

STUDIES OF COMPARATIVE FLEECE GROWTH IN SHEEP

I. THE QUANTITATIVE NATURE OF INHERENT DIFFERENCES IN WOOL-GROWTH RATE

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[Manuscript received November 5, 1948]

Summary

Since wool-growth rate is strongly influenced by the plane of nutrition, any measure of inherent wool-producing capacity in the sheep must take this into account, and the relation of these three factors to each other must be known. On general grounds, the relation of wool-growth rate to nutrient intake seems likely to follow the familiar law of diminishing returns which introduces the concept that for each sheep there may be an asymptotic value of wool-growth rate characteristic of the individual. From this and other considerations, it was postulated that these relationships could be described by an equation of the form

$$y/A = 1 - e^{-k'(x-x_0)/A},$$

where y = wool-growth rate, x = nutrient intake rate at or above maintenance levels, x_0 = the nutrient intake rate for which $y = 0$, A = the asymptotic value of y , and k' = a constant dependent on the nutritive qualities of the diet employed.

In this paper, an experiment is described which was designed primarily to test the validity of this generalization by comparing estimates of the parameter k' for sheep types contrasting widely in wool-producing capacity. Twelve Camden Park Merinos and twelve Corriedales individually fed were each divided into three groups of four sheep, one group being kept at a uniform intermediate plane of nutrition throughout, one group being transferred in four stages of six weeks duration from a high to a low plane, and one group transferred in four similar stages from a low to a high plane of nutrition. Equilibration periods of not less than 12 weeks were spent at the highest and lowest planes of nutrition before and after the reciprocal transfers were made. The diet used was of constant composition throughout and consisted of lucerne hay chaff 60 parts, rolled wheat 20 parts, and linseed meal 20 parts. No supplement of any sort was provided.

Data from the groups maintained at a uniform plane of nutrition revealed that factors other than the plane of nutrition were causing significant fluctuations in wool-growth rate which required assessment before the main issues could be examined. Wool-growth rate was found to have a significant positive association with the environmental air temperature. For the Uniform groups wool-growth rate increased by 0.048 ± 0.011 g. and 0.082 ± 0.021 g. per sheep per day per °F. in the Camden Park Merino and Corriedale respectively. Analyses on the data for the individual sheep showed significant differences between the regression coefficients for the individual Corriedale sheep. Evidence from the other groups suggested that the change in wool-growth rate (per °F.) increases with the plane of nutrition. It was postulated that the temperature effect was mainly due to cutaneous blood circulation changes which form part of the normal heat regulating response of the body.

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Another significant but inverse association revealed by the data of the Uniform groups occurred between fibre thickness and the amount of fleece carried by the sheep. For each growth increase of 1 lb. in fleece weight there was a mean reduction in fibre cross-sectional area of $6.72\mu^2$ in the Camden Park Merinos and $7.30\mu^2$ in the Corriedales. This phenomenon was ascribed to the effect of fleece covering on the moisture content of the skin and thereby on the tissue hydrostatic pressure, an increase in pressure causing compression of the follicle and the formation of a longer and thinner fibre with no change in the weight of wool produced per unit time. Considerations of tissue hydrostatic pressure were also invoked to explain why the effect of temperature on wool-growth rate was almost wholly brought about by an effect on length-growth rate in contrast to the effect of the plane of nutrition on both fibre thickness and length-growth rate.

The confounding effect of atmospheric temperature on the data for the sheep taken from a high to a low and from a low to a high plane of nutrition prevented a rigorous estimate of all the parameters in the above equation. However, the value of x_0 appeared to be close to zero, and by assuming that it was in fact zero, the other parameters could be estimated from the group mean data for the three groups. A small inaccuracy in the value of x_0 does not seriously bias the estimates of k' and A for the two breeds. The value of k' for the Camden Park Merinos was estimated to be 0.487 and for the Corriedales 0.422. Although the data do not provide standard errors for these estimates, the difference between the two breeds was not regarded as sufficient to dispute the main hypothesis embodied in the equation. The asymptotic value of wool-growth rate was found to be 5.3 g. and 21.9 g. per day respectively for the Camden Park Merino and Corriedale. Using the mean value of k' , 0.454, and putting $x_0 = 0$, a nomograph was constructed showing the family of curves corresponding to intervals of 5 g. per day in the value of A .

It was concluded that although the inherent wool-producing capacity of a sheep is difficult to assess in terms required by the equation, except under laboratory conditions, due weight must be accorded the relationships expressed, especially if Mendelian studies on wool growth in the sheep are to prosper. The experiment has also emphasized that studies on the physiology of heat regulation in the sheep, and especially the role of the skin, must be integrated with nutritional research if a complete understanding of fleece-growth phenomena is to be attained for application in experimental genetics.

I. INTRODUCTION

It is common experience that wool-growth rate is influenced by the environmental history of the sheep, particularly by the plane of nutrition. Consequently, any expression of the inherent productivity of sheep in terms of wool weight produced per unit time is indefinite unless the plane of nutrition is specified. Mere specification of the plane of nutrition, however, will not suffice unless the relation between wool-growth rate, plane of nutrition, and the maximum wool-producing capacity of the sheep is known. The purpose of this paper is to examine this relationship.

On general considerations it seemed likely that the relation of wool-growth rate to the nutrient intake would follow the familiar law of diminishing returns. The sheep as a living body is more adaptable than a mechanical engine and increases structurally and functionally in response to an increase in nutrient

intake, but does not do so *proportionately* and eventually reaches a maximum capacity for wool-growth rate. This point may or may not be reached before the maximum food capacity of the sheep. We thus have the concept of an asymptotic value of wool-growth rate characteristic of the individual.

The relationship may be further defined by restricting it to nutrient intakes above maintenance, unless, below maintenance, the nutrient intake value be adjusted to include nutrients supplied by the catabolism of body tissues. When so adjusted a nutrient intake below maintenance cannot be achieved in practice. However, for an *imaginary* nutrient intake of x_0 , where $x_0 \geq 0$, we may postulate that the corresponding wool-growth rate becomes zero. The value of x_0 may be taken as indicating the threshold above which wool-growth rate commences. It is impossible, from energetic considerations, to imagine a positive value of wool-growth rate corresponding to an imaginary adjusted nutrient intake of zero. Mathematically, the above conditions are met by the equation

$$y = A - Ae^{-k(x - x_0)} \dots \dots \dots (1)$$

where y = the wool-growth rate, x = the nutrient intake rate, x_0 = the nutrient intake rate for which $y = 0$, A = the asymptotic value of y , and k = a constant dependent on the particular foods used and representing the percentage decline in wool-growth rate increment per unit increase in nutrient intake.

This form of equation has been used to relate net energy to gross energy intake by Wiegner and Ghoneim (1930) in rabbits, and by Brody and Proctor (1933) and Brody (1945) in steers. It has been used to relate milk-yield to nutrient intake in dairy cattle by Jensen *et al.* (1942). Brody (*loc. cit.*) has also used the equation to describe the self-limiting phase of growth of populations and single organisms. To our knowledge the equation has not previously been used to describe the relation of wool production to nutrient intake in sheep.

Differentiating equation (1) we obtain

$$dy/dx = k(A - y),$$

which provides the concept that the conversion efficiency of an additional increment of nutrient intake is proportional to the degree of saturation of the physiological system involved in the transformation of the nutrients into wool. This concept formed the basis of a generalization of equation (1) proposed by one of us for the relation of milk-yield to the nutrient intake (Ferguson 1944). If we suppose that the physiological system for the transformation of nutrients to wool remains qualitatively the same for sheep of different productive capacities, equivalent degrees of saturation for such sheep are given by a single value of $(A - y)/A$. Thus we write

$$dy/dx = k'(A - y)/A$$

Integrating

$$y/A = 1 - e^{-k'(x - x_0)/A} \dots \dots \dots (2)$$

In this equation, A , while remaining a constant for a particular sheep, becomes a variable for different sheep. The value of k' remains constant for all sheep but depends on the nutritive qualities of the diet employed.

The validity of the generalization involved in equation (2) may be tested by comparing estimates of the parameter k' for sheep types contrasting widely in wool-producing capacity. The present experiment was set up primarily to make this comparison. The object of the experiment thus stated deals only with the quantitative nature of inherent differences in wool-producing capacity. The problem of the physiological nature of these differences requires further experimental investigation and is only briefly considered in this paper.

The experimental programme thus established provided the opportunity for the collection of data not directly concerned with our present objective. These extraneous data will not be considered here although a complete list of the observations made is included.

II. THE EXPERIMENT

(a) *The Experimental Design*

In attempting to estimate a particular relationship it is important to define the conditions under which the relationship is valid and to provide these conditions in the experiment.

As a primary condition, the plane of nutrition for our present purpose has been taken as the total consumption of nitrogen from a qualitatively suitable ration in which the composition remains unaltered at all levels of feeding. Under such conditions, clearly, the intake of any particular constituent of the ration is proportional to the intake of any other, but nitrogen was chosen as the most logical determinant of the amino acids assimilated, which in turn form the substrate of the keratin laid down in wool growth.

A further condition is that when fleece growth is being measured it should be in equilibrium with the plane of nutrition. Obviously, the period required before such equilibrium is established will depend on the magnitude and direction of the change in plane of nutrition and the physiological status of the animal. Equilibrium on nutrient intakes supplying less than maintenance requirements cannot be maintained once the supply of nutrients from the catabolism of body tissues becomes exhausted. If data obtained on nutrient intakes below maintenance are to be used, it would be necessary to adjust the nitrogen intake for the nitrogen supplied by the catabolism of body tissues. Such an adjustment cannot be made without data on the nitrogen balance of the sheep, so that for the present experiment it was decided to estimate the parameters A , k , and k' , and also x_0 from data obtained at or above maintenance levels. However, the measurement of fleece growth at levels below maintenance was included in the experimental plan.

Next, the sheep used must have reached their mature rate of fleece growth if the effects of differences in the plane of nutrition are not to be unduly confounded with age changes.

A complete test of the hypothesis can only be made by studying a wide range of sheep types, but with our limited facilities, it was necessary to reduce these to two, namely, the Camden Park Merino and the Corriedale. These types were selected since they contrast widely in a great range of characters, particularly in wool-producing capacity.

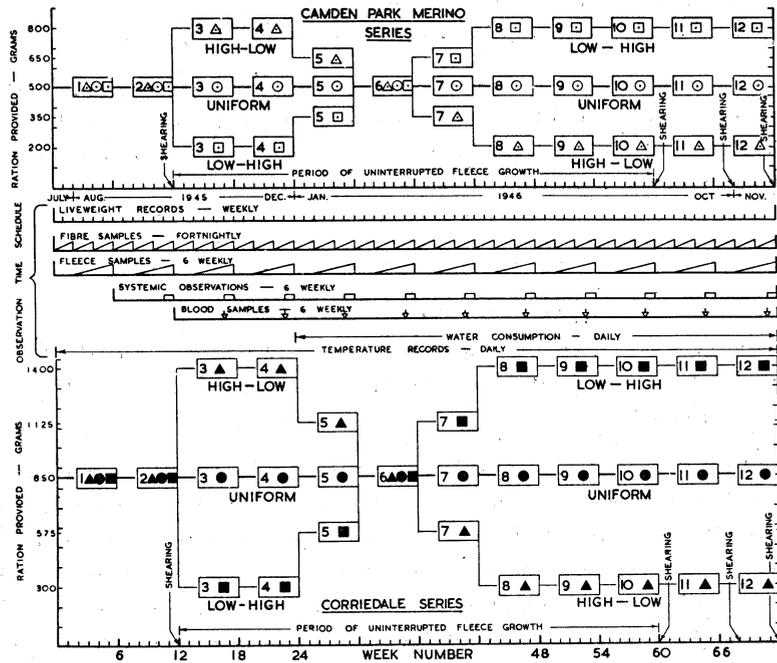


Fig. 1.—The plan and observation time schedule of the experiment.

The plan of the experiment is given in Figure 1. Each sheep type was represented by three groups of four sheep. Subject to restriction by liveweight, these sheep were allotted to their respective groups at random. In each series, the groups are hereafter referred to as the High-Low, Uniform, and Low-High groups respectively. The Uniform group was maintained on a constant plane of nutrition throughout to measure the effect on fleece growth of changing atmospheric or other environmental conditions common to all the sheep, as well as to provide some measure of possible time trends due to aging.

The High-Low group after a preliminary period of twelve weeks on the level of the intermediate Uniform group was raised in one step to a high plane of nutrition and brought down in four lesser stages of six weeks each to a low plane. The Low-High group followed the reverse procedure.

The five levels of intake of food per day thus established were, for the Corriedales, 1400 g., 1125 g., 850 g., 575 g., and 300 g. and for the Camden Park Merinos, 800 g., 650 g., 500 g., 350 g., and 200 g. The time intervals between successive observations varied for each character measured and are discussed later.

For about two months prior to the experiment, the sheep were allowed to become accustomed to their pens and during this period were fed *ad libitum* on lucerne chaff. In that time an estimate was made of the food capacity of the sheep so that the several levels of intake could be spaced over the full range of their appetite. Observations made in 1944 by one of us (Carter, unpublished data) indicate that the appetite markedly increases after shearing and then declines steadily until the next shearing. To avoid food residues this factor had also to be considered and the highest levels of intake for each sheep type were fixed somewhat below the estimated *ad libitum* capacity.

(b) *The Experimental Animals*

The Camden Park Merino ewes are direct descendants of the original Macarthur flock established at Camden, New South Wales, during the first decade of the last century. The flock has been maintained as an historic residue by the Trustees of the Estate and entirely closed to the introduction of outside blood for the past sixty or seventy years. This small flock thus constitutes one of the most highly inbred strains of sheep available and is particularly uniform in general type. The Camden Park Merino is not now of any commercial significance in Australian sheep-breeding. There is only one other Australian flock of a similar type in existence, also retained mainly for its historic interest. Both flocks typify the fine-wooled Australian Merino characteristic in this country of the period before 1870.

The sheep are small by modern standards although well-knit and vigorous, are almost entirely free from skin wrinkles and folds, and carry a fine fleece of high wax content. The skin supports a fibre population of moderate density. Their wool-productive capacity is low but not greatly below their modern equivalent. Initially they are nervous under restraint and may require some time to settle down to confined pen conditions. This is not regarded as an inherent characteristic so much as due to the relatively infrequent handling on their home pastures.

The Corriedale ewes were obtained from a stud flock at Trangie, New South Wales. By contrast, they are large, carry a strong fleece, low in wax content but high in suint. The fibre-population density of the skin is relatively low. These sheep have a moderate to high wool-producing capacity. They are, like the Camden Park Merino, relatively free from skin folds and wrinkles and this reduces the error of measurement of fleece-growth rate. They proved to have a more placid temperament than the Camden ewes under close confinement.

When the experiment started, the age of the Camden Park Merinos was about 23 months and of the Corriedales about 26 months.

(c) *The Diet*

The selection of a diet acceptable to sheep during long periods of close confinement and suitable for studies of this kind is difficult. In this experiment,

it was desirable to compound a food mixture with a sufficient concentration of nitrogen in available form to permit high intakes within the dry matter capacity of the sheep.

The fodder WB.3 used in the experiment, therefore, consisted of a loose mixture of good quality sun-cured lucerne hay chaff 60 parts, rolled wheat 20 parts, and linseed meal 20 parts. Apart from free access to clean tap water, the diet consisted of this mixture only, no mineral or other supplement being provided at any time during the course of the experiment. The full supply of fodder necessary for the whole experiment was mixed as one large batch to ensure

TABLE 1
SUMMARY OF THE PRINCIPAL DIETARY CONSTITUENTS PROVIDED AT EACH LEVEL
OF FEEDING

Plane of Feeding	Camden Park Merino Series						Corriedale Series					
	Amount provided per Sheep per 24 Hours						Amount provided per Sheep per 24 Hours					
	Dry Matter (g.)	Total Energy (kg. cal.)	Total Nitrogen (g.)	Total CaO (g.)	Total P ₂ O ₅ (g.)	Total Copper (mg.)	Dry Matter (g.)	Total Energy (kg. cal.)	Total Nitrogen (g.)	Total CaO (g.)	Total P ₂ O ₅ (g.)	Total Copper (mg.)
1 (High)	712	3240	24.6	10.1	6.3	8.0	1248	5680	43.2	17.6	11.1	14.0
2	580	2630	20.1	8.2	5.2	6.5	1000	4960	34.6	14.1	8.9	11.3
3 (Uniform)	445	2025	15.4	6.3	4.0	5.0	757	3440	26.2	10.7	6.7	8.5
4	312	1420	10.8	4.4	2.8	3.5	512	2330	17.7	7.2	4.6	5.8
5 (Low)	178	810	6.0	2.5	1.6	2.0	267	1215	9.3	3.8	2.4	3.0

reasonable constancy of composition. It should be noted, however, that this intention was not entirely fulfilled since at the end of Period 9 the stored fodder was accidentally damaged by water, and for the remaining periods, a new batch of similar ingredients was used. Throughout the experiment, samples were drawn daily from each individual ration, and bulked for each experimental period of six weeks into one lot which was subsampled for analysis. From these analyses the following mean values were obtained on a dry weight basis: crude protein (N x 6.25) 21.6 per cent.; crude fat (ether extract) 5.4 per cent.; crude fibre 19.1 per cent.; N-free extract 45.6 per cent.; ash 8.2 per cent. The diet also contained CaO 1.41 per cent.; P₂O₅ 0.89 per cent.; copper 11.3 μ g./g. The combustible energy of the mixture was 4.56 kg.cal./g. dry weight, whereas the mean moisture content as fed to the sheep was 10.9 per cent. The amounts of the principal dietary constituents provided at each of the given levels of feeding are summarized in Table 1. The nitrogen intake was calculated for each period from the analytical value obtained on the sample for that period (Table 2).

Analyses of duplicate subsamples of the bulked food samples in the first 7 periods gave ± 0.09 as the standard error of the individual values in Table 2. However, the error of the bulk sampling is unknown.

TABLE 2
NITROGEN CONTENT OF THE EXPERIMENTAL DIET

Period No.	1	2	3	4	5	6	7	8	9	10	11	12
Nitrogen												
Per Cent.	3.38	3.36	3.36	3.38	3.54	3.66	3.70	3.46	3.43	3.30	3.27	3.23
Dry Weight												

A digestibility trial with the mixture was carried out during Period 12. Six sheep were used representing each of the six groups in the experiment. The object of the trial was to obtain an average value for the apparent digestibility of the experimental diet. The sheep were confined in metabolism cages similar to those described by Marston (1935). The fodder and faeces were weighed and sampled over a period of 7 days. Subsamples of fodder and faeces were analysed for combustible energy and nitrogen content. The results are given in Table 3.

TABLE 3
SUMMARY OF DIGESTIBILITY TRIAL WITH THE FODDER WB.3

Breed	Sheep No.	Ration Fed (g. per 24 hr.)	Ration Consumed (g. per 24 hr.)	Nitrogen (g. per 24 hr.)		Digestible Nitrogen (%)	Energy (kg. cal. per 24 hr.)		Digestible Energy (%)
				Intake	Faeces		Intake	Faeces	
Corriedale	244	1400	1225	32.19	7.94	75.5	5008	1384	72.4
	247	850	850	22.80	4.38	80.8	3455	842	75.6
	246	300	300	8.06	1.38	82.9	1221	244	80.0
Camden	236	800	457	11.87	2.52	78.7	1770	464	73.8
Park	228	500	500	13.41	2.77	79.4	2031	510	74.9
Merino	227	450	450	12.07	2.52	79.1	1830	494	73.0

Unfortunately the trial was marred by the necessity for increasing the intake of sheep No. 227 shortly before the trial in order to keep her alive and by the refusal of sheep No. 244 and No. 236 to consume their whole ration towards the end of the trial. Circumstances made it impossible to continue the trial until perfect behaviour of all the sheep was obtained. Notwithstanding this, the digestibility coefficients for the several sheep show reasonable agreement. The values do not suggest any radical difference in the digestive abilities of the two breeds.

(d) *Observations and Methods*

(i) *General Husbandry*.—The animals were confined individually throughout the course of the experiment each in a small single pen measuring 5 feet by 4 feet, within a well-constructed sheep house, with concrete flooring, single course brick walls and fibrocement roofing provided with sky-lights. The sheep were thus entirely protected from direct sunlight, rain, and to a considerable extent from turbulent air movement which seldom exceeded 60 feet per minute within the pens. Under these conditions, it was not considered necessary to rug the sheep, though rugging was omitted for the further reason that it would interfere too greatly with the normal production of the skin secretions by altering the fleece micro-climate. An additional reason for excluding rugs was that they absorb these secretions to a degree sufficient to vitiate the results of the periodic chemical fractionations made.

All pens were cleaned daily, except at week-ends, between 8.0 a.m. and 9.0 a.m. by sweeping and liberal hosing, each animal being removed from its pen during the process. Movable wooden gratings were provided over half the floor of each pen, and this provision, together with the regular cleaning, tended to minimize soiling of the fleece and any risk of re-infestation with internal helminths. Food and water were provided in specially made galvanized iron troughs clipped to the iron railings at the front of each pen. Food was offered daily between 9.0 a.m. and 9.30 a.m. and the residues, if any, were collected and weighed. From Period 5 onwards, the daily water consumption was measured by filling each trough to a fixed mark while the sheep were consuming the new day's food ration. The daily food rations and residues were weighed to the nearest 5 g. and the daily water consumption measured to the nearest 100 ml.

The only occasions on which the animals were removed from their pens for any appreciable time were weekly for weighing, six-weekly for fleece sampling, and on three occasions to be photographed. All other manipulations (e.g. fibre clippings, skin biopsies, bleeding, clinical observations, etc.) were done with the animals standing quietly in their pens.

Periodic faecal examinations were made to estimate the degree and nature of helminth infestation. Phenothiazine was administered early in the experiment and thereafter the degree of infestation remained at an insignificant level.

(ii) *Fleece-Growth Rate*.—Fleece-growth rate was measured over the last four weeks of each six-weekly period by clipping the fleece from defined areas (10 cm. by 10 cm. approximately) on the midside of each sheep. The areas were delineated by tattooing. The sizes of the sample areas were measured at the conclusion of each period, first with the sheep in the lateral recumbent position on the table used for sampling, and again with the sheep standing normally in the pen. The size of each patch was determined by measuring the four sides of the square with a flexible celluloid rule and multiplying the mean of the dorsal and ventral by the mean of the anterior and posterior margins.

The fleece clipped from each sample area was weighed and the main components, viz. clean dry wool, wax, and suint, were determined. The "wax" fraction was separated by soxhlet extraction with carbon tetrachloride. The "suint" fraction was the cold water soluble material extracted after treatment with carbon tetrachloride. In the course of analysis the quantities of moisture and dirt in the samples were also obtained.

TABLE 4
RELATION OF FLEECE PRODUCTION ON MIDSIDE TO TOTAL FLEECE PRODUCTION
(CAMDEN PARK MERINO SERIES)

Group	Sheep No.	Skin Area (Periods 1 and 2)	Ratio of Value for the Whole Sheep to Value for the Sample Area				Ratio of Production per Unit Area over the Whole Sheep to Production per Unit Area of the Sample			
			Wool	Wax	Suint	Total Skin Products	Wool	Wax	Suint	Total Skin Products
High-Low	227	78.2	57.3	70.3	100.8	64.7	0.733	0.899	1.289	0.826
	232	83.8	63.5*	83.3*	88.1*	71.3*	**	**	**	**
	234	84.7	64.2*	74.2*	89.1*	72.1*	**	**	**	**
	241	80.0	60.7*	79.5*	84.1*	68.1*	**	**	**	**
	Mean	81.7	61.4	76.8	90.5	69.0	0.733	0.899	1.289	0.826
Uniform	225	80.1	59.6	103.6	100.4	72.9	0.744	1.294	1.253	0.910
	226	87.7	66.5*	87.2*	92.2*	74.6*	**	**	**	**
	228	78.2	58.4	72.9	92.4	64.9	0.747	0.932	1.181	0.830
	240	88.2	63.1	52.8	85.2	73.8	0.715	1.064	0.965	0.837
	Mean	83.6	61.9	79.1	92.5	71.6	0.735	1.097	1.133	0.859
Low-High	229	91.4	67.7	79.6	102.3	74.2	0.740	0.870	1.120	0.813
	233	91.6	80.2	107.6	92.9	88.5	0.876	1.174	1.013	0.964
	235	78.5	59.1	59.3	67.0	59.9	0.753	0.755	0.854	0.763
	236	79.9	62.1	98.0	72.7	71.9	0.777	1.227	0.910	0.901
	Mean	85.4	67.3	86.1	83.7	73.6	0.786	1.006	0.974	0.860
Grand Mean		83.5	63.5	80.7	88.9	71.4	0.761	1.027	1.073	0.856

* Estimated value. ** Sheep dead at time of estimation.

The relation of the sample fleece production to the total fleece production was estimated in the last period of the experiment (Period 12) by clipping the entire sheep in addition to the midside areas. A sample of the total fleece was analysed in the usual manner. In the same period, the surface areas of the surviving sheep were measured by means of the surface integrator described by Elting and Brody (1926).

Tables 4 and 5 show the ratios of total to sample fleece growth and total area to sample area for each sheep. The area ratios are those calculated for

Periods 1 and 2.* The ratios of fleece growth per unit area on the midside to fleece growth per unit area over the whole body are also shown. The differences between the groups are not significant and it may be concluded that the ratios were little affected by the plane of nutrition. Consequently, the ratios of total to sample fleece growth were used to estimate the total fleece growth in each period merely by multiplying the sample values of the fleece constituents by a factor constant for each sheep.

Theoretical reasons are given later to support the possibility that the ratio of total to sample fleece growth may have been influenced by the atmospheric temperature. It should be remembered, therefore, that the analysis of the influence of various factors other than the plane of nutrition on fleece growth applies strictly to fleece growth on the tattooed areas and that the proportionality between fleece-growth rate on the tattooed and total areas is established only for changes in fleece-growth rate due to changes in the nutrient intake.

The asterisks in Tables 4 and 5 denote estimated values of the ratios of total to sample wool, wax, and suint production for sheep which died before the end of Period 12.

(iii) *Fibre Thickness*.—A clipping of short lengths of fibre was taken every 14 days from a fixed location about 5 cm. anterior to the fleece sample area on the right side. This was done by first clipping the site with coarse cutter-heads on the electric clippers and then with fine cutter-heads. The fibre fragments obtained in this way were about 1 mm. in length and were formed in the follicles some days previously, the exact time being different for each sheep and depending on the rate of fibre-length growth. The fragments were mounted on a slide and the diameters of the projected images of a hundred fibres measured at a magnification of $\times 500$.

* The values were calculated by dividing estimates of the ratio of total to sample surface area for the missing sheep by the average value of the ratio of total to sample fleece growth per unit area. This procedure takes into account the differences between sheep in the ratio of total to sample area which result from individual differences in the size of area tattooed and from differences in body surface area, but assumes that the sheep did not differ from the breed average in the ratio of total to sample fleece growth per unit area. Estimates of the surface area of sheep in each period were made from equations relating surface area to liveweight, chest girth, and chest depth fitted to the data of Period 12. The equations were

$$\begin{array}{ll} \text{Camden Park Merino} & \dots S/W^{\frac{2}{3}} = 0.007 + 0.191 D/G \\ \text{Corriedale} & \dots \dots S/W^{\frac{2}{3}} = 0.054 + 0.393 D/G \end{array}$$

where S = surface area in square metres, W = liveweight in kilograms, D = chest depth in any units, G = chest girth in same units as chest depth. The ratio of total to sample area for each sheep did not appear to be influenced by the treatment differences and tended to remain fairly constant throughout the experiment. However, to avoid possible treatment effects, the mean values of the area ratios in Periods 1 and 2 were used in estimating the ratio of total to sample fleece growth for the sheep missing in Period 12.

For certain of the following analyses, the square of the mean fibre diameter multiplied by $\pi/4$ to give an estimate of the mean fibre cross-sectional area has been used, although it was realized that the shape of the cross section is seldom truly circular.

TABLE 5
RELATION OF FLEECE PRODUCTION ON MIDSIDE TO TOTAL FLEECE PRODUCTION
(CORRIEDALE SERIES)

Group	Sheep No.	Skin Area (Periods 1 and 2)	Ratio of Value for the Whole Sheep to Value for the Sample Area				Ratio of Production per Unit Area over the Whole Sheep to Production per Unit Area of the Sample			
			Wool	Wax	Suint	Total Skin Products	Wool	Wax	Suint	Total Skin Products
High- Low	246	117.0	100.6	132.3	129.3	113.2	0.860	1.132	1.105	0.968
	250	102.2	82.7	107.8	127.6	91.4	0.809	1.055	1.250	0.894
	251	99.1	81.3*	99.6*	111.3*	86.2*	**	**	**	**
	257	87.5	99.5	120.0	87.6	104.7	1.138	1.370	1.005	1.196
	Mean	101.4	91.0	114.9	114.0	98.9	0.936	1.186	1.120	1.019
Uniform	243	97.8	80.6	95.7	113.3	83.8	0.824	0.978	1.159	0.857
	245	95.3	83.7	78.9	120.9	84.8	0.877	0.827	1.269	0.890
	247	112.8	78.0	105.2	110.0	83.7	0.692	0.932	0.975	0.742
	253	117.4	96.3	127.1	167.4	103.3	0.820	1.082	1.426	0.880
	Mean	105.8	84.6	101.7	127.9	88.90	0.803	0.955	1.207	0.842
Low- High	242	95.4	78.2*	95.9*	107.1*	82.9*	**	**	**	**
	244	104.0	83.1	116.4	123.0	89.5	0.799	1.120	1.183	0.861
	248	114.2	80.3	99.4	89.7	82.9	0.703	0.870	0.785	0.726
	252	117.0	95.0	105.0	163.0	97.6	0.812	0.898	1.397	0.835
	Mean	107.7	84.2	104.2	120.8	88.2	0.771	0.963	1.122	0.807
Grand Mean		105.0	86.6	106.9	120.9	92.00	0.833	1.026	1.155	0.885

* Estimated value. ** Sheep dead at time of estimation.

(iv) *Fibre-Population Density*.—The fibre-population density was estimated by counting the number of fibres in several projections each of 1 sq. mm. of a histological section of the skin. Circular pieces of skin, 1 cm. in diameter, were taken from randomized positions on the dorsal region of each sheep by means of a special skin trephine. The technique described by Carter (1939) was used in the preparation of histological sections. The degree of contraction during preparation of the section, and the resulting effect on density, was determined by estimating the mean diameter of the mounted section and calculating its area. The estimate of mean follicle population density was corrected accordingly.

(v) *Fibre Length*.—A clipping of fibres immediately posterior to each mid-side sample taken at the end of every period provided material for the measurement of fibre-length growth. These measurements have not yet been carried out

but a provisional estimate of length was made for each sheep in each period based on the wool weight, fibre diameter, and follicle population of the tattooed area. The values of wool weight and fibre diameter for the individual periods were used to make this estimate but the follicle population per tattooed area was found to be relatively constant and the mean value for Periods 1-9 was used for each sheep. The fibre-population of the tattooed patch was determined from the fibre-population density, and the area of the tattooed patch measured in the standing position. For some regression analyses not used in this paper, however, an estimate of length was made based on weight of wool per tattooed area and fibre diameter in conjunction with the few available direct measurements of fibre length.

(vi) *Body Weight*.—The sheep were weighed at weekly intervals throughout the experiment at the same hour on each occasion.

(vii) *Body Conformation*.—Several linear dimensions were recorded at the end of each period. These were:

- (1) Standing height at withers.
- (2) Width of chest immediately posterior to the elbows.
- (3) Depth of chest immediately posterior to the elbows.
- (4) Chest girth immediately posterior to the elbows.
- (5) Length from the point of the shoulder to the tuber coxae.
- (6) Width between the tubera coxae.

(viii) *Systemic Reactions*.—At the end of each period after Period 1, observations were made of respiration rate, heart rate, rectal temperature, and skin surface temperature. Again, these measurements will not be considered in this paper except in so far as they may be used to interpret other results. The observations were taken during the afternoon of five days in the sixth week of each period. Skin surface temperature measurements were taken with a clinical thermometer and therefore must be regarded with caution.

(ix) *Blood Analyses*.—During one day of the fifth week of each period after Period 2, jugular blood samples were taken from each sheep between 9 a.m. and 9.30 a.m. at each collection. Determinations were made of blood sugar, blood non-protein nitrogen, blood ketones, serum protein, serum calcium, serum inorganic phosphorus, and serum magnesium. The results of those analyses are not considered in this paper apart from the association between blood non-protein nitrogen and wool-growth rate.

(x) *Atmospheric Temperature*.—The daily maximum and minimum atmospheric temperatures were recorded throughout the experiment at two places in the sheep house, one in the Camden Park Merino group of pens and one in the Corriedale group. The mean of the maximum and minimum daily values for the latter four weeks of each period was used in relating fleece growth to the atmospheric temperature.

(e) The Course of the Experiment

The experiment commenced on July 16, 1945, and observations continued for 72 weeks until the end of November 1946, although the main requirements of the design had been satisfied at the end of Period 9 (July 28, 1946), i.e. at the end of the 54th week.

Slight modification of the original experimental treatment levels proved necessary in order to keep alive, in the early periods, the sheep on the low plane of nutrition.

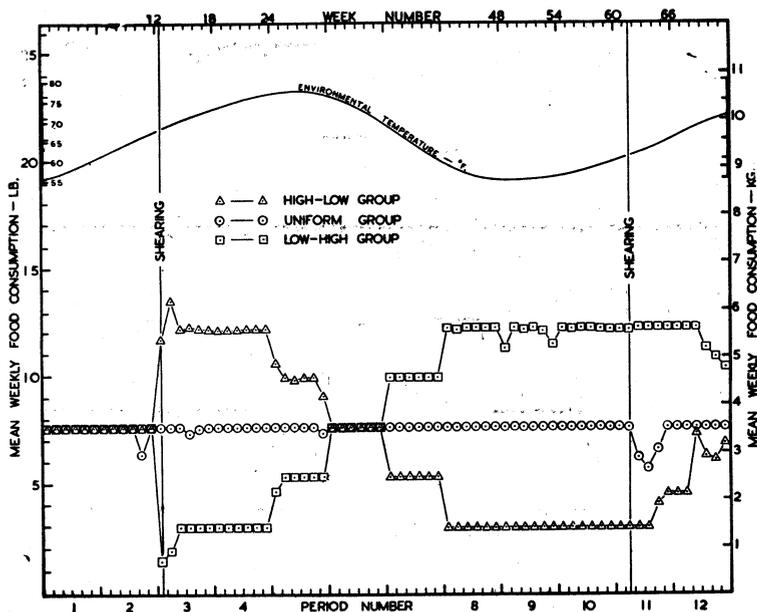


Fig. 2.—Camden Park Merino Series. The mean weekly food consumption per sheep.

During the first fortnight of Period 3, when the groups first received differential treatment, the feed levels for the High-Low groups were 1500 g., and 900 g. per day for the Corriedales and Camden Park Merinos respectively. The corresponding levels for the Low-High groups were 200 g. and 100 g. Before the commencement of the fleece-collection period in Period 3, the ration of the lowest level was increased by 100 g. for each breed and the ration of the highest level decreased by 100 g. The ration of the Uniform groups remained unaltered while the remaining levels of nutrition in the experimental schedule were altered to be half way between the Uniform and the Low, and the Uniform and the High levels respectively. The plan of the experiment in Figure 1 shows the amended levels. Figures 2 and 3 show the actual mean weekly food intake per sheep of each group during the experiment. The different levels received by the High-Low and Low-High groups for 14 days in Period 3, had the desirable effect of bringing the wool-production rate of these groups more rapidly into equilibrium with their respective food intake.

In Periods 11 and 12, the ration of the High-Low Camden Park Merino group was increased when it became apparent that the animals could not exist on the lower ration after they had been shorn at the end of Period 10. Even so, three sheep (Nos. 232, 234, and 241) in this group died from total inanition before the end of the experiment.

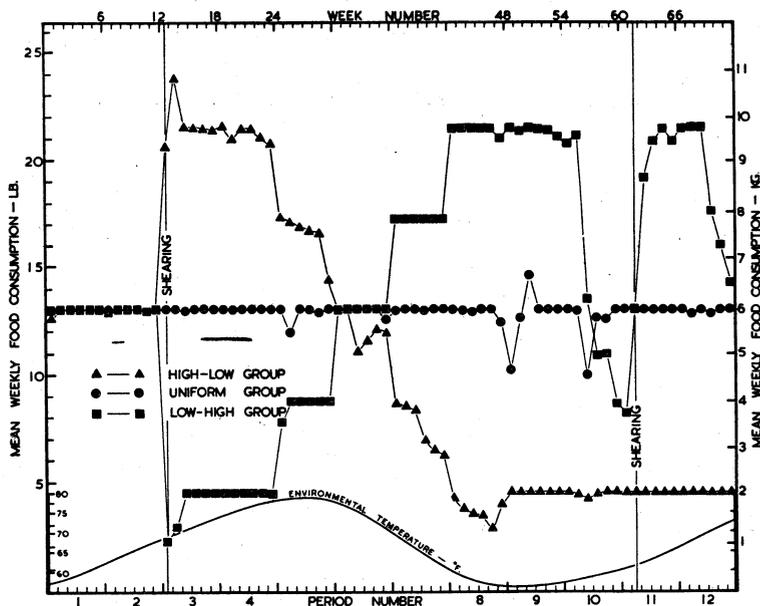


Fig. 3.—Corriedale Series. The mean weekly food consumption per sheep.

Loss of appetite occurred at various times, in three cases leading to death. The extent of inappetance may in part be appreciated from Figures 2 and 3. As mentioned earlier, the remainder of the first food mixture was unavailable in Period 10 and a fresh mixture of the same nominal composition was prepared. The feeding of this mixture was associated with inappetance in several sheep and consequent depression of wool-growth rate. In some cases, wool-growth rate appeared to be affected even though no decrease in food intake occurred. Sheep No. 242 in the Corriedale Low-High group did not recover her appetite and died in Period 11.

Sheep No. 251 of the Corriedale High-Low group showed decreased appetite in Periods 7 and 8 and died in Period 8. Sheep No. 257 in the same group showed decreased appetite in Periods 6 and 7. The observed wool-growth rate of these sheep in the above periods cannot therefore be regarded as being in the same state of equilibrium with the food intake as the wool-growth rate of the other sheep in the same group. Sheep No. 226 of the Uniform Camden Park Merino group showed decreased appetite in Period 11 and died towards the end of that

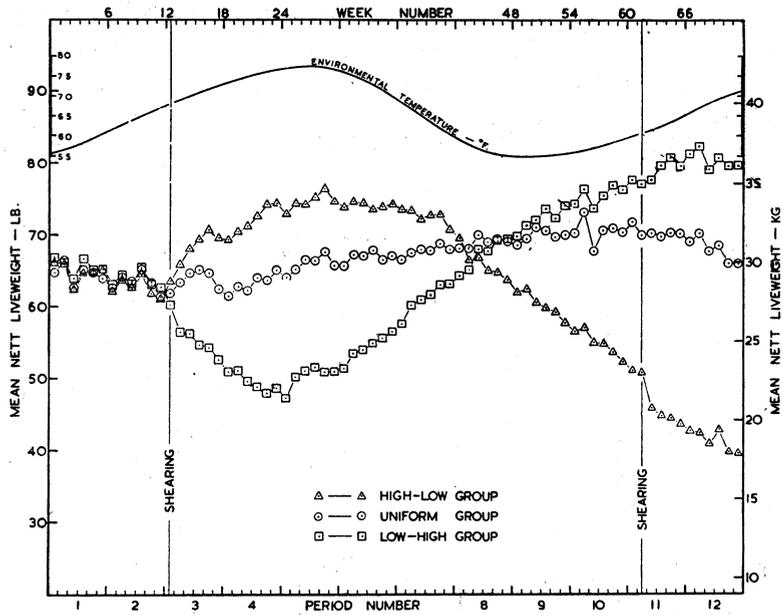


Fig. 4.—Camden Park Merino Series. The mean nett liveweight of the sheep.

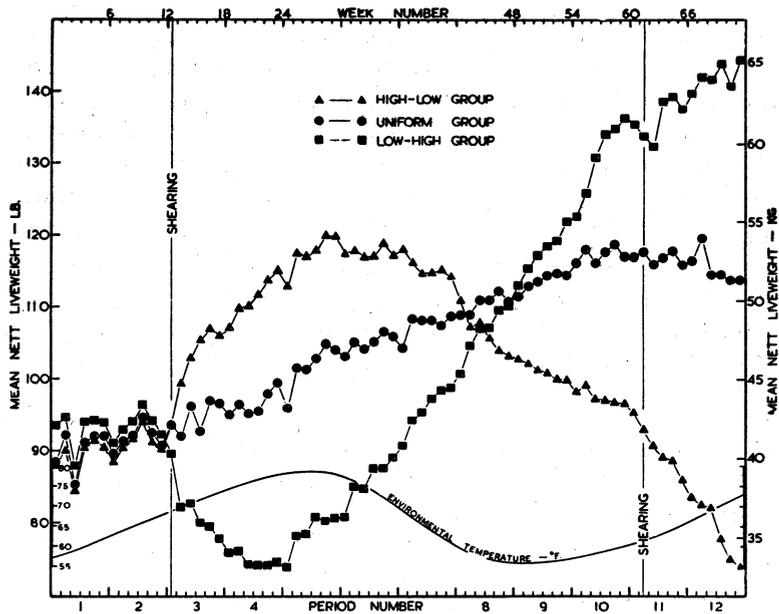


Fig. 5.—Corriedale Series. The mean nett liveweight of the sheep.

period. Transfer of sheep to the metabolism cages for the digestibility trial in Period 12 also caused some depression of appetite. Several substitutions of sheep were made before the trial was commenced.

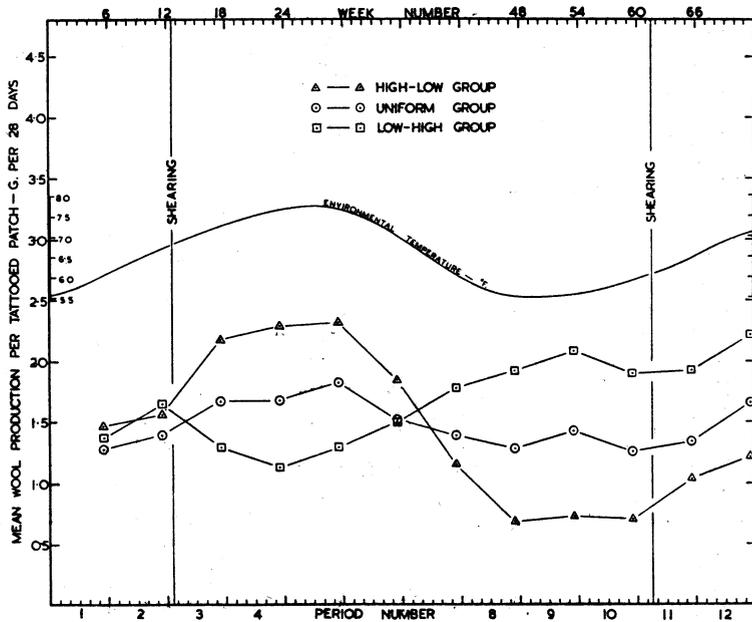


Fig. 6.—Camden Park Merino Series. The mean wool production per tattooed patch, expressed as dry weight per unit time.

The wool-growth rate of most of the Camden Park Merino sheep was low in Period 1 compared with later periods. This may have been due to the change from a ration of lucerne only to the experimental diet at the beginning of Period 1. It is a common experience in experimental work with hand-fed sheep that simple changes in the ration, sometimes, only a change in the batch of food mixture, with no alteration of constituents, can cause a marked disturbance of metabolism. One explanation offered is that a qualitative change in the ration may disturb the normal symbiotic relations of the ruminal flora leading to undesirable fermentations. In the later analyses of the relation of wool-growth rate, plane of nutrition and wool-producing capacity of the sheep, the Period 2 values of wool-growth rate have been used as an indication of the productive capacity of the sheep rather than the mean of the Period 1 and 2 values.

Most of the serious disturbances of the experimental programme occurred in the last three periods. They did not affect the essential aims of the main experiment which is to be regarded as completed at the end of Period 9.

Since helminthiasis, particularly trichostrongylosis, can appreciably alter wool-growth rate even with subclinical infestations (Carter, Franklin, and Gordon 1946) care was taken to see that this factor was excluded. Although all

sheep entered the experiment with a slight worm burden, mainly *Haemonchus contortus* and *Trichostrongylus* spp., this was almost eliminated in the early periods by the administration of phenothiazine and maintained at negligible levels thereafter. Owing to the system of pen hygiene made possible by the design and structure of the sheep house, there was very little risk of re-infestation, and the sheep may be considered to have been observed throughout under almost worm-free conditions.

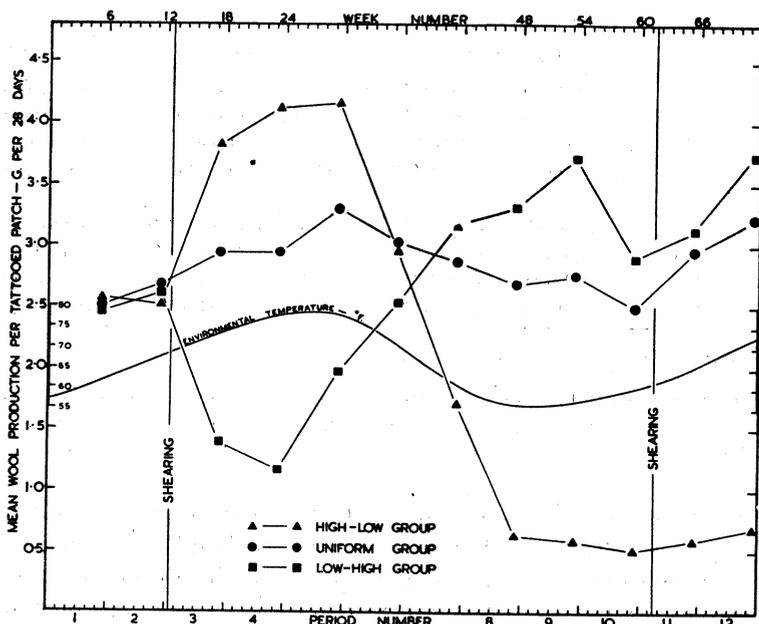


Fig. 7.—Corriedale Series. The mean wool production per tattooed patch, expressed as dry weight per unit time.

Apart from the cases mentioned above, all sheep survived the experiment without disturbance other than from minor extraneous causes. Very brief periods of inappetence were caused in two Corriedales, Nos. 250 and 257, the former by a transient abscess and the latter by a very mild fly-strike. In both cases, appetite had returned to normal within five days.

III. THE INFLUENCE OF FACTORS OTHER THAN THE PLANE OF NUTRITION ON WOOL-GROWTH RATE

(a) Experimental Results

The data for the Uniform groups revealed that influences other than the plane of nutrition were causing between-period variation in wool-growth rate. Analysis of this variation was necessary before the relation of wool-growth rate to the nutrient intake in the High-Low and Low-High groups could be adequately considered.

Partial regression analyses of the mean values for the Uniform groups show the dependence of wool-growth rate, fibre cross-sectional area, and fibre length, on atmospheric temperature, time (in periods of 6 weeks), fleece weight, and

TABLE 6
REGRESSION OF WOOL-GROWTH RATE (G. PER SHEEP PER DAY) ON ATMOSPHERIC TEMPERATURE, TIME, AND NITROGEN INTAKE FOR INDIVIDUAL SHEEP IN THE UNIFORM GROUPS†

Breed	Sheep No.	Independent Variate		
		Atmospheric Temperature (°F.)	Time (weeks)	Nitrogen Intake (g. per day)
Camden	225	0.0490 ± 0.0119**	0.0383 ± 0.0265	0.1878 ± 0.1391
	226	0.0526 ± 0.0089**	-0.0102 ± 0.0250	-0.2219 ± 0.1101
Park	228	0.0532 ± 0.0204*	0.0249 ± 0.0447	0.0234 ± 0.1491
Merino	240	0.0518 ± 0.0098***	0.0408 ± 0.0224	-0.0412 ± 0.0757
	243	0.0835 ± 0.0197**	0.2958 ± 0.0422***	0.2440 ± 0.0688**
Corriedale	245	0.1134 ± 0.0207***	0.1684 ± 0.0462**	0.5019 ± 0.1268**
	247	0.0601 ± 0.0169**	0.0816 ± 0.0372	-0.2244 ± 0.1143
	253	0.0928 ± 0.0186**	-0.0091 ± 0.0410	0.1820 ± 0.1276

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

† In the original partial regression analyses for this table, the term for fleece weight was omitted because in no case was there a significant association in the analysis of the group means (Table 7).

nitrogen intake (Table 7). The independent variate, fleece weight, represents the total fleece weight carried by the sheep calculated for each period by a proportionate division, based on sample fleece-growth rate of the fleece weight measured at shearing time. The term nitrogen intake was included to account for variation in the nitrogen percentage of the ration and occasional feed residues left by some sheep.

A further analysis was made of the regression of wool-growth rate on atmospheric temperature, nitrogen intake, and time by calculating the coefficients for the individual sheep in the Uniform groups (Table 6). The data on which these regression analyses were made are illustrated in Figures 6-11.

Table 7 shows statistically significant regression coefficients for the effect of atmospheric temperature on wool-growth rate and on fibre length for both breeds.

The effect of the environmental temperature on wool-growth rate, after adjustment for other variables would amount to a range of 44.1 per cent (Camden Park Merino) and 23.5 per cent. (Corriedale) of the mean wool-growth rate for the observed temperature range of 55° to 80°F. Wool-growth rate adjusted for the other variables is shown plotted against temperature in Figure 18.

The coefficients for fibre cross-sectional area and fibre length indicate that the effect of temperature on wool-growth rate was brought about by a change in length-growth rate rather than by a change in fibre thickness.

Table 6 shows that the regression of wool-growth rate on atmospheric temperature is positive and significant for each individual sheep.

Table 7 shows significant negative coefficients for the regression of fibre cross-sectional area on fleece weight in both breeds. Correspondingly, the coefficients for fibre lengths are positive in both breeds, significant for the Camden Park Merinos but not quite significant for the Corriedales.

TABLE 7
REGRESSION OF WOOL-GROWTH RATE ON ATMOSPHERIC TEMPERATURE, FLEECE WEIGHT, TIME, AND NITROGEN INTAKE FOR THE UNIFORM GROUPS

Breed	Independent Variate	Dependent Variate		
		Wool Weight (g. per day)	Fibre Cross-Sectional Area (μ^2)	Fibre Length (cm. per day)
Camden Park Merino	Atmospheric temperature ($^{\circ}$ F.)	0.0578 \pm 0.0110**	0.484 \pm 0.422	0.00802 \pm 0.000138***
	Fleece weight (lb.)	0.0478 \pm 0.0567	-6.724 \pm 2.169*	0.00199 \pm 0.000706*
	Time (periods)	0.0157 \pm 0.0175	-2.337 \pm 0.670*	0.000642 \pm 0.000218*
	Nitrogen intake (g. per day)	-0.0462 \pm 0.1032	4.126 \pm 3.951	0.00170 \pm 0.001287
Corriedale	Atmospheric temperature ($^{\circ}$ F.)	0.0818 \pm 0.0123***	0.391 \pm 0.587	0.000601 \pm 0.000124**
	Fleece weight (lb.)	-0.0342 \pm 0.0289	-7.296 \pm 1.383**	0.000534 \pm 0.000291
	Time (periods)	0.1382 \pm 0.0208***	0.439 \pm 0.994	0.001072 \pm 0.000209**
	Nitrogen intake (g. per day)	0.1908 \pm 0.0579*	3.147 \pm 2.771	0.001201 \pm 0.000583

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

The effect on fibre cross-sectional area amounts to decreases of $6.72\mu^2$ (Camden Park Merino) and $7.30\mu^2$ (Corriedale) per pound increase in fleece weight. Thus, the effect of fleece weight on fibre cross-sectional area after adjustment for other variables would amount to 13.5 per cent. of the mean cross-sectional area in the Camden Park Merinos and 11.8 per cent. in the Corriedales, for the ranges in weight shown by the two breeds in this experiment. The mean fibre cross-sectional area for each period, adjusted for other variables, is shown plotted against fleece weight in Figure 19. The adjustments were applied for the sake of uniformity though some variables had no significant effect.

The individual analyses (Table 6) show a variable effect of time in the different sheep. The time change in wool-growth rate is significant only for two of the Corriedale sheep. The trend is positive and it is concluded that these two sheep had not quite reached their mature wool-producing capacity.

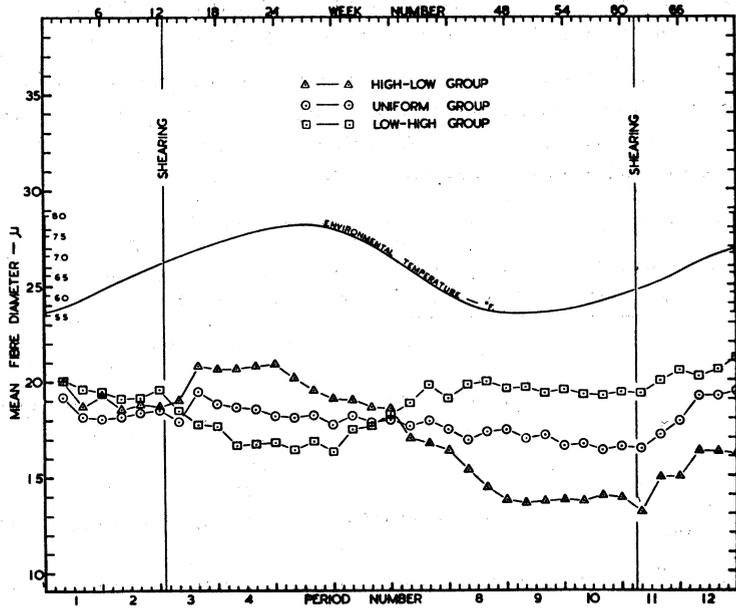


Fig. 8.—Camden Park Merino Series. The mean fibre diameter measured at a fixed position on the side immediately adjacent to the tattooed patch.

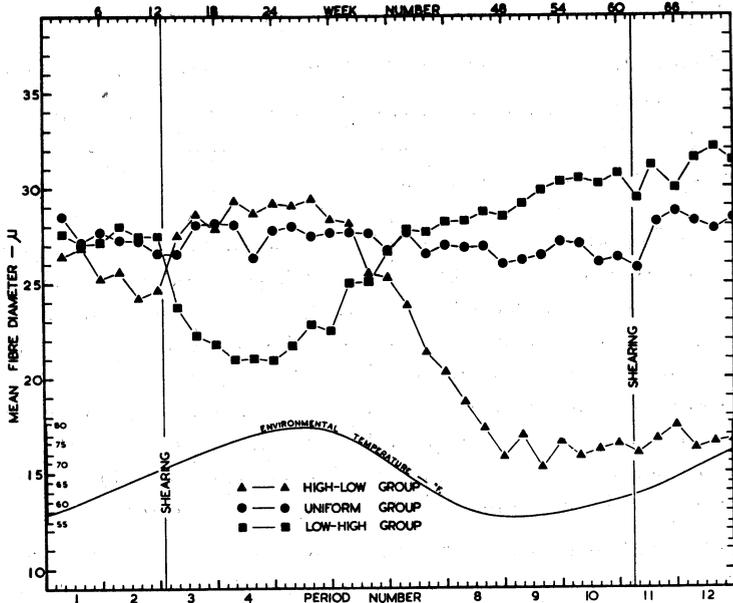


Fig. 9.—Corriedale Series. The mean fibre diameter measured at a fixed position on the side immediately adjacent to the tattooed patch.

(b) Discussion

There appears to be no reference in the literature to an unequivocal positive association between environmental temperature and hair growth in the mammalian coat. Strangeways (1933) observed an immediate decrease in the amount of hair produced when guinea pigs were removed from an environment of 60-70°F. and placed in a room with a temperature of 40-50°F. The production of hair remained at a minimum for 2 or 3 weeks and then returned to its normal level. Eaton and Eaton (1937) found a positive correlation between length-growth rate of hair on the human face and atmospheric temperature but did not observe whether the weight of hair produced was associated with the temperature. According to Marston (1935) external temperature changes "providing these were not great," did not have any measurable effect on wool-growth rate on frequently shaven skin patches such as we have employed in this work. Marston does not, however, say within what limits of temperature change his statement is intended to apply.

Our observation of a positive association between wool-growth rate and atmospheric temperature may appear inconsistent with the familiar appearance of the winter coat in furred animals. In the latter instance, however, one must remember that the hair fibres are not continually growing but attain their full length, enter a quiescent period, and are then shed (Trotter 1924; Dawson 1930; Strangeways 1933). The growth of the winter coat appears to be under the control of a neuro-endocrine mechanism (Bassett, Pearson, and Wilke 1944; Bissonnette and Bailey 1944) and this may not affect the production of continuously growing hair or wool. We suggest that our observed association between wool-growth rate and atmospheric temperature may be due to changes in the blood circulation of the skin in the course of its normal responses as part of the heat regulating mechanism of the body.

Although it has not been specifically demonstrated in the sheep, cutaneous vasodilatation with accompanying increase in blood volume and cardiac output has been demonstrated in various animals as a means of increasing heat loss by radiation and insensible water loss in hot environments (Barcroft *et al.* 1923; Pickering 1932; Freeman and Zeller 1937; Gagge, Winslow, and Herrington 1938; Grant and Holling 1938; Sunderman, Scott, and Bazett 1938; Hick, Keeton, and Glickman 1939; Thauer 1939; Scott, Bazett, and Mackie 1940; Barcroft and Edholm 1943; Naide 1944; Sams 1944; Spealman 1944; Ralston and Ken 1945; Spealman 1945; Barcroft, Bonnar, and Edholm 1947). Although there is apparently some dilution, the phenomenon appears to be largely one of redistribution of the circulating blood. Values of blood non-protein nitrogen which, with sheep on the same ration, may be taken as a crude measure of the blood concentration of wool substrate, showed no association with atmospheric temperature in the Uniform groups.

Increased hair growth on a circumscribed area associated with lesions of the nerves supplying it has been frequently reported. The phenomenon has been explained on the assumption that owing to functional interruption of the sympathetic innervation of the vessels in question (Kuntz 1945) the papillary blood supply has been increased. Kronacher and Lodemann (1930) quote a case in which resection of the sympathetic trunk on one side in the neck of a monkey led to an increased growth of the head hairs on the same side.

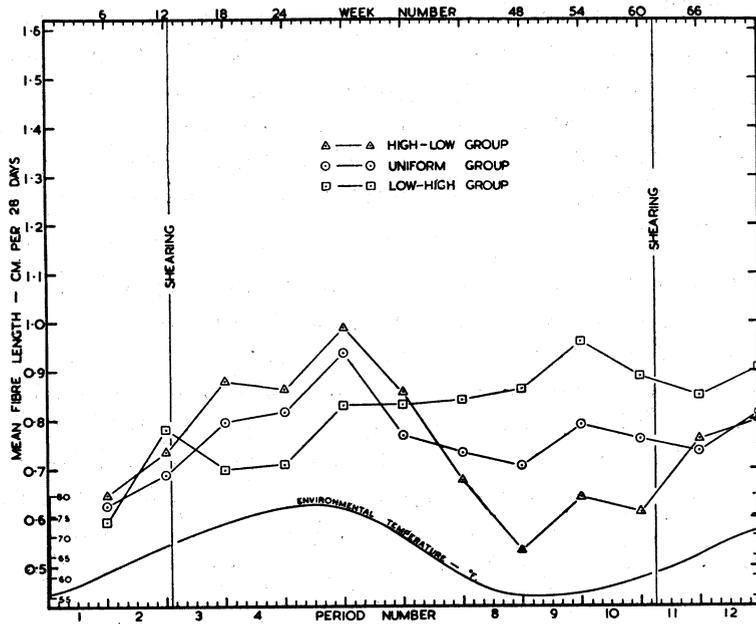


Fig. 10.—Camden Park Merino Series. The mean fibre length expressed as centimetres per unit time computed from wool weight and fibre diameter.

Haddow and Rudall (1945) demonstrated that the waves of active hair growth in the rat are associated with corresponding waves of vasodilatation.

The empirical evidence of an association between atmospheric temperature and wool-growth rate thus confirms the ample physiological expectation of such an association. However, the possibility of this phenomenon occurring has seldom been taken into account sufficiently in quantitative studies of wool growth.

The detailed mechanism of the circulatory responses of the skin to changes in the thermal environment will not be discussed in this paper. However, it should be noted that the relatively greater exposure of the periodically clipped fleece sample area to the thermal environment possibly causes a greater circulatory change on the sample area than over the remainder of the wool-bearing surface. This may be expected from the operation of local spinal and axon reflexes. The use of a constant ratio for converting growth rate of fleece sample to total fleece-

growth rate implies, therefore, a proportionality between sample and total fleece-growth rate which may not hold for all atmospheric temperatures. The ratios have been used nevertheless to render the data in the present analysis more comparable with the data used to relate total fleece-growth rate to the plane of nutrition.

It cannot be overlooked that an additional mechanism may be concerned in the relation of wool-growth rate to atmospheric temperature. Cutaneous vasodilatation besides providing an increased nutrient supply to the follicle also causes an increase in skin-surface temperature which may increase the activity of enzymes concerned in the synthesis of wool keratin.

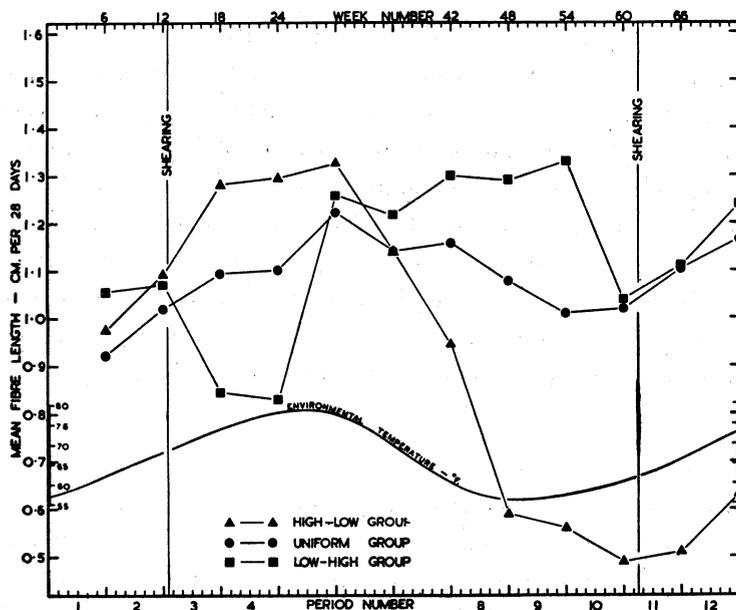


Fig. 11.—Corriedale Series. The mean fibre length expressed as centimetres per unit time computed from wool weight and fibre diameter.

The expression of the temperature effect almost wholly in increased length-growth rate may be explained by an increase in tissue hydrostatic pressure resulting from cutaneous vasodilatation. The increased follicle growth activity in taking the path of least resistance may be prevented from appearing as an increase in fibre thickness. Increased sweat-gland activity associated with increased atmospheric temperature may also contribute to an increase in tissue pressure. Furthermore we may note that changes in atmospheric temperature over the range observed did not cause any appreciable change in body weight (Figs. 4 and 5), when compared with the effect of the plane of nutrition. Consequently, an increase in atmospheric temperature is unlikely to cause an increase in surface area which would allow the fibre to expand laterally with increased follicle activity.

Similarly, the inverse association between fibre thickness and fleece weight may be explained as resulting from the effect of increasing fleece covering on the moisture content of the skin causing increased tissue hydrostatic pressure and deformation of the follicle. Rudall (1935) observed that removal of part of the fleece caused increased medullation of fibres on the shorn areas. However, he did not at the same time measure fibre thickness, and it is impossible to say what association between this dimension and atmospheric temperature was present in his sheep.

IV. THE RELATION OF WOOL-GROWTH RATE TO THE NITROGEN INTAKE

(a) *Experimental Results*

The influence of the plane of nutrition on wool-growth rate is summarized in Figures 6 to 13 in which the mean value for each group of wool weight, fibre diameter, fibre length, and number of fibres per sample area is plotted on a time scale. The mean atmospheric temperature for each period is also shown on each graph and the association of wool-growth rate with atmospheric temperature revealed by the earlier regression analysis is illustrated by the graphs. The influence of fleece weight on fibre thickness and fibre length is also shown, although the interpretation of the data for the latter three periods is complicated by the occurrence of inappetance associated with the feeding of the new mixture in Period 10 (Figs. 2 and 3).

The unexpectedly close association between atmospheric temperature and wool-growth rate seriously hampers the analysis of the relation of wool-growth rate to the nitrogen intake. Owing to the confounding effect of atmospheric temperature, the data for the High-Low and Low-High groups cannot be used to supply estimates for the individual sheep of the constants in equations (1) and (2). The group mean data for Periods 4 and 9 are free from this objection but only supply values of wool-growth rate at two planes of nutrition above maintenance, whereas three sets of values are necessary to estimate k , k' , A , and x_0 . However, inspection of the data revealed that the value of x_0 was probably very small, in which case, without serious bias, values of k , k' , and A could be estimated from two sets of values by assuming that x_0 was equal to zero.

Owing to the differences between the Camden Park Merino groups in productive capacity, as defined by the values for wool-growth rate obtained in Period 2, the data for these groups were adjusted by the regression of Period 4 and 9 values upon those of Period 2. The data for Periods 4 and 9 for each breed were then combined, giving values of wool-growth rate corresponding to the mean atmospheric temperature of the two periods, 64.6° F. (Camden Park Merino) and

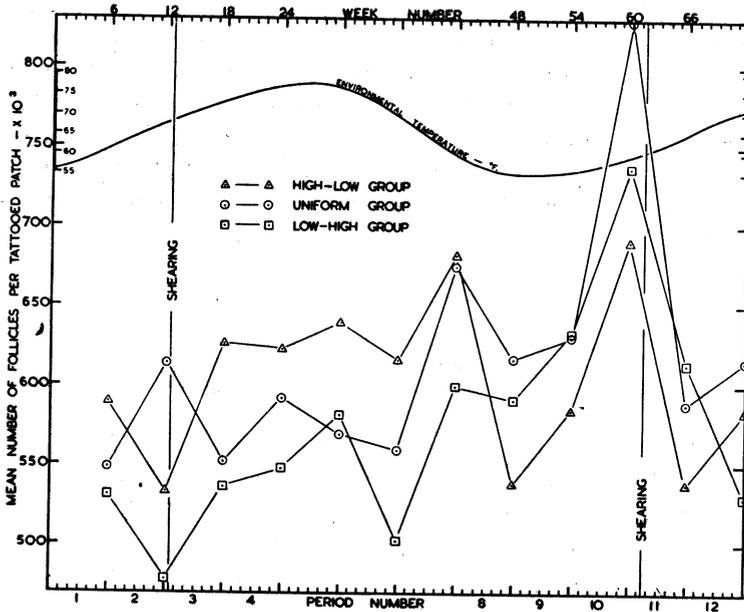


Fig. 12.—Camden Park Merino Series. The mean number of follicles per tattooed patch in thousands computed from periodic density estimates and measurements of the skin patch relaxed with the sheep standing.

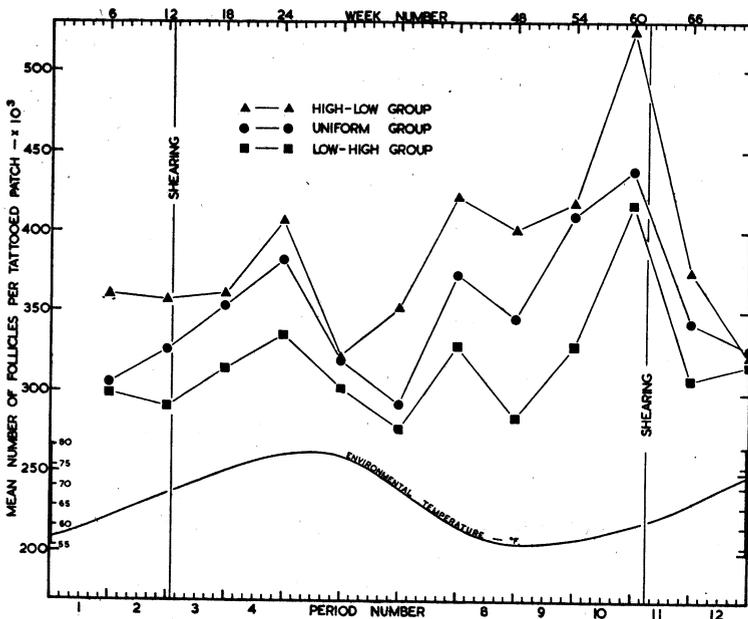


Fig. 13.—Corriedale Series. The mean number of follicles per tattooed patch in thousands computed from periodic density estimates and measurements of the skin patch relaxed with the sheep standing.

66.1° F. (Corriedale). Owing to the variable effect of atmospheric temperature on wool-growth rate in individual sheep (Table 6) it was not considered desirable to fit the equation separately to the Period 4 and the Period 9 data to obtain the effect of the temperature difference between these periods on the value of the constants. Also, further information on the effect of atmospheric temperature on the ratio of total to sample wool-growth rate is required before the effect of atmospheric temperature on the constants of equation (2) can be properly determined.

TABLE 8
THE REGRESSION OF CHANGE IN WOOL-GROWTH RATE PER UNIT CHANGE IN ATMOSPHERIC TEMPERATURE UPON THE NITROGEN INTAKE

Sheep No.	Camden Park Merino		Sheep No.	Corriedale	
	Regression Coefficient	Standard Error		Regression Coefficient	Standard Error
227	0.003985 ± 0.000413***		246	0.006476 ± 0.001736*	
232	-0.000379 ± 0.002238		250	0.006987 ± 0.002192*	
234	0.000854 ± 0.001802		251	—	
241	0.007031 ± 0.001748*		257	0.002832 ± 0.001658	

* $P < 0.05$. *** $P < 0.001$.

It is convenient to fit equation (1) to the data and to determine the value of A and k . k' is then given by the product of k and A . Equation (1) may be fitted by selecting a value of A and calculating the corresponding values of k for each of the two points. By successive approximation, the value of A corresponding to equal values of k for the two points is readily found.

The values found for the parameters A , k , and k' are shown in Table 9. The difference between the breeds in the value of k' cannot be regarded as significant. The data do not therefore dispute the hypothesis embodied in equation (2) generalizing the relation between wool-growth rate, nitrogen intake, and wool-producing capacity.

TABLE 9
ESTIMATES FROM THE EXPERIMENTAL DATA OF THE PARAMETERS IN EQUATIONS (1) AND (2)

Breed	A	k	k'
Camden Park Merino	5.3	0.092	0.487
Corriedale	21.9	0.019	0.422

As pointed out above, the fit of equations (1) and (2) to the data for the individual sheep in the High-Low and Low-High groups is complicated by the parallel change in nitrogen intake and atmospheric temperature. The effect of the two factors is synergistic in the High-Low group and antagonistic in the Low-High group. Furthermore, the wool-growth rate of the Low-High groups did not, in the intermediate periods, appear to be in equilibrium with the nitrogen intake. However, assuming the estimates of k' from the group means to

be valid for the individuals, the individual data may be used to supply estimates of the influence of the plane of nutrition on the effect of atmospheric temperature on wool-growth rate on the sample area. The individual data of the High-Low groups were used for this purpose.

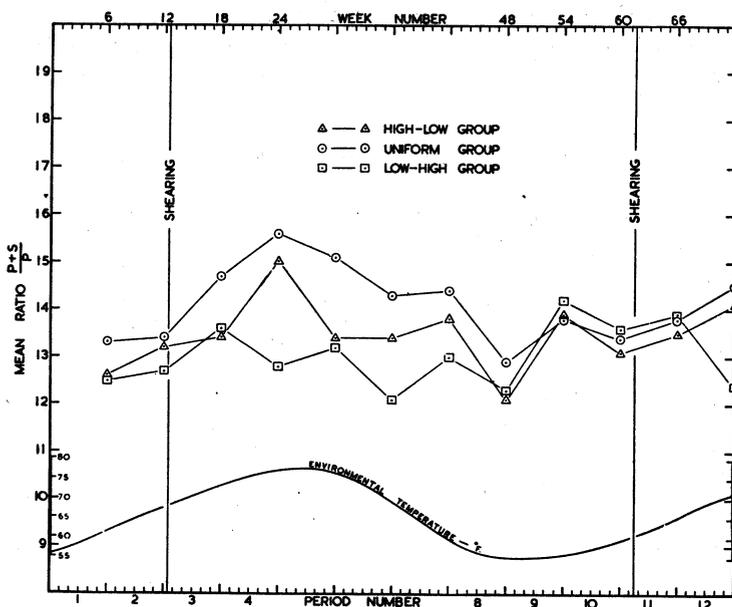


Fig. 14.—Camden Park Merino Series. The mean size of the hair follicle group measured by the ratio of the total follicle population (primary and secondary) to the primary follicle population.

The mean value of k' for both breeds, 0.454, estimated from the data of Periods 4 and 9, was used to estimate values of A for each sheep in the High-Low groups from the data of Period 2. The atmospheric temperature in Period 2 closely corresponds to the mean value for Periods 4 and 9. The theoretical wool-growth rate corresponding to the nitrogen intake in each period of each of the sheep in the High-Low group, was then calculated. The deviation of the actual wool-growth rate from the theoretical values may be ascribed to the temperature differences between each period and the mean value for Periods 4 and 9. The deviations in wool-growth rate were divided by the corresponding temperature deviations to provide estimates of the regression coefficient of wool-growth rate on atmospheric temperature for the planes of nutrition of the particular periods.*

The relation of this change per degree of temperature ($^{\circ}\text{F.}$) to the nitrogen intake for the individual sheep in the High-Low groups is shown in Figures 20 and 21. There is some indication that the influence of environmental temperature

* Only the data for Periods 2 to 9 were used for reasons given earlier. The relation for sheep No. 251 was omitted. This animal was sick in Period 6 and died in Period 7. The data for Periods 6 and 7 for sheep No. 257 were also omitted because of sickness in these periods.

on wool-growth rate increases with the plane of nutrition (Table 8). However, in these sheep, the higher levels of feeding occurred at the higher temperatures and *vice versa* so that from the data of the High-Low groups we cannot associate the apparent effect unequivocally with the plane of nutrition alone. For the present analysis, however, which aims at an adjustment for temperature to permit the fitting of curves for response to planes of nutrition, the present assumption will serve the purpose. A more detailed consideration will be given to the point in a later paper.

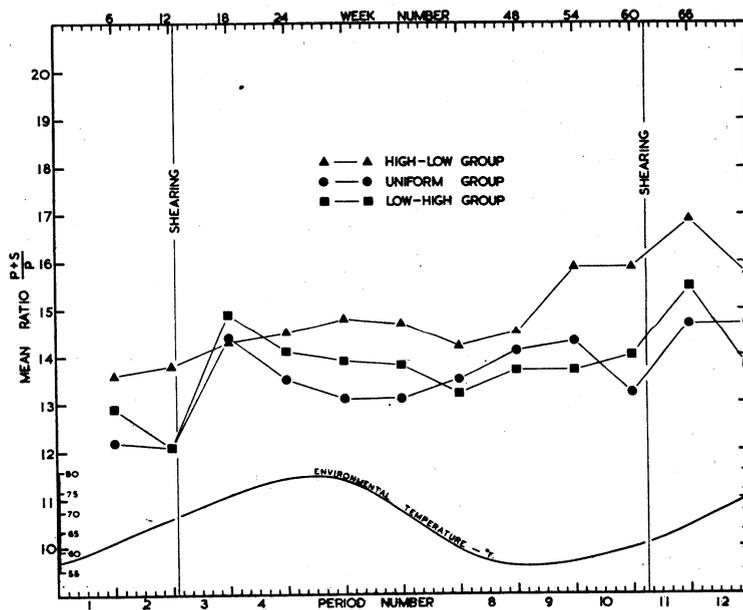


Fig. 15.—Corriedale Series. The mean size of the hair follicle group measured by the ratio of the total follicle population (primary and secondary) to the primary follicle population.

Straight lines were considered an adequate fit to the data of Figures 20 and 21. Adjustments to wool-growth rate for variation in atmospheric temperature were made by reading from the fitted line in each case the appropriate value per °F. change in temperature corresponding to each level of nitrogen intake. The fit of equation (2) to the individual data of the High-Low groups after this adjustment is shown in Figures 22 and 23.

If now the blood values for non-protein nitrogen be taken as a crude measure of the concentration of circulating wool substrate, it appears from the analyses that the influence of the plane of nutrition on wool-growth rate is due largely to a change in the blood concentration of these materials. Here is a contrast to the mechanism postulated for the influence of atmospheric temperature on wool growth, namely, changes in the rate and volume of the cutaneous blood flow. Figures 16 and 17 show the mean blood protein nitrogen of the six groups throughout the experiment.

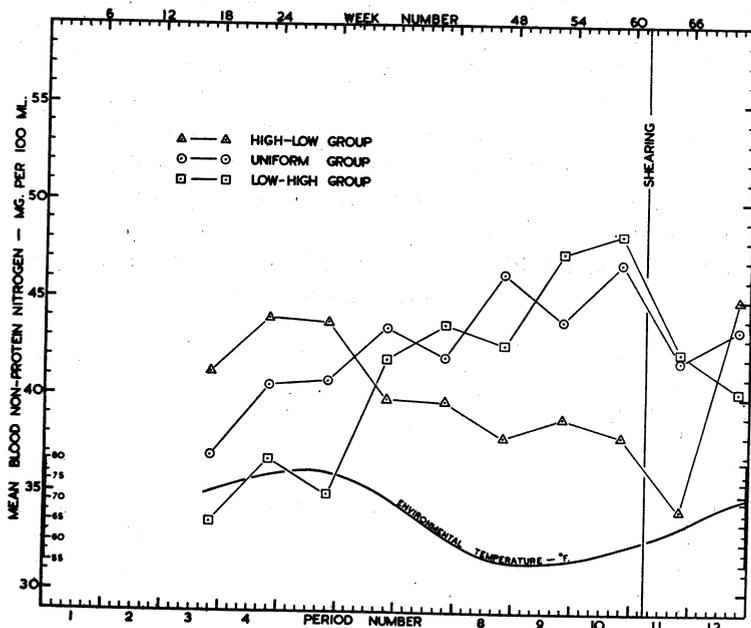


Fig. 16.—Camden Park Merino Series. The mean values for blood non-protein nitrogen.

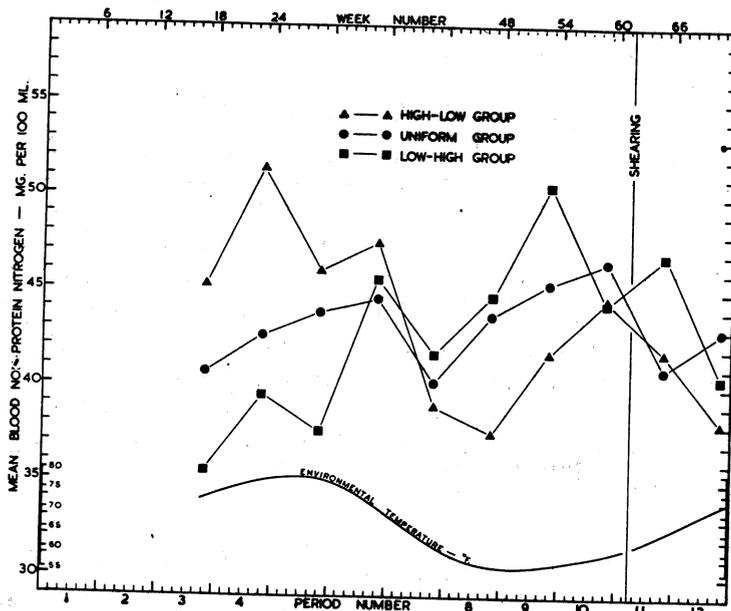


Fig. 17.—Corriedale Series. The mean values for blood non-protein nitrogen.

It may be noted in Figures 6 to 15 that the influence of the plane of nutrition on wool-growth rate is expressed mainly through changes in fibre-thickness and fibre-length growth rate with little evidence of change in the number of active follicles. From Period 8 onwards, however, there is slight evidence in Figure 12 of a decrease in the number of active follicles in the Camden Park Merino High-Low group, and by Period 12 in the corresponding Corriedale group also. This suggestion is supported by the histological picture in both of these groups, although the number of inactive follicles is small. In Figures 14 and 15, the ratio of total to primary follicles for each group throughout the experiment is shown. The graphs do not indicate any consistent effect of the plane of nutrition.

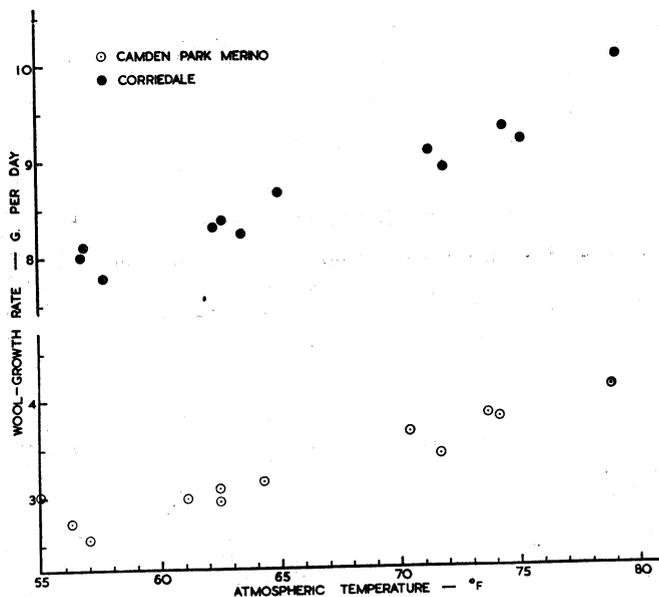


Fig. 18.—The relation of wool-growth rate (adjusted for the other variables) to atmospheric temperature.

From consideration of the factors affecting the relative expression of changes in wool-growth rate as changes in fibre thickness and length, it is apparent that the inherent fibre thickness and length of a fleece are not as precisely defined by the nitrogen intake and atmospheric temperature as is the total wool-growth rate. The generalization expressed in equation (2) can not be applied to the relations of fibre thickness and fibre-length growth to the nitrogen intake. The whole question of the responses in individual skin and fleece characters will be treated in another paper.

(b) Discussion

Although the close approximation of the values of k' for two contrasting sheep types is promising evidence that the same value may apply to other types, this conclusion is insecure without further experimental work. In any case, the

generality of a particular value of k' is limited to relationships in which the nitrogen is supplied from a particular diet. Indeed, the value of k' may be taken as a broad measure of the availability for wool growth of the dietary nitrogen. It is not to be expected, therefore, that data could be found in the literature which would be strictly comparable with the relationship expressed by equation (2).

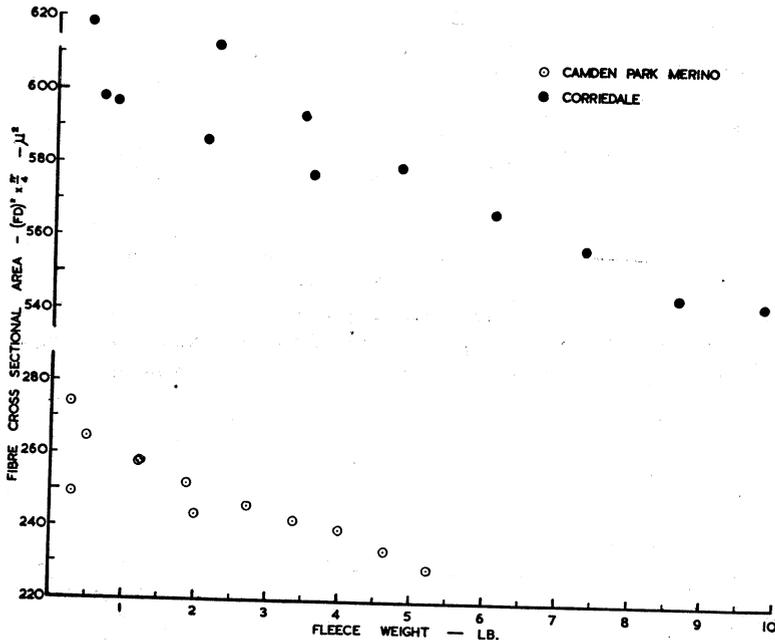


Fig. 19.—The relation of fibre cross-sectional area (adjusted for the other variables) to fleece weight.

Furthermore, in view of the apparent effect of environmental temperature on wool-growth rate, data obtained from sheep kept at different planes of nutrition at different seasons of the year need appropriate adjustment. In our experience, a period of about three months may be required before equilibrium between wool-growth rate and nitrogen intake is established after the plane of nutrition has been radically altered. Consequently, unless the animals be housed in constant temperature rooms, large seasonal differences in mean air temperature must be expected in experiments of this kind. The effects of this temperature fluctuation on wool-growth rate are important where the same sheep are being studied at different planes of nutrition. It is of lesser importance when several individuals or groups of sheep are being compared simultaneously at different planes of nutrition. It is of considerable importance if data from experiments at different laboratories are being studied.

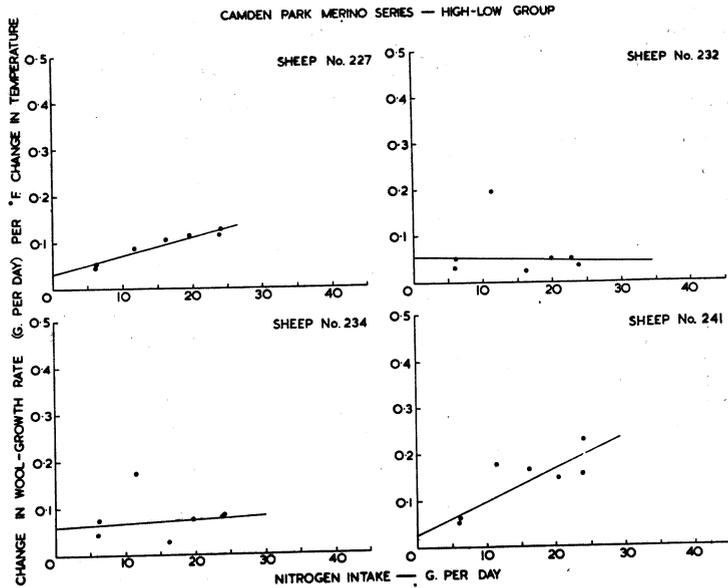


Fig. 20.—Camden Park Merino Series. The relation of the rate of change of wool-growth rate per degree of atmospheric temperature to nitrogen intake for the individual sheep in the High-Low group.

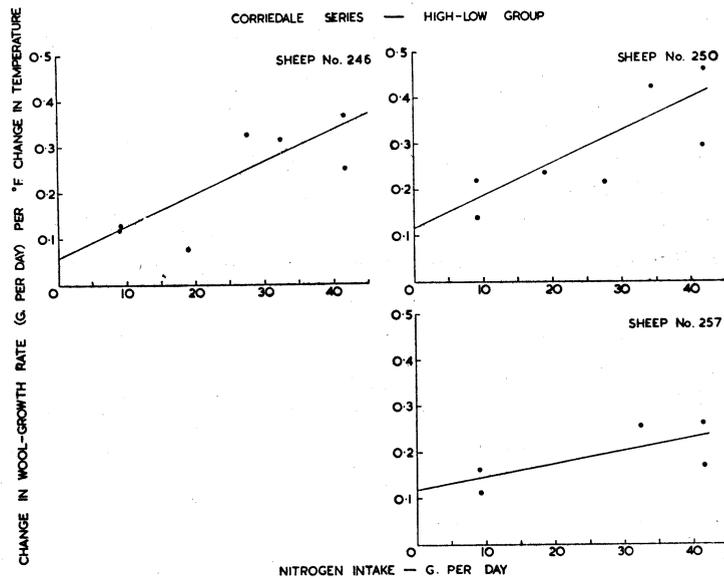


Fig. 21.—Corriedale Series. The relation of the rate of change of wool-growth rate per degree of atmospheric temperature to nitrogen intake for the individual sheep in the High-Low group.

However, data from two examples in the literature may be compared with the relationship given in equation (2) using the mean value of k' for both breeds, 0.454, and explaining deviations in terms of the factors discussed above.

TABLE 10
COMPARISON OF DATA DERIVED FROM LITERATURE WITH THEORETICAL VALUES
CALCULATED FROM EQUATION (2)

Reference	Sheep No.	A* Value (g. per day)	Nitrogen Intake (g. per day)	Actual Wool Growth (g. per day)	Theoretical Wool Growth (g. per day)
Maré and Bosman (1934): South African Merino Wethers. Age: 3 yr.	---	6.8	9.7	3.5	3.2
			12.7	4.0	3.9
			13.9	3.9	4.1
			16.9	4.6	4.6
Marston (1948): South Australian Merino Ewes. Age: 3½ yr. (Ascending Series)	522	17.1	3.67	1.5	1.6
			8.08	1.4	3.3
			12.90	4.6	5.0
			19.83	7.0	7.0
	547	21.5	3.48	1.3	1.5
			7.86	1.7	3.3
			12.51	3.5	5.0
			19.26	7.2	7.2
	558	49.0	3.38	1.1	1.5
			7.97	1.4	3.5
			12.60	4.8	5.3
			18.20	7.6	7.6
Marston (1948): South Australian Merino Ewes. Age: 3½ yr. (Descending Series)	550	6.6	4.18	1.0	1.7
			9.55	2.0	3.2
			15.05	3.2	4.3
			18.85	4.8	4.8
	559	12.4	3.95	1.6	1.7
			9.42	1.7	3.6
			15.55	4.4	5.4
			20.30	6.5	6.5
	572	136.0	4.62	1.5	2.1
			9.42	1.7	4.2
			15.20	7.1	6.7
			19.80	8.7	8.7

* A values were calculated from nitrogen intake and wool-growth values at the highest plane of nutrition for each series of data.

Maré and Bosman (1934) kept two groups each of 11 Merino wethers for 9 months, one on a high and one on a low plane of nutrition. For the next 9 months each original group was divided. For one subgroup the original treatment was maintained and for the other it was reversed. Mean values of wool-

growth rate observed for these four series of sheep during the 18 months of this experiment are set out in Table 10 with the theoretical values computed from equation (2). Although the data in this experiment were obtained with

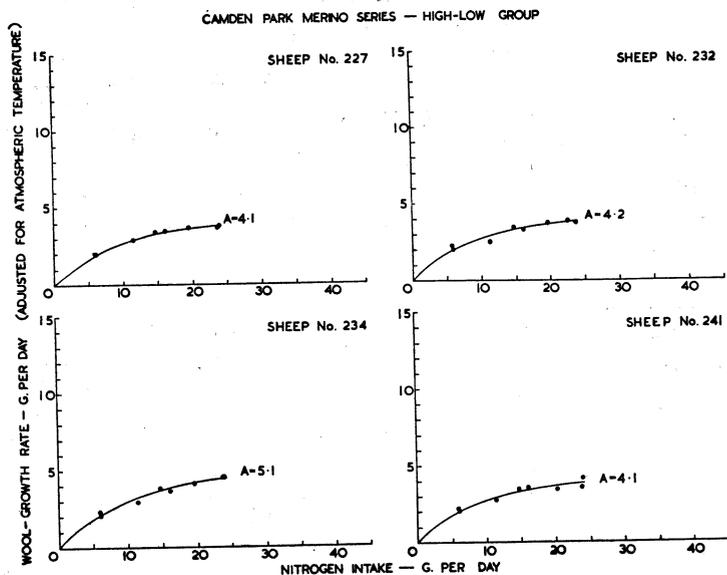


Fig. 22.—Camden Park Merino Series. The fit of equation (2) to the data (adjusted for atmospheric temperature) from individual sheep in the High-Low group.

a diet of different qualitative composition at high and low planes of nutrition and under unknown conditions of environmental temperature, there is reasonable agreement between observed and expected values. Environmental temperature fluctuations are, in this case, comparable for all 4 groups although unknown in relation to the conditions of our experiment.

Marston (1948*a*, 1948*b*) gives values of wool-growth rate and nitrogen intake at 4 planes of nutrition for 6 South Australian Merino ewes. These data were obtained by taking 3 of the sheep from a high to a low plane and, simultaneously, 3 sheep from a low to a high plane of nutrition. The sheep were kept for 10 weeks on each plane of nutrition and wool-growth rate with complete energy and nitrogen balance sheets determined during the latter 14 days of each such period. The observed values and these to be expected from the application of equation (2) are also set out in Table 10. In this case the two series of values do not agree very closely. Discrepancies may perhaps be explained partly by the seasonal trends in temperature of unstated magnitude occurring simultaneously with the changing planes of nutrition; partly, by the negative nitrogen balance of Marston's sheep at the lowest plane of nutrition; partly, by differences in the qualitative composition of the diet, perhaps requiring a different value of

k' ; and partly by slight differences in the method of estimating the wool-growth rate for each sheep from that used by us.

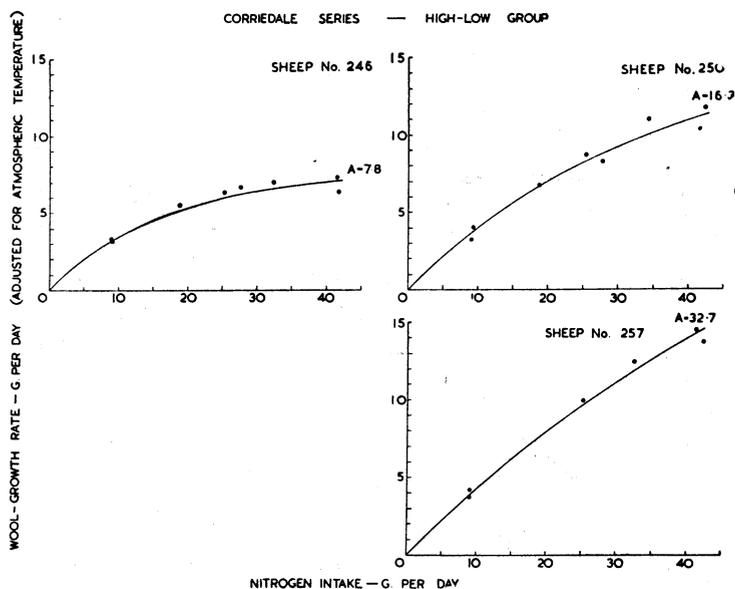


Fig. 23.—Corriedale Series. The fit of equation (2) to the data (adjusted for atmospheric temperature) from individual sheep in the High-Low group.

Figure 24 shows the theoretical curves derived from equation (2) relating wool-growth rate to nitrogen intake for sheep of different wool-producing capacities. The curves fan out from the origin, differences in wool-growth rate between sheep of different producing capacity becoming progressively greater as the nitrogen intake increases. It has been assumed here, as it has been in deriving k , k' , and A from our data, that $x_0 = 0$ in which case equation (2) may be written

$$y/A = 1 - e^{-k'(x/A)}.$$

This assumption seems reasonable on inspection of the data but rigorous proof must await further experiments. It is conceivable that the value of x_0 , although never large, is different for different individuals and is also influenced by the thermal environment. If this be true, it demonstrates that the assumption of $x_0 = 0$ made in this paper is an oversimplification. However, the comparison of the estimates of the parameters k , k' , and A made for the two breeds is relatively unaffected by inaccuracy in the estimate of x_0 . It is clear from Figure 24 that estimates of the asymptote A from single values of wool-growth rate and nitrogen intake using any predetermined value of k' become increasingly more accurate as the plane of nutrition rises. Further, there is no reason to suppose that the

standard error of measurement of wool-growth rate increases with the level of feeding sufficiently to nullify this consideration. In fact, it is more probable that the error decreases with an increasing quantity of wool measured.

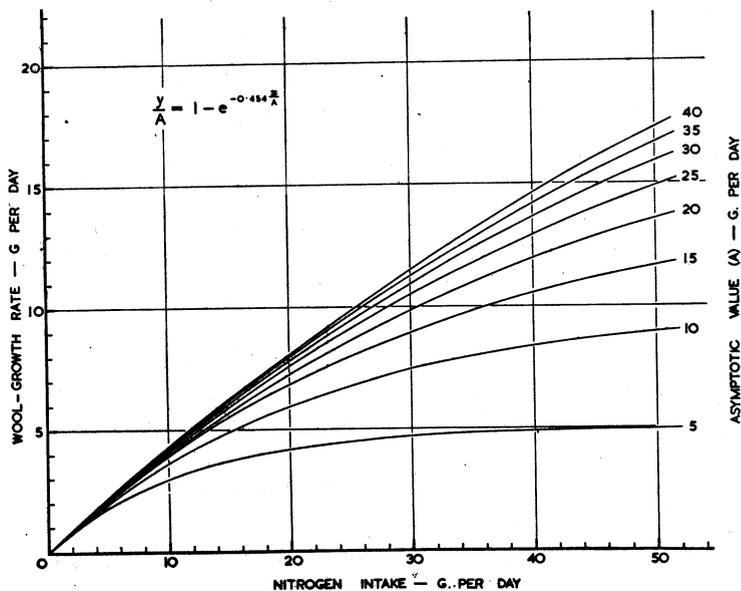


Fig. 24.—Theoretical curves derived from equation (2) relating wool-growth rate to nitrogen intake for sheep of different wool-producing capacities.

Figure 24 also demonstrates that the value of A is not a linear function of the corresponding values of wool-growth rate at ordinary levels of feeding. The value of A increases at a much greater rate than the corresponding wool-growth rate at a given nitrogen intake. For example, a difference in A value of 5 between 10 and 15 corresponds to a difference in wool-growth rate of 2.1 g. per day at a nitrogen intake of 40 g. per day. However, at the same nitrogen intake level, a difference in A value of 5 between 35 and 40 corresponds to a difference in wool-growth rate of only 0.4 g. per day. Thus the high values of A calculated for sheep Nos. 558 and 572 in Table 10 do not reflect proportionately large wool-growth rates at ordinary levels of feeding. Nor, in this case, can the values of A be taken as accurate estimates of productive capacity owing to the doubtful validity of applying equation (2) to Marston's data.

We may consider now the measurement of inherent differences in wool-growth rate in the light of equation (2). For laboratory studies the concept of an asymptotic value of wool-growth rate characteristic of the individual provides a possible method of expressing the inherent wool-producing capacity of a sheep independent of the plane of nutrition. From our data, it would seem desirable

to feed the sheep under observation at as a high plane of nutrition as possible to obtain the most accurate estimate of A . Moreover, since inherent differences in *ad libitum* food capacity constitute an important source of variation in productive performance, it is therefore preferable to feed *ad libitum* rather than at any fixed level. The self-chosen level of food intake thus becomes an additional important observation in itself directly relevant to the study of inherited performance in the sheep. However, before these concepts can find proper application in Mendelian studies of wool growth in the laboratory, more work is required to examine further the generality of equation (2) applied to various sheep types, as well as the effect of dietary composition and environmental temperature on the values of the constants x_0 , K , and A .

In field experimentation and in ordinary sheep breeding practice, the plane of nutrition cannot be known exactly for the individual, and the calculation of asymptotic values of wool-growth rate is virtually impossible. The observed growth rate of wool in the field under ideal pasture conditions is mainly the resultant of the separate inherent capacities for food consumption and for wool growth and the sheep's relations with its thermal environment. Wide variation in the *ad libitum* food capacity of sheep may be observed with individual feeding in the laboratory, and it is certain that equally wide if not wider variation may occur with natural grazing. The *ad libitum* food consumption of the Camden Park Merinos prior to beginning this experiment varied from 680 to 1250 g. of dry matter per day for the twelve individuals. The values for the twelve Corriedales varied from 1290 to 1950 g. per day. Wider variations may be expected in larger numbers of sheep. Assuming the nitrogen content of the dry matter in these cases to be reasonably high, say 3.0 per cent., these intakes provide 20.4 to 37.5 g. of nitrogen per day for the Camden Park Merinos and 38.7 to 58.5 g. per day for the Corriedales. From Figure 24 it is clear that such variation of intake in the Camden Park Merinos ($A = 5.3$ g. per day) would cause little variation in wool-growth rate, whereas in the Corriedales ($A = 21.9$ g. per day) the variation would be considerable. It is apparent, therefore, that studies under natural grazing conditions of the mode of inheritance of wool-producing capacity in sheep are likely to prove most unsatisfactory.

Selection of livestock under the conditions in which they are most commonly maintained, is a well-accepted aim in animal breeding. When sheep are kept at a moderately high plane of nutrition for any considerable part of the average year, such as in the most favourable Merino areas of Australia, desirable characters sought by the breeder include a high inherent wool-producing capacity (A value) and a high capacity and desire for food. Such characters would be poorly expressed when sheep are maintained at a low plane of nutrition with restricted grazing opportunity such as will occur in all areas during adverse seasons. With such unfavourable conditions, the selection of sheep for expected high production performance when the seasons improve, is likely to be relatively ineffective.

V. GENERAL CONCLUSIONS

The genetic component of wool-producing capacity in the sheep is difficult to assess. Differences in the biotic environment affecting the plane of nutrition by altering the amount and quality of food available, differences in the physical, especially the thermal, environment, and differences in the food capacities of individual sheep, all tend to complicate studies of the mode of inheritance of wool-growth rate and productive capacity in the sheep. The generalized equation postulated in this study as a means of relating wool-growth rate, nutrient intake, and wool-producing capacity, although requiring further research, seems to offer a more rational means of expressing the inherent capacity of a sheep for wool production than is commonly used. Considerable difficulties prevent the application of its concepts in genetic studies except under laboratory conditions. Nevertheless, in the breeding of sheep under natural grazing conditions, due cognizance must be taken of the relationships involved.

The differential effects on fibre thickness and on fibre-length growth rate of such factors as the plane of nutrition, thermal environment and amount of fleece covering, suggest that, in field experimentation, variation in either one of these two fleece characters alone cannot necessarily be regarded as reflecting a corresponding variation in total wool-growth rate. The explanation, involving differences in tissue hydrostatic pressure, postulated for the above effects, requires experimental substantiation.

The physiological mechanisms leading to changes in the moisture content of the skin which have been suggested to explain both the apparent influence of environmental temperature on total wool-growth rate and the progressive change in fibre configuration during fleece growth, offer for study a relatively unexplored field in the physiology of wool production. This implies that studies on the physiology of heat regulation in the sheep, and especially the function of the skin, must be integrated with nutritional research if a better understanding of fleece-growth phenomena is to be attained for application in genetic research.

VI. ACKNOWLEDGMENTS

The work described in this paper was carried out as part of the research programme of the Division of Animal Health and Production, C.S.I.R., and during the tenure by one of us (K. A. Ferguson) of the Walter and Eliza Hall Fellowship in Veterinary Science, University of Sydney. The authors are indebted to their colleagues, Miss H. Newton Turner of the Section of Mathematical Statistics for her advice and cooperation during the experiment; to Dr. M. C. Franklin for the chemical blood analyses; to Mr. N. F. Roberts for the numerous fibre thickness estimates made; to Mr. H. McL. Gordon for aid in the control of helminthiasis in the experimental sheep; and to Miss P. Davidson for the energy determinations. It is a pleasure to thank our assistants, Mr. W. Clarke, Mr. G. Shirley, Miss E. Baynes, Miss V. Croydon, Miss J. Grogan, and Miss E. McIntosh, for the enthusiastic manner in which they performed their duties.

Finally, we are especially indebted to the Trustees of the Camden Park Estate and to the owner of the Corriedale Stud for their generosity in donating the experimental sheep employed in this study.

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