Lambs' Genotype

Lambs' Genotype	♂ Singles	♀ Singles	♂ Twins	♀ Twins	Total
NN	5	11	6	7	29
N+	16	17	11	18	62
++	5	12	12	18	47
Total	26	40	29	43	138

Table 38
Expected and Observed Values for Weight
at 100 days

Lambs' Genotype		♂ Singles	♀ Singles	♂ Twins	♀ Twins
NN	Expected	64.28	55.74	52.86	47.19
	Observed	62.86	54.98	51.02	49.63
N+	Expected	68.74	60.20	57.32	51.66
	Observed	67.84	59.91	58.69	50.32
++	Expected	73.01	64.47	61.59	55.92
	Observed	75.26	64.15	60.16	55.22

(ii) Differences between genotypes pooling the mating groups.

(a) Body weights.

As the differences present appeared to be mainly between the lambs of different genotypes and not between the mating groups, it was decided to pool the mating groups and examine the differences between the three genotypes only. The method of analysis was the same as in the previous section with the three genotype groups in place of the ten genotype - mating groups. These results will not be presented as fully as those shown in the tables in the previous section, as in general they only confirm or extend these analyses.

The advantage of this further analysis is to confirm the results deduced empirically from the tables of estimated means and also to have an analysis based on larger sub-class numbers. This should increase the accuracy of the estimates of the genotype effects when the mating group effects are of little importance. The sub-class numbers and the classification for these analyses are shown in Table 37.

Unlike the previous analyses no significant interactions were found between the sex - birth rank effects and those of lambs' genotype. This was therefore examined further by comparison of estimated and observed mean values for both methods of classification. For the analysis by genotype - mating groups some difference in the results for singles and twins has already been shown, but in addition, groups with small sub-class numbers tended to differ in their expected and observed values. Examination of the present results showed a tendency for the expected values to underestimate the genotype differences for single lambs and overestimate them for twin lambs. Table 38 shows this for the values at 100 days

Table 39

Estimated Values of Mean Weights of Lamb Genotypes
Corrected for Age

Mean Age	30 Days	67 Days	100 Days	144 Days
Lambs' Genotype				
NN	26.13	43.59	55.06	64.47
N+	26.74	46.39	59.48	68.50
++	28.65	49.81	63.74	73.43

Table 40

Interactions Shown by the Analysis of Weight
Corrected for Previous Weight

Period	30-67 Days	67-100 Days	100-144 Days
Interaction between Genotype and:			
Sex - Birth rank	Present	Present	Present
Sex (Single lambs)	Present	Present	Absent
Sex (Twin lambs)	Present	Absent	Absent

of mean age, where it can be seen that the observed values indicate a smaller difference between genotypes for twin lambs.

Although these comparisons indicate a slight interaction effect, it was reasonable to analyse on the basis of the non-significant tests of interaction and use an estimate of genotype effects over all the sex - birth rank groups. The analysis of covariance of these effects corrected for birth date showed highly significant (P less than 0.001) differences at all the ages. The estimated values of the corrected mean weights are shown in Table 39. Apart from 30 days when the differences are between N-type lambs and the ordinary lambs, there appears to be a linear effect of N on the weight, as the mean weights of the heterozygous lambs fall between those of the homozygous and the ordinary lambs.

When the additional adjustment for the previous weights was added to the analysis of covariance, significant interactions were found. These are summarised in Table 40 which shows those sub-classifications of sex and birth rank where interaction was shown to be present on analysis. As a result, in order to analyse the lamb genotype differences, the data was broken down to those sex - birth rank classes where interaction was absent.

Thus for gains from 30 to 67 days each sex and birth rank was analysed separately. Over this period differences in favour of ordinary lambs were found for all groups except that of female twins. In addition, for the single lambs, rams showed greater differences than ewes. No genotype differences were found for gain in any groups from 67 to 100 days or for twin lambs from 100 to 144 days, but single lambs showed greater gains in the ordinary group over this last period.

These results are in general agreement with those deduced from the genotype - mating group analysis with the addition that

genotypic differences between ewe lambs appear to be less marked than those between ram lambs. This may be the result of the normal sex differences in that the rams or single lambs which grow faster are more penalised by the effects of the N genotype. This could be a similar effect to an environmental one causing slow growth and smaller differences.

Correction of the estimated mean weights for the height at withers made no difference to conclusions already reached in the previous section. Interaction was present at 67 days, when twins showed smaller differences than singles, but all the genotype differences were significantly in favour of the ordinary lambs.

(b) Body measurements.

An analysis similar to that used above showed no interaction for any age for height at withers corrected for birth date. Significant differences were found amongst the genotype groups for this measurement at 100 and 144 days, while those at 30 days approached significance. The estimated mean values are shown in Table 41 where it can be seen that lambs of NN genotype have a greater size than would be expected from their body weight. As all but three of these NN lambs were from ewes themselves derived from N-type stock, this confirms the observations made on the genotype - mating group analysis. These suggested that the N-type flock differed in other genetic factors besides N causing this greater size for a lower weight. These factors could be present as a result of the breeding policy within the N-type flock which for experimental reasons was based solely on wool, whereas selection of the ordinary Romney over a similar period has in addition been directed towards a type of sheep associated with meat production. Alternatively, the order of the differences could be the result

Table 41

Estimated Values of Mean Height at Withers (cms)
Corrected for Birth Date

Mean Age	30 Days	67 Days	100 Days	144 Days
Lambs' Genotype				
NN	42.7	48.4	51.9	54.4
N+	41.6	48.3	50.8	53.1
++	41.9	48.6	51.7	53.7

Table 42

Estimates of 'Leg Length' and depth of Thorax (cms)

Mean Age	Depth of Thorax		Leg Length	
	100 Days	144 Days	100 Days	144 Days
Lambs' Genotype				
NN	25.03	25.92	26.84	28.46
N+	24.80	25.75	26.02	27.31
++	24.88	26.11	26.78	27.58

Table 43

Average Changes in Measurements from Birth to
144 Days for all lambs

Measurement	Birth	144 Days	Difference	%Difference
Body Weight	10.09	68.87	58.78	582.6
Leg Length	20.06	27.78	7.72	38.5
Depth of Thorax	13.08	25.93	12.85	98.2

of the scale on which they have been measured not corresponding to the genetic scale; i.e., a scale such that the value for N+ is between those of NN and ++ lambs, and by which the action of N is additive.

The results for the corrected gain in height at withers were those which would be expected in order to obtain the differences in actual height at withers. There was, however, a significant interaction at 144 days when there were significant differences between single but not between twin lambs. This appears to be the result of the more rapid growth of the NN single lambs after weaning which is reflected in the comparative values (Table 41) of height at withers at 100 and 144 days. Although the differences in gain amongst twin lambs were very slight and not significant, they were sufficient to result in there being no interaction between singles and twins for actual height at withers at 144 days; i.e., those differences already present for twin lambs at 100 days were still present and slightly greater at 144 days although the differences amongst the gains were not significant. With such an effect it is possible for weights or measurements themselves to show no interaction although one is shown when these are corrected for the previous values.

Finally the differences for height at withers at 100 and 144 days have been examined to determine whether the differences are ones of 'leg length' or depth of thorax. There were no interactions for depth of thorax at these two times and the estimates for this measurement and those for 'leg length' obtained by subtraction from the height at withers estimates are shown in Table 42.

At 100 days the withers differences appear to be associated

with 'leg length', although the small differences in depth of thorax are in the same order, NN, ++, N+ as those of withers and leg length. At 144 days the greater height at withers of the homozygotes appears to be associated with the 'leg length' and not depth of thorax. This is in accordance with results at birth where it was apparent that depth of thorax was more closely associated with body weight than was leg length.

The difference between genotypes in height at withers at 144 days is about half that of the difference between a ram and a ewe lamb at this age and might not be detected by visual inspection if the animals were in the same condition.

Comparisons of the three variables at 144 days and at birth are of interest in relation to the results. The mean weights and measurements for all groups are given in Table 43. The major contribution to increases in height at withers is from increases in the depth of thorax and not the length of the leg. The percentage differences emphasise that there are far greater relative changes in weight after birth than there are in height at withers. This would suggest that there would be greater chance of environmental effects acting on body weight than on leg length after birth, which is in accordance with those results discussed in the review of literature which led to the taking of these body measurements.

4. Summary and conclusions for Section E.

It is not proposed to discuss the biological implications of these results in any detail until the end of the first part of this thesis. The purpose at this stage was to gather information as a basis for further experiments under more controlled conditions and also to examine views put forward on the lack of

'thrift' of the N-type sheep. It is clear, for this season and under these conditions, that these views had a basis of truth and that further investigation was worthwhile for research purposes and essential before any economic exploitation was considered.

The examination of the results has been essentially a statistical one in order to study the growth of the N-type flock as well as the effects of N. The use of matings of the type of IV and V in which heterozygous rams were mated to ordinary ewes has considerable advantages for this type of work as, apart from linkage, all effects other than those of N will be randomised in the two possible groups of offspring. The clear effect of N on growth is shown in Figure 2 which gives the curves for the individual ram single lambs from mating groups IV and V. This diagram illustrates the major difference found by the analysis, and the other conclusions are shown below in the form of a summary. It is this summary which will be used for future discussion.

General:

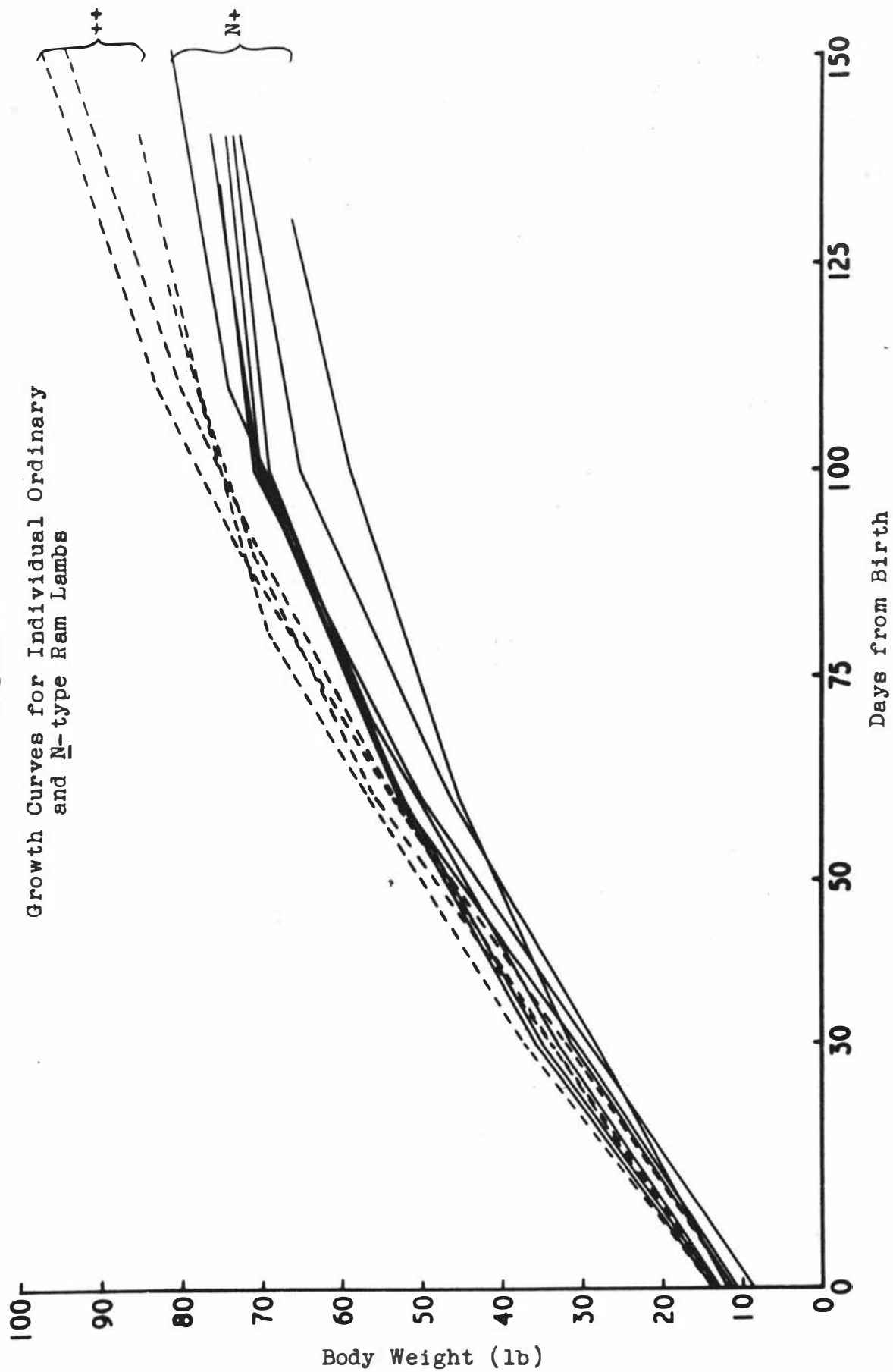
- (1) Twins showed a greater relative growth rate than singles between 30 and 67 days of age.
- (2) At 144 days of age twins had a lower weight for their body size than had single lambs.

Genotypic differences:

- (1) These were not, in general, linear functions of the sex - birth rank classification, the largest differences being shown by single lambs and the smallest by ewe twin lambs.
- (2) Full analysis indicated that mating group differences within the genotypes were likely to have been relatively

Figure 2

Growth Curves for Individual Ordinary
and $\bar{N}$ -type Ram Lambs



unimportant. These differences between mating groups will include maternal effects of the ewe either pre-natally acting on birth weight or post-natally acting via milk production and, in addition, possible differences associated with the sires. There may have been overall differences of these types associated with the N-type stock apart from effects of N.

(3) Analysis by lambs' genotype and sex - birth rank confirmed deductions from the full analysis and the analysis of weight at 30 days of age. These were:-

(i) Corrected weight gain differences between N-type and ordinary lambs from birth to 30 days led to weight differences between the genotypes of both sexes of singles and twins at 30 days.

(ii) Further differences in corrected weight gain occurred between the single lamb groups from 30 - 67 and 100 - 144 days, but these were more limited and may reflect the poor growth over the first few weeks of life.

(iii) Twin lambs showed no further differences after 67 days.

(iv) All differences showed NN lambs as the lightest and ordinary lambs as the heaviest, with N+ lambs as intermediate or similar to the NN lambs.

(v) It is concluded that the first six or nine weeks of life were the critical ones during which, for some reason, the N-type lambs did not grow as well as ordinary Romney lambs under the same conditions.

(4) This difference between N-type and ordinary lambs may be one associated with birthcoat type; the additional differences between the N+ and NN lambs being the result of other factors associated with the N-type flock.

(5) Correction for body size tended to increase the values of the differences between body weights of N-type and ordinary lambs.

(6) Body size, as measured by the height at withers shows NN lambs as the largest and N+ as the smallest, and this has been interpreted as an effect of the N-type stock although a possible alternative explanation of genetic scale has been pointed out.

(7) The difference in body size at 144 days appears to be associated with the length of the legs but the order of differences is probably too small to have much effect on the visible conformation of the animals if they were in similar condition. This assumes that there has been little penalty in growth of 'height at withers' compared with the poor growth in terms of weight.

F. Results from the slaughter of N-type and Ordinary Rams.

1. Review of previous work.

In the previous section it was shown that differences of weight had occurred between genotypes by the time that lambs are normally slaughtered for commercial purposes. Some difference in carcass quality was therefore to be expected as a result, but it was still necessary to find if there were any effects attributable to N apart from those arising from these weight differences.

An investigation of five heterozygous and five ordinary Romney sheep paired at different ages, had already been made at the College, and although this was primarily for other purposes, the weights of various joints and their component

tissues were available. This data was kindly made available by Mr. E.A. Clarke (now of Ruakura Animal Research Station), and an analysis was carried out by the present author.

Comparisons between the two types of sheep were made by means of analysis of differences between the regressions of the weights of the various parts on carcass weight. The conclusion was drawn that there were no differences in the relative weights of the joints or their component tissues except that the relative weight of the loin was slightly higher in the ordinary sheep as a result of a greater weight of fat in this joint. The small numbers of sheep made these conclusions tentative ones.

Complete dissection of a carcass or even of sample joints is a laborious technique if many animals are involved. As the data described above gave no indication of any important differences, a simple method was required for a preliminary examination of the lambs.

Palsson (1939) and also Walker and McMeekan (1944) have described methods of measurement of lamb carcasses, which reflect differences likely to be found on dissection. Clarke, Barton and Wilson (1953) described similar measurements to the ones used in this experiment. They involve measurements of the length of the carcass and of the hindquarter region. These latter give results which depend on the length of the leg of the animal and the shape of the joints of the hindquarter which are the most important commercially. In addition measurements are made on the cross-section of the carcass to determine the depth of sub-cutaneous fat and the dimensions of the cross section of the 'eye' muscle (*longissimus dorsi*).

If these measurements showed differences not explained by weight differences of the carcass then more detailed anatomical study of the lambs at various ages was intended. This

would be from a biological point of view rather than one of meat technology expressed by these measurements. These should , however, indicate whether this detailed approach was justified while at the same time answering the questions on the economic value of N-type carcasses.

2. Methods.

No homozygous animals were available for slaughter as the majority were required for future breeding purposes and consequently it was decided to avoid mating group differences by taking ten N+ ram lambs and ten ordinary ram lambs from mating group V only.

These 20 lambs were therefore starved overnight and slaughtered the following day. Before killing, a wool sample was taken from the side position for hairiness determination and the animal was weighed to obtain the 'empty live weight'. After slaughter the hot carcass weight was taken and also the weight of the various organs freed of connective tissue and blood. The organs weighed were the heart, liver, lungs, spleen and the kidneys. The left fore cannon bone was also cleaned and weighed and kept for measurement. Any abnormalities were noted.

The carcasses were then hung overnight and the following day the cold carcass weight and the measurements described above were obtained. For those measurements requiring it the cross section of the carcass was taken at the point at which the heart girth and depth of thorax measurements were made on the live animal. This was to obtain anatomical information in the event of differences being found for the live animal measurements when these were analysed. Such differences have already been shown to be unimportant and consequently these measurements will not be considered further.

Table 44

Measurements on the Left Fore Cannon Bone

Genotype	Length/Weight	Length/Circumference	Length(cms)
N+	0.329	2.27	10.65
++	0.309	2.19	10.56

Table 45A

Analysis of Covariance of Empty Live Weight Correcting for Age

Source	d.f.	Mean Square	F
Birth rank	1	570.16	13.28
Genotype	1	199.59	4.16
Residual	16	47.92	

For 1 and 16 d.f. $F = 4.49$ for $P = 0.05$

Table 45 B

Analyses of Covariance of Empty Live Weight(omitting two lambs)

(1) Corrected for age only

Source	d.f.	Mean Square	F
Birth rank	1	361.58	
Genotype	1	357.99	10.20
Residual	14	35.08	

(2) Corrected for age and medulla percentage

Source	d.f.	Mean Square	F
Birth rank	1	291.55	
Genotype	1	33.35	1.08
Residual	13	30.85	

Table 46

Estimated Mean Empty Live Weights at Constant Age (lbs)

Genotype	Singles	Twins
N+	70.6 (5)	62.1 (5)
++	82.5 (3)	68.4 (7)

The numbers in each sub-class are given in parenthesis.

3. Carcass measurements and organ weights.

The carcass measurements were analysed by analysis of covariance with the cold carcass weight as the independent variable, while a similar analysis was made for the organ weights corrected for the empty live weight.

In no case was significant difference found and any variation in the carcass weights was accounted for by differences in the empty live weight. Analysis of the weight and circumference of the cannon bones showed a tendency for those of the N+ lambs to be thinner relative to the length. The mean lengths are shown in Table 44 with the relative measurements. The slightly longer cannon bone of the N+ lambs can be attributed to the greater mean age of this group (1 week) and the lower relative weight and circumference to the slower growth of the lambs (Palsson and Verges 1952).

It was concluded that there were no differences in the economic or biological characteristics of the carcasses of the two groups that would not be expected from lambs showing different growth rates.

4. Empty live weight and medullation.

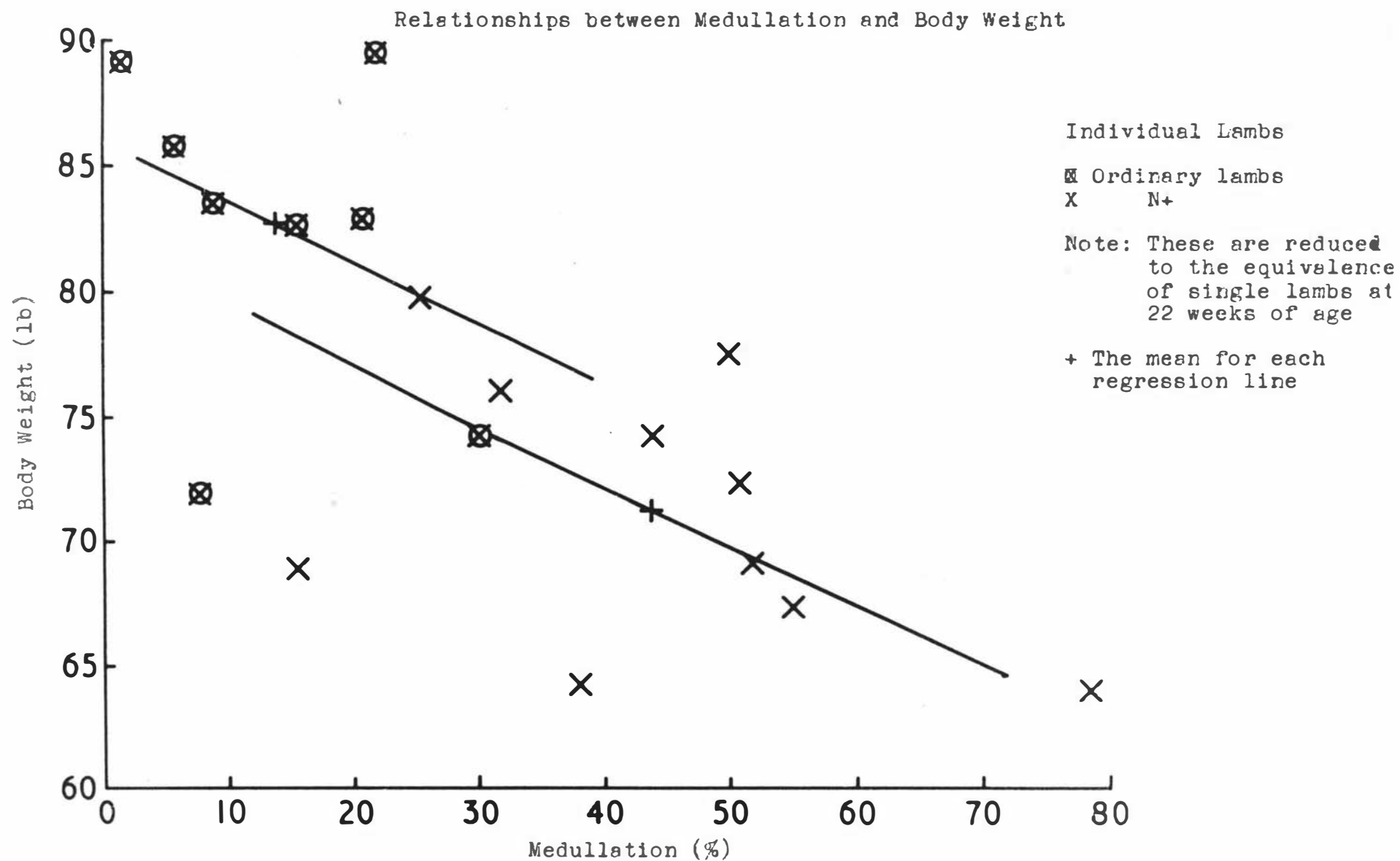
As all previous weights had been taken of lambs straight from the paddock, it was of interest to compare the empty live weights of the two groups. An analysis of covariance was made between the two genotype groups correcting for age and with a second classification of birth rank. This analysis is shown in Table 45 and the estimated weights at constant age are shown in Table 46. If the small numbers in the sub-classes are taken into consideration these results are in accordance with the previous analyses of live weight and it can be assumed that the differences found were not the result of variations in stomach content.

In taking the samples for the medullation test two ordinary lambs were omitted by accident and these are therefore excluded from the analyses shown in Table 45b. The first of these analyses is the same as that shown in Table 45A but in the second the percentage medullation shown by the benzol test (McMahon 1936) has been included as a further independent variable. The value of the partial regression coefficient of medullation on weight within the sub-groups of genotype and birth rank was $-0.24 (\pm 0.065)$, which is highly significant. The values of weight, corrected for age, have been plotted against the medullation values in Figure 3 with this regression value used to fit lines to show the relationship within the N type and ordinary lambs.

Whereas in the statistical sense, the differences in empty live weight are accounted for by the differences in medullation, this does not necessarily give the biological determination when such a large correlation exists. The biological interpretation of the benzol test is not straightforward, but in general the higher values would indicate a higher proportion of medullated and presumably coarser fibres. Schinckel (1953 and 1955b) has shown that for the Merino lamb, early growth can affect the composition of the subsequent follicle population. It is possible that within the N-type and ordinary lamb groups, the slower growing lambs had a lower fibre density and hence a coarser fleece and greater medullation. Alternatively, lambs with more halo-hairs at birth may show a coarser fleece at this later stage and these lambs may have a slower growth rate associated with the halo-hairs.

The data collected in this first year were not of the type to answer these questions but the importance of this benzol test result in planning future work was clear.

Figure 3



Summary of Section F.

- (1) It was concluded that further examination of the problem should be from the point of view of the relationships between growth and the various characteristics of the birthcoat and later fleece.
- (2) There was no evidence of any major differences in the anatomy of N+ or ordinary lambs at the age of 22 weeks nor was it considered likely that the carcasses of lambs of these two types would differ in their commercial value if the growth of the lambs was the same.
- (3) These remarks do not apply to the N-type 'carpet wool' flock as these were not available for slaughter. The data already analysed suggest that the lamb carcasses from this flock would be of lower commercial value than ordinary sheep because of the poorer lamb growth.

G. The Dorsal Spines of the Thoracic Vertebrae.

In the introduction it was stated that it had previously been suggested that the 'pointed' withers observed in N-type sheep were a pleiotropic effect of 'N' and that these were a reflection of the increased length of the dorsal spines of the thoracic vertebrae.

Hammond (1932) discussed the connection between horns and the length of the dorsal spines, suggesting after D'Arcy Thompson (1942) a mechanical necessity for such spines in horned animals to support the weight of the head on a cantilever principle. The mechanism whereby such a connection could arise in the development of the animal is not discussed. Von Borstal (1952) found longer dorsal spines in adult Cheviot ewes when

they were compared with ordinary New Zealand Romney ewes. This could not be attributed to the weight of the head, for neither breed is normally horned. The Cheviot, however, had greater musculature of the shoulder and the longer dorsal spines may have been associated with this.

Clarke (1952) in a comparison between heterozygous and ordinary Romneys at different ages found that the former had longer spines. The N-type sheep included one polled animal. Data from this comparison had been made available and the regression of the length of the fourth dorsal thoracic spine on head weight was calculated with the polled N-type sheep omitted. Limits at the 5% level of probability for the estimation of spine length from this regression equation were then found (Snedecor 1946) and it was then found that the polled N-type sheep fell outside these limits in that it had a greater spine length than would have been expected from the weight of its head. For the remainder of the sheep the results were those that would be expected if the greater spine length was the result of a greater weight of the head.

Later experiments by Clarke (1952), in which the weight of horns was stimulated by the use of increasing weights on the head of growing lambs, produced no effect on the length of the thoracic spines.

The data of Clarke was also examined to test the possibility that the longer vertebral spine was associated with greater length of other bones in the skeleton. However the cannon bone and the femur were the same length in both the N-type and ordinary sheep.

As these results are not conclusive it was decided to investigate the problem further by means of X-ray photography,

which enables study of the same sheep at different times without the variation in time being confounded with the variation between animals. This confounding is a major drawback of a technique where it is necessary to slaughter the animals to obtain the measurements required.

The technique was first investigated and validated using ten wether hoggets. These animals were X-rayed and measurements of the required bone lengths made from the plates. The animals were then slaughtered and measurements made of the actual bones after dissection. From the results obtained it was decided to use the plate measurement of the fourth thoracic vertebral dorsal spine for the subsequent work. When the magnification was allowed for, the plate measurement of this spine showed a correlation of 0.94 with the measurement of the actual dissected spine. With constant magnification, i.e. a constant distance between the plate and the tube, the plate measurement can be used for comparative purposes without conversion to the true measurement. The results for spine length given below are therefore 1.16 times the true measurement.

The lambs available were X-rayed at four weeks of age, 12 weeks of age and at about 10 months. Two homozygous (NN), two heterozygous and two ordinary ram lambs were measured for height at withers and X-rayed at each of these times. All the N-type rams had horns and the ordinary animals were polled although one of the latter showed a very slight scur growth.

In addition an NN ram which had been dehorned was available at four weeks but not at a later age as the de-horning led to abnormal horn growth and the animal had to be slaughtered. At ten months two polled N-type rams were available, one which

had been successfully de-horned and one which was naturally polled. In addition two ordinary horned rams were measured at this time, the horns on these animals probably being the result of a gene other than N (Dry 1955c).

Figure 4 shows the length of the fourth dorsal thoracic spine plotted against the height at withers less the length of spine, for the three times at which the measurements were made. The number of animals measured does not permit a statistical analysis but the measurements taken at ten months indicate that the longer dorsal spines are related to the presence of horns and not to the presence of N. The consideration of the spine lengths in relation to the height at withers shows that the greater lengths in these horned animals are not associated with greater lengths of the long bones of the fore limbs.

These results could be interpreted as a mechanical effect but it could be possible that the spines are slightly longer in horned animals at four weeks (Fig.4) when the horn growth is still slight. Also although the NN sheep had horns twice the size of the N+ sheep there was little difference in their dorsal spine length.

However although it is clear that further experiments are required to discover the mechanism of these relationships, the conclusion relevant to this thesis is that the longer dorsal spines observed in N-type sheep are the indirect result of horns and probably not directly associated with the action of N.

Figure 4A

Relationships between the Dorsal
Spines and Height at Withers

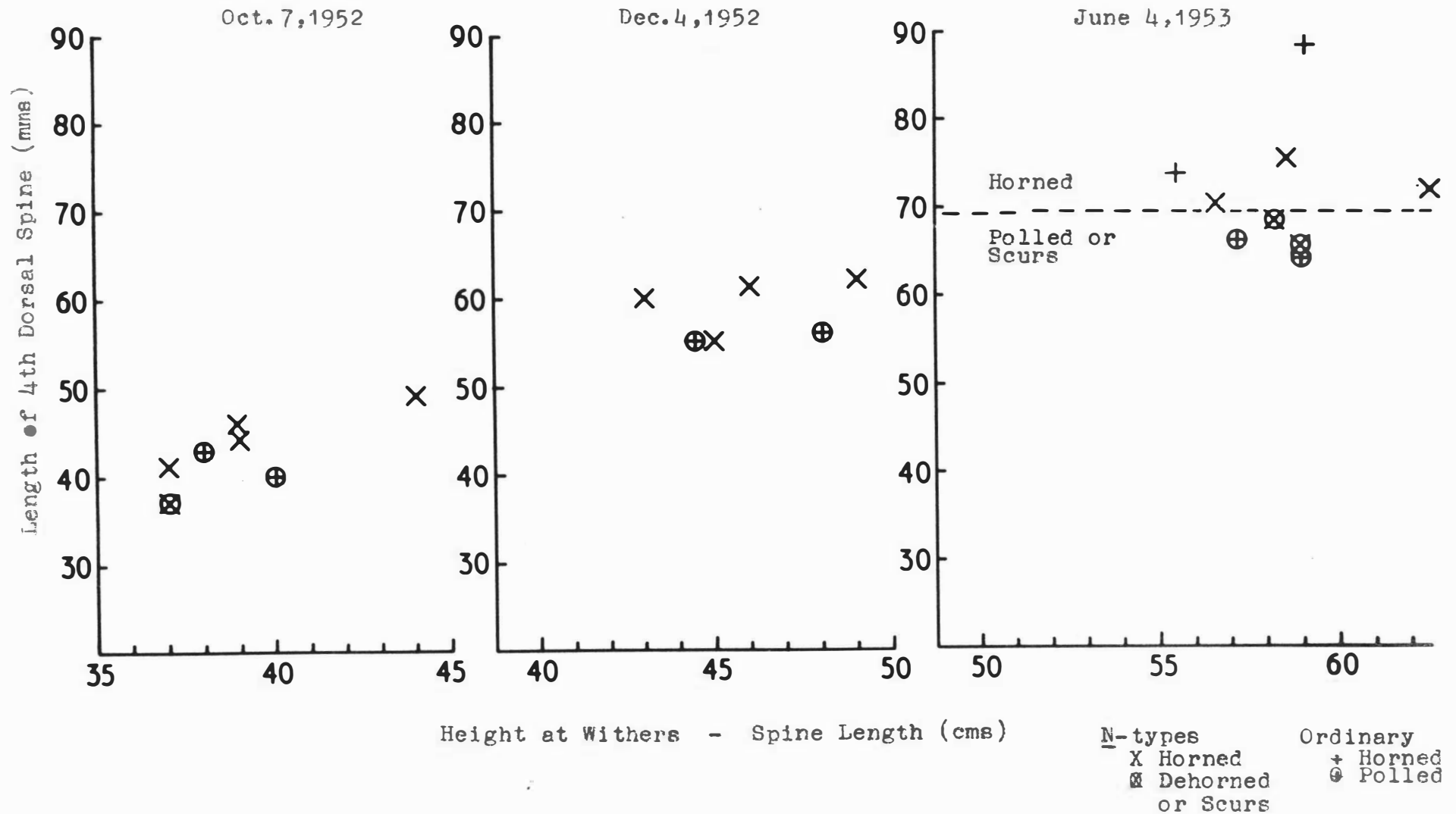
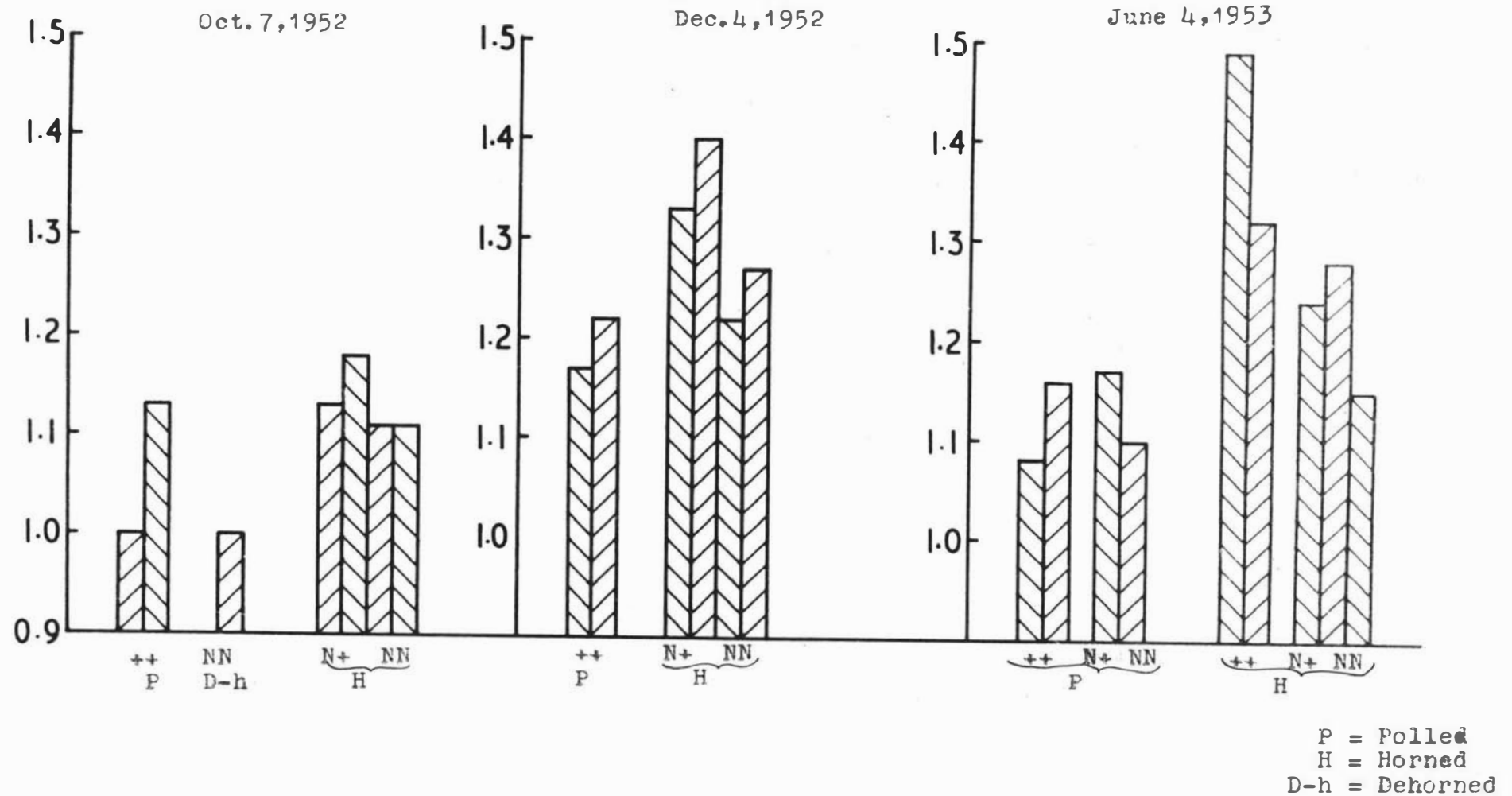


Figure 4B

Histograms of Values of Dorsal Spine
Length / Height at Withers (from
Fig. 4A)



IV. THE GROWTH OF THE EWE HOGGETS

All the N-type ewe lambs from the experiment just described were to be kept for future breeding purposes and it was decided to add 17 of the ordinary lambs to these to make up the maximum of 70 hoggets for which grazing was available. The 17 ordinary animals were chosen at random from those available using a table of random numbers (Fisher and Yates 1948). The main purpose in keeping these animals was to find out what effect the weight differences at the end of January would have on the survival of the different groups through the winter and ^{on growth} during the following spring. In addition, when the results from the slaughter of the 20 ram lambs were analysed, it was clear that some preliminary work on the biometrical description of fleece characteristics was required in order to plan the following year's experiment.

Conditions were generally good over the winter and these are reflected in the weight of the ordinary hoggets in the spring. This weight was above average for the district.

The mean weights of twins and singles of the different genotypes are plotted against the month of weighing in the form of a growth curve in Figures 5a and 5b. It was not considered necessary to carry out further analyses as that carried out for the growth of the lambs gave a clear idea of those differences which could be regarded as real. There were three deaths which are marked at the appropriate places on the 'curves', as removal of an animal would have a slight effect on the subsequent means by probably tending to select out the animals of lower weight. These deaths were all of N-type sheep, consisting of one homozygote and two heterozygotes.

Figure 5A

Growth of the Ewe Hoggets of the
Three Genotypes: Singles and
Twins Reared as Singles

Note: The straight line
is for comparison with
Fig. 5B

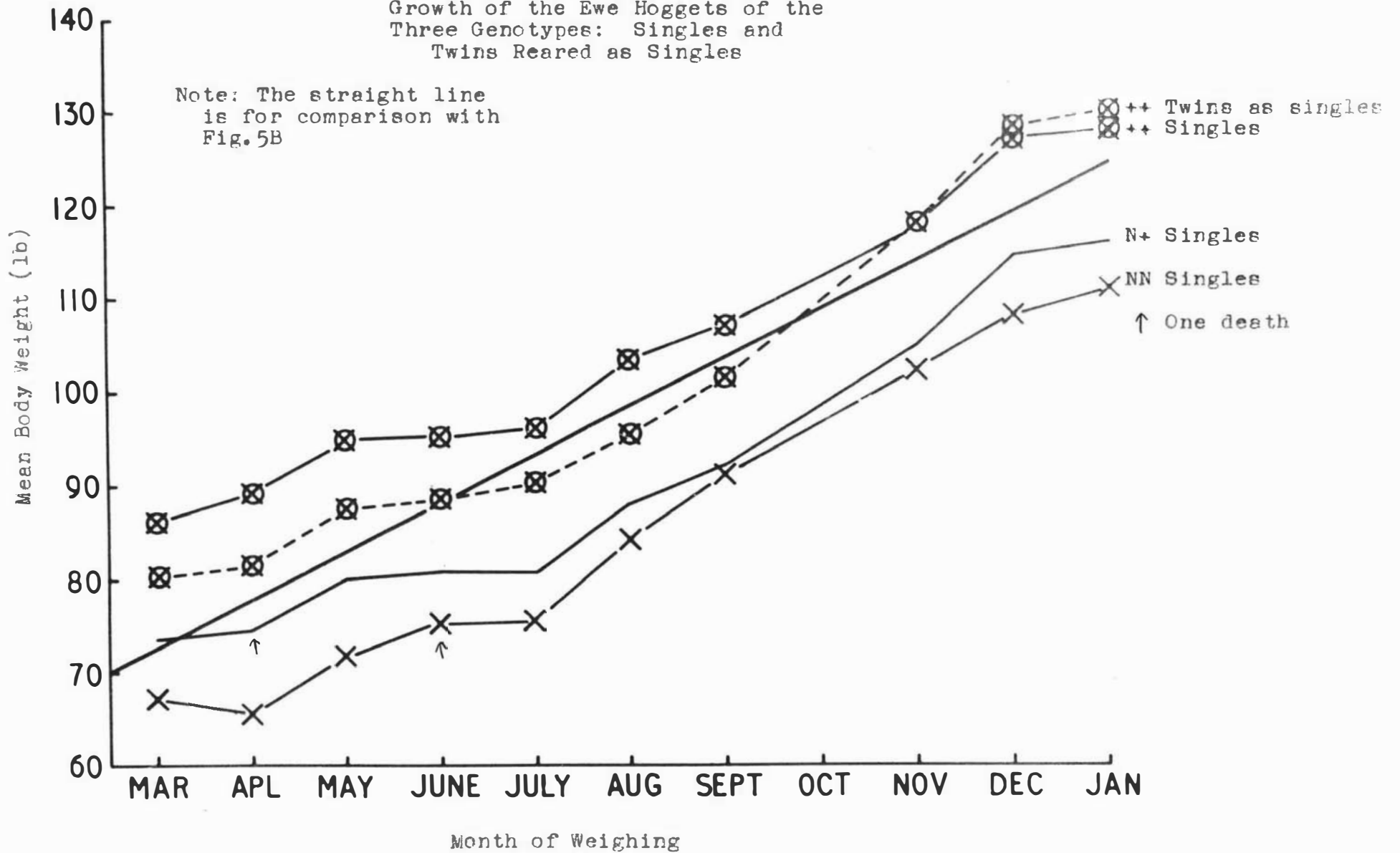
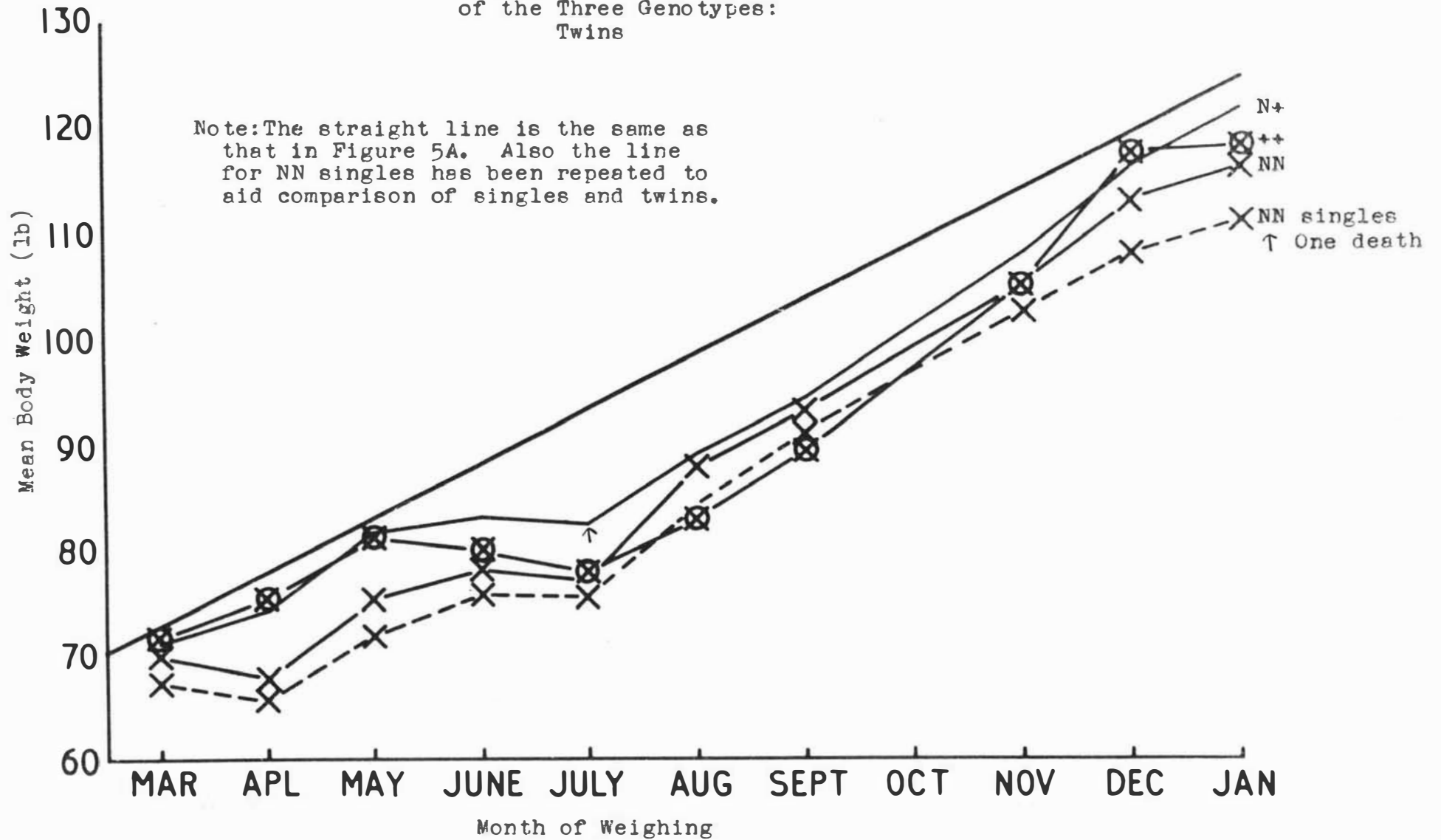


Figure 5B

Growth of the Ewe Hoggets
of the Three Genotypes:
Twins



It can be seen that for the single lambs similar differences of weight were maintained with a tendency for the N-types to form one group and the ordinary sheep another. After shearing, the heterozygous N-types and the ordinary sheep showed increased gain for a month whereas the homozygous N-types continued growing at much the same rate. The mean differences did not show any increase and a difference of, say, twenty pounds when the mean weight was 120 pounds is probably of less importance than a similar weight difference when the mean weight was 70 to 80 pounds.

When the twin sheep are compared with the single ones the interaction observed at the earlier stages can now be seen to be very marked. There is little difference amongst the three genotypes for the twin lambs and the relationship between twins and singles within the genotypes is somewhat unusual. For the homozygous N-types the twin lambs were heavier than the single lambs from March onward, while the heterozygous twins and singles are very similar. The ordinary lambs, however, showed a large difference, for the single lambs were considerably heavier. The twins reared as singles appear to be anomalous, the higher mean weight for the heterozygous animals being consistent for the four lambs in this group.

The occurrence of little or no weight increase during the months of May, June and July, followed by weight increases over the spring months appears from available records to be the normal pattern of growth for the Romney hogget in this district, it being usual for the ^{weights of} twins to approach those of the singles during the spring months.

The summary of conclusions from these curves is therefore:-

- (1) No changes occurred in the absolute mean weight differences between genotype groups for the single hoggets over the period from 6 months to 17 months of age.
- (2) There was a continued difference in the weights of singles and twins relative to their genotype.
- (3) Different genotypes may have reacted differently to shearing.
- (4) Heterozygous twins reared as singles were anomalous in that their weights were greater than those of the single lambs.

V. COMPARISONS OF HOGGET FLEECE CHARACTERISTICS

A. The greasy Fleece Weights

1. Lambs.

The lambs were shorn on the 30th December, 1952, and the greasy fleece weights were taken. Unfortunately it was not possible to weigh the lambs themselves at this time and the body weight used for correction was that taken three weeks prior to shearing. This weight is approximately equivalent to the shorn weight of the lambs and this has been assumed for purposes of comparison with the results obtained in the following year (Section IX, A 2)

Fleece weights for lambs and hoggets have been analysed in relation to their body weights which account for a considerable part of the variation in fleece weight. For the lambs an analysis of covariance, with body weight as the independent variable, has been made for the single and twin lambs separately. Initial plotting showed that any differences present were likely to be between the N-type group and the ordinary group and the

Table 47
Analysis of Covariance of Lambs' Fleece
Weights Corrected for Body Weight

Single Lambs

Source	d.f.	Residual	Mean Square	F	P
Total	64	12.274			
Within groups	63	11.926	0.189		
Difference	1	0.349	0.349	1.84	0.2

Regression coefficient within groups 0.044 ± 0.0062

The regression accounts for 45% of the variance within groups.

Twin lambs

Total	70	14.219			
Within groups	69	12.231	0.177		
Difference	1	1.989	1.989	11.22	<0.01

Regression coefficient within groups 0.041 ± 0.0068

The regression accounts for 33% of the variance within groups.

All measurements are in pounds.

analysis has therefore been carried out between these two main phenotypic groups and is shown in Table 47.

The regression coefficients within the genotype groups accounted for nearly half the variance of fleece weight for single lambs and about a third for the twin lambs. The estimated values of the regression coefficients for single and twin lambs did not show any real difference. The regression lines derived from the above analysis are shown in Figure 6 where it can be seen that although the regression lines are nearly parallel, twins have a lower fleece weight than singles at the same body weight. This could be the result of a lower weight of wool per unit of the fleece bearing area, or of a different fleece bearing area of the two birth ranks at the same body weight. This latter could be the result of more wool on the face or on the extremities of the single lambs, or of a different relationship between body weight and surface area. This last possibility is also suggested by the difference in the relationship of weight to height at withers between the birth rank groups (Section III, E3, (i) b)

This diagram also shows (Fig.6) that there was a tendency for the N-type single lambs to have a greater fleece weight for their body weight than the ordinary singles, although the difference could not be demonstrated as a real one. The presence of larger differences between the phenotype groups of the twin lambs may be associated with the higher halo hair 'coverage' of the twins shown in Section III, C2 (ii) which could lead to a larger difference in adult fleece type.

Fleece Weight - Body Weight Relationships for Lambs

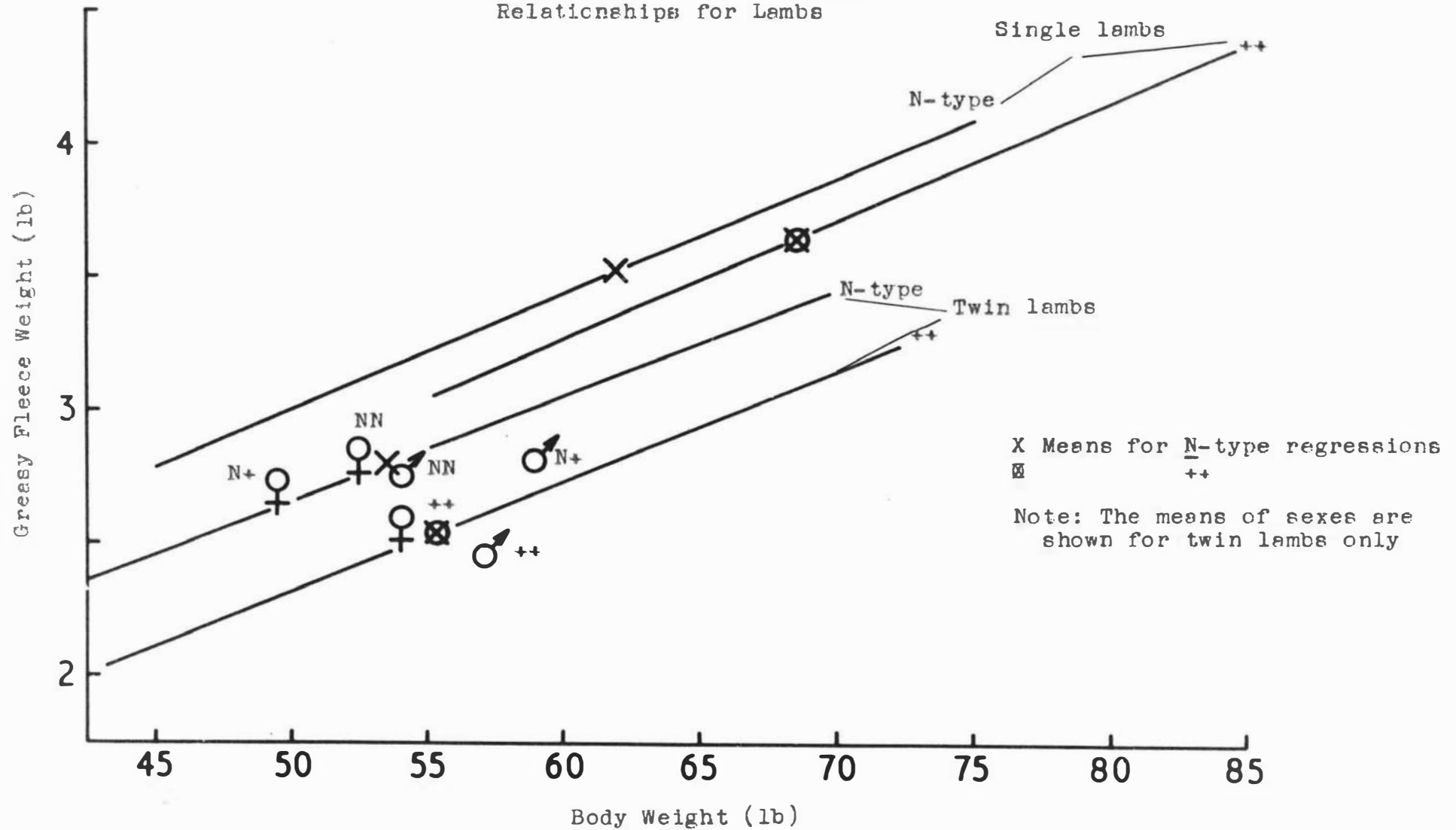


Table 48
Analysis of Covariance of Hogget Fleece
Weights Corrected for Body Weight

Source	d.f.	Residual	Mean Square	F	P
Total	65	129.616			
Within groups	64	123.718	1.903		
Difference	1	5.898	5.898	3.10	<0.1

Regression coefficient within groups 0.094 ± 0.0048

All measurements are in pounds.

Table 49
Hogget Fleece Weights Classified by Genotype

Genotype	NN	N+	++
Fleece weight	9.44	9.87	9.65
Fleece weight at the same body weight	9.87	9.90	9.19

All measurements are in pounds.

The means for male and female lambs have been plotted for the different genotypes in the twin groups and these show that there was a consistent tendency for ewe lambs to have a higher fleece weight for their body weight. This is shown by the position of the means relative to the appropriate regression line; the means for females are above and those for males below the regression line in each case. The reason for this is obscure at this stage.

2. Ewe hoggets.

Only a few ordinary hoggets could be kept to 15 months of age and it was considered that the numbers of each birth rank group were insufficient to estimate regression coefficients within these groups. Singles and twins have therefore been taken together for this analysis.

The observed and corrected means of the fleece weight are shown in Table 49, where the correction is for body weight. It can be seen that the differences are between N-type (NN and N+) and the ordinary hoggets. The value of the regression coefficient within these two groups was used to obtain the corrected values. There is a difference of about 0.7 lb (Table 48) in favour of the N-type sheep at constant body weight. It is possible that differences in the yield of clean wool could account for a part of this, but the yield of a coarse wool is likely to be greater than a finer one in which case the clean fleece weight differences would be greater.

Fraser (1952 b) reports no difference in fleece weight between N-type and ordinary sheep, this being required for his theory of competition between follicles; however, no corrections were made for body weight and details of the plan of experiment are not given. From the regressions and means

shown in Figure 7 it can be seen how consideration of fleece weight alone could lead to the conclusion that no differences existed; since the difference in body weight compensates for the difference in fleece weight. It could be argued that these differences disappear when the animals are older, but by this time the ewes will have been mated and lambing performance would have to be taken into account. Because of the effects of lambing on wool growth, the consideration of fleece weights prior to the first mating is a better guide to fundamental relationships between fleece type and fleece weights.

Figure 7 also shows the means of the different genotypes and birth ranks and it can be seen that the twin lambs still tend to show larger genotypic differences than the single lambs. The N+ twin lambs which were reared as singles (4 animals) appear to be completely anomalous as they had a far higher corrected fleece weight value than any of the other groups.

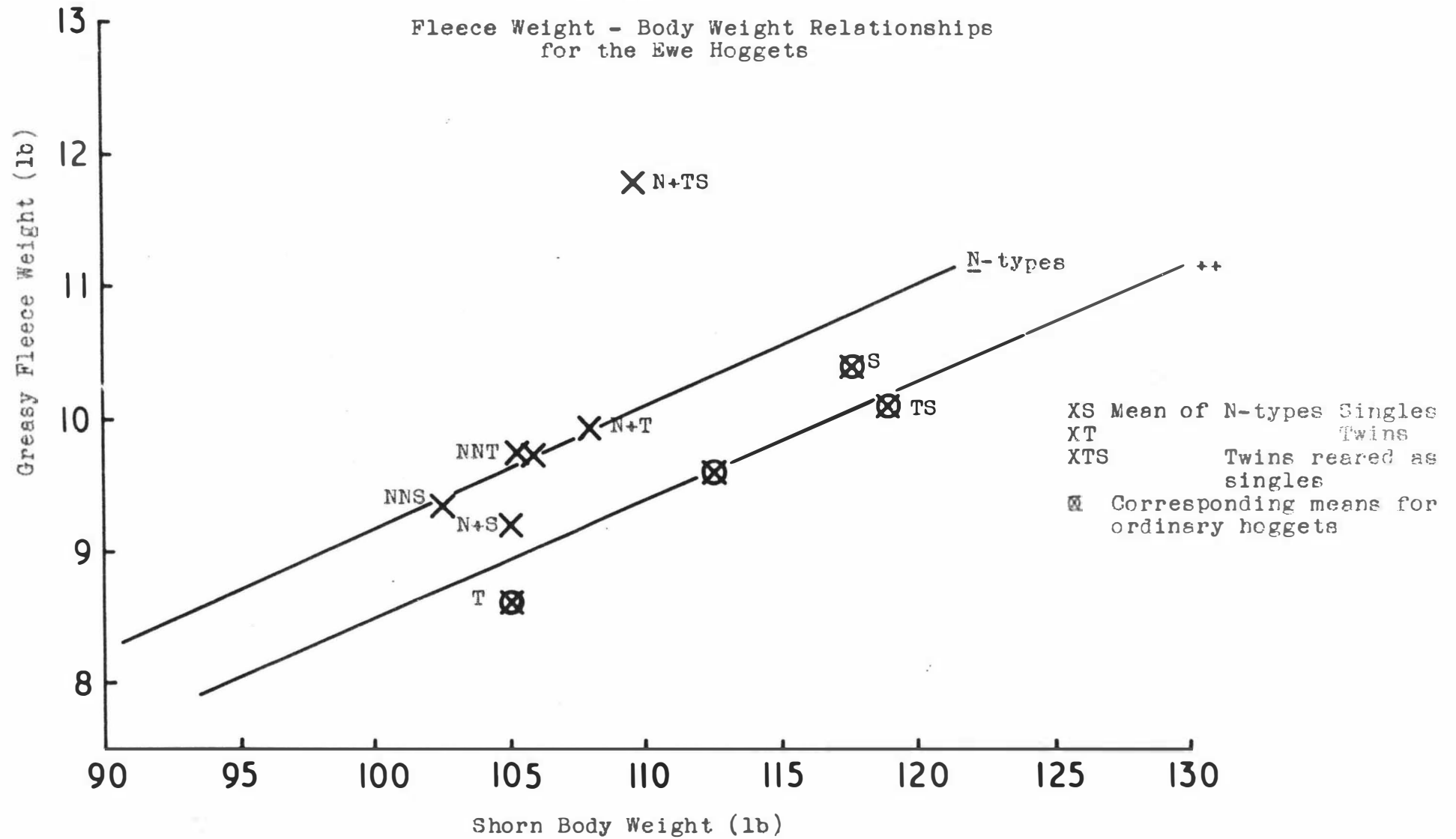
As all the animals were ewes, sex differences cannot be investigated but otherwise the results are similar to those obtained for the fleece weights of the lambs only with smaller differences relative to the greater average fleece weights.

Summary of Section V, A.

- (1) The N-type sheep showed a greater greasy fleece weight at constant body weight than the ordinary sheep.
- (2) There was a greater difference between the twin than between the single lambs and possible reasons for this are discussed.
- (3) It is considered that real differences in clean wool weight were likely to have occurred.
- (4) It is possible that ewe lambs had a greater fleece weight than ram lambs at the same body weight.

Figure 7

Fleece Weight - Body Weight Relationships
for the Ewe Hoggets



B. The Preliminary Biometrical Characterisation of the Hogget Fleece

1. Fibre diameters and proportions of fibre types.

The samples examined were those taken in March from the standard side position on the ewe hoggets. The simplest technique for examination would be by means of the medullometer test, for 'hairiness' was the principal fleece characteristic being studied. Some results from the medullometer test have been quoted for ram lambs in relation to their body weight in Section III, F 4. Some disadvantages of this test have been pointed out by Ross (1950) for samples of high medullation but as used here it was suitable for comparative work.

The major disadvantage for the present analysis lies in the interpretation of the results because the figure for percent medullation will depend on the length of the fibres, the diameter of fibre and medulla and also the proportions of the fibres which are medullated. In addition because of the different rates of growth of the fibres the result will vary with the time of sampling. — In the results here this will not be of importance for a particular set of samples taken together, as all the animals were shorn at the same time.

The medullometer test results showed higher values for the N-type sheep, NN being greater than N+. This would be expected on the known characteristics of their fleeces. However there was also a difference between single and twin lambs as the latter had a consistently higher value. As stated above this could result from various factors and the first of these to be considered was staple length. Figure 8 shows the mean values of the staple lengths for singles and twins

of each genotype plotted against the percent medullation. It can be seen that the higher test results are associated with greater staple lengths. It is not clear whether this association is a biological one or whether it arises at least in part from the nature of the test.

Therefore it is necessary to examine further the components of the medullometer test; i.e. fibre and medulla diameters and the proportions of medullated fibres.

Fibre and medulla diameters were measured by means of a projection microscope (X500) in which a millimetre scale resulted in units of 2 μ . This is the basic scale for all fibre and medulla diameter measurements in this thesis, but the tabulated results presented have been converted to μ for convenience in comparison with other work. The fibres on which measurements were to be taken had previously been sorted by their length into two main groups and snippets were taken from the middle of these fibres which were then immersed in benzol for measurement. No swelling of the fibres during the measurement time was observed as a result of the use of this medium which gave a strong contrast between the fibre and the medulla in the projected image. The refractive index of benzol falls within the limits suggested by the International Wool Textile Organisation for suitable mediums. The Becke line was used for the measurement of the fibre diameters (Anon 1952).

The previous sub-division of fibres into two groups, 'fine' and 'coarse', on length and macroscopic appearance, conveniently turned out to be also one of medullated and non-medullated fibres for all but a few animals. The main reason

Table 8

Relationship Between Staple Length
and Medullation Percentage

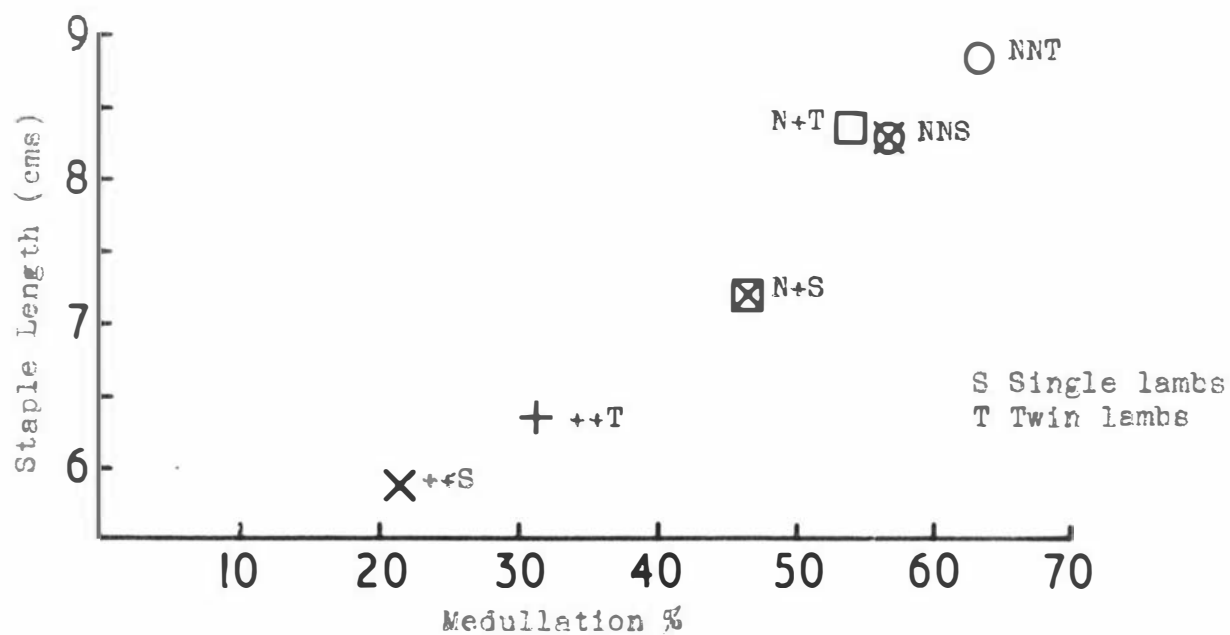
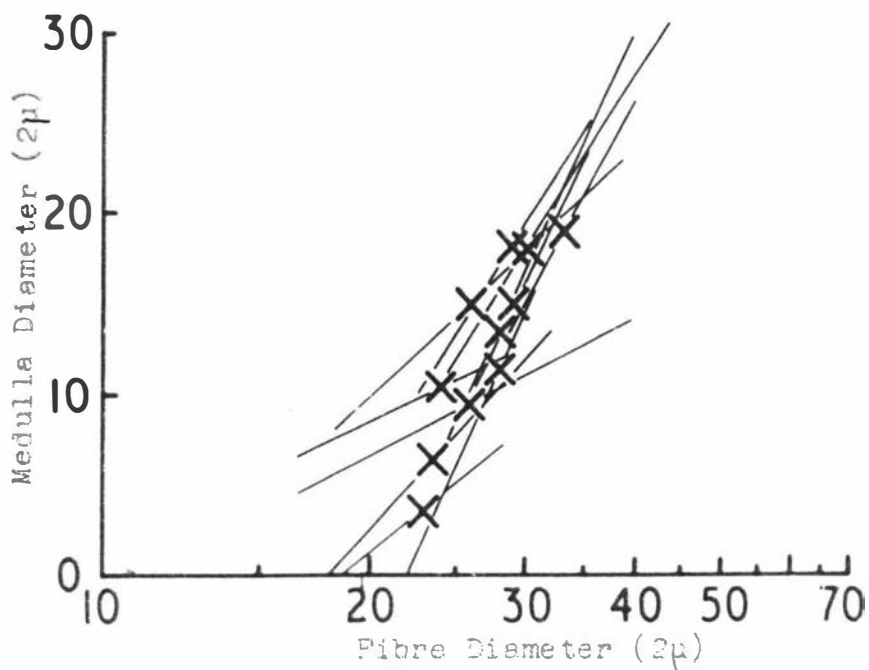


Table 10. Relationships between Fibre and Medulla Diameters
for Individual Sheep



for the use of this classification was to reduce the technical work as fewer fibres were needed for measurement. However, in addition, fibre diameters of samples from three sheep of different wool types were determined and the frequency distributions plotted. The number of 'coarse' and 'fine' fibres were also determined and the distributions in Figure 9 have been weighted accordingly. The total numbers of fibres counted and measured have been shown in each case. The distributions are those which might be expected from a review of other work and sheep number 191 in particular illustrates that the treatment of the diameters as two distributions is likely to be more efficient than the use of one overall mean and variance.

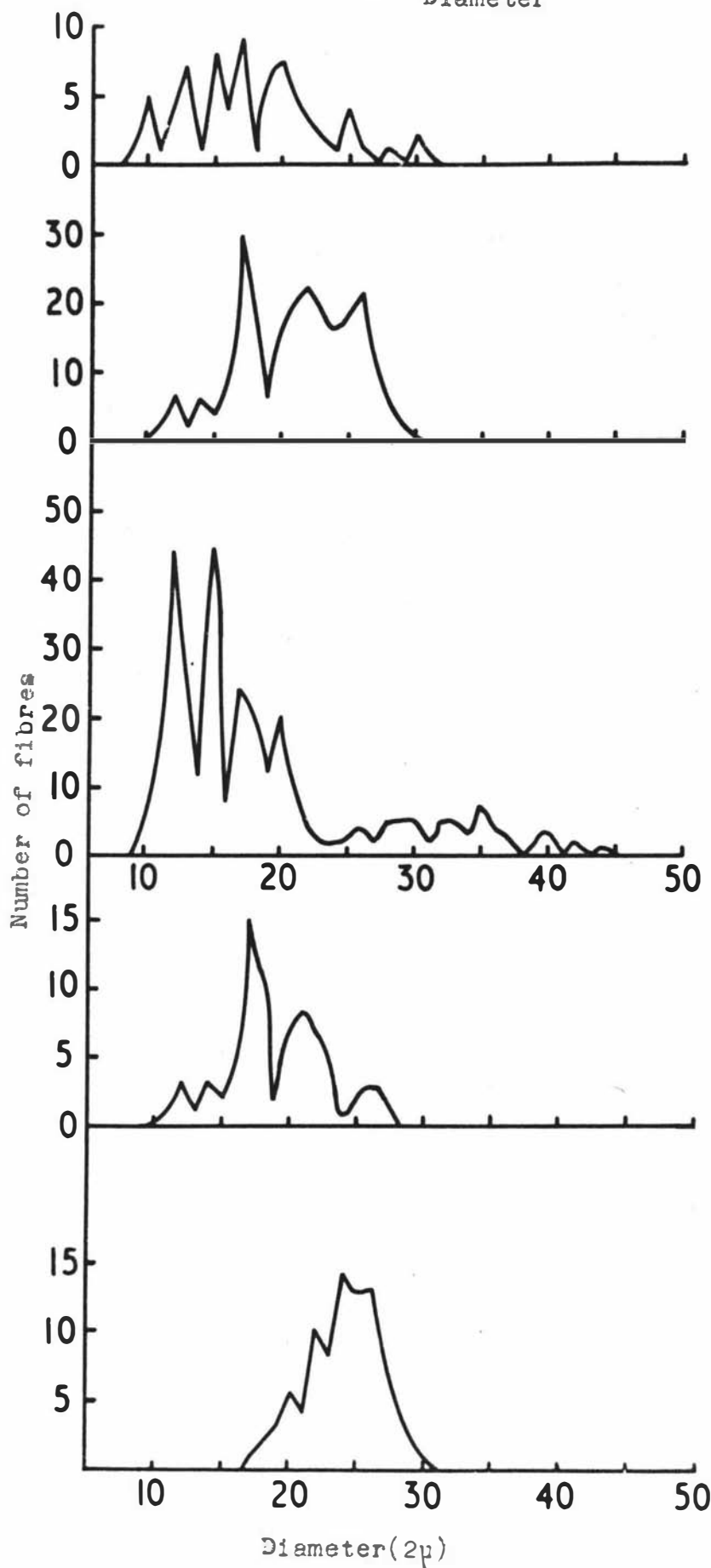
It was decided, therefore, to measure the proportions of fibres in the 'coarse' and the 'fine' groups and obtain the mean diameters of these groups separately. Thus instead of the overall mean fibre diameter, there are three variables to be considered: the 'coarse' fibre diameter, the 'fine' fibre diameter, and the percentage of 'coarse' fibres. About 300-400 fibres were counted in order to obtain this percentage.

The primary purpose of this section was a preliminary examination of fibre and medulla diameter relationships and also to consider various techniques. In addition the likely relationships of fibre diameters with other factors and also differences amongst genotype and birth rank groups, were required in order to plan the more detailed investigation the following year.

As large differences were present and as the variation amongst the sheep in fibre diameters was very large, it was found that the measurement of only ten fibres in each of the 'fine' and 'coarse' groups was sufficient. This is considerably less

Figure 9

Distributions of Fibre
Diameter



Weighted Distributions

Sheep 306 ++
No coarse fibres
70 fine fibres
measured

Sheep 276 ++
80 coarse and 80 fi:
fibres measured

Coarse/Fine 80/160

Sheep 191 N+
60 coarse and 60
fine fibres
measured

Coarse/Fine 60/240

Actual Distributions

Sheep 276
80 fine fibres

Sheep 276
80 coarse fibres

Table 50

Number of Hoggets Sampled in Each Sub-class

Genotype	NN	N+	++
Singles	10	13	5 (7)
Twins	6	19	6 (7)
Twins as singles	1	4	2 (3)

The figures in parenthesis are the totals for the 'fine' fibre diameters only, as a few of the ordinary lambs had no fibres classified as 'coarse'.

Table 51

Mean Values of the Various Fibre Characteristics Measured

The percentage of coarse fibres

Genotype	NN	N+	++
Singles	26.4	20.4	9.5
Twins	26.9	25.1	20.9
Twins as singles	34.7	29.5	18.6

The diameter of the coarse fibres (μ)

Singles	57.8	52.8	47.8
Twins	57.8	57.8	47.8
Twins as singles	51.4	56.4	41.8

The diameter of the fine fibres (μ)

Singles	30.2	31.6	36.0
Twins	31.8	30.4	34.0
Twins as singles	28.6	34.4	32.2

The diameter of the coarse fibre medulla(μ)

Singles	31.6	25.8	36.0
Twins	29.2	30.4	15.2
Twins as singles	21.4	25.8	13.8

than that normally used but, as the results show, under the circumstances described above it was sufficient to provide information for the planning of the following year's work. In the second part of this investigation the technique was improved and data on the accuracy of the results obtained and there is little doubt that the division of the fibres from coarse wooled sheep into sub-groups for measurement of diameter, both decreases the number of fibres required for measurement and also increases the meaning and value of these results.

The sub-class numbers involved and the means of the various measurements are shown in Tables 50 and 51. Because of the range in the variances of the 'coarse' fibre diameters a logarithmic transformation was used for estimation of the means and for the analyses. A similar transformation was used for the percentage of the 'coarse' fibres. The differences in Table 51 tend to be between the N-type and the ordinary sheep, although for single lambs the homozygous N-types (NN) tend to have larger values of 'coarse' fibre diameter, medulla diameter and percentage of 'coarse' fibres. Twins tended to have a higher value for the percentage of 'coarse' fibres for all genotypes but differences for other variables are not consistent. The higher 'fine' fibre diameter value for ordinary sheep suggests a lower overall variation in diameter of fibres from these.

Some preliminary work on the interrelationships of these variables based on all available data is shown in Table 52. Except for the ordinary twins the correlation between the percentage of coarse fibres and weight at 30 days was consistent within the sub-groups but not significant with the small numbers involved. Because of the lack of a

Table 52

Correlations Between Wool Characters

Correlations with the diameter of coarse fibres:

Variable	d.f.	r	P
Body weight	60	+0.026	n.s. (weight at time of
Fine diameter	60	+0.135	n.s. sampling)
% Coarse fibres	60	+0.128	n.s.
Staple length	57	+0.588	less than 0.001

Note: n.s. not significant p greater than 0.1

Correlations with the percentage of coarse fibres:

	d.f.	r	P
30 day body weight	60	-0.269	less than 0.05
'Coverage' of halo-hairs*	11	-0.671	less than 0.02

* N+ single lambs only. As the majority of twin lambs had almost complete 'coverage' the distribution was such that it was not possible to calculate a valid correlation for this group.

suitable grading which showed variation within heterozygous and homozygous animals on the same scale, further examination of the connection between birth coat and adult fleece was left until the second part of this investigation.

If these results are considered in the light of Schinckel's (1952) results for Merino sheep in Australia and Galpin's (1948) for the Kent Romney Marsh then a basis for future work can be suggested. These authors found that poor growth in the early stages of post-natal life had effects on the composition of the adult fleece, the former author finding that poorer growth led to a penalising of the formation of secondary follicles. In the sheep being considered here, both twins and N-types showed slower growth than normal single lambs over the first 30 days of post-natal life, twins in addition being penalised by their pre-natal environment. The longer staple length and higher percentage of coarse fibres in wool grown by twin lambs is consistent with a lower fleece density for these animals and the negative correlation between the percentage of coarse fibres and the weight at 30 days is consistent with a penalisation of secondary follicle formation over the first 30 days of post-natal life. The effect of 'coverage' which is likely to be negatively associated with actual halo hair density, (negative because of the nature of the scale) suggests also that the larger follicles producing halo hairs persist in the production of coarse fibres after these halo hairs have been shed. Alternatively, their presence may also affect the formation of secondary follicles either pre-natally or post-natally, the former being suggested by Dry's 'pre-natal check' discussed in the review of literature.

Table 53

Test of Homogeneity of the Regressions of
Medulla Diameter on Fibre Diameter

Source of variation	d.f.	Mean Square	F
Joint regression	1	989.151	greater than 100***
Between regressions	9	19.166	3.43**
Residuals	80	5.572	

*** P less than 0.001

** P less than 0.01

2. The relationship between fibre and medulla diameters.

The possibility of a relationship between diameters of fibres and that of their medulla is suggested by some of the work discussed in the review of literature. The general relationship between a coarse fleece and hairiness is well known, but the details of this relationship in terms of individual fibres for a particular sheep and, if such a relationship exists, how it varies between sheep, have not been investigated in detail.

In the present material a strong relationship was found between fibre and medulla diameters and an analysis has been made below to determine how this relationship varied between sheep and what factors might be affecting it.

Ten sheep were chosen at random with the restriction that all genotypes should be represented and an analysis made to test the homogeneity of the regressions of medulla diameter on fibre diameter. Table 53 shows that there were differences amongst these regression values but that a considerable portion of the variance was accounted for by the joint regression. These regression lines have been plotted in Figure 10 where it appears that the heterogeneity arises from those sheep producing fibres with little medullation. In such sheep the medulla was intermittent in some fibres and an equivalent continuous medulla diameter was estimated from the length of fibre observed (Ross 1950). For this reason results for the values below 20 (40 μ) on the fibre diameter scale must be considered with caution. In addition the use of a logarithmic scale for fibre diameter and an arithmetic one for medulla diameter means that a large difference in the regression value may have

little biological significance. The use of such scales has an advantage for this comparison as a straight line fit would not be the most accurate on other scales.

It was concluded therefore, that, apart from those fibres with small or intermittent medulla, then for any sheep there was a nearly constant relationship between medulla diameter and the fibre diameter and that this relationship, apart from a constant term, was the same for all sheep. The possible difference in constant term refers to the possibility that different sheep may have a different medulla diameter at a given fibre diameter although an increase in this given fibre diameter will lead to the same increase in medulla diameter for all sheep.

Auber (1950) suggests that medullation is a result of the failure of the necessary precursors for the formation of cortical cells to diffuse to the centre of the papilla where the medulla cells are formed. In addition, he showed that the mitotic rate in the papilla of those cells which would form the medulla, was lower than that of those which would form cortical cells.

Bullough (1952) has shown effects of "available energy" on the mitotic rate in the epidermis of the mouse and this suggests another possible limiting factor whereby medullation could be affected. The idea that medulla results from the failure of energy metabolites or keratin precursors to penetrate the papilla is supported by the fact that increase in fibre diameter after a certain stage takes place almost entirely by increases in the size of the medulla, i.e. the cortex can only increase up to a certain limiting thickness. If there was a lower concentration of precursors or metabolites available then it might be expected that there would be greater medullation of a fibre of a given diameter. Body weight has been shown to affect fleece

Table 54

Partial Regression Coefficients of Medulla Diameter(μ)
on Log Fibre Diameter (μ) and Body Weight(lb)
at the Time of Sampling

Variable	Coefficient	Standard Error
Log fibre diameter	166.45***	12.864
Body weight	-0.224**	0.080

*** P less than 0.001

** P less than 0.01

Note: Calculations were made directly on the diameter observations which were on a scale of two microns. Throughout this thesis the resulting regression coefficients and standard errors have been presented on a scale of one micron by means of a simple conversion.

Where the independent variable concerned is on a logarithmic scale there is no change required as the multiplication factor becomes an additive one and therefore affects only the constant term.

When the independent variable only is on a scale of two microns the regression coefficient and standard error must be multiplied by one half.

When the dependent variable is on a scale of two microns then a factor of two is used for multiplication.

In the multiple regression cases these rules also apply as where fibre diameter has been used as an independent variable it is on a logarithmic scale and the variances, and covariances with the other independent variable will not be affected.

The derivation of these conversions is by consideration of the variances and covariances and residual terms when the various components are changed according to the scale.

The diagrams illustrating the various coefficients are based on the original scale of two microns as they are only intended to show the relationships concerned and the actual values can be obtained from the tables.

weight, and although this may partly be a surface area effect it may for present purposes be taken as a rather crude measure of the level of energy or 'precursors' available.

A multiple regression analysis has therefore been made of medulla diameter on fibre diameter and body weight at the time the wool samples were taken. The partial regression coefficients were calculated within the genotype groups and are shown in Table 54. There were no differences amongst the genotypes and the coefficients are therefore representative of all the genotype groups. The significant partial regression of medulla diameter on body weight shows that lower body weights are associated with greater medulla diameter at constant fibre diameter, i.e. with less cortex. This suggests that the ideas presented above are worthy of further investigation.

This relationship of body weight also suggests an explanation for the observation of Burns and Clarkson (1949) that the medulla diameter was not correlated with the 'coarseness of fibre' as in a comparison of two sheep, one had a fine medullated fleece and one a coarse non-medullated one. It is possible that the net result of a lower body weight could be a reduction in overall medullation as a result of a concurrent lowering of the fibre diameter. This relationship is considered in the second part of this thesis where more data is available.

Summary of Section V, B.

The variables concerned with the type of fleece have been briefly examined to obtain preliminary information as a basis for further investigation. These results indicate:

- (1) Fibre diameter determinations for coarse woolled sheep are likely to be more informative if the multi-modal distribution is considered in its various parts.
- (2) There is evidence that consideration of N-type - ordinary and twin - single differences in an experiment to examine the inter-relationships of birthcoat type, early lamb growth and hogget fleece type would throw further light on those problems originally put forward.
- (3) There is a strong relationship between fibre diameter and the diameter of the medulla, and this relationship varies by a constant term between sheep according to their body weight.

VI. DISCUSSION OF PART ONE

The overall purpose of this year's work was to make as wide an investigation as possible under the existing facilities in order to determine the likely pleiotropic effects of the gene N and the nature of the problems connected with N-type sheep.

The only directly formulated problem was whether the N-type flock, as the result of the presence of the gene N, produced lambs with carcasses as commercially useful as the ordinary New Zealand Romney. This problem was approached with the initial null hypothesis that there was no difference of growth between the various groups of lambs in the matings set up. The null hypothesis was not accepted under the conditions described and no difference was found in the carcasses which could not be attributed to growth effects of N. Carcasses of the N-type carpet wool flock could not be examined but results from body measurements suggest that the carcass conformation might be poor for these animals even if they had showed faster early growth.

More detailed economic considerations are not the concern of this thesis, but from this point of view and from that put forward in the introduction of the possible use of these sheep for investigation in to the cause of certain genetic correlations, it was clear from these results that further investigations should involve fleece characters and that a preliminary investigation on such characters was required for the planning of future work.

This preliminary investigation showed that both these points of view could be satisfied by treating the problem as one of pleiotropy (as defined earlier) this probably being

one of the main causes of genetic correlations. Simple cases of pleiotropy are rare, for as the characteristic being examined becomes further in time and space from the original effect of the gene, the greater are the inter-actions resulting from other effects, both genetic and environmental.

On the evidence obtained so far, various hypotheses can be put forward as to the mode of action of the gene N. As in the majority of cases which have been examined by other workers, mainly in the mouse, the initial action occurs early in pre-natal life and is therefore capable of having effects on many subsequent developmental stages.

From this investigation there is little information on the pre-natal development or action of the gene. At birth, the N-type lamb has a large number of halo hairs resulting from larger primary follicles (Fraser, Ross and Wright, 1954), (Carter 1955), little being known of their numbers per unit area or their relationship to the secondary follicles. Without information on these variables it is not possible to relate such observed fleece characteristics at birth to characteristics of the rest of the animal; it is, however, possible to suggest various hypotheses at this stage.

Horn lumps, which later develop into the horns that are considered a pleiotropic effect (Dry and Fraser 1947), are observed at birth in most male animals on macroscopic examination. It is possible that the determination of cells which will later lead to the formation of horns, occurs at the same stage of growth as the initiation of the majority of the primary follicles, and that the formation of horns and of large primary follicles are related developmentally. A second pleiotropic effect that had been suggested was the longer dorsal thoracic vertebral

spines and the investigation described in Section III G suggests that these are a mechanical or physiological result of the presence of horns and will only result if the horns are present. The horns and these longer spines can, therefore, be provisionally considered as one branch of the developmental sequences in the pleiotropic action of this gene.

The brown pigmented fibres on the back of the neck at birth are usually halo hairs and again although there is no knowledge of the physiological processes involved, similar occurrences in other breeds of so-called 'red kemp' makes it a reasonable suggestion that this is a secondary effect of the larger primary follicles.

These effects were not examined further in this thesis, partly for technical reasons and partly because it was considered that the other effects now to be discussed were more important at this stage.

Galpin (1936) advances a theory relating the size of a follicle to the relative rate of growth of underlying tissues at the time of initiation of the follicle. This theory requires considerable further substantiation but it does suggest a mechanism whereby the size of the follicle is the result of underlying growth processes rather than direct determination by the cells forming the follicle itself. Post natal growth effects have been shown in this thesis to be associated with genotypes carrying the gene N. One possible hypothesis that must be considered at this stage is that the gene action is basically one on the growth and development of the animal as a whole, with the birthcoat type and subsequent effects on the fleece as secondary ones. This is an inexact idea at this stage as 'growth and development of the animal' is a somewhat

vague term, but available knowledge does not permit of more exact formulation. Evidence for this hypothesis is slight as there were no obvious differences between the animals at birth which could be related to birthcoat type; if it is true, however, then the growth differences obtained under the conditions of this experiment should be repeatable under different environmental conditions, a growth effect of this type being presumably little affected by the normal ranges of environment.

Alternative hypotheses can be based on the idea that the initial gene action observable morphologically is on the size of the primary follicles. These then produce large coarse fibres and the subsequent growth effects are then the result of the birthcoat type of the animal. This could occur in two main possible ways: the first could be the result of interaction of the climate with fleece type. The insulating properties of a 'hairy birthcoat' are presumably different from those of the ordinary birthcoat of the New Zealand Romney and effects on the metabolism of the animal are not unlikely. Again, little is known of these possible effects but Fletcher and Reid (1953) report a lowering of body temperature by about 1°F and a fall in respiration rate when shorn lambs were compared with unshorn lambs at a high environmental temperature. These results were similar to some obtained by the author for another purpose using adult sheep and with a temperate environment. Leveck (1948) reported a marked difference in weight gain of 0.31 pounds per day for shorn lambs contrasted with 0.12 pounds per day for unshorn controls. These results indicate that effects of fleece type on growth as a result of different insulating properties of the fleece are not unlikely and if this is so then these effects should vary from year to year and the results obtained for this year should not necessarily be repeatable.

A second way in which fleece type could affect growth is by the demands made by the follicles on the available precursors in the blood stream. To what extent a follicle is controlled by the endocrine or other systems is not known; if there is any form of direct control then the metabolism of the follicle and the consequent formation of wool will be co-ordinated with the general metabolism of the animal. If, however, the follicle is mainly self regulating and controlled only by the level of the various required metabolites in the blood stream, then the presence of a larger follicle with a larger circumference and area for diffusion could lead to the removal of substances required for other metabolic processes and, if these were at a critical level, result in a retardation of the general growth of the animal.

There is little evidence for this hypothesis on the work done so far; there were fleece weight differences but the fact that they were greater for the twin lambs which showed less growth differences, does not support the idea. Barnicoat et al (1951) showed a higher milk production for ewes suckling single N-type lambs for the second to fourth week of life. This probably reflects the lamb's requirements as single lambs do not at first take all the milk that can be produced (Wallace 1948, and other authors). However this comparison is confounded with seasonal effects and cannot be considered further.

The main virtue of the hypothesis at this stage lies in future uses of N-type sheep for research into problems associated with such ideas. There could be environmental interactions according to the feed available and growth differences would not be necessarily repeatable under this hypothesis. A simple general test for it would be the comparison of N-type

and ordinary sheep under two planes of nutrition. A combination of these last two hypotheses is also possible to explain results so far.

If the causes of the observed growth differences are ignored there are still further pleiotropic effects to be considered. These concern the effects of growth and of the birthcoat type on the fleece of the fully developed animal. Schinckel's and Galpin's results have already been quoted and the preliminary results on the N-type sheep have been given in the previous section. These indicate that the growth of the animal can affect the numbers of new follicles formed and hence the final follicle proportions and the fleece density (follicles per unit area). The fleece density will also depend on the expansion of the skin, which is directly related to body growth. Birthcoat type is related to follicle size which is variable over time, and this also could have a direct effect on follicle proportions or the proportions of 'coarse' and 'fine' fibres. The gene 'N' may also affect these characters indirectly through growth by one of the methods suggested above, and further effects could arise from the direct action of the environment on growth as shown for instance for pre-natal environment, by the differences between single and twin lambs at birth.

Effects of growth in terms of body weight have also been shown on the medullation of the fibres where this occurs and further investigation was required to confirm this.

The rest of the investigation in the second part of this thesis arises directly from this discussion, with the addition of the necessary collection of objective data on the birth coat.

PLATE II
An Ordinary Ram Lamb and an N-type Ram Lamb
(after shearing) from the Second Year's
Experiment



Ordinary

N-type

PART TWO

A STUDY OF THE RELATIONSHIPS BETWEEN BIRTHCOAT TYPE AND THE GROWTH OF THE LAMB, AND THE SUBSEQUENT FLEECE TYPE

VII. INTRODUCTION

The discussion of the first year's work showed the need for the examination of three main topics in more detail.

These were:-

- (1) Determination of whether the differences in growth in weight occurred under different seasonal and other environmental conditions.
- (2) Examination of the relationships between birthcoat type, growth of the animal and the changes in the fleece over the first six months of post-natal life.
- (3) The obtaining of basic data by measurement of the birthcoat characteristics of the N-type Romney relative to the ordinary New Zealand Romney with reference to possible effects on the animal of the pre-natal environment.

As the main interest now lay in N rather than in the N-type carpet wool flock, comparisons between heterozygous N-type and ordinary Romney sheep only, would lead to a simplification of the analyses and of their interpretation. Knowledge from this simple comparison could then be used in any future experiments on commercial or other aspects of the homozygous 'carpet wool' flock.

The first of the above objectives could be approached in a similar way to the previous work with more attention to controlled conditions for the ewes from the time prior to mating until the weaning of the lambs, and also with more frequent weighings of the lambs over those periods when differences of growth rate had previously occurred.

The second objective was primarily based on the hypothesis that differences of post-natal growth, however caused, and also differences of birthcoat type, could in turn lead to differences in the number of fibres added to the fleece from secondary follicles. The work of Galpin (1948) and Schinckel (1953) suggested that this could, by altering the density of the fleece, affect certain characteristics of the fibres of that fleece. In addition, differences in medullation associated with the weight of the animal and the diameter of the fibre had been shown to exist and confirmation of such differences and their relationships was required.

The third point was essential to this second point if differences in fleece development were shown to be associated with birthcoat type. Possible differences of halo hair density between single and twin heterozygous lambs have been shown in the first part of this thesis, and these could also lead to differences in the mature fleece. In addition it was desirable for all purposes to have measured results on birthcoat types to use in conjunction with the eye gradings and for interpretation in terms suitable for comparison with work on other sheep breeds.

These three objectives fitted into the study of pleiotropy by consideration of:

- (1) Pre-natal effects deduced from differences amongst new born lambs.
- (2) Post-natal growth effects following from these differences or from more direct effects closer to the original gene action.
- (3) The chain of events arising from either or both of these causes and leading to the observed differences between the heterozygous and ordinary sheep at five months of age.

Table 55
The Mating Plan

Mating Group	I	II
Parental genotypes		
Ram	++	N+
Ewes	25N+	25++
Lambs expected		
N+	12	12
++	12	12

VIII. THE PLAN AND METHODS OF THE EXPERIMENT

A. The Matings.

The N-type animals were those used in the previous year's experiment. The ewes were those used in mating group III supplemented by a few from mating group II. The ram was that used in mating groups III and IV. The 25 ordinary ewes and the ram were made available from another experimental Romney flock. All the ewes were six or seven years old except for a few N-type ewes which were required to make up the numbers.

Various possible mating plans were considered, but those in which genetic effects of the rams and the ewes and also environmental effects associated with the ewes could be estimated, were rejected because of the small sub-class numbers which would be involved. However the previous year's work had showed the genotype of the ewe to be relatively unimportant compared with that of the lamb and the final plan used confounds possible pre-natal and milk production effects of the ewe on the lamb with the genetic differences of the rams and ewes. The mating plan is shown in Table 55 where it can be seen that it is a straightforward reciprocal mating relative to N. For this reason the difference between mating groups will be called the reciprocal mating effect to distinguish it from the mating group effects in the previous part.

B. THE DATA COLLECTED

1. Before lambing.

The ewes were joined with the rams after a short 'flushing' period under uniform conditions. The dates of mating for

individual animals were noted to find if there were any differences in gestation period associated with the lamb's genotype or with ^{the} reciprocal mating effect.

When the rams were removed the ewes were run in randomised groups for the rest of the experiment. The ewe's weights were recorded at intervals until the lambs were weaned, the exact intervals being based on practical considerations. A wool sample from the side position and a measurement of the height at withers were also made.

2. During lambing.

The weight, birth rank, sex, phenotype, halo hair grading and date of birth of each lamb were recorded in the paddock within a maximum of 20 hours after birth and a wool sample was taken from a tattooed area on the loin position for determinations of halo hair and total densities and also of fibre and medulla diameters.

3. During the growth of the lamb.

The weight and height of withers of each lamb were recorded once a week for the first six weeks thus covering in detail the period when the growth differences were previously observed. A further wool sample was taken at three and six weeks of age to determine changes in and relationships with, those characteristics measured at birth. This six weeks period covers that of the maximum addition of post-natal secondary fibres in the Romney sheep (Goot 1941)

After this period weighing was at less frequent intervals and the lambs were weaned about four weeks before being shorn. Greasy fleece weights were recorded at shearing and body weights taken the previous day and two days later.

The experiment ended eight weeks after shearing, at which time the final wool samples were taken. These would represent the first growth of the hogget fleece after all or nearly all follicles would be laid down and growing fibres.

4. Wool sampling methods.

If a wool sample is taken from a measured area of skin and scoured and weighed, then weighing a known number of fibres will give an estimate of the number of fibres in that area or per unit area. In addition the sample can be used for diameter and medullation determinations, fibre type counts and any further fibre measurements required. This technique has been used by various authors for lambs but little accurate information is available on the errors involved under the particular field conditions likely to be encountered in this experiment. It was therefore assumed that the lambs were bilaterally symmetrical and duplicate samples were taken on either side of the backbone just behind the last rib. These were processed as separate samples so that an analysis of error could be made at any stage of the determination of the several variables from which fleece density was calculated.

As the fibre types are identified by their tips (that is the pre-natal portion of the fibre) and also as Rudall's (1935) and Coop's (1953) work suggested the possibility that sampling affects wool growth, the same area was not sampled twice but the area immediately adjacent was used. The areas were about $2 \times 1\frac{1}{2}$ cms. It was originally intended to use a balanced incomplete block or similar experimental design so that this position effect, the duplicate sampling effects and the time of sampling/^{effects} could be estimated. However there was a possibility of less than three

lambs in a sub-class and an additional difficulty of non-orthogonality of the sub-classes so that a satisfactory design could not be achieved without waiting until all the lambs were born, when it would be too late to obtain the sample at birth.

The final design adopted involved sampling the loin position (Henderson 1953) at birth on all the lambs. At six weeks the sample was taken immediately to the rear, while at three weeks the sample was adjacent to the boundary of the other two, on the ventral side. This design makes it impossible to distinguish between effects resulting from position and those from the time of sampling. However the latter are clearly greater than the former which in all probability would be too small to be detected by the methods used here.

The technical details of sampling are described in the section below and methods of treating the samples are dealt with in conjunction with the analyses of the errors involved.

The samples after shearing were taken so as to cover the positions of the birth and six weeks samples. Shedding of the birthcoat fibres was examined after three weeks to ensure that premature shedding did not affect the results.

C. Technical and Husbandry Details

The experimental area where the sheep were grazed has been described by Clarke, Barton and Wilson (1953). The area is divided into acre paddocks and the sheep were moved once a day over a five day rotation. For mating, the sheep had to be divided into the two mating groups and these groups were run on paddocks with fertiliser treatments which had been shown over ten years of trials to have no differential effect

on the sheep grazing the pasture. No differences in weight gain were observed between the groups over this period.

Mating dates were obtained by ~~the~~ noting those ewes marked by the ram for which purpose the ewes were identified by a stencilled number on the flank. Ewes marked when not in oestrus could be identified by their returning to the ram when true oestrus occurred.

After the rams were removed, the ewes were randomised into two groups which were rotationally grazed such that both random groups covered all the paddocks in one period. This rotation was continued during lambing and ewes that had lambed were left in the paddock and rejoined the main group when they were again in that paddock five days later.

The data from the newborn lambs was collected every morning. Halo hair gradings were checked by the assistant who had graded the previous year's lambs. The wool sample was taken by putting the lamb over one's knee to ensure a constant position of the lamb and ease of sampling. A stencil was used to mark the sampling squares on the wool of the animal and a hypodermic needle used to mark the skin with tattoo. The use of an ordinary tattooing instrument was not satisfactory at this stage because the tattoo was removed by the very dense wool. This technique was apparently successful at the time but subsequently the marks could only be found with difficulty. The wool was sampled by clipping very carefully with scissors close to the skin, following the marks. All the sides and the diagonals of the area were then measured with dividers and rule to the nearest millimetre. It was found that with practice the areas sampled were rectangular or nearly so.

After lambing had commenced and until the majority of lambs were over six weeks of age, each group was yarded every fifth day when the rotation brought them to the paddocks adjacent to the yards. All lambs were then weighed and measured for height at withers for estimation of this data on an exact weekly basis. Lambs within three days of three or six weeks of age were taken out for wool sampling and all those animals not so required returned to the paddock as soon as the weighing was complete. This meant that the majority of animals in each group were not in the yards for more than an hour every fifth day. The lambs for sampling were placed across a board on the yard fence in a similar position to that for sampling at birth. When the tattoo marks could not be located the previously sampled area was used as a guide. The new dimensions of this original area were not measured because of this difficulty and reclipping the cut fibres and measuring the skin thus exposed would have meant keeping the lambs in the yards too long unless further technical help had been available. The keeping of yarding and handling to a minimum was considered an essential part of an experiment on growth rates and as no halo hairs are formed after birth and this fibre type is easily recognised, area increases for the N-type animals could be estimated from the changes in the density of these fibres. The animals were checked for possible shedding of the halo hairs at each weighing.

After they were shorn the lambs were randomised into five groups and kept without further rotation. The randomisation was repeated after each fortnightly weighing. The final wool sampling was carried out by using a padded box like a small vaulting horse over which the animals were placed in a similar

position to that used for previous samplings.

All measurements and all samples were taken by the author with one or more assistants to record data or help with the holding of the animals. For this reason possible observer differences in data collection have not been considered. Feed was plentiful over the entire period of the experiment but the weather was generally unfavourable from lambing until shearing except for a few weeks.

The timetable of events for comparison with Part One was:-

<u>Date</u>	<u>Event</u>
March 6	Ewes weighed; numbers stencilled; rams joined with ewes
April 13	Ewes weighed
April 30	Ewes weighed; wool sampled; height at withers taken; randomised into two groups. Rams removed.
May 20	Ewes weighed
July 15	" "
Aug. 18 - Sept. 1	Majority of lambs born
Aug. 24	1st five day weighing of lambs
Aug. 29; Sept. 4, 8, 13, 18, 23, 28; Oct. 3, 8	Weighing and sampling
Sept. 18	All lambs docked (with iron) All ram lambs left entire
Oct. 15	Ewes and lambs weighed
Nov. 6	Lambs weighed
Nov. 20	Lambs weighed and weaned; graded for horns. Ewes disposed of.
Dec. 4 and 14	Lambs weighed
Dec. 15	Lambs shorn and fleece weights taken
Dec. 17	Lambs weighed
Dec. 31	Lambs weighed
Jan. 14	Lambs weighed
Jan. 28	Lambs weighed; height at withers and depth of chest measured; graded for horns
Feb. 10	Final wool samples taken
Feb. 11	Final weights taken

D. The Treatment of the Wool Samples

1. Estimates of fleece density.

(i) Technical

Sampling methods have been described and the resulting samples were first weighed and scoured using a synthetic detergent (Teepol) and warm water. Because of the small size of the fibres special care was required in scouring so the samples were shaken in a flask until clean and then filtered off on a wire gauze on which they were washed with warm water and finally a small amount of alcohol to hasten the drying. The samples taken at birth were washed twice in this way to ensure removal of placental material. The samples were then placed on a filter paper to dry at air temperature and humidity. The filtrate from the washings was checked at intervals to ensure that no small fibres were passing through the gauze.

All samples collected during lambing and the following six weeks were dealt with in this way the same day as sampling, while those from the lambs after shearing were scoured during the following two days.

After drying for four or five days the samples were weighed, the slight variations in temperature and humidity in the laboratory being considered unimportant in comparative work of this type. The weights taken prior to scouring were used as a check on possible errors, there being a close relationship between the two weights.

After weighing the procedure varied slightly for the samples taken at the different times:

For those taken at birth and six weeks, the samples from the N-type lambs were sub-sampled by continuous splitting of the sample and random choice by the tossing of an unbiased coin, until there about 400 fibres left. These were then sorted into halo-hairs* and other fibres, the two groups then being counted and placed in a small envelope. The ordinary lambs had very few halo hairs so all those in the sample were counted. Two hundred of the remaining fibres were then counted out for weighing. If there were more than 20 halo-hairs these were weighed separately and allowed for in the density calculations.

All the envelopes, first with, then without the samples, were then weighed to the nearest 0.2 mgm, using an aperiodic balance. These were all done during one weighing period thus obviating the necessity for a standard sample for humidity corrections.

The samples taken after shearing were treated in a similar manner, only the fibres were not sorted into types and about 300 fibres were weighed for each sample. From these data and knowledge of the area sampled the following variables were obtained or calculated:

* These included Dry's super-sickle A'. In fact there is a continuous distribution from halo-hairs to the larger super-sickle fibres which has tended to additions to the terminology of fibre types as more samples have been examined. This continuous distribution is not considered of importance here as the main basis has been one of fibre diameter; the important point was that those fibres classed as halo-hairs at birth were also classified in a similar manner at six weeks and in addition the classification should correspond to that on the live lamb when given a 'halo-hair grading'.

Table 56

Analysis of Sampling Errors in the Weight of Wool
per Unit Area

Source of Variation	d.f.	Mean Square	Expected Mean Square
Sheep	32	180.984	$E + 2S$
Positions	1	0.380	$E + 33P$
Interactions(Error)	32	39.847	E

Estimates of the Variance components:

Error (E) 36.5%
Positions (P) — 1.1%
Sheep (S) 64.6%

If A sq cms is the area sampled

W gms is the weight of the scoured sample

w mgms is the weight of n fibres

Then density = fibres /sq cm

$$= W/A \times n/w \times 10^3 \text{ fibres/sq cm}$$

The densities have been expressed as 1000 fibres/sq cm for analysis and presentation.

For the ordinary lambs: If m' is the total number of halo-hairs
then halo-hairs/ sq cm = m'/A

For the N-type lambs: If $p\%$ is the percentage of halo-hairs in
the sub-sample

$$\text{then halo-hairs/ sq cm} = p.W.n/ A.w.$$

The weight of 1000 fibres = $n/w \times 10^3$

This last expression is a useful one for the measurement of average follicle production.

(ii) Estimates of error

The duplicate samples were kept separate throughout this process and at each stage the errors associated with that stage were estimated by means of the analysis of variance for N-type and ordinary lambs separately. The estimation of error for W for the N-type lambs at birth is given in detail in Table 56.

The existence of a negative component of variance is not theoretically possible and is the result of errors of estimate associated with the method. However the component for sheep is

Table 57

Errors in the Estimation of the Components of Fleece
Density for N-type Lambs

Sampling Time	Standard Deviation based on Error(E)	Coefficient of Variation as Percentage	Variance due to Sheep as percent	Coefficient of Variation for the Mean of Positions
<u>Mgms of wool per sq cm</u>				
Birth	6.31	12.8	64.6	9.0
6 weeks	13.32	10.2	62.4	7.2
Hogget	9.64	8.0	52.6*	5.6
<u>The weight per 1000 fibres (mgm)</u>				
Birth	1.57	6.5	93.8	4.7
6 weeks	7.74	12.4	72.0	8.8
Hogget	3.17	4.7	91.5	3.3
<u>The fleece density as 1000 fibres per sq cm</u>				
Birth	0.315	15.0	46.7	10.6
6 weeks	0.362	16.5	64.9	11.7
Hogget	0.164	9.2	66.3*	6.5
<u>The percentage of Halo-hairs**</u>				
Birth	1.34	5.0	92.6	3.6
6 weeks	2.21	13.5	62.5	9.5
<u>The Halo-hairs per sq cm.</u>				
Birth	69.12	16.6	74.7	11.7
6 weeks	49.57	27.0	67.8	19.1

* Position bias significant at 5% level

**A transformation $p = \sin \phi$ was used for this data.

the best for comparison with other work or measurements, and represents the amount of variation which is associated with the item of interest; that is, sheep.

Other measurements of error are the standard deviation and the coefficient of variation as a percentage which latter can be compared with estimates of 'percentage error' being roughly equivalent to the maximum 'percentage error' for 80% of the observations. These are given in Table 57, with in addition, the coefficient of variation for the means of the duplicate samples. The presence of a significant position bias has been indicated but in no case was it large enough to be considered of importance when the means of the positions were to be used.

The major source of error in the density estimations lies in the estimates of weight of wool per unit area. This was probably associated with the measurement of the area, which is not easy to make accurately on the live animal. The sampling errors of halo-hair numbers at six weeks have also led to lower accuracy in the weight per 1000 fibres as halo-hairs made a major contribution to the wool weight at this stage.

Similar estimation of errors for the ordinary lambs are shown in Table 58. It can be seen that the weight of wool per unit area is again a major source of error. In addition, the small size of the fibres at birth led to lower accuracy for the weight per 1000 fibres. This may have been the result of difficulty in counting the fibres for weighing. The reason for the bias for the right position for the six weeks 'weight of 1000 fibres' is not clear but that associated with weight of wool per unit area in both types of sheep is probably associated

Table 58

Errors in the Estimation of the Components of Fleece
Density for the Ordinary Lambs

Sampling Time	Standard Deviation based on Error	Coefficient of Variation as Percentage	Variance due to Sheep as percentage	Coefficient of Variation for the Mean of Positions
<u>Mgms of wool per sq cm</u>				
Birth	3.35	13.1	68.0	9.2
6 weeks	10.64	12.5	45.9*	8.9
Hogget	9.14	7.8	43.0*	5.5
<u>The weight per 1000 fibres (mgm)</u>				
Birth	0.89	9.3	59.5	6.6
6 weeks	3.01	8.1	80.2*	5.7
Hogget	3.42	5.7	75.5	4.0
<u>The fleece density as 1000 fibres per sq cm</u>				
Birth	0.376	13.7	67.0	9.7
6 weeks	0.314	13.6	61.0*	9.6
Hogget	0.167	18.5	42.1*	6.0

* Position bias significant at 5% level.

with the practice of sampling from the left side in every case. This should have little effect on the final results when the means of the two positions are taken. The lower variance due to sheep at the hogget stage was the result of the variance associated with this position bias.

When the possibility of large differences being present and the number of sheep sampled (67) are considered, these results were considered satisfactory for the purpose required when the position means were used. However future work should be of greater accuracy if the sources of errors are known and can be concentrated upon. The results for density show the desirability of designing experiments using methods of this type so that the errors can be estimated and fluctuations resulting from these errors not attributed to seasonal or other effects. The sample taken at three weeks was not dealt with after scouring, being kept in case the additional information was required.

2. Measurement of fibre diameters.

(i) Technical

The six weeks sample was measured first and initially the halo hairs were measured and recorded separately from the remainder of the fibres. However this method involved too much time and the system finally used for all the samples was as follows.

A snippet was taken from the base of a randomly selected staple, thus representing the diameter just prior to sampling, and immersed in benzene as a medium and placed on a slide for viewing under the projection microscope described in the first part of this thesis. A count was made of A, B and O type fibres, that is, large, small or no medulla (Burns 1953) following

a type of classification described in the review of literature. The first 20 fibres of each group were then measured for diameter and medulla diameter except when A type fibres were rare in which case only ten were measured. For the large fibres in the birth sample some difficulty was experienced in a few cases due to twisting and for A type fibres the major axis has been taken in cases of doubt; for the remainder any elliptical tendency has been randomised, the part of the fibre in the centre of the screen being taken sufficiently far from the cut end to avoid any collapsed medulla. A light yellow filter was used between the light source and the slide which saved eyestrain and also made the Becke line somewhat clearer. About 150 fibres were counted in each sample and in all about 15,000 fibre diameters were measured.

(ii) Estimates of error

The analyses of the errors from the duplicate samples were carried out in a similar way to those above and are shown below for the samples at birth and post-shearing as being representative of the two extremes of wool type. It is difficult to compare these results with published work which is mainly on the Merino sheep which has considerably lower fibre diameters and variation than animals being considered here. In general this technique should detect overall differences of from 2 to 4 μ between two groups of five sheep but the additional information on the components of the mean is a considerable advantage over methods which determine the mean diameter only. Cross-sectional methods are of doubtful value with the extremely large fibres concerned in some of the samples because of the collapsing of the large air spaces in the medulla.

Table 59

Errors in the Estimation of Fibre Diameters (μ)

Sampling Time	Standard Deviation (Error)	Coefficient of Variation (percent)	Variance due to Sheep (per cent)	Coefficient of Variation for Position Mean
---------------	----------------------------	------------------------------------	----------------------------------	--

N-type Lambs

The diameter of the O-type fibres

Birth	1.35	6.0	60.3	4.3
Hogget	1.86	5.2	79.0*	3.7

The percentage of O-type fibres**

Birth	5.89	11.0	85.4	7.8
-------	------	------	------	-----

The weighted diameter

Birth	1.87	6.0	72.3	4.2
Hogget	1.89	4.6	65.4*	3.3

Ordinary Lambs

The diameter of the O-type fibres

Birth	0.98	3.6	63.9	2.6
Hogget	1.93	5.1	65.9	3.6

The weighted diameters

Birth	as for the O-type fibres			
Hogget	1.70	4.4	68.5	3.1

* Position bias significant at the 5% level

** The percentage of O-type fibres is only given where the error is sufficient to affect the estimation of the weighted diameter.

The errors associated with the measurement of diameters are shown in Table 59. The reasons for the position bias are not clear but this was not considered of importance as the means of the position values were used. Therefore the coefficient of variation in the final column reflects the errors for the values used in the analyses. For the ordinary lambs there were very few medullated fibres at birth and therefore the weighted diameters were very similar to those of the O-type fibres.

Unless stated to the contrary all the variables used in the subsequent sections on wool have been arrived at by the methods described above. They are based on the means of the two symmetrical positions and the values for the positions were arrived at independently.

Table 60

The Sub-class Numbers for the Analyses
in Section A

Ewes Genotype	Lambs Genotype	Ram Singles	Ram Twins	Ewe Singles	Ewe Twins	Total
N+	{ N+	6	2	1	8	17
	{ ++	4	2	-	2	8
++	{ N+	1	4	3	5	13
	{ ++	1	8	4	7	20
Totals		12	16	8	22	58

IX. RESULTS

A. The Differences Between N-type and Ordinary Lambs

1. Weight gains.

The method of analysis and estimation of the differences between groups was that described in Section III D 2. The groups included in the model were for estimation of the reciprocal mating, the genotype and the sex - birth rank effects. Twins reared as singles were omitted from the analyses in this section as there were insufficient for reasonable estimation.

The numbers of lambs in each sub-class under the above classification are shown in Table 60. The genetic implications of these numbers were discussed in Section III,C 2 (i)

The form $\text{Log}_e w_2 - \text{Log}_e w_1$, if w_1 and w_2 are the weights at two successive times, has been used in the analysis of possible differences of relative weight gain. These values have also been used in the sections on the various components of the fleece and thus the results throughout are comparable. In the event of differences being found, they have been discussed in terms of the live weight for comparison with the first part.

Mean differences in birth date between the genotype groups and between the mating groups were only of the order of one day and have not, therefore, been corrected for.

The results of the analyses have been summarised in Table 61 where the values of the estimated differences have been given for those groups between which they were considered real.

There was no evidence of any significant genotype effect on birth weight or the subsequent gains of the lambs, nor was the

Table 61

Results from the Analysis of Birth
Weight and Subsequent Gains

Source	d.f.	Birth Weight	Mean Squares		
			Birth to 6 weeks	6 weeks to Shearing	Shearing to Final Weight
<u>The Tests of Interaction</u>					
Interaction	10	0.402	0.0025	0.011	0.0037
Within Subclasses	42	1.240	0.012	0.0061	0.0033
F		less than 1		1.82	1.13
<u>The Tests of the Group Effects</u>					
Genotypes	1	0.012	0.030	0.0080	0.0013
F		less than 1	2.95	1.13	less than 1
Mating Gps	1	0.546	0.108	0.026	0.013
F		less than 1	10.67**	3.70	3.79
Sex - Birth rank	3	21.362	0.011	0.025	0.011
F		19.80***	1.13	3.58*	3.48*
Residual	52	1.079	0.010	0.0071	0.0033

* F significant at the 5% level

** F 1%

*** F 0.1%

The estimates of the differencesMating groups birth to 6 weeks: 0.091 in favour of group I
(N+ ewes)

Sex - Birth rank. Birth: Singles greater than twins.
Males greater than females
6 weeks to shearing: Twins greater than singles
Males greater than females
Shearing to final weight: Twins greater than
singles.

relative effect on single and twin lambs shown by the tests of interaction. The slight advantage of lambs from mating group I (N+ ewes)* in growth over the first six weeks could be a genetic effect or alternatively it could be associated with a greater milk supply from these ewes. In the latter case a differential effect between singles and twins might have been expected but there was no evidence that this was so. It is of interest to note that the twin lambs had a greater relative growth than the single lambs after six weeks of age which suggests that milk supply is not a limiting factor after this age.

When the individual growth curves were examined in conjunction with this analysis, it was clear that the previous year's results were not confirmed and as a result, the hypothesis that N had a basic action on growth was rejected. The alternative hypothesis of an environmental interaction with birthcoat type was therefore favoured. Because of the possibility of other factors being present and because no further results were available, this conclusion does not necessarily apply to the homozygous (NN) sheep in the carpet wool flock.

The mean growth curves from the two years' work are given in Figures 11, a - d, for male singles, female singles, male twins and female twins respectively. It can be seen that the lack of difference in 1953 resulted from the faster growth of the N-types and somewhat slower growth of the ordinary lambs.

* Note: This difference in relative growth rate is equivalent to a body weight difference of three pounds at six weeks for lambs having a birth weight of ten pounds and having weights of about 35 pounds at six weeks.

Figure 11A

Mean Growth Curves for Each Group in
1952 and 1953: Ram Lambs

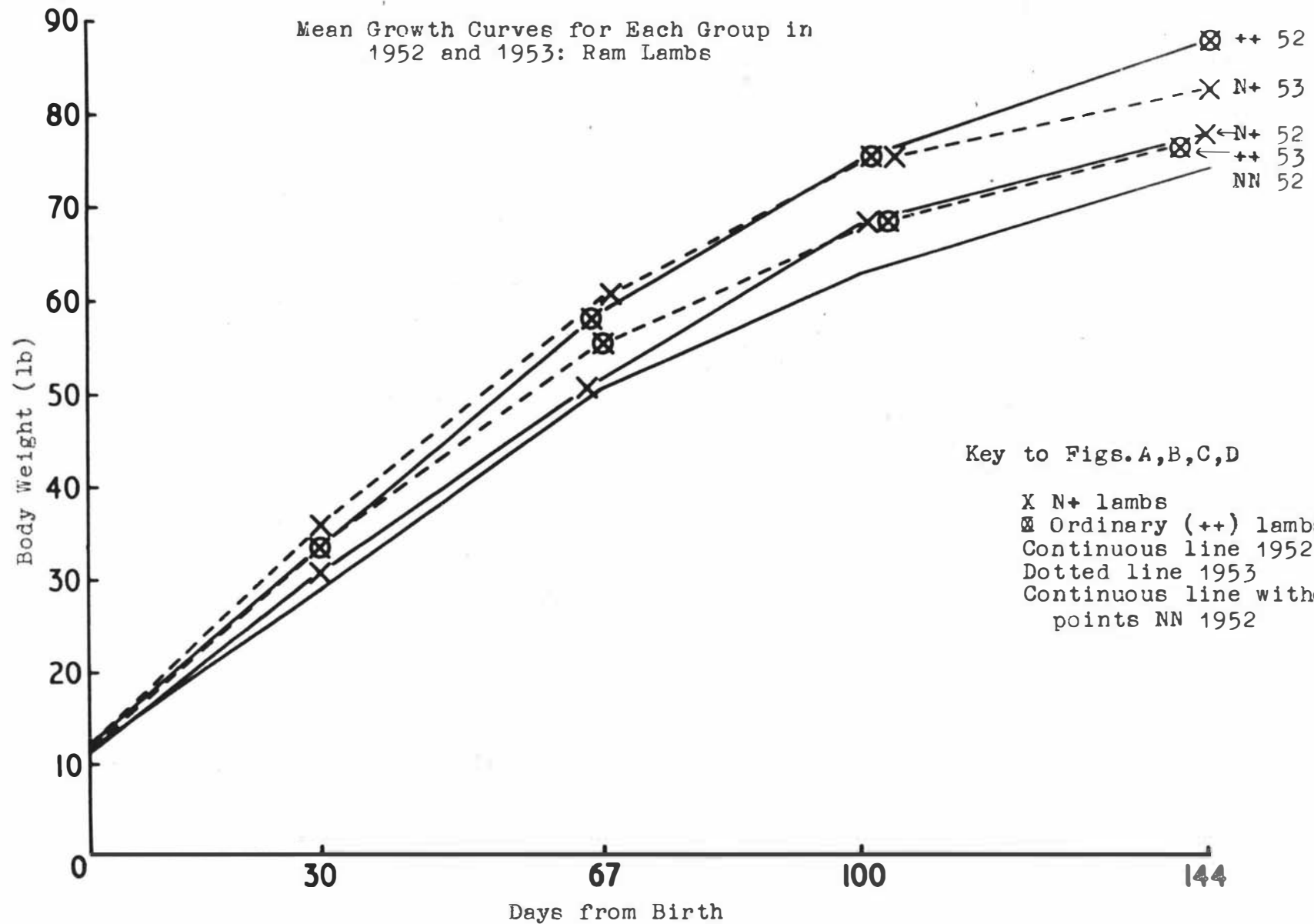


Figure 11B .

Mean Growth Curves for Each Group
in 1952 and 1953: Ewe Singles

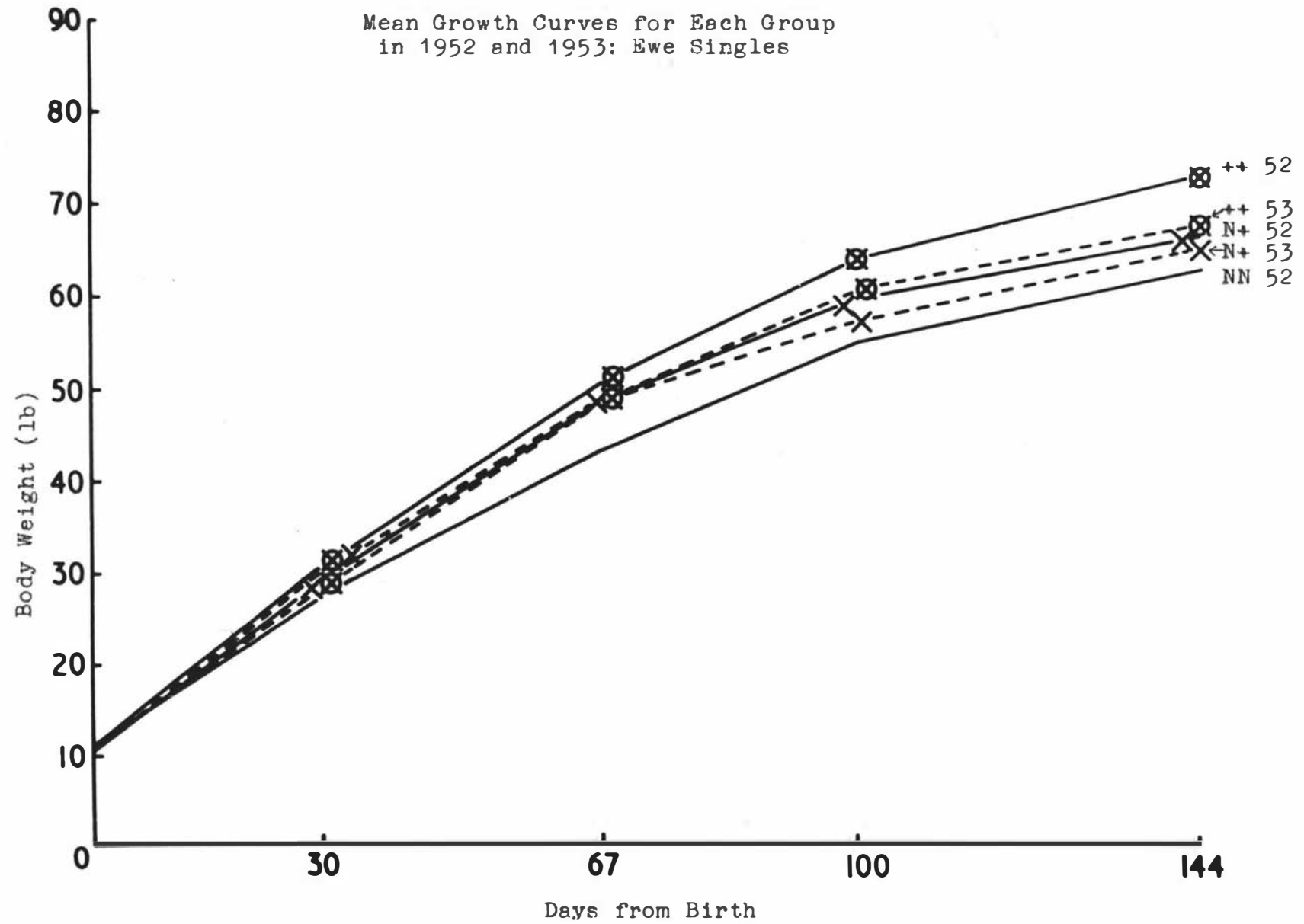
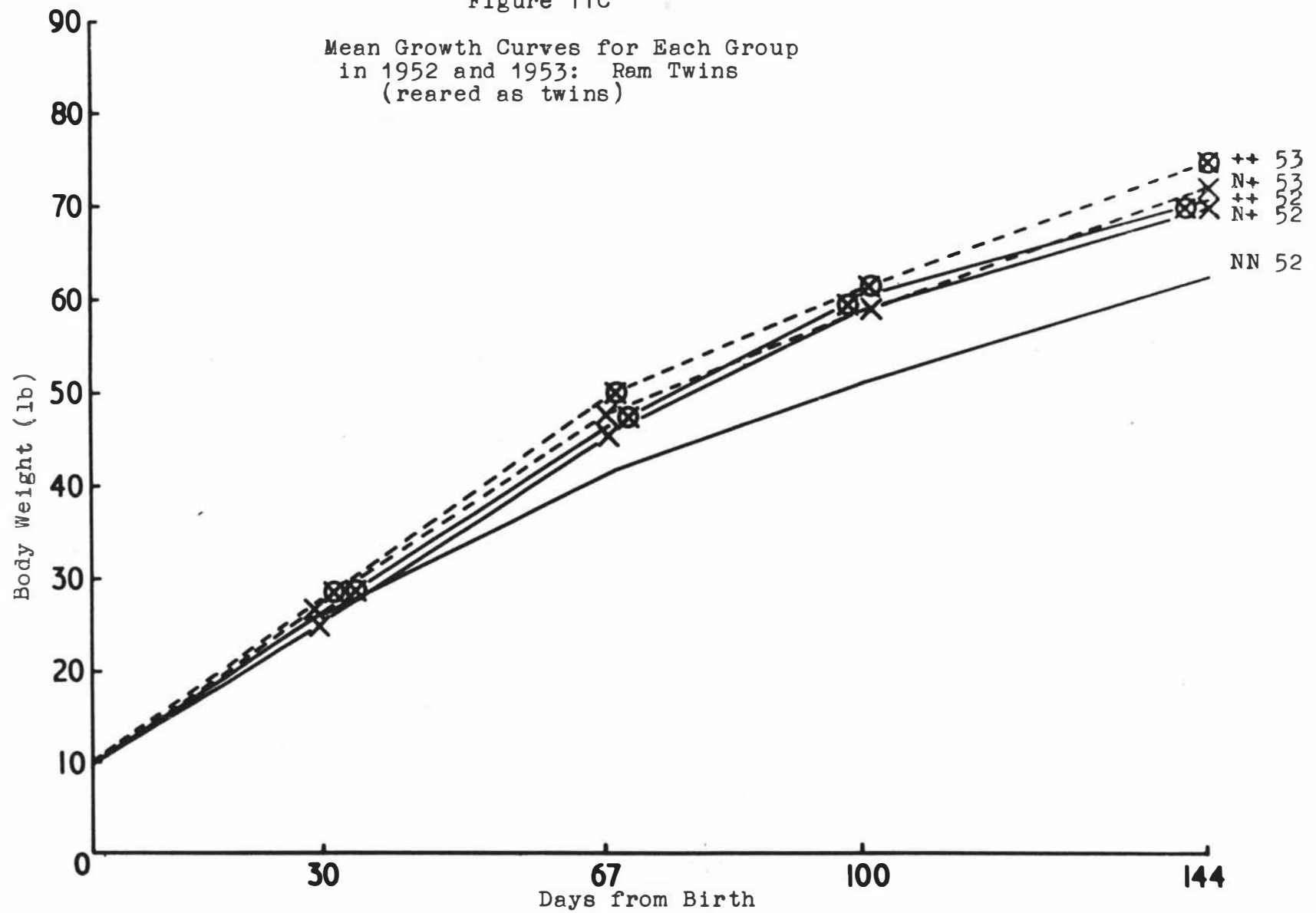
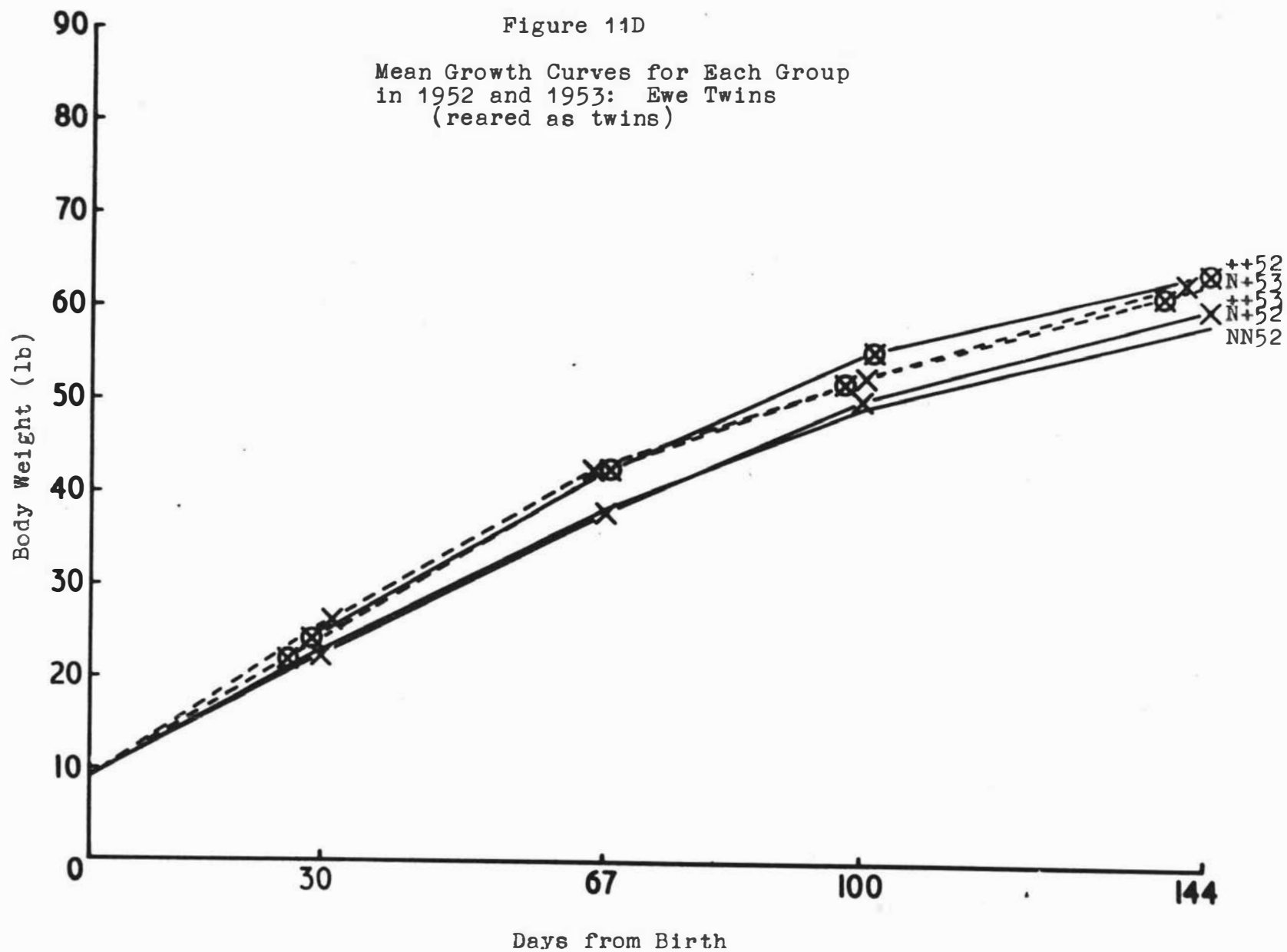


Figure 11C

Mean Growth Curves for Each Group
in 1952 and 1953: Rem Twins
(reared as twins)





Up to 30 days of age, when differences were detected in the first year, there was no slowing of the growth of the N-types while the ordinary sheep were the same in both years. This suggests that nutrition was not a limiting factor to this stage unless the requirements of the N-type lambs are considerably higher than those of the ordinary animals, thus leading to a penalisation of the former only if there is any limitation of the ewes' milk supply. If this was so, the effect would be expected to be greater for twins unless they had different metabolic requirements associated with the relatively smaller surface area. There is no consistent evidence on this aspect from these results.

If the birthcoat type is of any importance in determining the lamb's reaction to its climatic environment then the different weather conditions over the two spring seasons might possibly account for the different results. The spring of 1952 was generally warm and dry while that of 1953 was cold and wet, which would suggest that the 'hairy' birthcoat was a disadvantage under the warmer conditions of 1952. Further experiments are required before any further comments can be made, except that the precautions taken in yarding and weighing the animals which have been described were probably adequate otherwise there would have been a general slowing of growth of all groups in 1953.

It can also be seen that the homozygous animals in 1952 were consistently lower in weight than any group in the same or the following year.

Therefore the main conclusion from this work on lamb growth is that lambs having a 'hairy' birthcoat as a result of N

Table 62
Fleece Weights (lb) and Shorn Body Weights(lb)
of the Lambs

Group	Body Weight	Fleece Weight	Corrected Fleece Weight
N+ Singles	65.5	3.6	3.6
++ Singles	62.3	3.1	3.2
Difference	3.2	0.5	0.4*
N+ Twins	53.7	2.8	3.1
++ Twins	56.0	2.4	2.6
Difference	- 2.3	0.4	0.5***

* Difference significant at 5%level
*** 0.1%level

Table 63
Regression Coefficients of Fleece Weight
on Body Weight for the Two Years

Birth Rank	1952		1953	
	Coefficient	s.e.	Coefficient	s.e.
Singles	0.044	0.0061	0.047	0.0078
Twins	0.041	0.0068	0.029	0.0089

Table 64
Comparison of Shorn Body Weights with Those
Taken Six Weeks Before Shearing

Genotype	Male Singles	Male Twins	Female Singles	Female Twins	Weighing Time
N+	71.9	53.8	55.0	48.8	Before shearing
	72.0	58.0	54.3	51.8	Shorn
++	65.0	55.9	58.5	48.0	Before shearing
	64.4	60.2	59.0	51.2	Shorn

may show slower growth than ordinary lambs under the same conditions. In addition this slower growth follows from some environmental interaction associated with fleece type and this aspect requires further investigation. These further investigations should be on nutritional or climatic factors and would need to be carried out over a number of years.

2. The fleece weights of the lambs.

An analysis of covariance showed differences of the greasy fleece weight when corrected for the body weights taken two days after shearing. Table 62 shows these body weights with the fleece weights and also the fleece weights corrected to a mean value of 64 pounds body weight. The regression coefficient used in each case for correction was that calculated within the genotype groups for each birth rank. The values of these regression coefficients for 1952 and 1953 are shown in Table 63 and it can be seen that they are in good agreement for the number of animals concerned.

The regression lines, with those from 1952, are shown in Figure 12, and it can be seen that apart from the ordinary single lambs which have a small mean difference, the slopes and the relative mean values are remarkably consistent. The previous difference found between singles and twins on the one hand and N- type and ordinary sheep on the other is therefore confirmed by the second year's work.

It will be remembered that in 1952 body weights taken three weeks before shearing had to be used for correction and it was stated that these were likely to be comparable with those body weights taken just after shearing. Mean values at these two times are available for the 1953 lambs

Figure 12

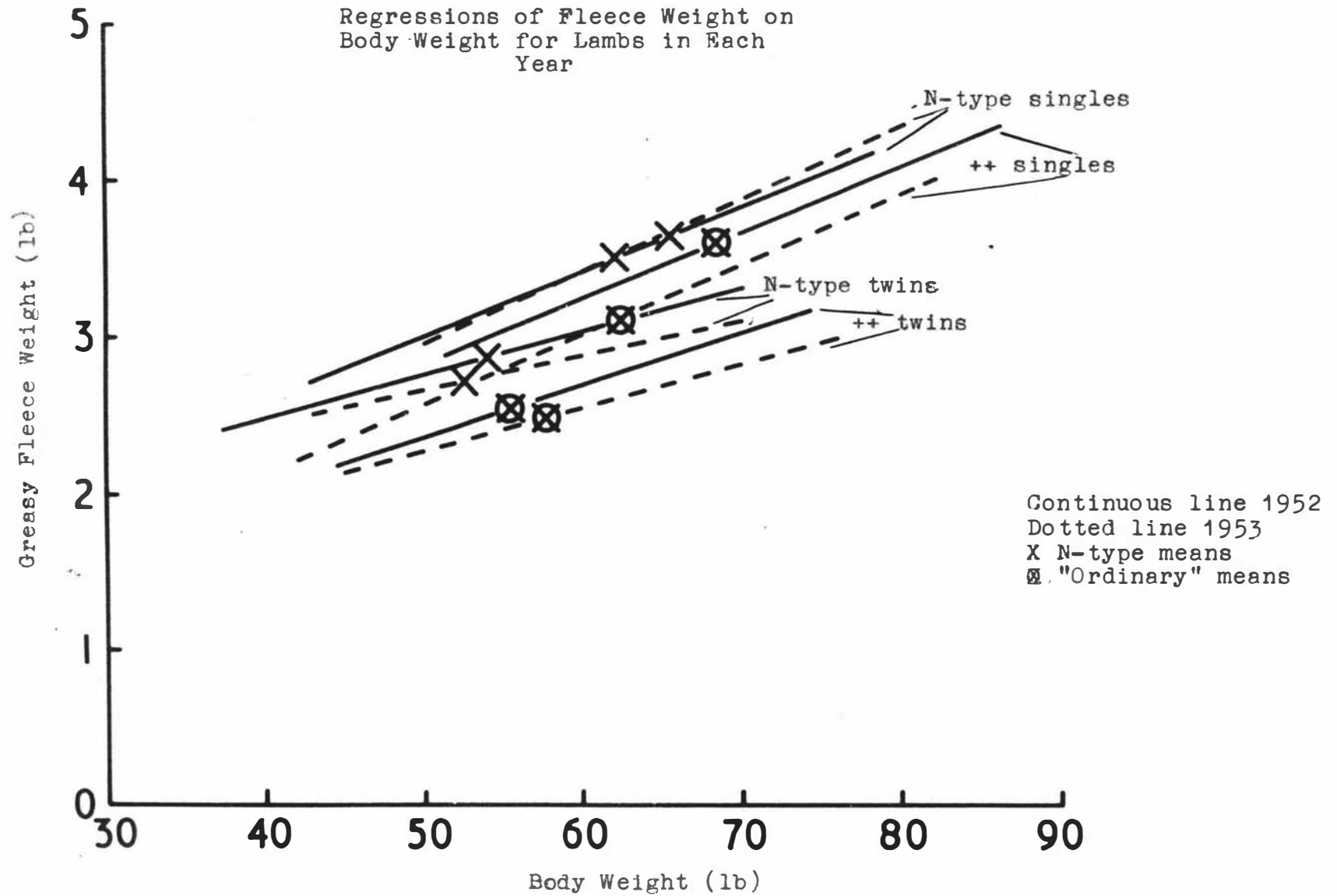


Table 65
Results from the Analyses of the Fleece
Densities (1000 fibres/sq cm)

Source	d.f.	Birth	Six Weeks	Hogget
<u>The Tests of Interaction</u>				
Interaction	10	0.210	0.225	0.116
Within	42	0.217	0.311	0.066
Sub-classes				
F		less than 1		1.74
<u>The Tests of the Group Effects</u>				
Genotypes	1	4.869	0.183	0.417
F		22.60***	less than 1	5.49*
Mating groups	1	0.260	0.735	0.00006
F		1.21	2.49	less than 1
Sex -	3	0.307	0.092	0.146
Birth rank				
F		1.43	less than 1	1.92
Residual	52	0.215	0.295	0.076

* — Significant at the 5% level
*** 0.1% level

The estimates of the differences

For genotypes, the Ordinary lambs had more fibres than the N+ lambs
by: Birth 610 fibres/sq cm
Six weeks 120 fibres/sq cm (not significant)
Hogget 180 fibres/sq cm

and are shown in Table 64. There is little difference in the mean weights of single lambs at these two times of weighing but for the twin lambs there is a bias of about four pounds in favour of the shorn weights. If this is allowed for on the diagrams in Figure 12, it will be seen that the means for 1953 now fall on the 1952 lines and it was therefore concluded that the use of weights taken at different times relative to shearing in the two years in no way invalidates the conclusions above.

3. Fleece densities

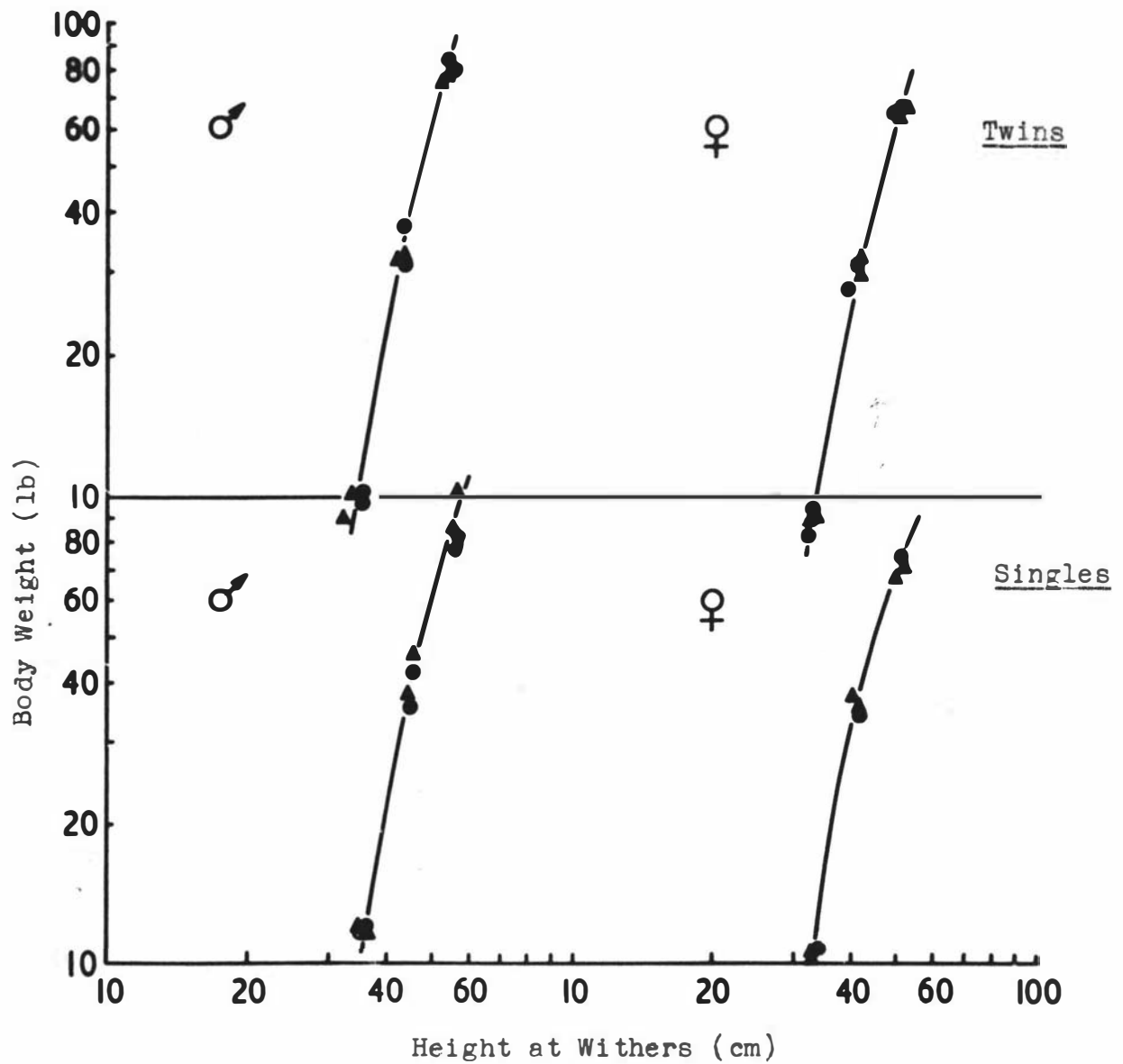
Fleece densities as determined were analysed using the same model as that used for the relative weight gains and the summary of the analyses of variance is shown in Table 65. The only real differences are those between genotypes at birth and at the final sampling when the N-type density was lower than that of the ordinary lambs. The higher sampling errors at six weeks may in part account for the non-significance of the result at this time but there clearly must have been more fibres added to the N-type lambs' fleeces over the period from birth to six weeks, as skin expansion was presumably similar in the two groups. These differences will be discussed below when the factors contributing to them are considered.

4. The height at withers.

The means for the height at withers and body weight at birth, six weeks and the end of the experiment have been plotted for each sex, birth rank and genotype in Figure 13 in which both variables are on a logarithmic scale. Little difference can be seen between the relationships of these variables for

Figure 13

Relationships Between Weight and
Height at Withers (1953)



▲ N-types

● Ordinary

Note: The mean of
each reciprocal
mating group is
plotted

the two genotypes ~~for the two genotypes~~ and it was therefore considered unnecessary to carry out a more elaborate analysis except at birth where the graphs indicate a possible difference, in particular for the male twins. As it has already been shown that there were no significant weight differences an analysis of variance was made of the height at withers at birth. This showed that the ordinary animals were significantly larger by about one cm. This result is not in agreement with that obtained the previous year and requires further confirmation before any conclusions can be drawn concerning it.

5. Summary and conclusions for Section IX,A.

As no differences between genotypes in body growth were apparent in 1953, it has been assumed that differences in fleece development during the early growth of the lamb were the result of birth-coat differences and of variations amongst individual lambs in their rate of growth. As there was no significant correlation between halo-hair density and growth rate ($r = 0.16$ 31 d.f.) over the first six weeks it can be assumed that birthcoat type and growth rate were independent for this year's work. This assumption leads to simpler interpretation of some of the results from multiple regression analysis to be presented below.

The remainder of the results and analyses therefore are concerned with the type of fleece at 25 weeks of age arising from lambs with varying birthcoat types and growth rates.

Summary:

(1) The growth differences found between genotypes in 1952 were not confirmed and the hypothesis of a basis action of N on growth was rejected. Alternative hypotheses were put forward in terms of environmental interactions with birthcoat type.

- (2) Fleece weight when corrected for body weight showed the same relationships in 1952 and 1953; N-type lambs had heavier fleeces than the ordinary lambs, and single lambs had heavier fleeces than twin lambs.
- (3) Differences in the number of fibres per unit area were detected at birth and at about 25 weeks of age. Ordinary sheep had a higher density than N-type sheep.
- (4) Apart from a possible difference at birth, the relationship between height at withers and weight was the same for both genotypes and the conclusion that the gene N has little or no effect on body proportions relative to body weight in the first 25 weeks of post-natal life, is similar to that arrived at the previous year for heterozygous N-type and ordinary animals.
- (5) There being no growth differences between genotypes, the remainder of the analysis is concerned with the effects of individual growth variations and birth coat type on the hogget fleece characteristics.

B. Factors Affecting Fleece Density

It should be emphasised that the density measured was that of the ~~coarse~~ fibres which had become sufficiently long to be included in the sample. Therefore the results presented here apply to active follicles which have produced sufficient fibre for it to be included in the sample and actual follicle densities may have been greater at the time the sample was taken. On the other hand it is not possible to state that the follicle density at a previous period is being measured by this method, as skin expansion will have taken place since the

time that these fibres represented all the follicles present.

The analyses that follow are based on all lambs in a genotype group, including all possible birth ranks unless it is stated otherwise. On this basis there were 33 N-type and 34 ordinary lambs.

1. Fleece density at birth.

The lower density of the N-type birthcoat has already been established in Section IX, A 3, and it is reasonable to suppose that this could be the result of a suppressing effect of the larger primary follicles from which the halo hairs are produced. Fraser and Short (1952) offer evidence for this type of effect and Fraser, Ross and Wright (1954) showed that halo-hairs came from large primary follicles. This being so then an animal with a higher halo-hair density would be expected to have a lower overall fleece density.

In the first part of this thesis it was shown that variation occurred in halo-hair 'coverage' in that 'coverage' was greater for twin than for single lambs. (Section III, C 1) This grading would be expected to be related to halo-hair density. Figure 14 shows the 'coverage' gradings for 1953 plotted against the halo-hair density with the fitted regression line. The 'coverage' gradings are on a logarithmic scale. Although there is some scatter of the means of each 'coverage' grade, the relationship is a significant one. The numbers concerned are small but the estimate of the regression shows that an increase of one 'coverage grade' is equivalent to an increase of 313 halo hairs per sq cm on the loin position.

As the result of the ideas in the first paragraph of this section, it was decided that an examination of the factors affecting halo hair density was the first logical step in determining those factors affecting overall density.

Figure 14

Halo-hair Densities Corresponding
to the 'coverage' gradings

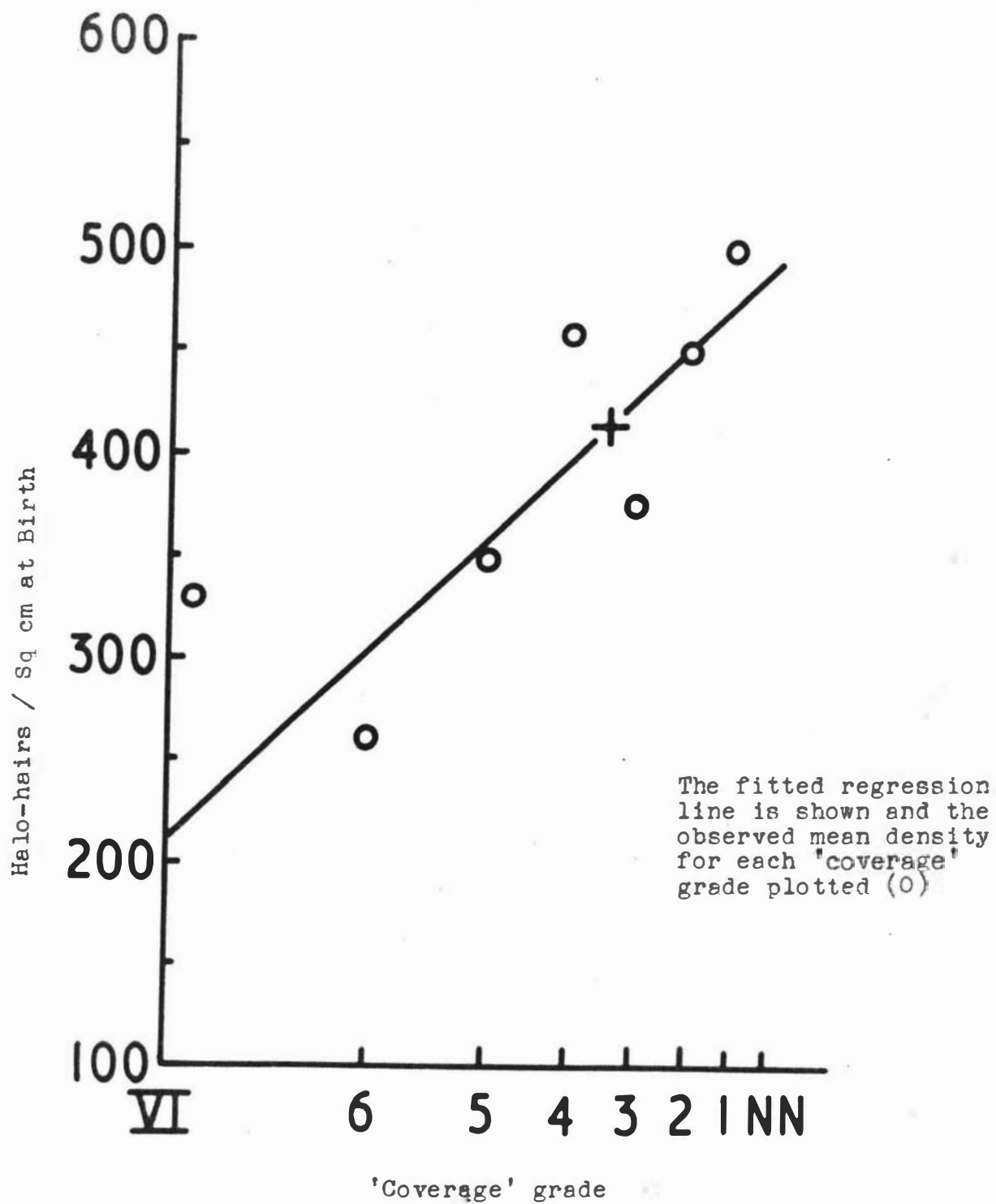


Table 66

Partial Regression Coefficients of Halo-hair Density
on Height at Withers and Birth Weight for the N-type
Lambs

Source	d.f.	Mean Square	F
Regressions	2	29,310.26	1.84
Residual	30	15,893.25	
<u>The coefficients</u>			s. e.
Height at withers		-27.10	14.113 (p = 0.075)
Birth weight		+10.85	15.033

The primary follicles are laid down early in foetal life before differences in the size of the animals, from pre-natal or from genetic effects, are likely to have occurred. Therefore even if the number of large follicles producing halo-hairs was fairly constant between lambs, subsequent differences in growth and skin expansion would lead to differences in the density of these large follicles at birth. This being so, then the density at birth should be inversely proportional to some measure of the size of the animal. If this relationship occurs then the variance unaccounted for will be some measure of the presence of factors affecting the original number of large primary follicles laid down.

The height at withers and the birth weight are two probable measures of size and therefore a multiple regression of halo-hair density on these two independent variables, was calculated for the N-type lambs only. The halo-hair density was too low to make this worthwhile for the ordinary lambs.

The results in Table 66 suggest a real connection between halo-hair density and the height at withers. This regression line is shown in Figure 15 with the means for single and twin lambs and for the two mating groups. It is apparent that if the twin lambs are adjusted for their lower height at withers, then the difference between twins and singles in halo-hair density disappears.

The residual variance is considerably higher than would be expected from the errors of measurement alone (Section VIII, D,2,ii) and it is concluded that there may be other factors affecting the number of large primary follicles originally laid down. The difference in halo-hair density between the two mating groups, not explained by the slight difference in the size of the lambs, confirms this idea.

In order to examine the total fibre density at birth, a multiple regression of density on the height at withers and birth weight was calculated, but no significant relationships were found. But it has just been shown that there is a decrease of halo-hair density associated with the larger lambs, therefore there must be an increase in the other types of fibres to compensate for this; i.e. the less the halo-hairs per sq cm the more other fibres there are per sq cm. Therefore the relationship between halo-hair density and total density has been studied further.

As the halo -hair density was directly estimated from the total density, it would be misleading to draw conclusions from the relationship between these two variables. However the percentage of halo-hairs was estimated from counting fibres and the density was estimated from the weight of wool per sq cm divided by the weight per 1000 fibres. It is possible that the errors of density and halo-hair percentage are related to a slight extent due to sampling fluctuations in the fibres taken to count and estimate the weight per 1000. However the main error in density has been shown to be the result of the weight per sq cm (Section VIII, D,2,ii) and also the means of duplicate samples have been used, therefore it was considered valid statistically to correlate the halo-hair percentage and the total density.

A further point to be considered however, is a possible mathematical relationship, for if in one sq cm there are h halo-hairs and k other fibres,

$$\text{then density} = h + k$$

$$\text{and halo-hair proportions} = h / (h + k)$$

The consequences of this relationship are shown below for the particular result obtained.

The relationship was calculated as the regression of total density on halo-hair percentage, which was found to be highly significant and negative. The value of the regression coefficient showed that for an increase of 1% in halo-hairs there was a decrease of 25 fibres per sq cm.

Now, using the symbols above, it is known that:

- (1) $h + k$ is not constant
- (2) $h/(h + k)$ is not constant

therefore

- (3) h is not constant.

It is, however, a possibility that k is constant and if so then an increase in h will lead to an increase in both $h/(h + k)$ and also in $h + k$.

This is then a positive relationship between halo-hair percentage and total density whereas the one obtained was negative.

Therefore k cannot be constant.

Therefore if h is increasing, k can either be decreasing or increasing.

If k is increasing then $h + k$ must also increase and for $h/(h + k)$ to decrease then k must increase faster than h (1)

If k is decreasing, then $h/(h + k)$ is increasing and for $h + k$ to decrease, then k must be decreasing by a greater amount than h is increasing.....(2)

Both (1) and (2) are possible interpretations of a negative relationship between halo-hair percentage and total density and they both show that an increase of one halo-hair will lead to a decrease of more than one other fibre. This suggests that the presence of halo-hairs leads to a suppression of the

Table 67

Estimated Numerical Relationships Between
Halo-hair Percentage and Total Density
(fibres / sq cm)

Halo-hair %	Total Fibres	Halo-hairs	Other Fibres
10	2250	225	2025
20	2000	400	1600
30	1750	525	1225
40	1500	600	900
No halos	2500	0	2500

formation of some secondary follicles or to the suppression of the growth of fibre from these follicles. The likely nature of this relationship is shown in Table 67 where it has been applied to the case of a mean density of 2000 fibres per sq cm and a mean halo-hair percentage of 20. It is based on the regression value that indicates that an increase of 10% halo-hairs is equivalent to a decrease of 250 fibres.

Figure 16 shows this regression of total density on halo-hair percentage with the mean for the ordinary lambs plotted. The position of this mean suggests that the difference in density of the birthcoat of N-type and ordinary lambs is largely explained by the density of the halo-hairs of the former.

Calculation of the partial regressions on total density of the height at withers and the birthweight for ordinary lambs showed a relationship between increased size and decreased density. Again it was the height at withers and not the birth weight which gave the significant coefficient. Halo-hair density would be insufficient to have any suppressing effect, but the parallel with the above results for an effect of 'size' on fleece density at birth is of interest and is discussed below.

The means for the various results for single lambs and for all twins at birth are shown in Table 68, and these with the significant regressions mentioned above are plotted in Figures 15, 16, and 17.

Before discussing these results it is as well to consider the probable timing of events prior to birth. The work of various authors discussed in the review of literature suggests that the primary follicles are laid down before the nutritional and other factors of the pre-natal environment have had much

Figure 15

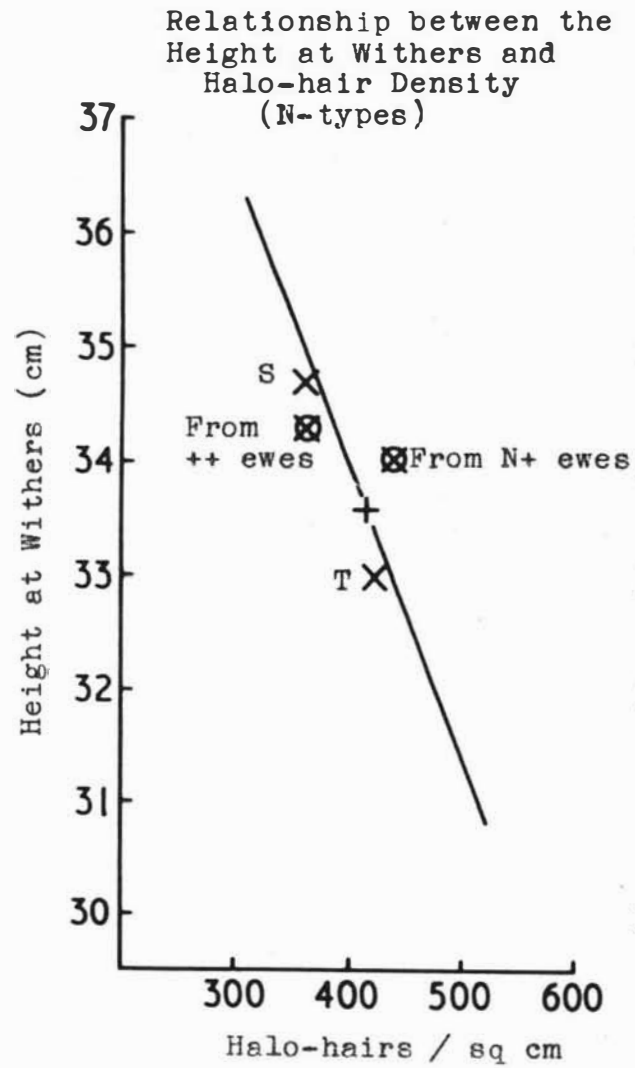


Figure 17

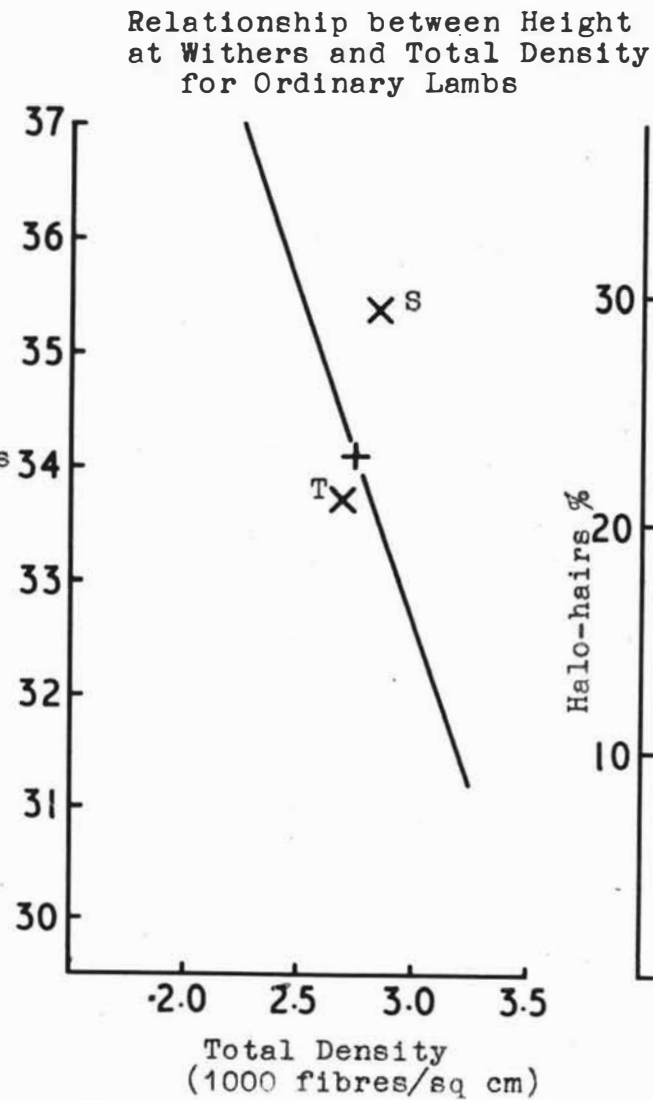


Figure 16

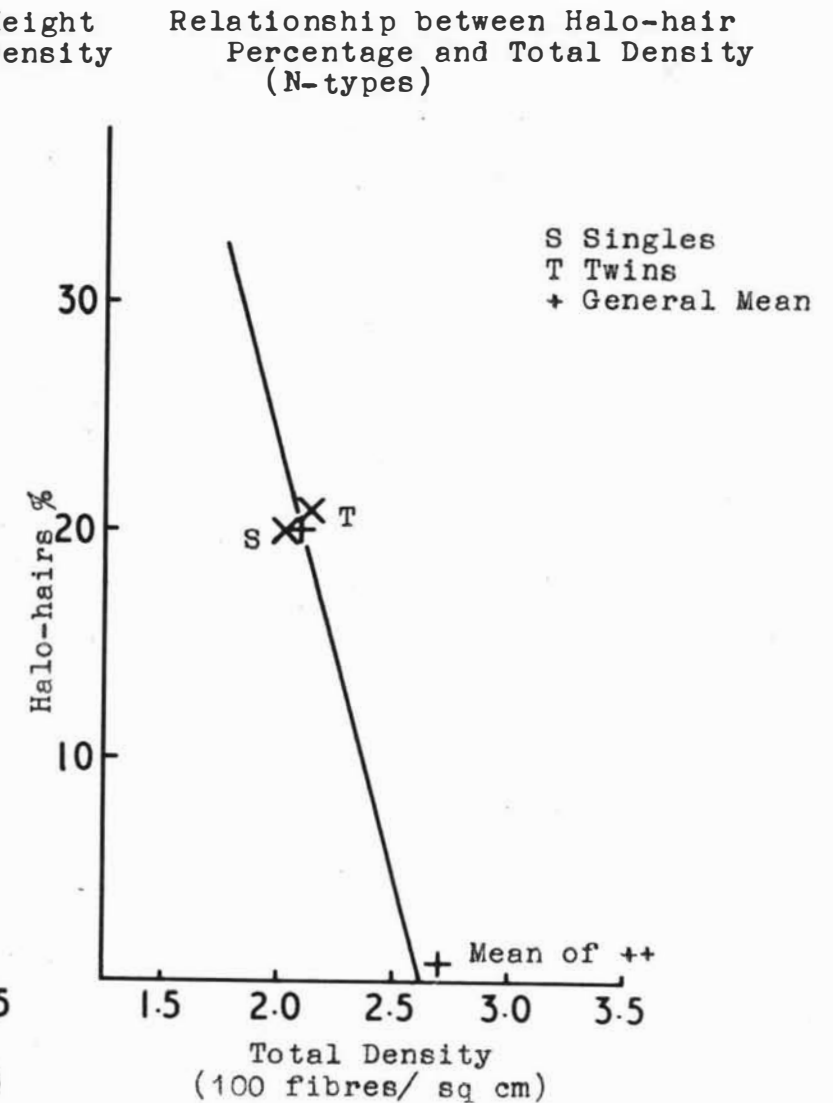


Table 68
Means of the Densities at Birth and Related
Factors

<u>N-types</u>	Height at Withers	Halo-hair Density	Total Density	Halo-hair Percentage
Singles	34.61	378.2	2.017	20.08
Twins	33.24	432.7	2.134	20.50
Total	33.69	414.5	2.096	20.36
<u>Ordinary</u>				
Singles	35.40	7.2	2.822	-
Twins	33.68	4.9	2.722	-
Total	34.13	5.5	2.749	-

opportunity to affect the size of the animal. By the time the secondary follicles are being formed and are starting to grow fibre and, in particular for the last six weeks before birth, these factors become important and variation in the sizes of the animals at birth result.

When this course of events is considered and also the fact that follicles starting to produce fibre a week or less before birth will not have a fibre included in the sample, then the following explanations of the results in this section can be put forward.

- (1) The higher halo-hair density of N-type twins is the result of lesser skin expansion probably in the last few weeks prior to birth.
- (2) Other factors also affect halo-hair density probably by acting on the number of halo-hair producing primary follicles originally laid down. These are shown by a possible reciprocal mating effect and by the large amount of variance not accounted for by height at withers.
- (3) There is some suppressing effect of large primary follicles on the formation of new secondary fibres about six weeks before birth and this leads to a difference in the fleece densities of N-type and ordinary lambs at birth. There is no difference in the observed total densities of single and twin lambs, but if all these animals had had the same skin expansion over the last 3 or 4 weeks, after the majority of the pre-natal secondary follicles were added then the twins would have had a lower density than the singles. As, in fact, the skin expansion of twins over this period would be less than that of the single lambs, the lower density of the twin lambs expected under the hypothesis

of suppression, would not be observed.

(4) The lower density associated with greater height at withers for ordinary sheep could be the result of different skin expansions during these last few weeks, but twin lambs have a slightly lower density associated with smaller size. This could be the result of suppressing factors during the development of the secondary follicles, which cannot be measured without using skin sampling techniques. But it is reasonable to suggest that a somewhat similar situation to that of the N-types exists, with similar densities being measured at birth as the result of differential skin expansion since the formation of the major number of secondary follicles.

In both N-type and ordinary sheep these results should reflect a lower secondary / primary follicle ratio for twin lambs as found by Schinckel (1953) for the Australian Merino and confirmation by such an approach is desirable.

2. The fleece density at six weeks of age.

Fleece density at six weeks of age will depend on the density at birth, the skin expansion between birth and six weeks and the number of new fibres added, relative to those already present. Because of difficulty with the tattooing technique, no direct estimate of either skin expansion or of the number of new fibres was available. It was therefore decided to approach the problem in terms of the changes in density from birth to six weeks. These were also the variables in which there was most interest because of the possible relationships between density and fibre diameter and hence fleece type.

The following theoretical relationship can be derived between these variables mentioned above on which the six weeks

density will depend:

If d_0 is the density at birth

d_1 is the density at six weeks

$q\%$ the percentage of fibres formed post-natally present in the six weeks sample

$$q' = 1 - q$$

s is the relative skin expansion i.e. the area at six weeks of 1 sq cm at birth

Also let there be b fibres in 1 sq cm at birth

and let there be a fibres added to this area up to six weeks

Then $d_0 = b$ and $d_1 = (a + b)/s$

$$\text{as } q = a/(a + b) \quad \text{then } q' = (a + b - a)/(a + b)$$

If both sides of this last expression are multiplied by s

$$\text{Then } sq' = b.s/(a + b) = d_0/d_1$$

That is, a simple relationship exists between the density changes, the skin expansion and the number of fibres added.

The densities at six weeks are known for a given density at birth and given some measure of the corresponding skin expansions, the above relationships can be calculated. Given this result, then the number of fibres which have to be added to an original square cm to give such relationships can also be obtained.

Estimates of relative skin expansion have been obtained for the N-type lambs by means of the relationship:

$$\text{Relative skin expansion} = \frac{\text{Halo-hair density at birth}}{\text{Halo-hair density at 6 weeks}}$$

No additional halo-hairs are added to the fleece after birth (Dry 1935) and no shedding was observed before this time. These estimates were liable to a fairly large error and in

Table 69
Relationship Between Weight Gain and
Skin Expansion

Source	d.f	Mean Square	F	
Regression	1	1.090	12.17	p less than
Residual	31	0.090		0.01

The value for k (W in lb) 1.445

The regression equation $y = 1.445x - 0.922$

Table 70
Partial Regressions of Six Week Fleece
Density on Weight Gains and the Density
at Birth

Genotype	d.f.	Weight Gain Regression	s.e.	Birth Density Regression	s.e.
N+	30	-0.847	0.759	+0.428	0.262
++	31	-1.831	0.530	+0.280	0.123

addition were not available for the ordinary lambs. However, use can also be made of the relationship between relative skin expansion and relative weight gains. Various authors have shown a relationship of the type:

$$\text{Skin area (S)} = cW^k$$

where W is the weight at a particular time and c and k are constants. Where W is in kilograms, k has been shown to have a value of 0.67 for various breeds of sheep at different ages (Brody 1945)

Now if $S = cW^k$ then $\log_e(s_2/s_1) = k(\log_e W_2 - \log_e W_1) + c$ where s_2/s_1 is the relative skin expansion over a period for which W_1 is the initial weight and W_2 the final weight. The expression $(\log_e W_2 - \log_e W_1)$ will then represent the relative weight gain.

This is a simple regression relationship and the values of k and c can be calculated by least squares methods. Estimates of these parameters were obtained for the N-type lambs using the estimates of relative skin expansion obtained above and the relative weight gains over the period birth to 6 weeks.

Table 69 shows the relationship thus calculated and the equivalent value of k for W in kilograms was 0.648 which is in reasonable agreement with the more general estimates of Brody cited above. On the basis of this equation it was decided to use weight gains for the calculations connected with density, which would thus be the same for both groups of sheep, and then interpret them in terms of the skin expansion.

The relationship between weight gains and skin expansion being established, it was now possible to calculate a multiple regression of six weeks density on weight gains and birth density

Table 71

Calculation of the Values in the Expression
 $sq' = d_0/d_1$

Birth density $d_0 = x_1$	Skin expansion $s = x_2$	6 week density $d_1 = y$	Fibres in original sq cm	New fibres	q%
1.0	1.5	1.87	2805	1805	64
3.0	1.5	2.73	4095	1095	27
1.0	2.5	1.71	4275	3275	77
3.0	2.5	2.57	6425	3425	53

The x_1 , x_2 and y refer to the multiple regression equation.

The densities are in the form 1000 fibres per sq cm.

for the required interpretation in terms of skin expansion. These regressions are shown in Table 70. The errors for the N-type group are somewhat high for satisfactory estimates, but these values will be the best estimate of the relationships and the consequences of these are of interest.

The results are shown in diagrammatic form in Figure 18 where the regression of density at six weeks on that at birth is shown for the various values of skin expansion derived from those of weight gain. For the N-type lambs the equation for theoretical skin expansion derived from the multiple regression values for weight gain by use of the estimated values of c and K , was:

$$\text{6 week density } y = 0.43x_1 - 0.30x_2 + 1.56$$

This equation will give an equivalent result to that obtained by estimating densities for a given weight gain and birth density and then converting for the appropriate skin expansion. Thus the validity is not affected by the possible relationships between x_1 and x_2 . In the equation, x_1 is the birth density and x_2 is the skin expansion on a logarithmic scale. Thus theoretical values of six week density can be derived for various values of x_1 and x_2 and when one sq cm at birth is considered then the number of fibres in this original sq cm after expansion to the six weeks value is:

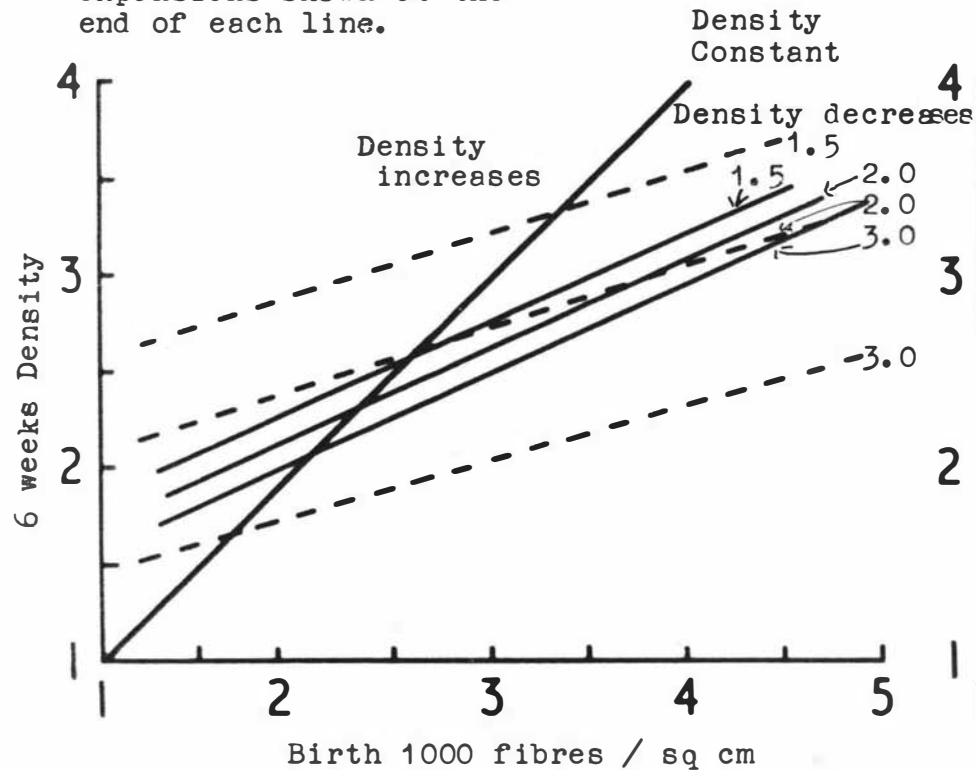
Density at six weeks $\times$ skin expansion.

The number of new fibres can then be estimated as this value less the density at birth, that is, the number of fibres already in the area. Then $q\%$ will be the number of new fibres as a percentage of the total fibres in the area at six weeks. Thus we have the variables required for the relationship derived above ($sq' = d_0/d_1$). A sample of

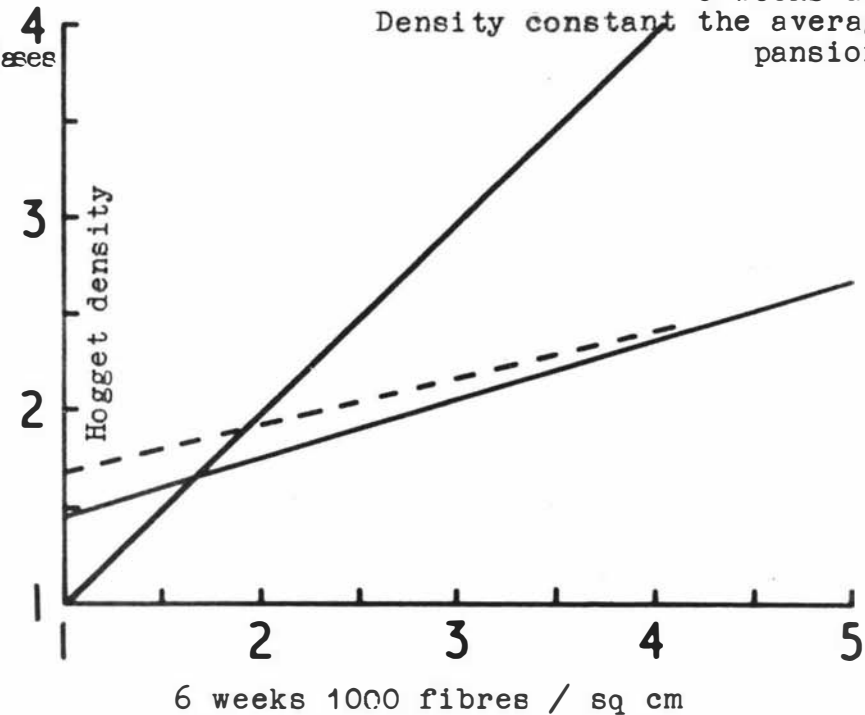
Figure 18

Regressions of Density on the
Previous Density

Partial regressions of
6 weeks density on birth
density for the skin
expansions shown at the
end of each line.



Partial regressions
of hogget density on
6 weeks density for
the average skin ex-
pansion



Continuous line
N+
Dotted line
Ordinary

the calculation is given in Table 71.

Results obtained in this way for the N-type and the ordinary lambs are plotted in Figures 19 and 20 with the theoretical curve $d_0/d_1 = 1$. When plotted in this way a separate curve is obtained for each value of birth density. Each curve shows the percentage of new fibres which will result from a given skin expansion. The number of fibres which must ^{have} been added to the initial sq cm to give the result are shown for skin expansion intervals of 0.5. In addition, the position of a value relative to the line $d_0/d_1 = 1$ is a measure of the change in density; e.g. in Fig. 19 for a birth density of 1.0 (1000 fibres per sq cm), a skin expansion of 3 means that 80% of the fibres at six weeks will be new, that is 4000 fibres. The new density must be $5000/3 = 1.67$ that is an increase in density. The same skin expansion for a birth density of 3.0 (3000 fibres per sq cm) will give a six weeks density of $7600/3 = 2.53$, i.e. a decrease of density.

These are the theoretical curves which best represent the density and weight gain data and any confirmation of them from other data is of considerable interest when the indirect method by which they were obtained is considered. For the N-type sheep it was possible to obtain estimates of the values of $q\%$ for individual animals and check them against the values obtained for the above relationships for a given birth density and weight gain (skin expansion). The values for $q\%$ were obtained as follows:

If x is the halo-hair percentage at birth

y is the halo-hair percentage at 6 weeks

a the actual number of halo-hairs in a given original area

b the total fibres at birth

c new fibres added up to 6 weeks

Figure 19

Relationships leading to Six Weeks Density:
N-type lambs

Unchanged Density
 $d_0/d_1 = 1$

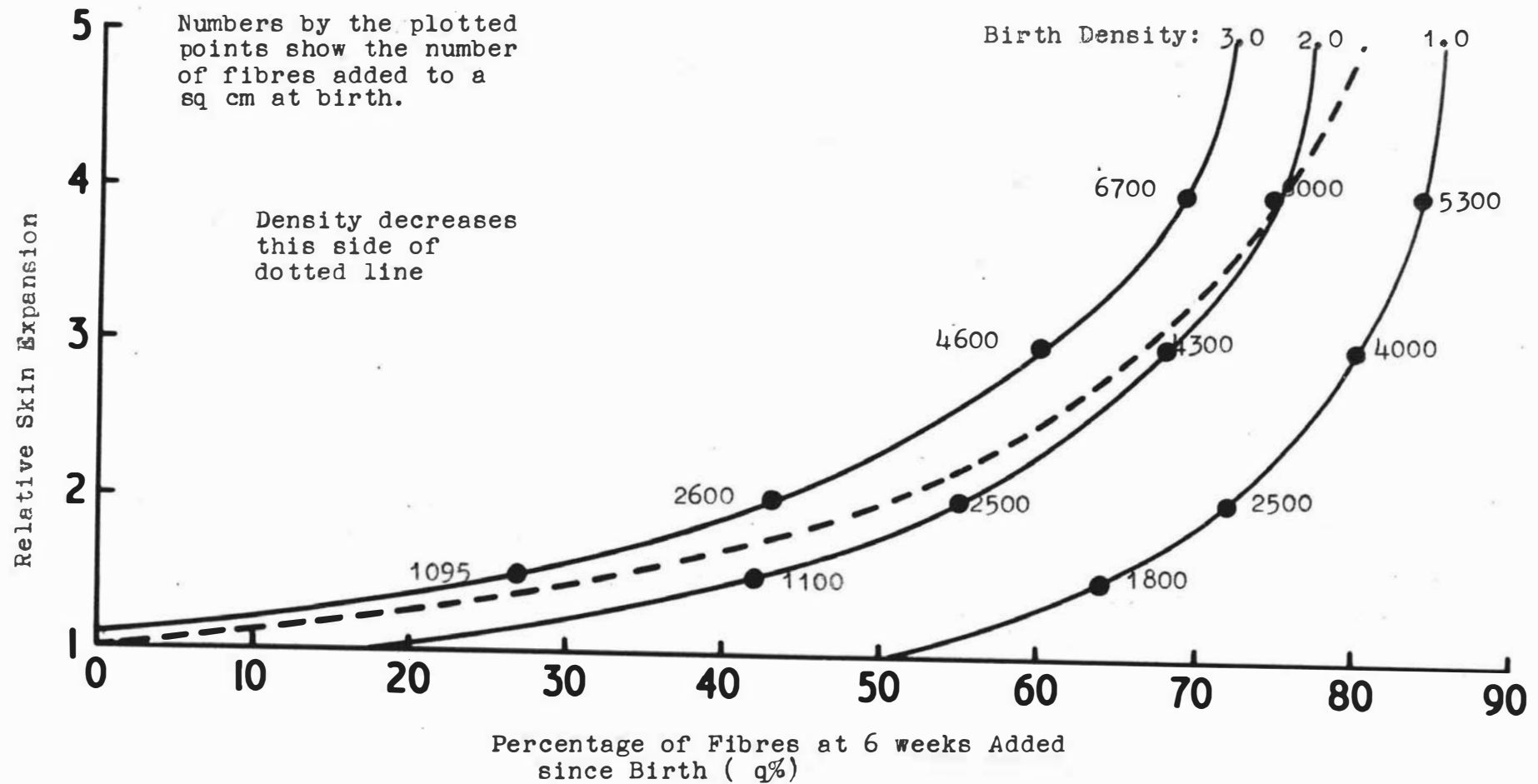
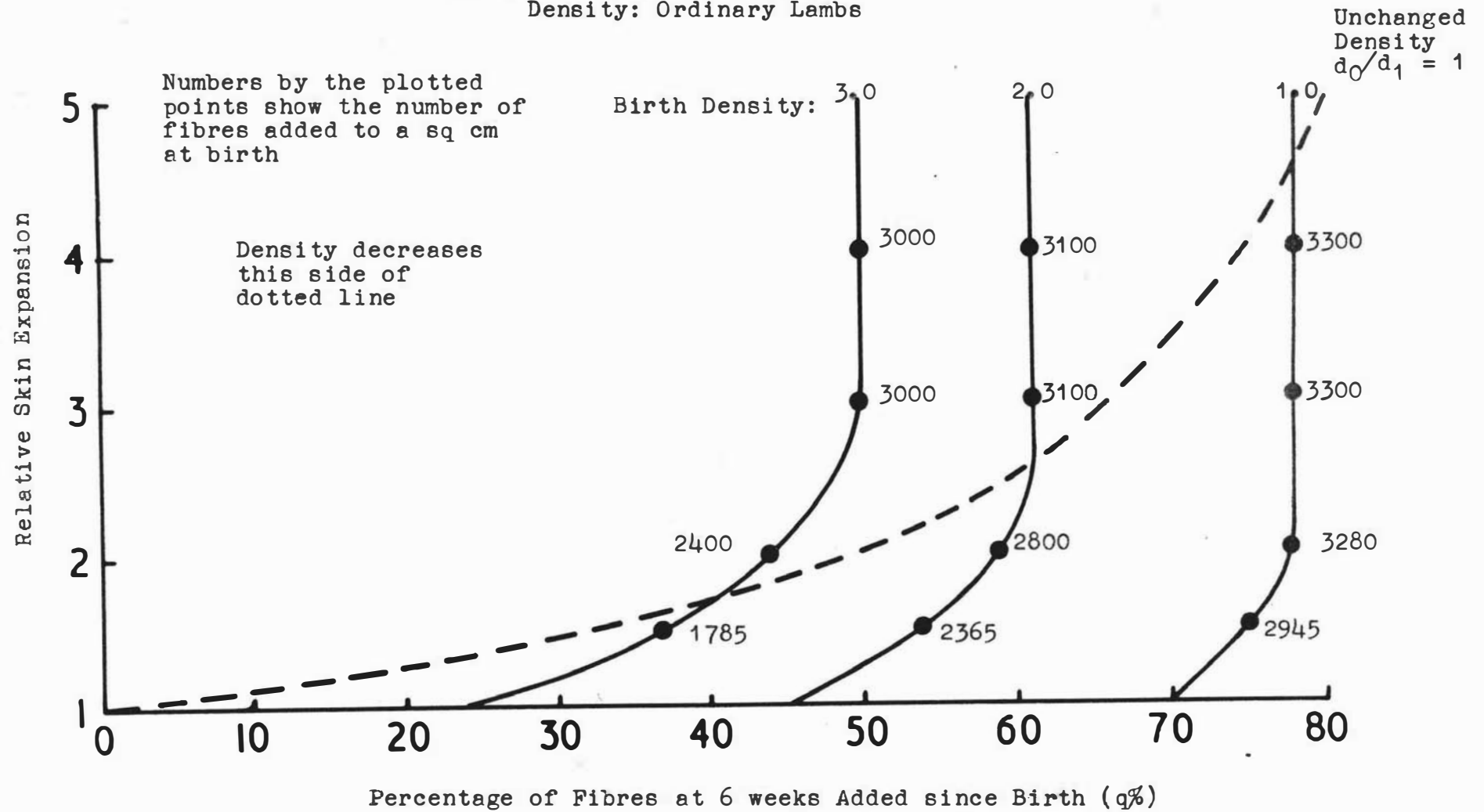


Figure 20

Relationships leading to Six Weeks
Density: Ordinary Lambs



Then $x = a/b$ and $y = a/(b + c)$

and $1 - (y/x) = 1 - b/(b + c)$

therefore $(x - y)/x = c/(b + c)$ which is a convenient form for calculation of $q\% = 100.c/(b + c)$ from x and y .

Figure 21 shows the values of $q\%$ calculated in this way, plotted against those values expected from the curves derived from the density relationships, with the regression lines and also the line expected if the relationship was perfect. The correlation of 0.56 (31 d.f.) which has a probability of < 0.001 of arising by chance can be considered good agreement when the possible errors in both the variables are considered. It will be seen from the diagram that the theoretical curves based on density somewhat underestimate the penalisation of the added fibres for low values of $q\%$, that is, high initial density and low skin expansion.

A similar diagram for the ordinary sheep is shown in Figure 22 where expected and observed values of d_0/d_1 are compared. This is not as satisfactory as the comparison used for the N-types as d_0 will be common to both expected and observed values making the comparison virtually one of expected and observed densities at six weeks. The agreement is again satisfactory ($r = 0.69$ 32 d.f.) and it was concluded that the theoretical curves estimated from the density and weight gain relationships showed a reasonable representation of the actual relationships of the various factors occurring during the first six weeks.

Considering the theoretical curves it is seen that the N-types add a greater number of fibres than ordinary lambs for skin expansions greater than 2.5 tending to a maximum of about 6000 compared with a maximum of about 3000 for the

Figure 21

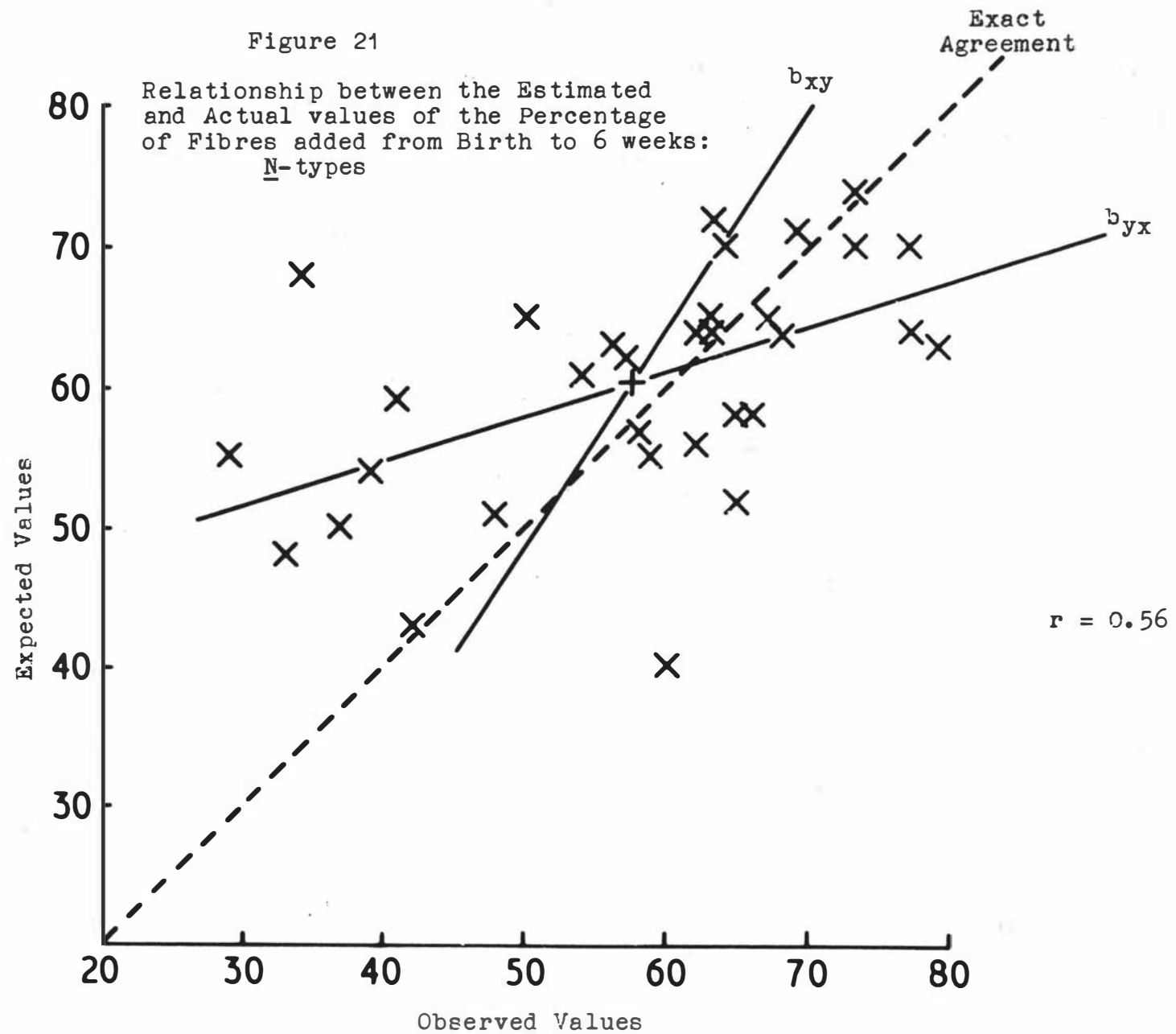
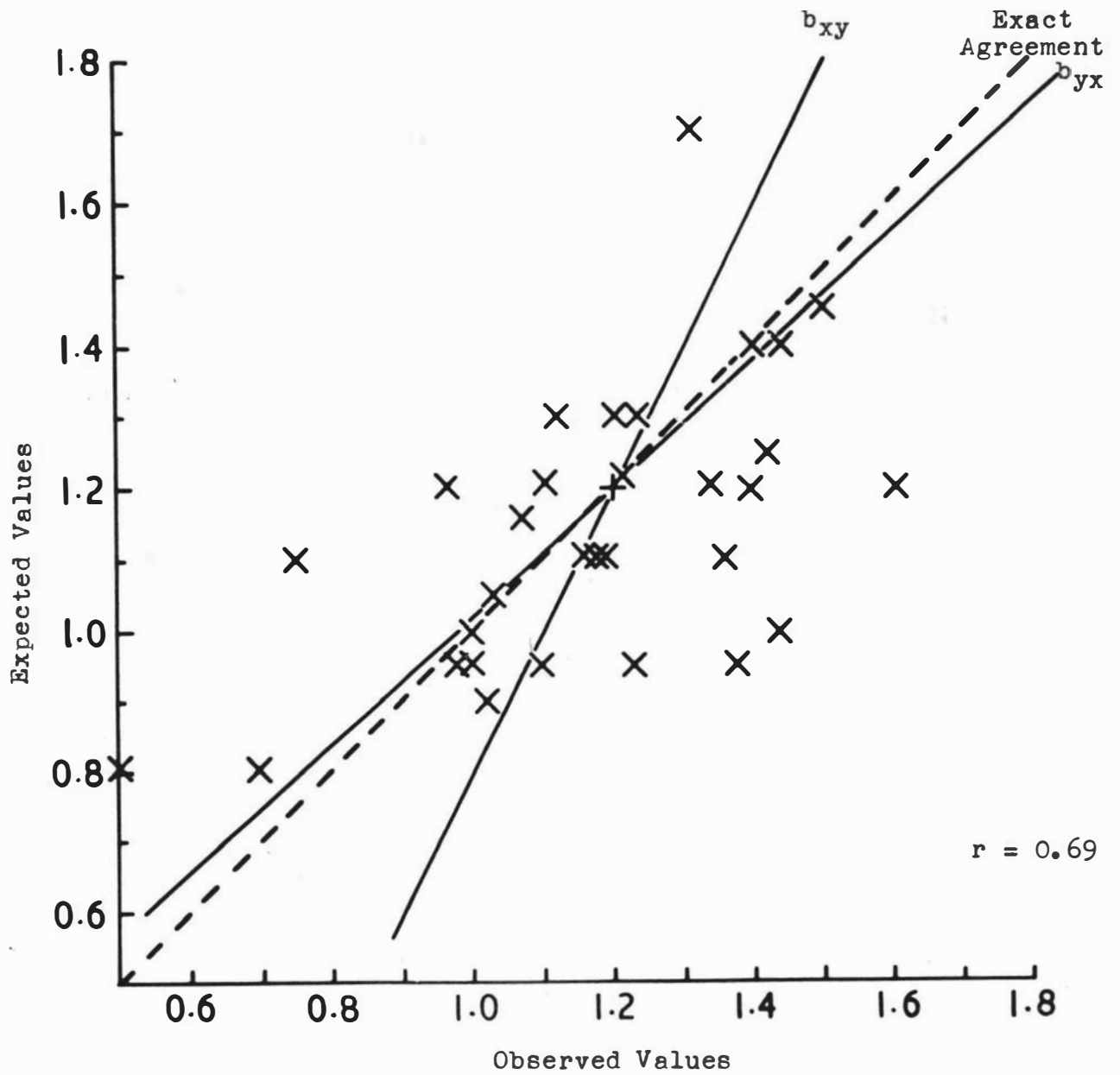


Figure 22

Relationship between the Estimated
and Actual Values of d_0/d_1 : Ordinary
Lambs



ordinary lambs. This latter figure appears to be in fair agreement with that obtained by Henderson (1953) for high - high plane lambs sampled in the loin position. (Henderson's Text fig.7. The original area of his enclosed position would have been from 1.0 to 1.5 sq cms.) This difference between N-types and ordinary lambs would explain the lack of a difference between the two genotypes of density at six weeks, but may be the result of non-active follicles at birth in the N-type rather than a major difference in the number of follicles added over the first six weeks.

Within genotypes it can be seen that for the lower skin expansions (less than 2.0) more fibres are added to those animals showing a lower initial fleece density which suggests a continuation of the suppression effect occurring pre-natally. This idea is strengthened by the lesser number of fibres added to N-type lambs at skin expansions of 1.5. In general it can be stated that for normal growth (skin expansion 2.5 or greater) N-types will tend to make up the deficiency of density at birth, but if slow growth occurs then the density at six weeks will still tend to be lower, there being a continuation of the penalisation of new fibre addition which occurred before birth.

A further experiment of this type using actual follicle counts would be of great interest, this approach having the advantage of bringing together density changes, ^{body} growth and numbers of new fibres in one overall relationship which involves both the mathematical and biological consequences of density changing as the result of both skin expansion and the addition of new fibres.

Summary of conclusions for six weeks density:

- (1) The number of new fibres added to the fleece from birth to six weeks is penalised, by a higher birth density or by the presence of halo hairs, when there are low weight gains or skin expansions (less than 2.0)
- (2) For skin expansions greater than 2.0 for N-types and 2.5 for ordinary lambs the number of fibres added is independent of the initial density.
- (3) For skin expansion greater than 3.0, ordinary lambs will add a maximum of 3000 fibres to an initial square cm so that greater skin expansion has no effect on the number of fibres added. N-type sheep differ in adding a greater number of fibres up to a skin expansion of 4.0 when a maximum of 6000 fibres is reached.
- (4) At skin expansions greater than 2.5 N-type sheep will add more fibres to an initial area than will ordinary lambs.
- (5) It is a mathematical consequence of these results that lambs with a low initial density will tend to increase it and those with a high initial density will tend to decrease it, the amounts depending on the skin expansion and the genotype of the lamb.
- (6) The results are in accord with those of Dry(1935), Galpin (1948), Schinckel(1953 and 1955 a & b) and Short (1955 a & b), who suggest that slow initial growth will penalise the addition of fibres or the development of the secondary follicles producing these fibres during the early growth of the lamb.

3. The density eight weeks after shearing.

A similar approach was adopted in analysis of this density and the multiple regression of the hogget density (about 25

Table 72

Partial Regressions of Hogget Density on Six
Weeks Density and Weight Gains

Independent Variable	N+ Coefficient	s.e.	++ Coefficient	s.e.
Weight gain 6 weeks to shearing	-0.972	0.645	+0.269	0.478
Weight gain shearing to hogget sample	+0.088	0.765	-0.583	0.924
6 weeks density	+0.307**	0.090	+0.243**	0.076

** Significant at 1% level

weeks of age) on six weeks density and on weight gains from six weeks to shearing and shearing to the hogget sampling were calculated for each genotype.

Weight gains (skin expansion) no longer appear as important as does the density at six weeks, the results being non-significant and inconsistent, except for the partial regression on six weeks density. The equations from this latter value^{are} plotted for the two genotypes in Figure 18.

The skin expansion over this period will have been of the order of 1.5 and a mean density of 2.0 at 6 weeks gives values of d_0/d_1 (from the Fig.18) for N-types of 0.75 and ordinary lambs of 0.95, which means that approximately 1000 more fibres will have been added to an original sq cm at birth, fewer being added to the N-types than to the ordinary lambs. This latter point is also suggested by the high negative value of the partial regression coefficient (i.e. density changes due to skin expansion only), for N-types for weight gains from six weeks to shearing, although there is a likelihood of its being a chance effect.

However this slight difference between N-types and ordinary lambs is sufficient to lead to the difference in favour of a higher density of the latter at 25 weeks of age, which was shown by the analysis of variance in the previous section. In general this period is of less importance for the addition of fibres to the fleece and it is reasonable to conclude that the effect of these on density is largely determined by growth in the first six or eight weeks of post-natal life and after this differences in skin expansion reflected in the final adult size of the sheep will determine the final characteristics of the fleece as far as they are affected by the density.

Summary:

(1) The density at the time that the final sample was taken depended on the density and number of fibres already in the fleece at six weeks, and of the small proportion of new fibres added over this final period it is probable that ordinary sheep added more than the N-types.

(2) It was concluded that the final fleece density of the adult sheep would be dependent on the density at six or eight weeks and subsequent skin expansion to the final adult value.

These results will be considered as a whole in the final discussion which will be based on the summaries of these sub-sections.

C. Factors Affecting Fibre Diameters.

1. The mean weighted diameter.

The initial calculations have been made using the weighted diameter, after which those components contributing to this weighted diameter are considered.

If P_A, P_B and P_O refer to the proportion of fibre types A, B and O respectively and x_A, x_B and x_O are the means of the diameters for each type, in a particular wool sample, then the weighted diameter was calculated as:

$$x_A P_A + x_B P_B + x_O P_O \text{ where } P_A + P_B + P_O = 1$$

The values used for the analysis were the means of the weighted diameters for the duplicate samples calculated independently. In considering the distribution of these weighted diameters, two points must be considered. Firstly by the Central Limit Theorem if the measurements comprising the individual means are normally distributed then the means themselves must be normally distributed. Secondly, the sum of linear functions of normally

distributed variables will also be normally distributed. (Cramér 1946) It has therefore been assumed that the weighted mean is normally distributed and that the usual statistical methods can be used.

Many workers have shown a connection between fleece density and mean fibre diameter, and also relationships between the weight of the animal and wool production, increased production taking the form of increased length and diameter of the individual fibres. After all follicles have been laid down, then apart from follicles ceasing and renewing production, changes in the weight of a sheep could lead to changes in skin area with the consequent density and correlated fibre diameter changes. The relationships between these various factors as a whole do not appear to have been considered, except perhaps by Galpin (1948) who, however, has not considered the weights of the sheep and has relied on mathematically derived rather than observed relationships. These theoretical relationships, moreover, are not accurate when medullation is present as they depend on the specific gravity of the wool fibres which can only be regarded as a constant when no air spaces are present.

The weighted diameter for the present data has been examined for each genotype and sampling time in terms of birth weight or weight gains prior to sampling, and density. This was done by means of a multiple regression to determine the independent effects of these variables on the weighted diameter.

The actual weight was used at birth and for the other two periods the weight gains from birth to six weeks and shearing to final weighing respectively were used. The use of shorter periods, over the time the diameter measured was produced, was not practicable as the weight gains were insufficient; this means

Table 73

Partial Regressions of Weighted Diameter(μ)^Q on
Weight (or Weight Gain) and Density (1000
fibres per sq cm)

Sampling Time	Genotype	d.f.	Residual Variance	Regression Coefficients			
				Weight gain@	s.e.	Density	s.e.
Birth	N+	30	8.636	+0.360	0.330	-4.233**	1.411
	++	31	1.686	+0.390*	0.166	+0.617	0.392
6 weeks	N+	30	9.319	+5.251	4.815	-2.297*	1.099
	++	31	6.337	+3.491	3.709	-2.086	0.994
Hogget	N+	30	7.538	+9.413	6.356	-2.076**	1.507
	++	31	7.663	+14.230	10.194	-2.940	1.988
Hogget within genotypes		63	7.358	+10.938*	5.334	-3.624**	1.092

* significant at 5% level

** significant at 1% level

@ Weight at birth and previous weight gains for 6 weeks and hogget.

Q The data was calculated in units of 2 microns and then regression coefficients and standard errors multiplied by 2 and residual variances by 4 (see Table 54, page 94)

Table 74

Regression of the Diameter of O type fibres (μ)* on
Halo-hair Density

d.f.	Coefficient	s.e.	t	p
31	- 0.00667	0.00246	2.71	0.01

*See footnote Table 73

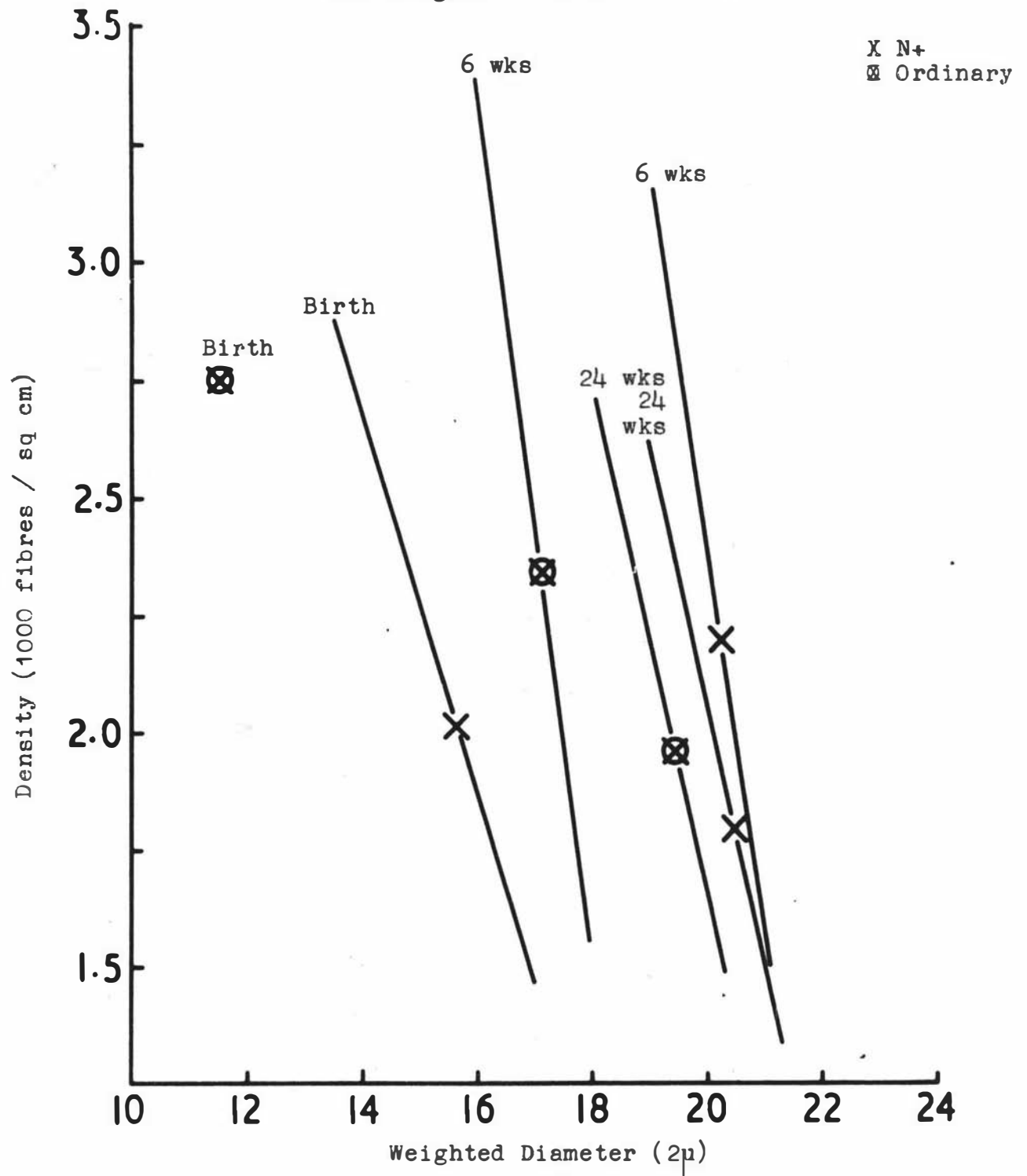
that an assumption is involved of either a high correlation between weight gains over 6 or 8 weeks and over the time the diameter was formed or a strong relationship between diameters of any particular section of the fibre over the period considered. Both these assumptions are reasonable unless there is a sudden check of the growth of a particular animal from some cause. These results are shown in Table 73, and the partial regressions and means for the density and weighted diameter are plotted in Figure 23.

The N-types consistently showed a higher weighted diameter for a given density, this being confirmed by analysis of covariance for the six weeks and post shearing sample, differences being significant at the 0.001 and 0.01 levels of probability respectively. A slightly greater change in diameter of N-type fibres for unit change in density was also consistent at the three sampling periods.

At birth there was no significant relation between density and diameter for the ordinary sheep while that shown for the N-types cannot be interpreted as cause and effect as it has already been demonstrated that a high halo-hair percentage (which will tend to increase weighted diameter) will lead to a lower fleece density. An effect of density on diameter of samples at birth from N-types can be demonstrated however by calculating the regression of the mean diameters of O type fibres on halo-hair density giving the result in Table 74. The small value is the result of the units used and it indicates that a decrease in diameter of 0.66μ will occur for each increase of 100 halo-hairs / sq cm. This is confirmatory evidence for the idea of a 'suppressing effect' of halo-hairs on the later formed fibres (or follicles).

Figure 23

Relationships Between Density
and Weighted Diameter



The partial regressions for weight or weight gains are consistently positive but have high standard errors. For this reason the regression within groups was calculated for the final sample, which reflects conditions most likely to be met with in the adult sheep, so as to increase the available degrees of freedom for the estimation of error. The significant relationship thus obtained shows that in terms of body weights of two animals of the same fleece density, the lightest being 70 lbs weight and the other 80 pounds (the two having been the same weight at shearing) the mean fibre diameter of the heavier animal would be greater by 1.54 μ . This represents a difference of 0.14 ($\log_e$) in relative growth rate which would be a fairly large one for growth over this period.

A further point of interest from Table 73 lies in the comparison of residual variances of the weighted diameters. That of the N-types increases to six weeks and then decreases again to the post-shearing stage, while those of the ordinary lambs increase from a low variability to one similar to that of the N-types at the final stage. This may be the result of the tendency for low densities to increase and high densities to decrease which was shown in the previous section, but the increased variance of the ordinary sheep is of particular interest when the wide range of hogget fleece type found the previous year for ordinary sheep is considered.

2. The components of the mean weighted diameter.

The mean weighted diameter was made up of the means and proportions of three types of fibres A, B and O. The changes in these components over the three time periods are shown in Figures 24 and 25 respectively; mean weighted diameters are

also included in the former diagram.

For the O-type fibres the diameters show an increase over the period, this increase being significantly greater for N-types at the 25 weeks sampling. The N-type fibre measurements at six weeks are likely to include more new fibres which may lower the mean value of diameter, although those fibres which showed the tip under the lanometer were omitted as they would only have been in the initial stages of growth.

When considering the changes in the diameter of the A and B type fibres shown in Figure 24, it is also necessary to consider the changes in their proportions in the sample (Figure 25) The reason for this is the changes in the fibres from birth to six weeks. For instance a super-sickle fibre under Dry's (1935) classification may show a thinning at birth so that a section at this point will be a B type whereas a section at six weeks will be an A type. Similarly a curly-tip fibre may be O type at birth and B type at six weeks.

This change is associated with an increase in weighted diameter and B type fibre diameter and also with a large increase in the mean diameters of the A type fibres. In addition there is a sharp decrease in the proportion of O types, that is unmedullated fibres, in spite of the number of new and probably smaller fibres added. The mean value of 40% for O types at six weeks indicates that even if all the fibres present at birth were medullated at six weeks, some of the new fibres must also be medullated, as there were more than 40% of new fibres present at this stage. The addition of new fibres results in the percentage of A types being virtually unchanged in spite of the change of some fibres from B to A types over

Figure 24

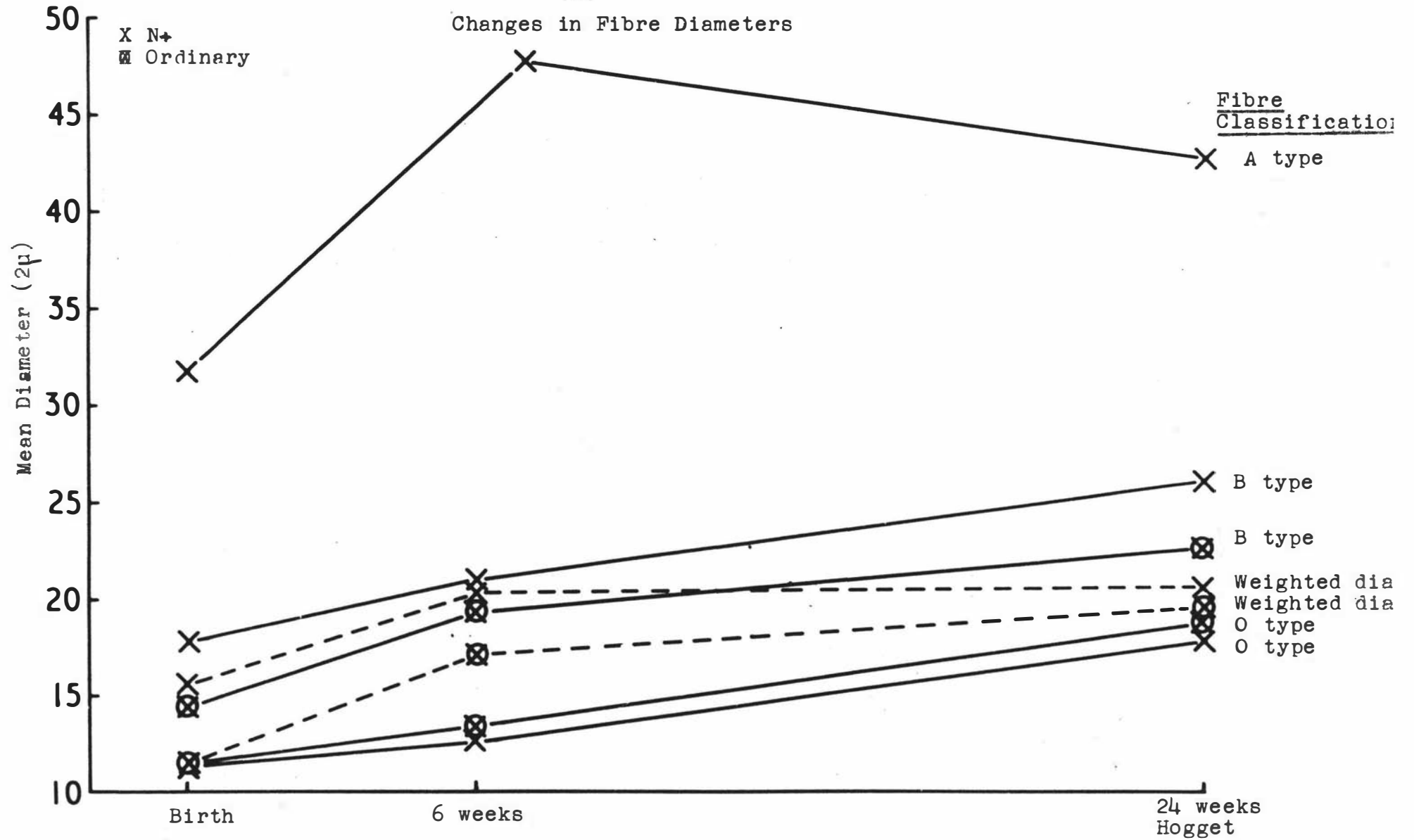


Figure 25

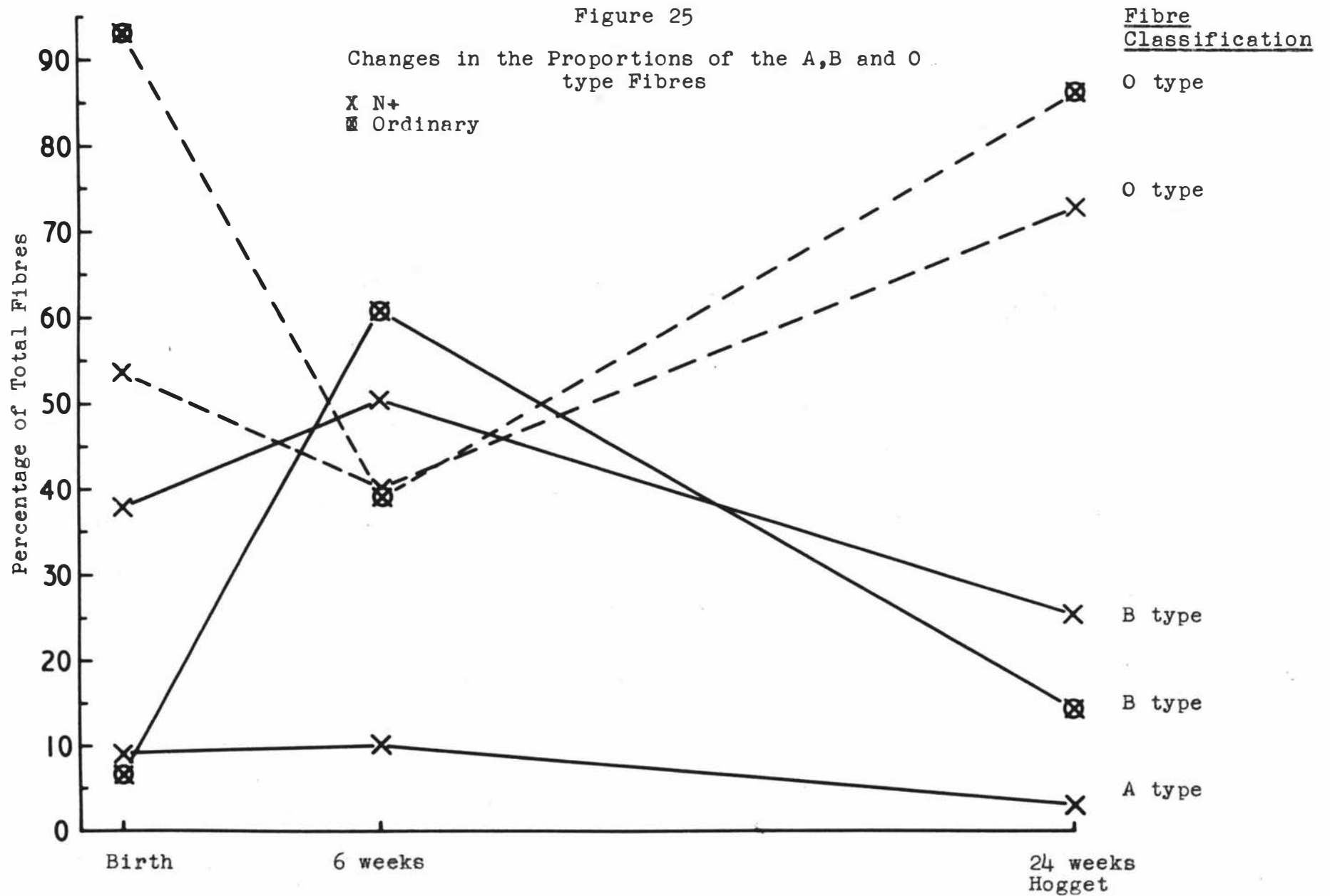


Table 75

Correlation Coefficients between the Mean
Diameters of O and B type Fibres

	Birth	Six Weeks	25 Weeks
N-type	0.231	0.0059	0.198
Ordinary	0.217	0.510**	0.462*
The degrees of freedom:			
N-type	30	31	31
Ordinary	12	32	21

* Significant at 5% level
** 1%

the period. It is difficult to determine at this stage whether there is any significance in this constant value in relation to effects already described concerning the addition of new fibres.

From six weeks to the hogget stage there is a decrease in the difference between mean values of the component fibre types from the N-type animals. This agrees with a similar result observed for the variance of the weighted diameter (Table 73) Also over this stage there is a marked decrease in the numbers of medullated fibres, the reason for which will become clear when medullation is discussed below.

The correlations for each genotype, between mean diameters of the various fibre types at each sampling are shown in Table 75. Those between A type and other fibres are not shown as in no case were they significant. The different degrees of freedom are the result of some fibre types not being present on all animals. The absence of any correlations for the N-type sheep indicates that the assumptions made earlier concerning the normal distribution of the weighted diameters, will hold whatever the distribution of the means of the various fibre types. The full assumptions are required for the ordinary lambs.

The biological meaning of a lack of correlation is not clear because the increase in the mean of any group may result in the larger fibres in that group becoming the smaller fibres of the type above. The presence of a correlation suggests that it is possible that one population of fibre diameters may be being dealt with in the ordinary lambs.

Follicle measurements, making use of the classification into primary and secondary follicles, are required to determine the meaning of the relationships between the fibre types.

Table 76
Regressions of the A type Proportions on the
Halo-hair proportions

Time of Sampling		Coefficient	s.e.	d.f.
Halo-hairs	A types			
Birth	Birth	+0.440***	0.108	31
6 weeks	6 weeks	+0.666*	0.279	21
6 weeks	Hogget	+0.878**	0.228	16

* Significant at 5% level
 ** 1%
 *** 0.1%

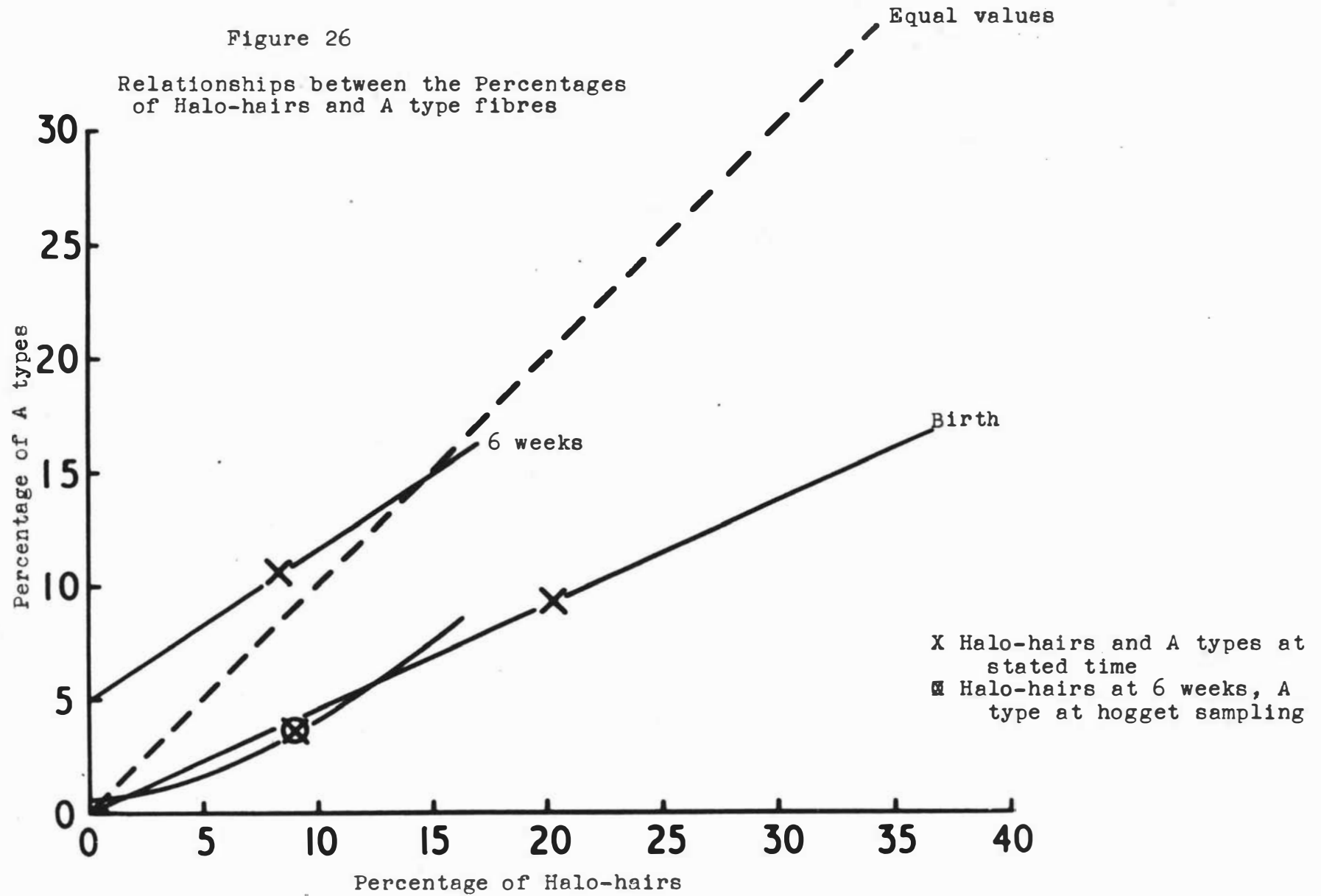
In Section VIII,D,2 it was stated that for the measurement of the diameter at six weeks, the halo-hairs were separated out for measurement as an individual group, but that the method was abandoned in favour of direct classification under the lanometer into A, B and O types. Consideration of the relationship between proportions of A type fibres and halo-hairs shows that this would lead to slight underestimation of the proportion of A types for these first few sheep but hardly enough to affect the main results. It should be noted that this would have no effect on the weighted diameter as non-halo-hair A types would occur in the B-type classification for these sheep.

In addition to this relationship, that between halo-hair proportions and A type proportions at birth was calculated and also that between halo-hairs at six weeks and A types at the post-shearing stage. These are shown in Table 76. The percentage of A type fibres at this stage had a skewed distribution and therefore zero values are omitted and the transformation $p = \sin^2$ (Fisher and Yates 1953) has been used.

These regressions are plotted in Figure 26 with the appropriate means. The mean value of $\frac{\text{halo-hair}}{\text{percentage}}$ at six weeks for those sheep having no A type fibres in the sample at 24 weeks was 6.54 which value would give an expected value of 2.3% instead of zero from the calculated regression. It is possible that the omission of the zero values has biased the fit of the regression, but at this stage the establishment of the relationship is considered more important than its exact nature. Remembering that some new fibres will have been added over this period the result suggests that the majority but not all of the halo-hairs may be succeeded by A type fibres (not necessarily kemps), if it is assumed that no other follicles have started to produce these larger fibres.

Figure 26

Relationships between the Percentages
of Halo-hairs and A type fibres



The other two results indicate that not all halo hairs are A types at birth (or a little before birth) and also that at six weeks, lower halo-hair percentages appear to be associated with more fibres which are A types at this stage but not at birth. It is possible that the super sickle-fibres come from follicles capable of producing fibres equivalent to halo-hairs but which fail to do so except over the pre-natal period prior to the secondary follicles being laid down and also over the post-natal period of rapid skin expansion.

3. Summary of Section IX C

- (1) Mean weighted diameters and fleece density were inversely proportional for each genotype and each time of sampling except for the ordinary lambs at birth.
- (2) The diameter of O fibres at birth decreased with increased halo-hair density of the N-type lambs.
- (3) For the post-shearing sample weight gains had a significant positive relationship with fibre diameter at constant density when partial regression coefficients within genotype groups were estimated.
- (4) A tendency was observed for the variances of mean fibre diameters of N-type and ordinary lambs to converge as the lambs became older.
- (5) Consideration of the individual means of fibre type diameters making up the weighted mean showed overall increases from birth to six weeks, these being most marked in the larger fibre types. In addition there was a tendency for the variability to be reduced between six weeks and final sampling, with, however, little change in the value of the mean weighted diameters over this period.

- (6) O type fibres from N-type sheep had a smaller diameter than those from ordinary sheep at the post-shearing stage.
- (7) Consideration of the correlations between means of fibre types at the various sampling times showed no relationships amongst those from N-types, but a positive relationship between B type and O type fibres existed for the ordinary lambs at six weeks and final sampling.
- (8) The relationship between A type fibres and halo-hairs was considered. It is reasonable to suppose that halo-hairs were generally followed by A type fibres but histological evidence is required in support of this.
- (9) Of the halo-hairs from the N-type lamb birth samples about a half must have been classified as B type fibres under the projection microscope.
- (10) At six weeks all halo-hairs examined were A type fibres and in addition some other of Dry's fibre types must have been classified in this group.

D. Factors Affecting Medullation

In the first part of this thesis it was shown that the diameter of the medulla of a fibre was strongly related to the total diameter of the fibre and the weight of the sheep from which it was taken. The 'hairiness' of the fleece will then depend on the diameter of the fibres comprising it and the condition of the animal. 'Hairiness' has been quoted previously as being one of the principal observed pleiotropic effects of N at all stages of growth and in particular for the adult stage when birthcoat fibre types can no longer be recognised. Events leading to the different densities and diameters of fibres have

Table 77

Partial Regressions of Medulla Diameter on Log Fibre
Diameter (μ)[Ⓐ] Fleece Density (1000 fibres / sq cm)
and Weight Gains for B type Fibres at the Three
Sampling Times

Time of sampling	d.f.	Weight Gains@ Coefficient	s.e.	Density Coefficient	s.e.	Fibre Diameter Coefficient	s.e.
Birth							
N+	29	-0.204	0.209	+0.634	0.942	+27.198***	5.272
++	10	-0.009	0.366	-0.582	0.947	+32.258**	7.150
6 weeks							
N+	29	+1.473	3.741	+0.715	0.648	+21.785***	4.492
++	30	+3.411	4.015	+1.867	1.177	+22.981**	7.537
Hogget							
N+	29	-16.736*	8.367	+1.539	2.041	+60.907***	7.275
++	19	+1.783	4.219	+2.231	1.527	-1.626	4.868

* Significant at 5% level

** 1%

*** 0.1%

Ⓐ See footnote to Table 54 (page 94)

@ Body weight used at birth.

now been described and the final stage is therefore the examination and possible confirmation of the effects of these variables and the animals' condition, on medullation.

Multiple regressions have therefore been calculated for B type fibres and each genotype at the different sampling times. These multiple regressions were of mean medulla diameter on the relative weight gain (or birth weight), the fleece density and the appropriate mean fibre diameter. The results are shown in Table 77. A natural log scale was used for the fibre diameter means as preliminary plotting and the previous year's results with those of Ross (1950) indicated that this would lead to a better straight line fit for this variable.

The only regression coefficients showing a real departure from a zero value, apart from those for fibre diameter, were those of weight gains of N-type lambs from shearing to the time of the post-shearing sample. This effect of weight gains is considered confirmatory evidence for the result obtained in the first part; that is, that the condition of the sheep has an effect on the amount of medulla in a fibre from that sheep.

Density does not appear to be of any importance at any stage and therefore has been omitted from the regressions for A type fibres which are shown in Table 78, which are simple regressions of medulla diameter on fibre diameter except at the hogget stage when the additional variable of weight gain has been included.

The results in Table 78 are for N-type lambs only and the difference in numbers of degrees of freedom for the residual variance are the result of some of the lambs having no A type fibres in the particular sample.

Table 78

Regression Coefficients for the A type Medulla Diameters on Log Fibre Diameters (μ)^Q for the Three Sampling Times, with the Partial Regressions at the Hogget Sampling

Sampling Time	Birth	6 weeks	Hogget Weight Gains	Fibre Diameter
Coefficient	+57.815***	+93.046***	+0.0846	+62.010***
s.e.	5.018	4.774	22.386	15.947
d.f.	30	31		15

*** Significant at 0.1% level

^Q See footnote to Table 54(page 94)

Table 79

A Comparison of the Partial Regression Coefficients Obtained for Medulla Diameters in the Two Years

Year	Genotypes	Weight Gains Coefficient	s.e.	Fibre Diameter Coefficient	s.e.	d.f.
1952	NN,N+,++	-16.132**	5.867	72.288***	5.961	54
1953	N+	-16.736*	8.367	60.907***	7.275	29

* Significant at 5% level

**

1%

0.1%

The means and the fibre diameter regressions from both these tables have been plotted in Figure 27. At the hogget stage the non-significant regression for ordinary sheep has been omitted, and the regression obtained the previous year over all genotypes, at about the same period, included.

Before discussing these regressions and the possible differences between them it is as well to consider to what extent the results, after shearing, for the two years agree, and to do this the fibre diameter regression for 1952-53 has been expressed in terms of natural logarithms, and the partial regression on live weights has been expressed in terms of the weight gains appropriate to the mean value. The resulting partial regression coefficients, with those obtained in 1954 and the standard errors are shown in Table 79.

When the different conditions and methods of arriving at these results are considered, the ~~results~~ results are remarkably consistent, there being no real difference between years for either coefficient. The coefficient for weight gain indicates that a difference in this value which results in a difference of 10 pounds for sheep initially of the same weight, will result in a difference of about two microns in the medulla diameter at constant fibre diameter, the lighter sheep having the greater medulla. In effect this means that fibres from a lamb showing retarded growth will show medulla at a lesser diameter than fibres from a lamb growing well. In Section C however, it was shown that retarded growth would also tend to reduce the diameter of the fibres at a given fleece density. Consideration of the overall effect on the medulla for a 10 pound weight advantage shows that although fibre diameter will be increased by 1.54

Table 80

Means of the Medulla and Fibre Diameters(p)
for the B type Fibres at the Three Sampling
Times

Genotype	Birth		6 weeks		Hogget	
	Fibre	Medulla	Fibre	Medulla	Fibre	Medulla
N+	35.4	13.2	41.6	18.0	52.0	17.6
++	28.8	7.0	38.6	14.0	45.2	6.6*

* Intermittent medulla (see text)

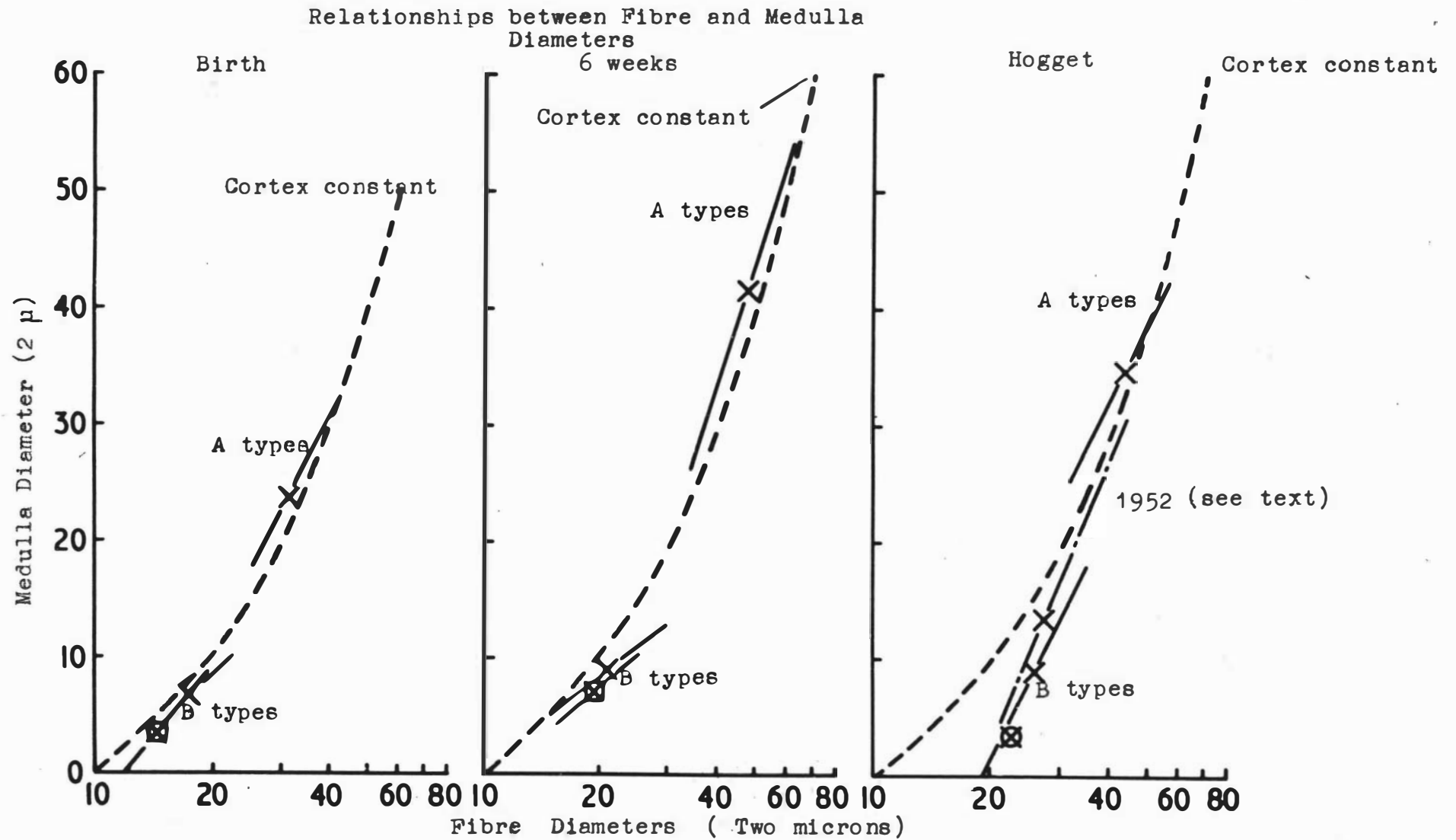
microns, the medulla will tend to decrease by 0.7 microns.

This is subject to errors of estimate of the multiple regression equation and to the limitations of the range over which it is valid, but it suggests that apart from density and possible unknown effects, vigorous growth will not lead to increased fleece medullation (except perhaps in terms of the medullometer when the greater length of medullated fibres is also measured). The reservation with regard to density is necessary because a large weight increase in an adult sheep may lead to decreased density and correlated increased diameter over and above that resulting from the weight gain alone. In addition a sheep that grows well as a hogget is likely to have grown well as a lamb, which as has been shown, might also lead to a lower density. Therefore because of this density effect, coarse fibres and consequent medullation could be associated with a vigorous well grown sheep.

The comparison of the results for the three time periods for 1953-54 is of interest, as they show that the medulla and fibre diameter relationships are not the same for each of these periods. Means for each genotype and time period are shown in Table 80, the means for the fibre diameters being reconverted from the log scale.

From Figure 27 and Table 80 it is clear that the N-type and ordinary lambs show very similar relationships between medulla and fibre diameter ~~relationships~~ at birth and that any differences in medullation of the fleece are the result of the larger fibres of the N-type. At 6 weeks the A type fibres, which are all from N-type lambs, have shown an increase in medulla corresponding to the increase in diameter. B type fibres

Figure 27



X N+
 □ Ordinary

Cortex constant: i.e. For values on this line increase of fibre diameter takes place by increase of the medulla only.

from the N-type have also shown a proportional change, no difference of medulla diameter at constant fibre diameter being shown by analysis of covariance.

A difference (P less than 0.001) does exist, however, between N-type and ordinary sheep at six weeks of age, the latter having fibres with a lower medulla diameter for a given fibre diameter. A simple explanation for this would be the heavier drain on the keratin precursors in the blood stream of the N-type sheep, which were adding considerably more fibres to the fleece at this stage.

For the post-shearing sample, it is clear without analysis, that the medulla diameter is now considerably less for a given fibre diameter. A value of about 40 microns is reached before medullation occurs. Examination of the fibres suggests that this difference lies largely in the size of the cells of the fibre, individual air spaces being of the order of 10 microns compared with about 1 micron previously. The non-significant connection between fibre and medulla diameters for the ordinary sheep at this stage is probably the result of the intermittent nature of the medulla in the majority of the fibres measured at this stage. As the variation between medulla and no medulla is of the order of the air space size, medullas greater than 10 μ would be required to establish relationships.

Although it is beyond the scope of this thesis it is suggested that a histological investigation of cell dimensions and numbers in medullated and non-medullated fibres would reveal that the results observed here are the result of progressive changes in the size of the cortical cells until medullation occurs. After this the expansion of the medulla air spaces is likely to be the main factor contributing to increase in fibre diameter. The changes in relative sizes of

the length and breadth of the cells may also explain the relationships between fibre diameter and length observed by many authors.

Auber (1950) has dealt in considerable detail with those follicles which produce medullated fibres in the fleece of the Herdwick sheep. He suggests that medullation is the result of the failure of 'pre-cursors' to penetrate to those cells eventually forming the bridges between the medulla air spaces. If weight or weight gains are related to such 'pre-cursors', and the fibre diameter relationships suggest that they are, then the increase of medulla diameter at constant fibre diameter for lesser weight or weight gains offers confirmatory evidence for these ideas. The few values quoted by Auber for medulla and fibre diameters fall fairly close to the regression lines calculated earlier in this section, but the evidence is insufficient to draw any conclusions concerning breeds other than the Romney.

The work of Bullough and Johnson (1951) on the effect of available energy on mitotic rate in the epidermis of the mouse is also suggestive. It is possible that the low mitotic rate in the centre of the papilla of the wool follicle which leads to the formation of medulla cells may result from the lack of available energy. Medulla formation could thus be the result not of a shortage of keratin pre-cursors but of those metabolites required for cell division.

If such ideas can be further verified then the differences in medulla diameter at constant fibre diameter might well prove a useful index for work on the availability to the wool follicles of keratin or other pre-cursors in the blood stream. The higher values of relative medulla diameter for the birth and six weeks

samples when there is a high fleece density and when considerable numbers of new follicles are starting to produce fibres, adds force to the argument that an approach of this type would be of use.

In general the results in this section show that the hairiness of the birthcoat and later fleece of the M-type sheep can in part be considered a consequence of the diameters of the fibres composing that fleece. The examination of 'hairiness' then becomes largely a problem of identifying those factors which lead to fibres of different diameter, which problem has been attempted in the earlier sections. In addition, studies of 'hairiness' should consider the availability of the precursors of keratin and other factors which are required to form the cortical part of the fibre.

E. The Relationships Within Individual Fibres

1. The pre-natal and post-natal fibre diameter.

This section is essentially a preliminary study which was made in order to form a basis for correlating the results obtained above with those of previous workers. The approach used in this thesis has been one which has enabled the determination of the relationships between the development of the fleece and body growth. Previous work has been concerned initially with the morphology of the fibres and then with the inter-relationships of the resulting fibre types (Dry 1935) (not the A, B and O types used in previous sections) and the follicles which produce them.

The results in previous sections are based on fibre diameters and their relationships. A possible connecting link between the two approaches is by consideration of the diameter relationships within a particular fibre. An increase in the post-natal

diameter of a fibre has been shown by Ross (1950) and in addition it has been found in this thesis that a high halo-hair density is associated with a lower diameter of O type fibres. It was also found that a rapid increase occurred in diameter after birth, particularly for the larger fibres. This increase and the lower diameters of O type fibres also correspond to the rapid addition of new fibres after birth and the possible restrictions on them before birth.

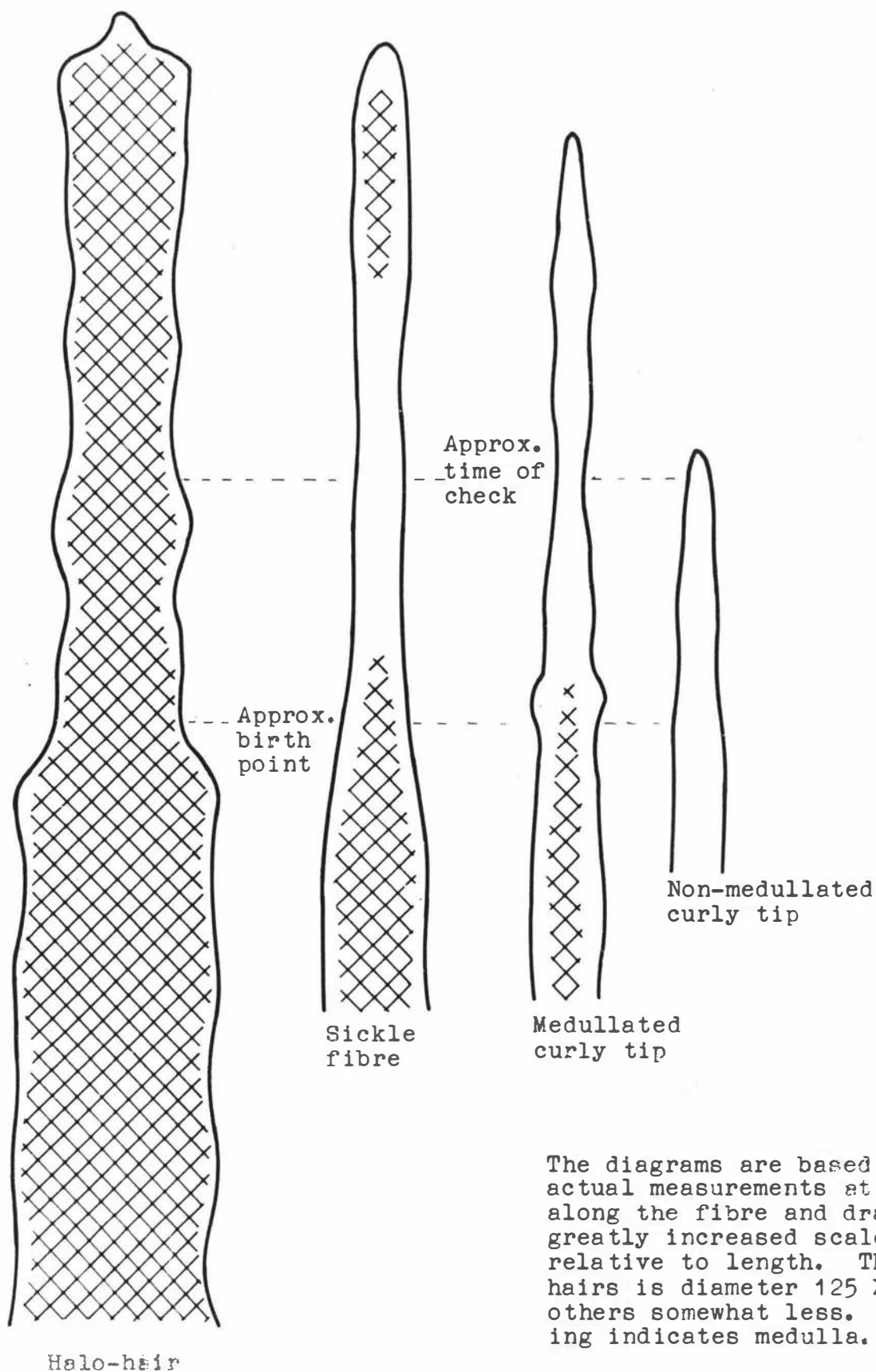
To examine these factors for individual fibres those from ten sheep of both genotypes and of both birth ranks were measured for changes between pre-natal and post-natal diameter. Figure 28 shows the variations in diameter for four of Dry's fibre types from initiation to six weeks after birth based on measurements at intervals along the fibre. These are included as a guide to the remaining data which was obtained by measuring diameters of individual fibres at the six weeks level and at the thinnest pre-natal portion (major axes throughout); i.e., the section of maximum pre-natal check.

Regressions of the difference between these two diameters on the six weeks diameter were calculated. The six weeks value was chosen because it probably approaches the maximum value of fibre diameter for a particular follicle initiated pre-natally over the period being considered. The six weeks value (independent variable) was selected to give as wide a range as possible for a particular sheep, the least squares regression technique being valid under these conditions. Twenty fibres were measured for each sheep as this was found sufficient to determine the relationship.

The individual regressions for the 10 sheep were all different from zero, the values of F (1 and 18 d.f.) varying from

Figure 28

Diagrams of Fibre Types from
Initiation to Six Weeks



The diagrams are based on actual measurements at intervals along the fibre and drawn with a greatly increased scale for diameter relative to length. That of halo-hairs is diameter 125 X length, the others somewhat less. Cross hatching indicates medulla.

Table 81

Differences Between Regressions of Six Weeks
Diameter (μ) on the Reduction in Pre-natal
Diameter (μ)

Source	d.f.	Mean Square	F
Joint regression	1	8830.134	Very large***
Differences	9	23.714(s_1)	5.24***(s_1/s_2)
Residuals	180	4.523(s_2)	
Differences within genotypes	8	20.802(s_3)	4.60***(s_3/s_2)
Between genotypes	1	47.013(s_4)	2.26(s_4/s_1)

*** Significant at 0.1% level

Table 82

Differences Between the Regression in Table 81
Analysed for Each Genotype.

N-types

Source	d.f.	Mean Square	F
Joint regression	1	7770.226	Very large
Differences	4	11.064	1.55
Residuals	90	7.152	

Ordinary lambs

Joint regression	1	1106.921	Very large
Differences	4	30.540	16.12***
Residuals	90	1.895	

*** Significant at the 0.1% level

The joint regression coefficients: N-type 0.616
Ordinary 0.502

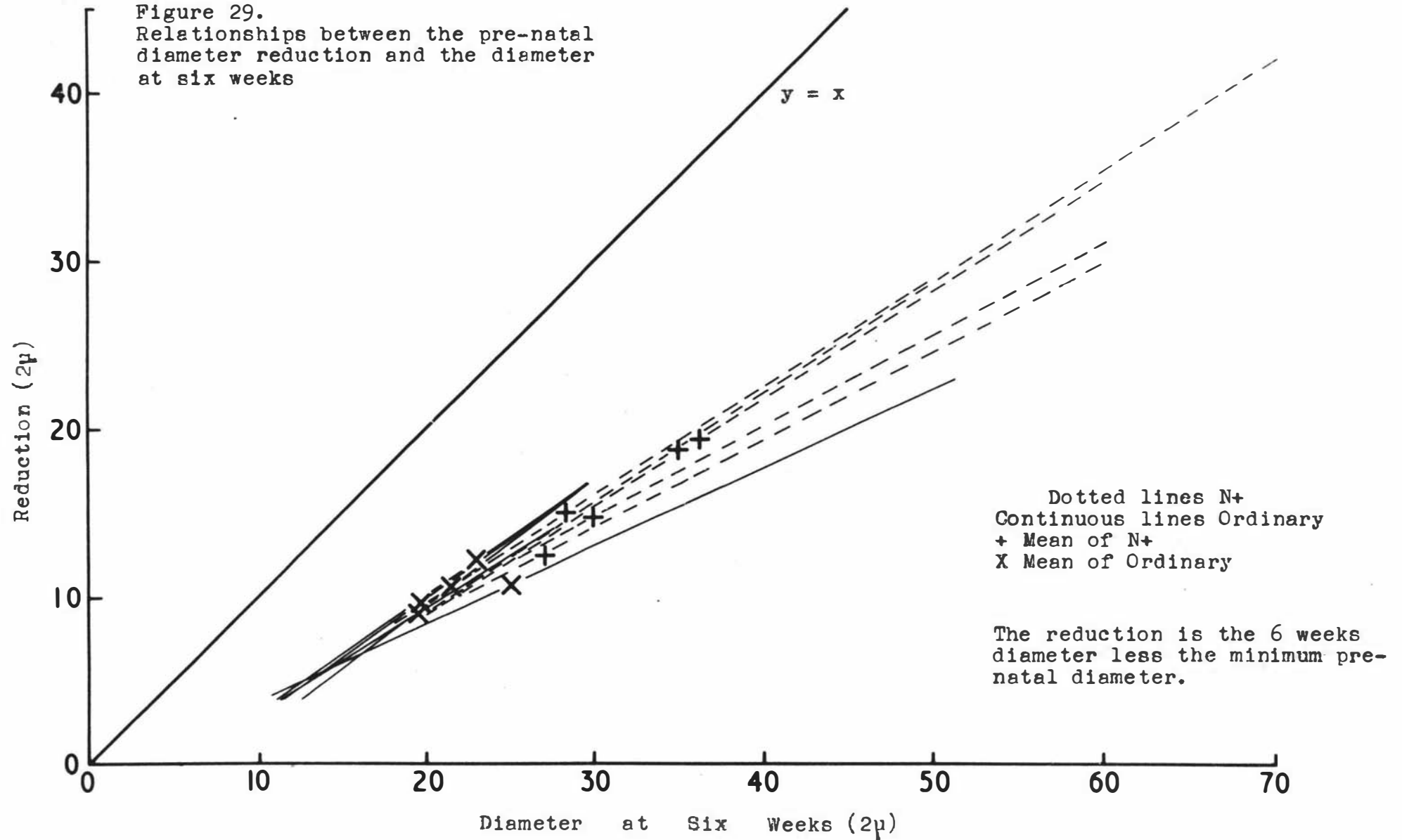
7 to 239. The values of the coefficients varied from 0.3957 to 0.8080 and these regressions with the means have been plotted in Figure 29.

Table 81 shows the analyses of the possible differences amongst these regressions. There is no difference between the genotypes but there is an overall difference and also one within genotypes. This difference within genotypes has been further analysed and Table 82 shows it to be the result of variation amongst the regressions for the ordinary animals and not amongst the N-types. Further consideration of the plotted regression lines shows one lamb deviating considerably from the remainder. Examination of the results on growth and on density and diameter for this lamb showed that it had grown very slowly from birth to six weeks and as a result showed an increase in density due to the low skin expansion. As a result of this there was likely to be a smaller increase in diameter than normal.

The line $y = x$ in Figure 29 indicates the maximum theoretical reduction, i.e. no fibre growth from a follicle before birth. Similarly, the x axis will represent the minimum reduction, i.e. the fibres would be the same size pre- and post-natally.

These regressions show that the larger the fibre diameter at six weeks then the larger will be the reduction in diameter pre-natally. In addition, the large amount of variance of this reduction which is accounted for by the six weeks diameter suggests that the reduction is very similar amongst sheep and depends on the six weeks fibre size. This diameter at six weeks approaches the maximum diameter a fibre attains and may depend on the original size of the follicle when it is formed, which may be determined very largely by genetic factors. Thus, a larger follicle can have a greater variation than a smaller one in the

Figure 29.
Relationships between the pre-natal
diameter reduction and the diameter
at six weeks



size of the fibre it produces in response to different conditions.

Factors affecting fibre diameters just prior to birth and at six weeks have been discussed and it is suggested that a combination of these conditions acting at the time a particular section of fibre is formed, with the original follicle size, will determine the diameter of the fibre at that time.

2. Discussion in relation to previous work.

The morphology of a fibre depends on the shape of the tip and changes in its diameter and medullation. The data presented offer no relationships with classification by the tip structure but do, however, show possible relationship in diameter changes. Medullation has been discussed in the previous section where it was shown to be strongly related to fibre diameter. This confirms observations by Ross (1950) and although further work is required to determine whether the relationship differs for the different fibre types of Dry (1935), the results seem directly in accord with the previous work.

The main purpose of this section therefore is to consider the relationships observed here on diameters and densities with their possible causes and those observed by Dry (1935), Fraser, Ross and Wright(1954) and Fraser (1952).

Dry (1935) discusses the various fibres of the birthcoat and their division into various fibre types. These have been tabulated and discussed in relation to the follicles from which they grow by Fraser, Ross and Wright (1954) and Ross(1954) The range of fibre diameters for various types have been given by Ross (1950)

These fibre types can be arranged in the probable order of their appearance on the lamb, to form arrays. The order of their appearance is determined by the type itself in the case

of pre-curly-tip fibres and by the number of curls in the pre-natal portion of the curly-tip fibres. The justification for this is based on follicle dissection by Rudall and Hefford (unpublished) and by Ross (1954)

The essential features of this work are firstly the occurrence of a thinning of the pre-natal portion of the fibres which, with medullation, partially determines its type classification; and secondly, the occurrence in some arrays of fibres with a diameter less than that of fibres formed before and after them in the array i.e. there is a decrease in diameter and length from those fibres formed initially until the first of the curly-tip fibres and then an increase in the diameter of the later formed fibres. There are considerable variations in the extent of these smaller fibres in the different arrays.

These observations are attributed to a checking force, the pre-natal check, which acts at some period before birth. By considering variations in its time of onset, its strength and its falling off, the various types of arrays can be explained.

The work on individual fibres earlier in this section confirms the reduction in part or all of a fibre pre-natally and indicates that for this aspect of the check, fibre types could be explained in terms of this thesis, i.e. reductions in diameter and consequently medullation, as a result of the density relationships. Further work on the relationships of these diameter changes with data from the various fibre types is required to confirm or add to these results.

It is clear that this aspect of the check is very similar for both N-type and ordinary lambs, which with the results of Dry and Stephenson (1954), indicates that a further appraisal is required of Fraser and Hamada's (1954) speculations on the

position of the pre-natal check in the evolution of the fleece.

The second aspect of the check is difficult to assess in the terms of this thesis without more detailed work on the fibre types. However at this stage it seems reasonable to suggest that those follicles laid down or starting fibre production, at the time that there is considerable crowding of follicles (Ross 1945) may be penalised. For N-types this is the stage that skin expansion and halo-hair density are probably the limiting factors in the determination of the number of fibres at birth, and follicles formed after this period may suffer less from these effects and produce the larger curly-tip fibres found further down the array. Where skin expansion is insufficient the suppressing effects may continue long enough for all subsequent fibres to be checked as in the 'Plain' array.

This does not explain all the features of the check and the arrays, and more work is required in relating the arrays to the type of result obtained on density and diameter in this thesis. Further evidence of the effect of primary fibre size on both numbers and sizes of secondary fibres is offered by Fraser and Short(1952) and when it is considered that the majority of these results were forecast by Dry from the array technique then the importance of relating his technique to those of diameter measurement is clear.

Fraser (1952 a and b) has considered the development of the N-type fleece in terms of fibre length growth and follicle efficiency. If the latter is directly related to fibre diameter and in turn to length growth of the fibre, then the results given here are in general agreement with those of Fraser and his expression for the pre-natal check of efficiency as a function

of time becomes diameter as a function of time. This then is the first aspect of the check which has been discussed above. Fraser's efficiency concept is considered further in the general discussion.

It can be seen then that in spite of the necessary difference of approach used in this thesis, the results are in general accord with those derived by other means and although more detailed investigation is required on the various fibre types and arrays in the terms used here, such an investigation is likely to prove rewarding.

PART THREE

CONCLUSIONS.

A. The Pleiotropic Effects of the Gene N

The science of genetics has always been dependent on those differences between organisms which can be determined by eye appraisal or by measurement. If two organisms have the same phenotype but different genotypes, then differences amongst their offspring must be relied upon for deductions concerning these parental genotypes. In this work the differences between two known genotypes have been relied upon to determine those series of phenotypic manifestations dependent, the one upon another, and upon external events, which are known as pleiotropy in the wider sense of Gr neberg (1938)

It is now proposed to consider these results in terms of the pleiotropic effects of the gene N in the New Zealand Romney sheep and also the evidence for these effects. There will clearly still be gaps in the knowledge so far obtained so that certain stages are still little more than guesswork; but it is considered that there is sufficient evidence presented in this thesis to draw up a general plan of the pleiotropy. Within the framework of this plan, further research can then be carried out, not only with N-type sheep, but with the ordinary Romney and other breeds, on factors underlying genetic and phenotypic correlations amongst fleece and body characters.

'N'. PLEIOTROPIC EFFECTS PRIOR TO BIRTH

Fig. 30 Thesis

DEVELOPMENTAL STAGE

PRIMARY FOLLICLE FORMATION

OTHER GENETIC FACTORS

N

GENOTYPE FOR HORNS

LARGE PRIMARY FOLLICLES

POTENTIAL HORN PRODUCING CELLS

LARGER FIBRES & HALO-HAIRS

ACTIVE HORN CELLS

DIFFERENT SKIN EXPANSIONS

VARIATIONS IN HALO HAIR DENSITY

PIGMENT DEPOSITION

FIRST WAVE OF SECONDARY FOLLICLE FORMATION

COMPETITION OR SUPPRESSION EFFECTS

PROPORTIONAL REDUCTIONS IN FIBRE DIAMETER

LESS SECONDARY FIBRES

SMALLER MEDULLA DIAMETER

DIFFERENT SKIN EXPANSIONS

BIRTH

OBSERVED VARIATION IN HALO-HAIR DENSITY

VARIATION WITHIN A LOW TOTAL DENSITY

BROWN FIBRES ON BACK OF NECK

THE 'HAIRY' BIRTHCOAT

HORN LUMPS

FIG. 31 POST-NATAL

- Primary chain of events } 'N'
- Secondary effects
- Effects other than 'N'

Dotted lines Evidence doubtful or not known.

The various main stages of the pleiotropic effects derived from the comparisons of ordinary and N-type lambs, are shown in diagrammatic form in Figures 30 and 31. It is proposed to discuss each of these stages with reference to the relevant summaries of the sections from which the evidence is derived.

Some simplification is clearly required in the presentation of a diagram of this type and it is hoped to make this clear in the following discussion based on the developmental stages shown in the left hand column. Different colours have been used to help in the interpretation but should not be considered as absolute divisions. Red indicates the more direct chain of events from the initial gene action; blue environmental or non-related genetic effects; and green secondary effects usually derived from the other two. There are, of course, no such real exact distinctions after the early stages.

There is little direct evidence yet available concerning the first stage, when primary follicles are initiated. It is suggested that the initial gene action is one causing the formation of a number of large primary follicles (large being used as a term of comparison with the ordinary Romney, in the diagrams). This explanation is the simplest one and as it accounts for subsequent events it is therefore unnecessary to consider the problem of fundamental pleiotropy or otherwise until further evidence is available. Evidence for independent determination of the hair follicle type can be found in the work of Hardy (1951) and of Billingham and Medewar (1948). In addition, Ross (1954) states that the larger primary follicle of the N-type occurs at an early embryonic stage and "therefore these genes probably affect its follicle anlagen".

The relationship with horns at this stage requires histological

investigation, but the occurrence of scurs in a large proportion of the ordinary male offspring of a heterozygous ram and of the occasional N-type animal with little or no horn growth is not unusual. These observations suggest that the gene, by related but independent action to that on the follicles, stimulates the production of horns if the animal ~~if the animal~~ is of the appropriate genotype. Independent is used in the sense that horns can be produced without a hairy birthcoat although this may be the result of genetic factors other than N (Dry 1955c). This effect has been shown in the diagram with the dotted lines indicating a considerable amount of doubt.

The mechanism of pigmentation is also unknown, but its presence in large A type fibres of other breeds, where it is usually known as 'red kemp', makes it reasonable to suggest that it is a secondary effect arising from the already occurring large halo-hair fibres.

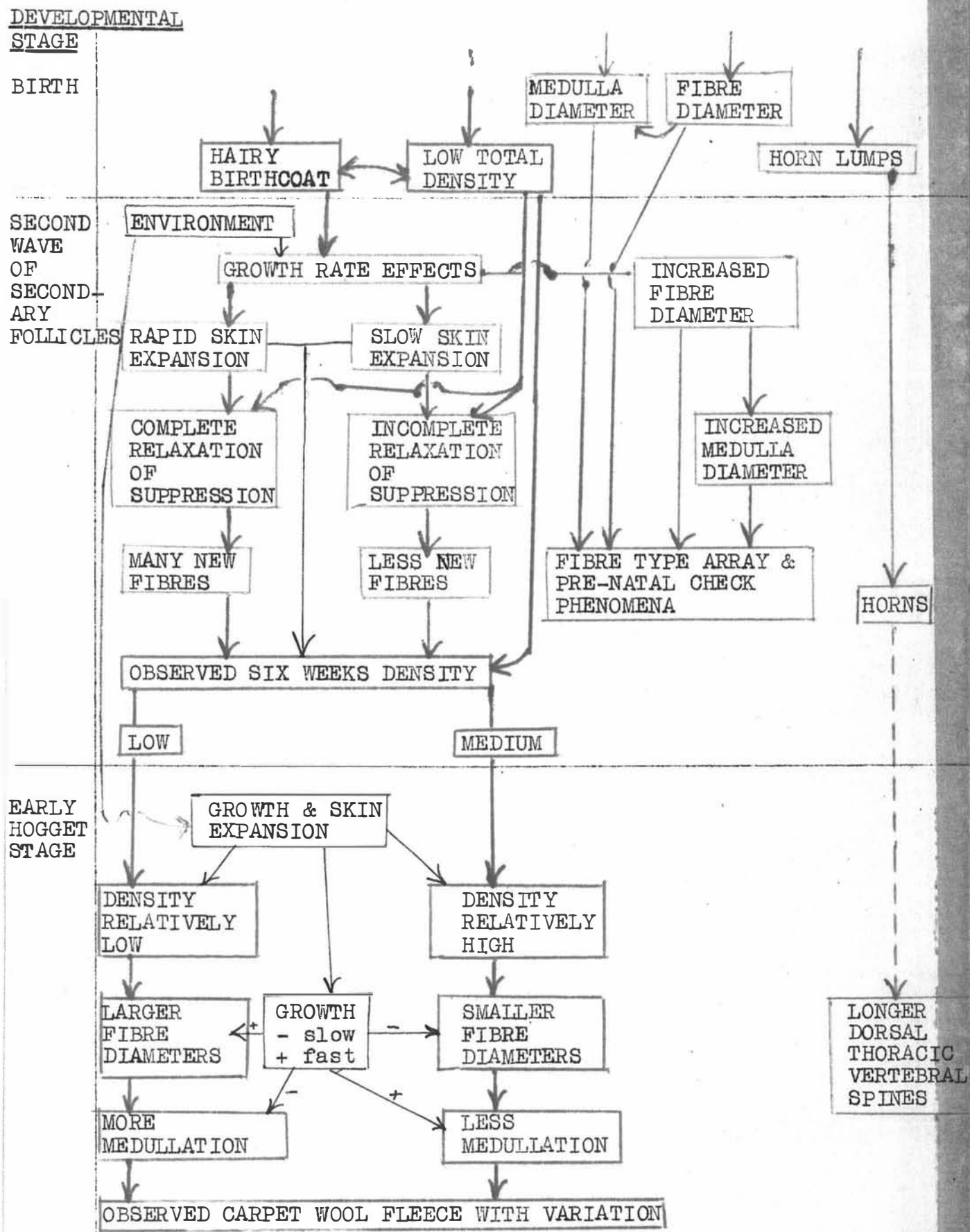
After the primary follicles are formed any differential skin expansion that occurs will cause variations in the density of these follicles, this effect increasing as the foetuses develop. This will cause differences in halo-hair density, apart from those resulting from possible differences in the original number of primary follicles producing these hairs. Differences between the reciprocal mating groups suggest some genetic determination of this initial density and the results from examination of halo-hair density variation indicated other factors besides skin expansion. This has been shown in the diagram by the term 'other genetic factors'.

The first wave of secondary follicles will start to form soon after the primaries and it is suggested that the presence of large primary follicles will either suppress the formation of

a number of secondaries, or alternatively or as well, will lead to a delay in the follicle producing a fibre. The work of Ross (1954) would suggest the latter as she found no overall difference in secondary / primary ratio at birth between N+ and ordinary lambs, although the data was limited. The possibility of a lower density of primary follicles in the N-type lambs must also be considered. If this does occur it is not likely to be a major effect, for then the N-types would have a higher secondary / primary ratio at six weeks when the total densities were nearly equal. Further evidence comes from the work of Short(1955) and Schinckel(1955) who showed that the potential follicle population of the Merino sheep is determined before birth. The subsequent effects of body growth are on the development of these 'embryonic' secondary follicles. If a similar situation occurs in the Romney sheep then the maximum in fibre numbers observed in Section IX,B,2 would be explained by the development of all potential follicles under optimum conditions.

The possible existence of a suppression or competition effect has been shown by Fraser and Short (1953) who found a negative correlation between the secondary/primary ratio and the size of primary follicles. They also found a similar relationship between fibre size and the distance and size of adjacent fibres. The evidence shown in this thesis supports these ideas, for lower fleece densities were found for N-type sheep at birth and these were shown to be associated with the proportions of halo-hairs present. Also, the size of a secondary fibres was found to be negatively related to the halo-hair density. In addition there was a diameter reduction at the approximate time of the formation of the secondary follicles, there being a reduction of all fibres in proportion to their maximum diameter.

Fig. 34



See Text for full explanation. All terms 'low', 'high', etc. are comparative with ordinary Romney and when in pairs, as for the carpet wool, they also indicate how the variation arises.

All these observations suggest a limiting effect at work associated with the presence of large halo-hair producing follicles.

If these ideas are accepted then the observed phenotype at birth can be explained on the assumption of single initial gene action shown in the diagram. At birth the major phenotypic characteristic of the N-types is the large number of halo-hairs in the birthcoat with differences in their abundance between and within the birth rank grouping of singles and twins. This is partially explained by the different conditions pertaining pre-natally and, as discussed above, by possible additional genetic factors acting on the number of primary follicles which are large enough to produce halo-hairs. This genetic difference is also indicated by the difference between the heterozygous and homozygous N-types, the latter having greater numbers of halo-hairs, judged from 'coverage'.

The brown fibres on the back of the neck have been discussed and no further details are available at the birth stage, except that only rarely does the pigment extend to the skin, usually being confined to both medulla and cortex of the halo-hairs. It is therefore considered as a secondary effect.

The formation of 'active' keratin producing cells would account for the appearance of horn lumps at birth.

After birth, the environment, considered here as all non-genetic effects, becomes of paramount importance. The interaction of seasonal conditions with the birthcoat type can, in their resulting effects on weight growth, with additional direct environmental effects, cause considerable variation in growth rates over the early part of a lamb's life. These are shown in the discussion on the two years' results on growth rate and weights.

These variations, possibly acting in part through skin expansion, lessen or remove the pre-natal limiting factors, and lead in turn to variation in the number of new fibres added to the fleece. The large relative medulla diameter at this stage suggests that the space between the follicles and the size of those follicles are not the sole limiting factors at this stage. It suggests that in addition the availability of keratin precursors or other necessary metabolites in the blood stream may also be of importance. In this respect the relationship between the size of the follicle and the area available for diffusion could be determining factors, diameter being directly related to circumference. The exact nature of these relationships requires a more detailed investigation than that undertaken here, but it indicates that there could be profit in such work.

A combination of these various events will lead to the density observed at six weeks which in turn bears a relationship to the mean diameter of the fibres. This complex of genetic and environmental relationships is therefore likely to be of considerable importance to the determination of the final characteristics of the adult fleece. This arises from the relationship between six weeks density and that at the Mogget stage and the relationship of the latter to mean fibre diameter at the time.

The pre-natal check has been added to the diagram at this point, it being suggested that the observed fibre type array phenomena are in part the morphological manifestation of the events described. The differences in medullation between fibres can be explained, in general, by the fibre diameter changes, as has been shown in Section IX,D. The possible relationships between these results and those derived from fibre type arrays has been discussed in Section IX,E. Other variations in arrays could arise from the environmental causes described, and, in

addition, more detailed investigation might show differences in response to these amongst different follicle types. This latter term could include secondary follicles in different positions relative to the primary group. There is, however, no evidence for this type of interaction in this work which is more of a general than a detailed nature.

Goot(1941) suggests that the majority of fibres are added to the fleece of the New Zealand Romney by three months of age and there is no evidence in this work to contradict this. Fibres were added between six weeks and the hogget stage but in fewer numbers. This would indicate that the peak had been passed by the former sampling and numbers added may well have declined to near zero at three months to give this result.

The fibre diameter at the February sampling was related to density and to the weight gains since shearing, the latter being a positive relationship independent of any connection arising out of possible relationships between weight gain and density. The density to this stage has been discussed and from this stage until the final adult size is reached, will presumably depend on the skin expansion. If, as suggested by Galpin, (1948) there is some variation in follicle numbers resulting from the degeneration of follicles and the formation of new ones after the main development stage, then there may be further variations in density from this cause. The importance of this is difficult to judge as it is not clear from Galpin's paper, to what extent the variation observed in the number of fibres in a given area is the result of experimental errors, which errors could exaggerate the observed variation when it is examined by means of percentages of an original number of fibres which itself is liable to error.

The correlation between A type fibre numbers and the numbers of halo-hairs (the numbers being relative to the total density) at six weeks suggests that this latter is of importance in the final fleece type, although it could be the result of indirect action through density effects.

The relationships between weight or weight gains and the diameter of the fibre and its medulla have been shown for young sheep (24 - 34 weeks of age) only, but it seems likely that a similar type of relationship will be found to hold for adult sheep. However this is still a subject for further investigation before a final decision can be made. The positive and negative signs in the diagram (Figure 31) indicate whether increased growth will increase (+ve) or decrease (-ve) the medulla or fibre diameters.

The other marked effect at this stage is the growth of horns, in particular in the male N-type, and this has been shown in Part I to be connected with the conformation of the shoulder region, that is, the longer dorsal spines of the thoracic vertebrae.

The evidence here is still by no means conclusive, except that the long spines seem to be connected with the horns, rather than with the 'hairy' fleece. It is not possible to accept a mechanical explanation of direct induction of bone growth by the heavier head acting through the ligamentum nuchae and associated ligaments; but it is reasonable to consider it as a secondary effect of pleiotropism associated with horns until further evidence on early developmental stages is available.

Whether these pleiotropic effects described, approach a full explanation of the observed differences between the

adult N-type and ordinary Romney sheep, remains to be seen in the light of further work of a more detailed and accurate nature. However, this general statistical approach within a framework of pleiotropy, using comparative methods, gives a background for both more detailed research and for trials of an economic nature.

B. Final Discussion

In the general introduction to this thesis, the initial problem was stated as one of the carcass quality of the N-type sheep. It was then shown that a study of growth was a necessary prelude to a study of carcass quality. As the sheep to be compared differed only in the coarseness of their fleeces, it appeared that the investigation could also be profitably used for consideration of the factors underlying some of the observed phenotypic and genetic correlations between characters of the New Zealand Romney.

These various objects could all be approached by treating the problem as one of investigation of the pleiotropic effects of N. The results of this investigation have been covered in the first part of this discussion where the conclusions have been presented within a framework of the possible pleiotropic effects.

Considerations of an economic nature can be based on this framework, but possibly of more importance is the information which can be obtained by the use of these sheep and which is likely to apply to the New Zealand Romney which comprises the majority of sheep in the country. Such information including that already obtained should form a basis for research on problems of body growth and fleece production, both of great importance for an industry based on the dual purpose sheep.

The methods used here have been, of necessity, crude; but the use of the comparative method where large differences

are present and of sufficient animals to obtain objective levels of probability for the results by the use of statistical analysis, has yielded a considerable amount of information.

Apart from this use of N-type sheep such an approach seems required to link the work of the population geneticist with that of histologists and physiologists, who are concerned with more detailed work involving a few animals. The former has its dangers in that the reactions of the individual animal can be forgotten and the latter in the inductive use of results which make no allowance for the natural variation in a population of animals from which the sample (random or otherwise) of two or three sheep may have been taken.

The approach adopted here, which is more detailed than that normally used for population genetics but at the same time considers biological variation, offers the connecting link. An example is that of medullation, whereby results here can be interpreted in the light of the ~~more~~ detailed histological work of Auber (1950) and at the same time throw some light on a previously observed correlation between fleece weight and hairness (Rae 1952)

Another approach that has arisen from the examination of the fleece of the N-type sheep is that of Fraser (1953_a) who has attempted to fit a simple general pattern to all types of fleece. The part of this pattern which depends on constant fibre substrate needs consideration in the light of both the fleece weight differences indicated in this thesis and the possible misinterpretations on Galpin's (1948) analysis shown by Lockhart (1956). In addition, the similarity between some of Fraser's theoretical distributions for follicle 'efficiency'

and observed distributions for fibre diameter are of interest. On present knowledge Fraser's 'efficiency' might be considered synonymous with fibre diameter, and in fact has been based on the closely correlated measurement of fibre length. This does not allow for medullation and it appears to this author that the efficiency of a follicle would be better based on the production of fully keratinised cortical cells. This would then fit in with physiological investigations on the pre-cursors of keratin and also with economic considerations based on fleece weight and fleece quality. It would be an approach to the true efficiency of the follicle and this could then be considered in terms of the diameter and length of the fibre produced. This information is not at present available, but an approach has been indicated and it would be of interest to know whether under this definition of efficiency, a large follicle producing a medullated fibre is in fact as efficient as a smaller follicle producing fully keratinised cells. Results presented, of a very preliminary nature, suggest that the former may be more efficient but that a maximum is reached at a certain follicle size. Also included in this approach should be investigations on the effects of available energy on mitotic rate as this may be a further limiting factor in follicle production. Bern, Harkness and Blair (1955) have results from radio-autographic studies which suggest that keratinisation is an active synthetic process above the mitotically active hair bulb. Thus there are two possibly distinct processes underlying fibre growth.

Although this type of approach using N-type sheep or other breeds is likely to be valuable, the use of N-types for other types of research should not be forgotten. Investigation could also be made into factors affecting the weight of

wool grown per unit area. Schinckel (1956) has shown this to be independent of body weight, and similar results have been obtained on two tooth ewes by the present author (unpublished). These results should be related to those in which body growth has been shown to affect density and also fibre diameter and length with their possible consequent effects on weight of wool per unit area.

The most valuable method at the moment appears to be the one making use of the mating of heterozygous N-type with ordinary Romney sheep thus giving approximately half of each type of offspring. There are then two groups differing only in the genotype by N, apart from any linkage effects. In addition, maternal effects can be assumed to be automatically randomised and hence few difficulties in interpretation should arise.

The use of this mating, or of variations of it such as for instance making use of heterozygous with heterozygous sheep to give all three genotypes in the offspring, has been demonstrated in this thesis for a study of pleiotropy. This has only ~~been~~-indicated a general framework and an extension of these methods could be made to ecological studies, such as the response of lambs of different birthcoat type to different climatic conditions; metabolic studies, comparing the relative efficiencies of the animals for wool growth and body growth; to detailed studies of the follicle and its physiology; to morphology and histology; and, in fact, to any aspects of the biological study of the sheep. All studies of the sheep for any purpose must eventually be concerned directly or indirectly with its unique properties of growing a continuous wool fibre.

When one considers the extent of our present-day knowledge of the sheep, which does not extend to the reaction of sheep of different types to different environments or to their requirements for the maximum balance between wool growth and meat production, then some approach of this type is required. Such an approach should yield a considerable amount of information in a comparatively short time and bring our knowledge of the sheep to something beyond that of general statistical surveys and management trials. The use of such additional devices as shearing as a simple experimental treatment should also yield its share of information, there being remarkably little known of the biological effects of this standard annual practice.

A basic plan for a nucleus stock of N-type sheep, with continual outcrossing is shown in Appendix II. This could be varied according to the type of animal required for experimental purposes, but it is necessary to set up such a flock from which animals of reliable history, genetic and environmental, could be drawn.

With such a flock, and the appropriate facilities, our knowledge of the biology of the sheep can be increased, with subsequent benefits to the primary industry of this country and other countries dependent on the sheep for a major part of their economy.

APPENDIX I

The Identity of Weight Corrected for Previous
Weight and Gain Corrected for Previous Weight
in the Covariance Analysis

Let y be the weight at the time of interest and x the previous weight. Then $y - x$ will be the weight gain.

Let all sums of squares be expressed as deviations from the relevant mean.

$$\begin{aligned} \text{Then the regression } b_{y.x} &= E \, xy / E \, x^2 \\ b_{(y-x).x} &= E \, x(y-x) / E \, x^2 \\ &= (E \, xy / E \, x^2) - 1 \end{aligned}$$

$$\text{i.e. } b_{(y-x).x} = b_{y.x} - 1$$

For the simple case of analysis of covariance the residual sums of squares will therefore be:

$$\text{For } y \text{ corrected for } x : E y^2 - b^2 E x^2$$

where b is $b_{y.x}$

$$\begin{aligned} \text{and for } (y-x) \text{ corrected for } x : E(y-x)^2 - (b-1)^2 E x^2 \\ = E y^2 + E x^2 - 2 E xy - b^2 E x^2 + 2 b E x^2 - E x^2 \end{aligned}$$

$$\text{but } 2 b E x^2 = 2 E xy \quad \text{therefore} = E y^2 - b^2 E x^2$$

The two methods therefore give identical residual sums of squares.

If the sums of squares are expressed directly with the term for correction for deviation from the means, an exactly similar result is obtained.

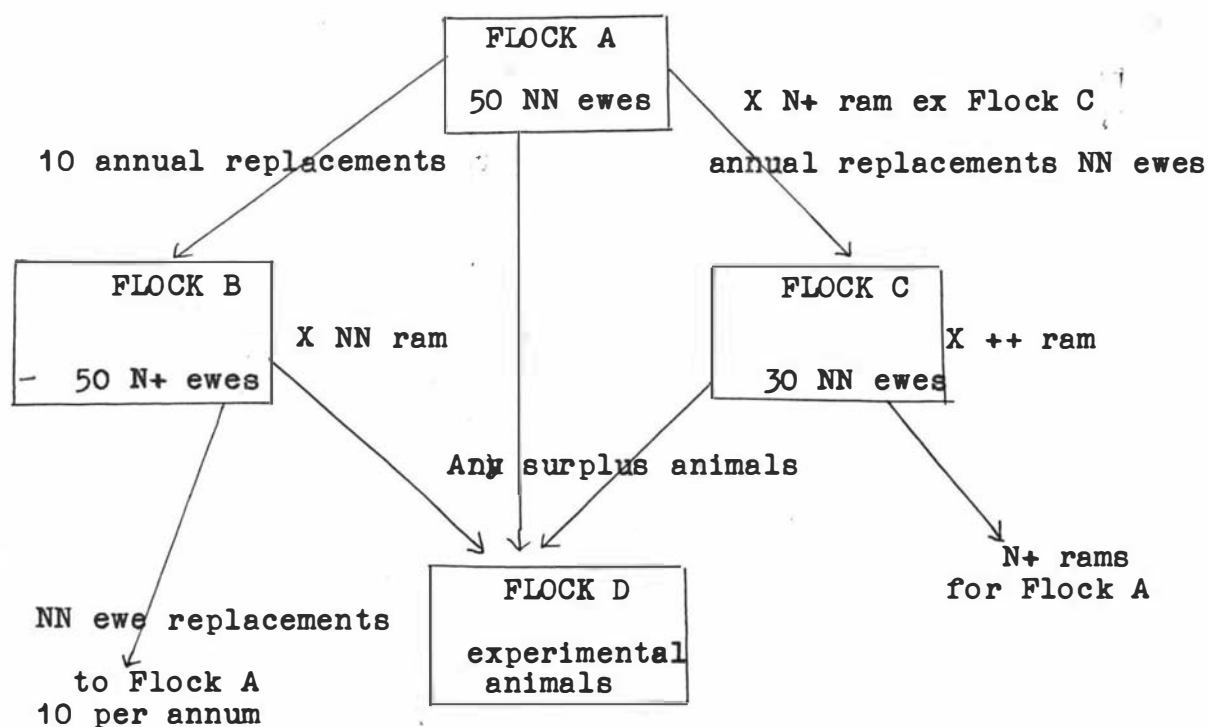
It can also be shown that the estimates corrected for regression are the same except for the subtraction of the mean of x in the case of the corrected weight gain.

The proof~~for~~ for the multiple regression case follows a similar method using reduction formula (Weatherburn 1949) to express the multiple coefficients as simple ones.

It should be noted that this identity is not true for the reverse case when x is corrected for y or $(y-x)$

APPENDIX II

Figure 32. Plan for a Permanent N-type Research Flock



The plan is for about 200 sheep, divided into 4 units for administrative purposes.

Flock A is the nucleus flock of 50 NN ewes of 5 age groups of 10 ewes each. This flock is mated each year to an N+ ram to supply replacements for Flocks B (N+) and C (NN).

Flock B, of similar age composition, would be mated to an NN ram from Flock A, the maximum relationships being a half sib. This would supply NN ewe replacements for Flock A.

Flock C would be kept for outcrossing NN ewes to an ordinary Romney ram to produce N+ rams for mating with Flock A, thus

avoiding any intensive inbreeding.

Surplus stock, required for experimental purposes could be kept in Flock D which will vary according to requirements.

Such a scheme would enable a supply of rams of various types and ages to be available at any time. Ewes would be available from Flock D, or if a large number were required then rapid expansion from the nucleus stock would be a comparatively simple matter.

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