THE SPATIAL RELATIONSHIPS BETWEEN CENTRAL PRIMARY SKIN FOLLICLES DURING THEIR DEVELOPMENT IN SHEEP

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Summary

The spatial patterns of central primary follicles have been measured during development and compared on six body positions and between Romney × Southdown cross and Merino sheep. The patterns are similar in both breeds on all the body positions investigated and appear to be constant between 70 and 140 days of foetal age.

The actual measurement of spatial relationships shows that the distribution of central primary follicles is highly uniform, and gives support to the idea that these follicles may compete for space during their initiation.

The marked directional trend of the trio groups does not appear to be associated with a directional component in the spatial arrangement of central primary follicles.

I. Introduction

The wool follicle population in a wide range of sheep breeds is composed of two major follicle types—primary and secondary. These are characteristically distributed in groups or bundles consisting of three primary follicles and a variable number of secondary follicles. The arrangement of follicles into groups and the pattern of follicles within these groups are both associated with the developmental sequence of the follicle population (Hardy and Lyne 1956). Further, the angular orientation of any trio group bears a marked relation to those of other trio groups about it. Thus there are general consistent patterns both within and between follicle groups.

The concept of competition between wool follicles was originally designed to explain differences in the shape of the tip curl of fibres formed by central and lateral primary follicles (Fraser 1951). Several other aspects of the fleece have since been attributed to the effects of competition (Fraser and Short 1960). It is not known whether competition occurs for follicle-forming substrate, for fibre-forming substrate, or for both; nor is it known whether an interaction between follicles results from their relative spacing. Fraser and Short (1952) showed a negative correlation between the size of any one fibre and the size and distance of those adjacent to it, but Ryder (1957) gave evidence to show that this was not necessarily due to spatial competition between adjacent fibres. Similar methods aimed at demonstrating spatial competition clearly must make allowance for the developmental sequence of the follicle population.

The results presented here deal with the spatial relationships between central primary follicles. They are part of a project whose objects were twofold. Firstly, it

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was undertaken to analyse on a quantitative basis the general spatial relationships between follicles; to compare these relationships during follicle development on different body positions and in two sheep breeds. Secondly, it was hoped that the results might indicate some aspects of the determination of fleece structure and in particular provide further evidence on the nature of competition.

II. Materials and Methods

(*a*) *Experimental Material*

The foetuses were from 6-year-old fine-woolled Australian Merino ewes and 5-year-old Romney ewes. The Merino ewes were mated to a Merino ram of the same strain, while the Romney ewes were mated to a Southdown ram. Foetuses were obtained at 10-day intervals from 60 to 140 days of gestation, the last day of the oestrus in which conception occurred being taken as the beginning of pregnancy. Data have been collected from a total of 22 foetuses.

(*b*) *Treatment of Skin Samples*

Duplicate skin samples were collected from each foetus from six body positions. These were poll, neck, shoulder, back, midside, and britch, and correspond respectively to positions C, D_1, E_1, F, F_1, and H_1 described by Stephenson (1957). Up to 90 days of foetal age inclusive, skin samples were collected with a 0·5-cm trephine, while those from older foetuses were taken with a 1·0-cm trephine. Duplicate sections have been analysed in some of the 90- and 110-day material only.

Skin samples were fixed in Zenker's solution and stored in 50% alcohol prior to histological treatment. Those from 60- and 70-day-old foetuses were prepared as a series of whole mounts and stained with Ehrlich's haematoxylin. Only two series of these from 70-day-old foetuses were found satisfactory for viewing under the projection microscope. All other material was sectioned before mounting by methods similar to those described by Clarke (1960). A triple staining technique with Ehrlich's haematoxylin, eosin, and picric acid was found satisfactory.

(*c*) *Methods of Describing and Measuring the Spatial Pattern*

Clark and Evans (1954) have described a measurement of spatial relationships among individuals, the criterion used being the distance from an individual to its nearest neighbour. The measurement indicates the manner and degree to which the distribution of individuals in a population departs from that of a random distribution. Individuals are chosen randomly, and a series of distances from each to its nearest neighbour is obtained. The mean distance to the nearest neighbour that would be expected if the individuals of that population were randomly distributed is also calculated, and the ratio of the observed mean to the expected mean is used as a measure of departure from randomness. The value of the ratio, R, may vary according to $0 \leqslant R \leqslant 2 \cdot 1491$, and departures of R from unity, toward either $2 \cdot 1491$ or zero, indicate trends in the spatial pattern toward maximum spacing or aggregation respectively.

Letting ρ = density and $\bar{r}$ = the mean observed distance to nearest neighbour, then (cf. Clark and Evans 1954)

$$R = 2\rho^{\frac{1}{2}}\bar{r}.$$

The calculation of an R value for each follicle population involves measurements of density and of mean distance to nearest neighbour. Density estimates were made from follicle counts taken with the aid of a projection microscope and corrected for shrinkage of the section during processing (Carter and Dowling 1954). As nearly as possible, interfollicle measurements were all made at mid-sebaceous gland level. By means of the projection microscope, an area of the follicle population was recorded on paper by drawing around the outer root sheath of each follicle. An outline of the complete section at a low magnification was superimposed over the drawing and a centre of the drawn field marked in relation to this. Magnifications were recorded from the projected images of a standard slide graticule.

Twenty individual distances were measured in each field to give a mean distance to the nearest neighbour. Primary follicles not identified as centrals or laterals have not been used as either centres or nearest neighbours, but it is not known whether the exclusion of these follicles from the population in which measurements were taken has in any way affected the results. For the purposes of comparing R values, analyses of variance have been carried out on untransformed data (Clark and Evans 1954).

(*d*) *Methods of Dealing with Distortion in the Mounted Section*

On no occasion was the mounted section the same diameter as the original skin sample and seldom was its shape circular. True distances to nearest neighbour will be affected by these changes in shape. Fraser and Short (1952) corrected interfollicle measurements on the basis of the ratio of the area of the section taken from the animal to that of the mounted section after shrinkage. For the purposes of this work two corrections have been compared, both based on the following assumptions:

(1) That distortion in any one direction is uniform across the section and is not an edge-effect. Estimates of density across the section do not indicate major differential shrinkage.

(2) That the outline of the section represents a true reproduction of the embedded sample and that all areas within the section are the same depth below the skin surface.

(3) That the original skin sample was in fact circular.

The two corrections were as follows:

Correction I.—Distances were measured as they appeared on the drawn field. These were all subjected to a single correction given by the ratio of the original (trephined) skin sample diameter to a mean of four equally spaced section diameters, one of these being made to correspond with the maximum section diameter.

Since in each section the correction parameter for adjusting observed density estimates is the inverse square of that used for adjusting mean distance to nearest neighbour with correction I, the R values obtained from these measurements define the spatial patterns existing in the distorted sections.

Correction II.—For the purposes of this correction method each section has been regarded as an ellipse. Distances were first corrected to those which would exist in a circular section of diameter equal to the maximum diameter XY in the actual section (Fig. 1(a)). Distortion from the circle to the ellipse has no component parallel to XY.

Let F_1F_2 (Fig. 1(b)) represent the centres of two follicles as they appear on the distorted section. Figure 1(b) is an enlarged portion of the shaded area in Figure 1(a).

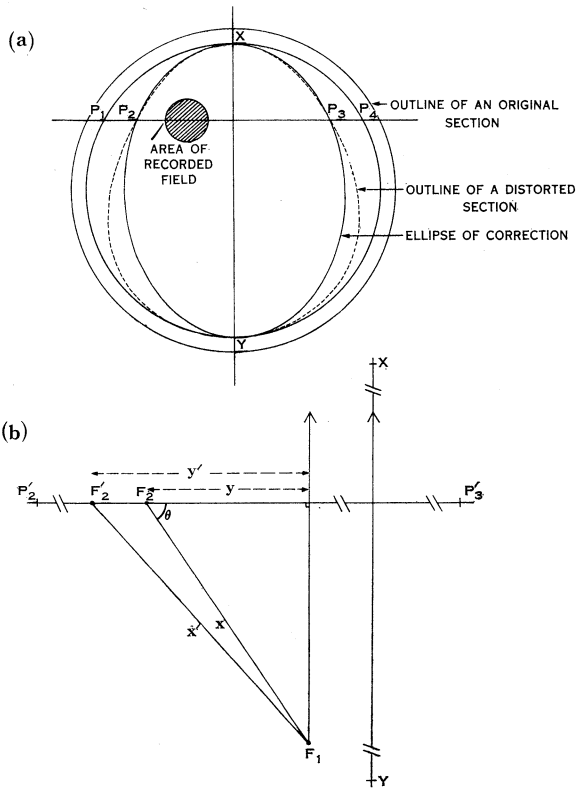

Fig. 1.—Method of correcting interfollicle measurements for distortion in the section.

Let F'_2 be the position of F_2 before shrinkage. This point will lie on the line through F_2 and perpendicular to XY. With the symbols in Figure 1(b):

$$x' = x \sin\theta(1+k^2)^{\frac{1}{2}}/k,$$

where

$$k = y/y' \tan\theta.$$

Thus a corrected distance x' can be obtained from the observed distance x with a knowledge of θ and the ratio y/y'. From Figure 1(a) and on previous assumptions

$$y/y' = P_2P_3/P_1P_4.$$

Since the area of the drawn field cannot be regarded as a point within each section, a mean of the ratios given by five chords similar to $P_1P_2P_3P_4$ was used to calculate y/y'. These were equally spaced over the projected field.

A set of tables was constructed giving various correction factors for 5° intervals from 0 to 90° and various values of y/y' ranging from 1·0 to 1·5 at 0·01 unit intervals. Having applied the appropriate correction factor to each individual distance within one section, a second correction of the ratio of the trephined skin sample diameter to the length XY was made.

It should be noted that the nearest neighbour to a given follicle on the drawn field will not necessarily be the nearest after applying the correction. In cases where the distances to several neighbours vary only slightly, a correction must be applied to each in order to determine the nearest neighbour before distortion took place.

Forty skin samples, taken in duplicate pairs and used later to estimate errors in the R values, were also used to compare mean distances to nearest neighbour adjusted with both correction factors. The variation in mean distance to nearest neighbour between duplicate sections was similar for the sets of data based on each correction. The difference in the means of the two sets was only 0·1% of an overall average value. Therefore, it was concluded that both corrections yield similar and equally reliable values of mean distance to nearest neighbour. Consequently the resultant values of R will be unaffected by the use of either correction. The results presented later have been adjusted with correction II.

(e) *Directional Trends in the Spatial Pattern of Central Primary Follicles*

Although the value of R associated with spatial distributions is useful in comparing different populations, it does not describe any given population completely. In particular it does not specify whether a distribution incorporates a directional component, a feature which, if existent among central primary wool follicles, may play a part in determining the position of lateral primaries, to form the marked trend in the direction of trio groups.

The presence of a directional trend would presumably affect the distribution of directions of distances to nearest neighbour which would otherwise be expected to occur randomly in all directions within each section. However, the effects of distortion have also altered the distribution of directions of distances between follicles, and these to some extent may have masked small directional trends in the undistorted section.

III. Results

(a) *Accuracy of the Method*

From four foetuses (two from each breed and aged respectively 90 and 110 days) duplicate skin samples from each body position (except the poll) were prepared. The errors in estimating an R value on a given position of a foetus fall into two classes: errors in measuring density, and errors in measuring a mean distance to nearest neighbour.

(i) *Density*.—Up to 100 days of foetal age, direct counts of central primary follicles could be made. Beyond 100 days the size of the field in which all primary follicles could be satisfactorily classified as centrals or laterals became small, and the error in estimating density increased correspondingly. Consequently in the older material, central primary density was obtained from a total primary count adjusted according to the ratio of centrals to laterals. This ratio is likely to be constant after 90 days of foetal age (Schinckel 1955).

TABLE 1

MEAN RATIOS OF LATERAL PRIMARIES TO CENTRAL PRIMARIES ON TWO 100-DAY-OLD FOETUSES OF EACH BREED

Breed	Position					Mean
	Neck	Shoulder	Back	Midside	Britch	
Romney × Southdown	1·73	1·65	1·70	1·58	1·67	1·67
Merino	1·63	1·64	1·63	1·46	1·62	1·59

Analysis of Variance*

Source of Variation	Degrees of Freedom	Mean Square
Between foetuses	3	
Between breeds	1	0·0267
Error	2	0·0126
Within foetuses	16	
Within positions	4	0·0157
Breed × position	4	0·0018
Error	8	0·0047

* All comparisons non-significant.

Little data has been recorded on the ratio of lateral primary to central primary follicles. Ross (1954) gave a value of 1·9 in heterozygous *N*-type Romney foetuses, while Narayan (1961) has given values ranging from 0·98 to 1·41 in seven Rajasthan sheep breeds. The results for four 100-day-old foetuses in the present series are given in Table 1. The accompanying analysis of variance on the raw fractions shows the difference between Romney × Southdown and Merino values to be non-significant. An average value of 1·63 has been used to estimate central primary density beyond 90 days of foetal age in both breeds.

Mean values of central primary density and the errors from duplicate sections are shown in Table 2. An average of 85 follicles in the 90-day material and 236 follicles in the 110-day material was counted for each section. The high coefficient

of variation at 90 days results from two markedly different duplicate estimates. Neglecting these, the coefficients of variation are similar at both ages and agree closely with those given by Stephenson (1958).

TABLE 2

MEAN VALUES AND ERRORS* FOR CENTRAL PRIMARY DENSITY (FOLLICLES/MM^2)

Duplicate sections from five body positions on four foetuses

Breed	Age (days)	Position					Mean
		Neck	Shoulder	Back	Midside	Britch	
Romney × Southdown	90	24·0	24·1	35·9	26·7	22·4	26·6
	110	9·5	10·5	14·1	11·0	9·7	10·9
Merino	90	20·6	23·5	33·6	26·9	28·0	26·5
	110	9·4	11·8	18·0	13·4	13·2	13·1

* Between duplicates:

90 days: S.D. = 4·46, coefficient of variation = 16·8%.

110 days: S.D. = 1·04, coefficient of variation = 8·65%.

(ii) *Mean Distance to Nearest Neighbour.*—The mean values for mean distance to nearest neighbour in the duplicate material are shown in Table 3, together with

TABLE 3

MEAN VALUES AND ERRORS* FOR MEAN DISTANCE (MM) TO NEAREST NEIGHBOUR

Duplicate sections from five body positions on four foetuses

Breed	Age (days)	Position					Mean
		Neck	Shoulder	Back	Midside	Britch	
Romney × Southdown	90	0·159	0·179	0·138	0·160	0·176	0·162
	110	0·273	0·258	0·215	0·252	0·268	0·253
Merino	90	0·191	0·168	0·148	0·162	0·170	0·168
	110	0·264	0·234	0·204	0·220	0·236	0·231

* Between duplicates:

90 days: S.D. = 0·0142, coefficient of variation = 8·6%.

110 days: S.D. = 0·0058, coefficient of variation = 2·4%.

the errors between duplicate sections. The higher between-duplicate variation at 90 days has resulted from measurements recorded from the same two sections which influenced the density errors at this age.

The mean values of R for the duplicate material, each obtained as a function of density and mean distance to nearest neighbour, are given in Table 4. The

TABLE 4

MEAN R VALUES AND THEIR ERRORS*

Duplicate sections from five body positions on four foetuses

Breed	Age (days)	Position					Mean
		Neck	Shoulder	Back	Midside	Britch	
Romney × Southdown	90	1·52	1·75	1·64	1·65	1·66	1·64
	110	1·68	1·66	1·61	1·67	1·67	1·65
Merino	90	1·73	1·61	1·71	1·68	1·77	1·70
	110	1·61	1·60	1·73	1·61	1·71	1·65

* Between duplicates:

90 days: S.D. = 0·164, coefficient of variation = 9·8%.

110 days: S.D. = 0·193, coefficient of variation = 11·7%.

coefficients of variation at both ages are similar, and suggest that the two pairs of 90-day sections responsible for the higher coefficients of variation in both components of R are not characteristic of the series.

TABLE 5

MEAN VALUES OF R, OF CENTRAL PRIMARY DENSITY ρ (AS FOLLICLES/MM^2), AND OF MEAN DISTANCE TO NEAREST NEIGHBOUR $\bar{r}$ (IN MILLIMETRES)

Each entry is the mean of six body positions on each of two foetuses*

Age (days)	Romney × Southdown			Merino			Mean		
	R	ρ	$\bar{r}$	R	ρ	$\bar{r}$	R	ρ	$\bar{r}$
70	1·69	36·2	0·142	1·70	41·0	0·134	1·70	38·6	0·138
80	1·70	28·4	0·164	1·70	35·0	0·147	1·70	31·7	0·156
90	1·70	21·3	0·186	1·73	31·0	0·157	1·71	26·3	0·172
100	1·61	14·5	0·218	1·63	20·2	0·184	1·62	17·4	0·201
110	1·68	10·5	0·251	1·68	12·0	0·235	1·68	11·3	0·243
120	1·65	7·9	0·301	1·66	9·7	0·270	1·65	8·8	0·286
140	1·69	4·7	0·394						

* Only one foetus included from each breed at 70 and 110 days.

(*b*) *Density, Mean Distance to Nearest Neighbour, and* R *Values during Development*

Mean values of R and their components during development are summarized in Table 5. Replicate pairs of foetuses from each breed were included at all ages

except 70 and 110 days, where measurements on only one foetus from each breed were taken. An insufficient number of adjacent central primary follicles was identified in the Merino material after 120 days of age, and calculation of comparable R values was not possible in this breed.

TABLE 6

ANALYSIS OF VARIATION IN R VALUES

All comparisons non-significant

Source of Variation	Degrees of Freedom	Mean Square
Between foetuses	19	
Age	5	0·0311
Breed	1	0·0070
Age × breed	5	0·0128
Replication	8	0·0105
Within foetuses	97	
Position	5	0·0128
Position × breed	5	0·0135
Position × age	25	0·0110
Position × age × breed	25	0·0065
Error	37	0·0085

The variance analysis on the R values for foetuses from 70 to 120 days of age inclusive is shown in Table 6. The results make allowance for three missing section records after methods given by Snedecor (1948).

TABLE 7

REGRESSION COEFFICIENTS FOR THE LOGARITHMS OF MEAN DISTANCE TO NEAREST NEIGHBOUR AND OF FOLLICLE DENSITY ON THE LOGARITHM OF AGE

Breed		Poll	Neck	Shoulder	Back	Midside	Britch
Romney × Southdown	Density	−3·11	−3·79	−2·77	−3·88	−3·56	−3·68
	Mean distance	1·81	1·83	1·42	1·98	1·81	1·87
Merino	Density	−3·58	−4·75	−3·66	−4·61	−4·15	−4·05
	Mean distance	1·74	2·48	1·69	2·05	1·94	1·77
New Zealand Romney and N-type sheep	Density*	−3·15	−3·93	−3·44	−3·74	−3·11	−4·11

* After Stephenson (1958).

The changes in density and mean distance to nearest neighbour with age have been analysed by similar methods to those described by Stephenson (1958). Within positions the logarithms of these values have been separately regressed with the logarithms of age. Records for the 70- and 80-day material in which the initiation of

central primary follicles may not be complete have been excluded. Regression constants are shown in Table 7 along with the results for total primary density obtained by Stephenson in New Zealand Romney and *N*-type sheep.

The values of the regression constants for density are of opposite sign and about twice the values obtained for mean distance to nearest neighbour. Between positions there are no consistent differences between the regression coefficients for density and twice the values of those for mean distance to nearest neighbour when the signs are ignored. These facts also suggest that R is constant between 90 and 120 days in the Merino and between 90 and 140 days in the Romney × Southdown.

TABLE 8

PERCENTAGES OF DIRECTIONS OF MEAN DISTANCES TO NEAREST NEIGHBOUR FALLING INTO THREE RANGES

Values are for two foetuses from each breed at each age

	90 Days			100 Days			120 Days			Combined Mean		
	S_1	S_2	S_3	S_1	S_2	S_3	S_1	S_2	S_3	S_1	S_2	S_3
Correction I												
High distortion	44	24	32	39	34	27	38	29	33	38	33	29
Low distortion	39	41	20	39	32	29	32	36	32			
Correction II												
High distortion	17	22	61	12	25	63	17	30	53	20	29	51
Low distortion	24	37	39	24	29	47	25	34	41			
Percentages expected if the directions of distances were distributed at random										31	33	36

(c) *Directional Trends in the Spatial Pattern of Central Primary Follicles*

The directions in which nearest neighbours among central primary follicles lie in any distorted section tend to be along the line of maximum distortion. On choosing nearest neighbours with correction II, these directions tend to lie in the direction of least distortion. Both these tendencies increase as the level of departure from circularity in the section increases. These features are illustrated in Table 8, which gives the percentages of directions falling into each of three ranges—two associated with the minimum (S_1) and maximum (S_3) section diameters respectively, and a third (S_2) covering the remainder of directions not included in S_1 and S_3. The proportion of these percentages expected in any range if the directions of measurement were randomly distributed, are also shown in Table 8. Different proportions in each range merely reflect that the ranges were not of equal size.

Within each section a general direction of the trend of the trio groups was assessed subjectively and represented an average direction of lines drawn through the two lateral primaries of each trio group. This direction appeared to vary independently of both the directions of maximum and minimum shrinkage in each

section. Further, a lining up of the trio group arrays in adjacent duplicate sections did not produce any similar correspondence in the two directions of greatest (or least) distortion between these duplicates.

Seven sections at 120 days of age showed less than 10% differential shrinkage in the directions of greatest and least distortion. In this material, the directions of distances to nearest neighbour were distributed randomly.

IV. Discussion

The differences in density estimates between duplicate sections appear to be independent of those for mean distance to nearest neighbour, since the correlation between these two variables within the duplicate pairs is non-significant. Stephenson (1958) found the coefficient of variation of density counts between duplicate skin samples to be no greater than that for counts on different areas of the same section. Further, the standard deviation of mean distance to nearest neighbour between duplicates is similar to the sampling variation of the mean within a section. Therefore the relative errors between duplicates in the square root of density, and in mean distance to nearest neighbour, indicate the extent to which either component has affected the between-duplicate variation in R values. The coefficient of variation for root density is slightly more than half that for density, and is about $1\frac{1}{2}$ times larger than that for mean distance to nearest neighbour. Thus greater precision in estimating R values will be best achieved by increasing the accuracy with which density counts are made.

An overall mean R value of 1·67 shows that the spatial distribution of central primary follicles is highly uniform in the direction of maximum spacing. Clark and Evans (1954) measured a value of 1·14 among trees which they suspected were subject to spatial competition. The high values of R obtained here support the suggestion made by Stephenson (1959) that central primary anlagen, once present, may inhibit the initiation of new central primaries within a certain radius, a system which has also been proposed as a determinant of the position of thorax bristles in *Drosophila melanogaster* (Stern 1954). If the position of follicles is influenced in this way, and if the differences in density over the body during development are real, then the radii of inhibition must vary over the body. It also seems likely that the range of inhibition on any given position varies during development, since Stephenson (1959) showed the rate of primary follicle formation to vary on different body positions after allowance had been made for different rates of skin expansion. However, this may have resulted from analysing central and lateral primaries as a single population.

The differences in R values between the two sheep breeds are small and non-significant. It is concluded that the final fleece type is not dependent upon the spatial arrangement of central primary follicles. However, the pattern of central primaries is not completely uniform: some follicles have more space about them than others. Therefore the possibility cannot be excluded that the relative size of any fibre within a small area is influenced by the amount of free space about it after allowance has been made for the effects of developmental competition.

There is no indication that the spatial pattern of central primary follicles alters between 70 and 140 days of foetal age. Therefore, firstly, the introduction of new central primary follicles into the population, and secondly, the increases in skin expansion as development proceeds, do not appear to alter the spatial pattern among these follicles. Presumably the rates of skin expansion in different directions on any one of the six body positions investigated do not differ markedly.

The estimates of total primary density at 90 days in the Merino foetuses are very similar to those found by Schinckel (1955) in the same breed at this age. Values for the Romney × Southdown foetuses are less than those given by Stephenson (1958) for New Zealand Romney and *N*-type sheep at 90 days, but the value for midside is similar to a figure given by Ryder (1956) for the Romney. The differences in central primary density and mean distances to nearest neighbour between the two breeds, shown in Table 5, are accounted for completely by differences in body surface area calculated from the foetal weights.

The change in central primary density with age, after initiation is complete, is presumably a result of skin expansion. After 90 days the rate of decrease which is given by the regression of log density on log age should be the same as the rate of decreasing density in all primary follicles. The regression constants calculated from the Romney × Southdown material are in fact similar to those given by Stephenson (1958) for New Zealand Romney and *N*-type sheep. The differences in ranking between some positions, while possibly reflecting a breed difference, may have resulted from sampling variation, since the number of foetuses used in the estimates was small, and the coefficient of variation for the regression coefficients was about 10%. The higher regression constants obtained for the Merino breed result from a greater rate of increase in body weight between 90 and 120 days of age for the foetuses sampled in this breed. Generally, however, the weight increases in Merino foetuses are less than those of the Romney × Southdown foetuses (Stephenson and Lambourne 1960).

Among central primary follicles, the directions in which distances to nearest neighbour lie in the undistorted section appear to be distributed at random; there is no evidence for a directional component in the spatial pattern of these follicles. This suggests that the position or positions of greatest free space about any central primary bear no directional relationship to similar positions about other central primaries. Since there is a marked directional trend in the relative orientation of trio groups, the position of lateral primary follicles seems to be determined by some factor additional to those influencing the position of central primaries. Whether this extra control is connected with the central primaries themselves may become clear after the spatial pattern of all primary follicles has been analysed.

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