AN ANALYSIS OF GROWTH PROCESSES IN CATTLE COATS AND THEIR RELATIONS TO COAT TYPE AND BODY WEIGHT GAIN

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Summary

Hair regrown on a clipped patch of skin during each of nine intervals covering a period of 13 months was sampled, counted, and measured. Methods of estimating the rate of appearance of new hairs, the proportion of follicles with growing hairs, the duration of growing and resting phases of follicles, and linear growth rate of hairs are described. Results obtained from 70 animals are presented. Seasonal changes in the various parameters, and their roles in producing seasonal changes in coat type, are analysed and discussed. Replacement of hairs occurred continuously and amounted to slightly more than two hairs per follicle per year; rates of replacement were highest in spring and in summer. The number of growing hairs and the time for which each hair grew were much lower in summer than in autumn.

Differences between two breed types (Africander crossbreds, and Herefords and Shorthorns) and between steers and heifers and effects of clipping the whole body are analysed.

Differences in coat type between animals were a function of (1) total number of new hairs produced per thousand follicles, (2) the seasonal pattern of shedding and replacement, (3) mean number of growing hairs during the year, which reflects duration of the growth phase of the follicles, and (4) mean hair diameter. Weight of hair grown was a function of mean number of growing hairs and their diameter and medullation. Gain in body weight was significantly associated with total number of new hairs only, and not with other components of coat type or weight of hair. Differences between animals in linear growth rate of hairs, though significant, were not important in correlations with other characters.

The results, taken together with those of previous studies, are relevant to the significance of coat type as an index of thrift in cattle.

I. Introduction

Strong associations of coat type with temperature regulation, tropical adaptation, nutritional condition, and growth rate have been shown by Bonsma (1949), Yeates (1955), Dowling (1956), Turner and Schleger (1960), and Hayman (1965). Attempts to define objectively the characteristics of coats responsible for these associations have been made by Dowling (1959), Schleger and Turner (1960), and Hayman (1965). The attributes studied have been either assessments of coats *in situ* or measurements made on hair samples and skin samples. Progress has been made towards defining critical attributes but the results are largely empirical and the relative importance of various measurements varied under different circumstances. Schleger and Turner (1960) pointed out the degree to which different measurements

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are correlated with each other and suggested that they are subject to a common physiological influence, which might be elucidated by more intimate studies.

Analyses of cattle coats and hair samples are complicated by the extreme variability of hair characters and by the fact that individual hairs vary greatly in age and stage of development at any time, because of continuous shedding and replacement.

In this study the processes of growth and replacement of hairs are examined with a view to building up a picture of the way in which different types of coat are developed. As a first stage, the processes responsible for seasonal changes in coats are analysed, and then differences between animals in these processes and the relative importance of the differences are assessed.

II. Materials and Methods

A group of about 80 calves at the National Cattle Breeding Station, "Belmont", Rockhampton, provided the material for this study. They were born in November 1956 and included approximately equal numbers of the following four breed groups: Hereford, Shorthorn, Africander × Hereford, Africander × Shorthorn. Following preliminary clipping of the sample site in May 1958, they were first sampled in June 1958, and then at intervals varying from 28 to 55 days. The females were removed from the experimental group to enter the breeding herd in January 1959 when the last sample was taken from them, but sampling was continued on the males until June 1959, thus completing a full cycle of 12 months of sampling, representing 13 months of hair growth. For purposes of another experiment (Turner 1962), the whole body of half of the animals of each breed and sex group was clipped at each sampling date, up to January 1959.

As the Hereford and Shorthorn origins did not affect results significantly, the four breeds have been combined into two groups; British and Africander cross. Results are presented from four male groups (British breed and Africander cross, both clipped and unclipped) and three female groups, totalling 70 animals, measurements not having been made on the Africander cross, unclipped females. Results on females cover only May to January and it was only during this period that the treated animals were clipped.

At each sampling date, hair and skin samples were taken from the region of the last intercostal space, skin samples being taken either from a position adjacent to the hair-sampling area or from the corresponding region on the opposite side of the animals. On each occasion, the site was brushed free of loose material and a hair sample was taken with a single blow of small-animal clippers from the middle of the area which had been clipped at the time of the previous sampling. Mean length and mean width of the sampled area (about 40 cm²) were determined, and the surrounding area was then clipped in preparation for subsequent sampling.

Hair samples were weighed and at least two subsamples, each representing a complete hair staple of 3–6 mg, were taken and weighed. Weights were adjusted to standard humidity conditions. The individual hairs in each subsample were teased out and hairs were mounted on a strip of transparent adhesive cellulose tape about 15 in. long to which a strip of millimetre graph paper was subsequently applied. The number of hair ends on each strip was counted, pointed ends and blunt (cut) ends being counted separately. From these, the number of hairs with two cut ends and the number with one pointed end were calculated. Using the weights of subsample and of sample, and the area sampled, these counts were converted to number of pointed (new) hairs and number of blunt (old) hairs per square centimetre of skin. The number of hairs per subsample was mostly in the range of 250–500. If calculated densities from duplicate subsamples showed poor agreement (one 20% higher than the other), further subsamples were taken and mounted.

Under a dissecting microscope, against the millimetre backing, lengths of 75 hairs of each subsample were measured, lengths of pointed and blunt hairs being recorded separately. Under a standard microscope with an ocular micrometer, at ×320 magnification, diameters and degree of medullation of the blunt hairs among these 75 were recorded.

Skin samples were collected at each sampling date and used for determination of number of follicles per square centimetre of skin, according to the procedure described by Turner, Nay,

and French (1962). The skin samples were weighed, and this weight provided a good measure of skin thickness (Hayman *et al.* 1966).

Coat scores, on a scale from 1 (very sleek) to 7 (very woolly) (Turner and Schleger 1960), were recorded by two observers at various times during the year preceding the experiment and during the experiment, and the mean of all scores on each animal was used in analyses.

Body weights were recorded at intervals before and during the experiment, but comparative growth rates during the experiment may have been disturbed by a few subclinical cases of *Lantana* poisoning, so gain of each animal during a 5 months growing season immediately preceding the experiment is used in analyses of relations between coat characters and gain. The stability of coat type ratings and of their relation to preceding or succeeding gain have been shown by Turner and Schleger (1960).

One animal which showed distinct clinical symptoms of *Lantana* poisoning has been excluded from the main data and the results for it are treated in a separate section.

III. Treatment of Data

The hair samples collected represented the hair regrown on approximately the same patch of skin during nine successive experimental intervals throughout a year. The regrowth is made up of new (pointed) hairs which appeared above clipping level since previous clipping, and of old (blunt) hairs which were cut at previous clipping but grew further during the interval. In interpreting counts of these hairs the following assumptions and principles are adopted:

(1) The cycle of a hair consists of a period of growth followed by a period of quiescence, before shedding. Individual hairs do not cease growth and then subsequently resume growth. Shedding, and initiation of a new hair, are virtually coincident (Hayman and Nay 1961). The time lapse from effective commencement of growth of a hair in the follicle bulb to its appearance at clipping level (approx. 2 mm above skin level), at 0·3 mm per day (Fig. 2), would be about 10 days.

(2) No uncut, club ends, representing loose, shed hairs, were detected in the samples. Any that may have remained in the regrown stubble were apparently brushed out before sampling. Hairs are therefore cut *in situ* and at the same level above the skin surface at each sampling. All hairs harvested have grown during the interval between samplings, and their lengths represent the amount by which they have grown in the case of old (blunt) hairs, and the amount by which they have grown since reaching clipping level in the case of new (pointed) hairs. Clipping level is the reference point throughout.

(3) The minimum interval from cessation of growth of a hair to its shedding is longer than the sampling interval of 1–2 months. This assumption is confirmed by data to be presented. It follows that all hairs that have grown during the interval are harvested, an extension of (2) to its converse.

(4) Blunt hairs collected at a given sampling represent all hairs that were growing before the previous sampling and have continued to grow for some part at least of the intervening interval. The count of blunt hairs therefore equals the number of hairs growing at the time of the previous sampling.

(5) The number of follicles per unit area of skin changed as the animals grew during the experiment and also differed between animals (Turner, Nay, and French 1962). In the main data, counts of pointed and blunt hairs and derived counts of emerging and growing hairs are therefore expressed as number per 1000 follicles. Random error could have been reduced by smoothing successive follicle densities, but this might have introduced a bias and was avoided. Actual follicle densities are shown in Table 1.

TABLE 1

MEAN NUMBERS OF FOLLICLES PER SQUARE CENTIMETRE

Date	British Breed, Clipped		British Breed, Untreated		Africander Cross, Clipped		Africander Cross, Untreated
	Male	Female	Male	Female	Male	Female	Male
June 17	1697	1419	1574	1417	1316	1171	1242
June 30	1638	1419	1512	1351	1254	1160	1205
Sept. 22	1448	1316	1484	1292	1208	1171	1370
Oct. 20	1435	1412	1411	1153	1039	1135	995
Dec. 10	1386	1196	1541	1219	983	995	1184
Jan. 27	1353	1272	1391	1142	1092	1035	1030
Mar. 23	1189		1215		1051		998
Apr. 29	1232		1245		1029		976
June 16	1131		1151		1022		934

(6) Average lengths of phases of the follicle cycle can be calculated. The total cycle length, i.e. the average time from initiation of a new hair to its shedding and replacement by another new hair, is equal to the time taken for the total number of new hairs emerging to equal the total number of follicles. The growth phase, i.e. the average time from initiation of a new hair to its cessation of growth, is equal to the time required for the total number of new hairs appearing to equal the number of growing hairs. These principles are illustrated in Figure 1. Only the mean lengths of these phases can be calculated; no information can be obtained on the variation in cycle length between follicles on the same animal at the same period of the year.

(7) For any sampling interval, data on the number of growing hairs and rate of initiation of new hairs can be used to calculate the mean number of days for which new hairs and old hairs respectively were actually growing during the interval. For instance, if during an interval of 30 days the number of growing hairs per 1000 follicles declined from 100 to 80, and 35 new hairs appeared, then only 45 of the original 100 hairs continued to grow throughout the whole interval. The other 55 ceased growing during the interval and, assuming that cessation was evenly distributed over the month, grew for an average of 15 days. The mean growing period of the 100 blunt hairs was therefore $[(45 \times 30) + (55 \times 15)]/100 = 21 \cdot 75$ days. Hence, from the mean length of these hairs, their mean linear growth rate can be calculated.

Similarly, emergence of new hairs is regarded as evenly distributed over an interval, so that the mean time for which they grow is half the interval, unless the number of growing hairs at the end of the interval is less than the number of new hairs, when allowance must be made for new hairs which appeared early in the interval and ceased before its end.*

(8) When calculations of follicle phases, etc. involve the period May–July, the results for June–August 1958 are regarded as following those for April–June 1959, and mean results for the overlapping period May 8 to June 16 are used.

IV. Validation of Assumption 3

On one occasion an extra sample was collected from each of 11 animals. Following the clipping of the normal sampling site on the left side in July, routine samples were collected from this site in September and October, at intervals of 54 and 28 days respectively. In July the corresponding site on the right side was also preclipped, and this area was sampled only in October, after 82 days.

The expectation is that the sum of new (pointed) hairs collected in September and October from the left side should equal the number from the right side in October. In fact, while new hairs during the total period ranged from 276 to 1077 per square centimetre in different animals, means by the two methods of sampling were 639 and 667 respectively, an insignificant difference of 28 ± 34.

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* If I = interval between samplings 1 and 2,

$\quad P$ = number of pointed hairs at sampling 2,

$\quad B$ = number of blunt hairs at sampling 2,

$\quad b$ = number of blunt hairs at sampling 3,

D_B and D_P = mean time for which blunt and pointed hairs, respectively, collected at sampling 2, were growing during the interval I,

then, if $b \geqslant P$,

$$D_B = \{(b-P)I + \tfrac{1}{2}I[B-(b-P)]\}/B$$
$$= I(b+B-P)/2B,$$

and

$$D_P = \tfrac{1}{2}I.$$

If $b \leqslant P$, and F is the fraction of the interval taken for the number of new hairs to equal the number of growing hairs, i.e.

$$FP = b + (I-F)(B-b),$$
$$F = B/(P+B-b),$$

and G is the fraction of the interval over which b new hairs appear, i.e.

$$G = b/P,$$

then

$$D_B = \tfrac{1}{2}FI$$
$$= \tfrac{1}{2}IB(P+B-b),$$

and

$$D_P = [\tfrac{1}{2}bGI + \tfrac{1}{2}I(P-b)(F+G)]/P$$
$$= I[P(b+B)-b^2]/[2P(B-b+P)].$$

Similar types of calculation are used for fixing the points on the time scale at which mean growth rates and diameters are plotted (Fig. 2).

Furthermore, if hairs growing in July and present as blunt hairs in September were still not shed by October, the blunt hairs collected in October from the right side would equal the number collected in September from the left side. Blunt hairs from the right side in October averaged 226 per square centimetre, less by 66 ± 33 than the number from the left side in September. The difference is not statistically significant.

It is concluded that no new hair appearing during a sampling interval of 82 days was lost during that interval, and that no significant number of the hairs growing at the beginning of the interval was lost by the end. For the shorter sampling intervals actually used (28–55 days), the assumption that all hairs growing at the beginning of an interval are still present at the end, i.e. that the quiescent period is not shorter than the sampling interval, appears justified.
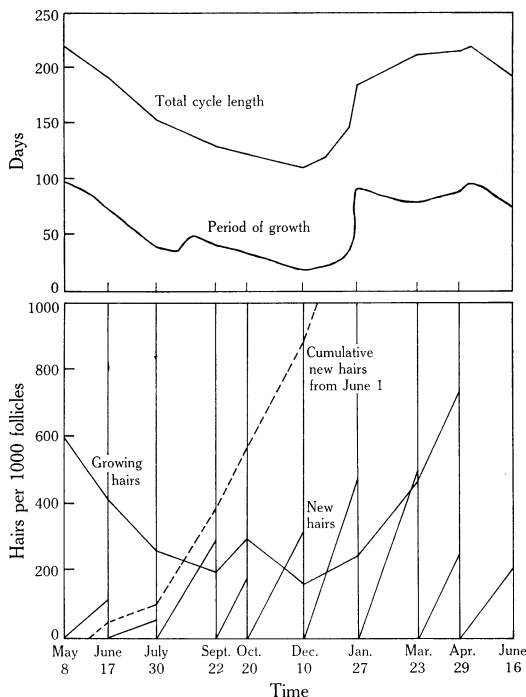

Fig. 1.—Numbers of new hairs and of growing hairs in British breed untreated males at each sampling; and calculated mean lengths of growth phase and of total follicle cycle for hairs commencing growth at indicated dates.

V. RESULTS

(a) Parameters of Hair Growth and their Seasonal Variation

Various results for the combined group of Hereford and Shorthorn males which were not subjected to whole-body clipping are shown in Figures 1 and 2. Results for the different breed, sex, and treatment groups will be compared in Section V(b).

At the bottom of Figure 1 is shown the number of new hairs per 1000 follicles which appeared between successive sampling dates. The slopes of these curves, representing numbers of new hairs per 1000 follicles per day, are plotted in Figure 2. This curve shows a peak of 10 new hairs per day in January and a minimum at 1·2 hairs per day in July. Although it is not strongly expressed in this group, there is also

a peak in October. From the mean results for all animals (Table 2), the rates of entry of new hairs have been calculated, and Figure 4 shows that the spring and summer peaks are of approximately equal height.
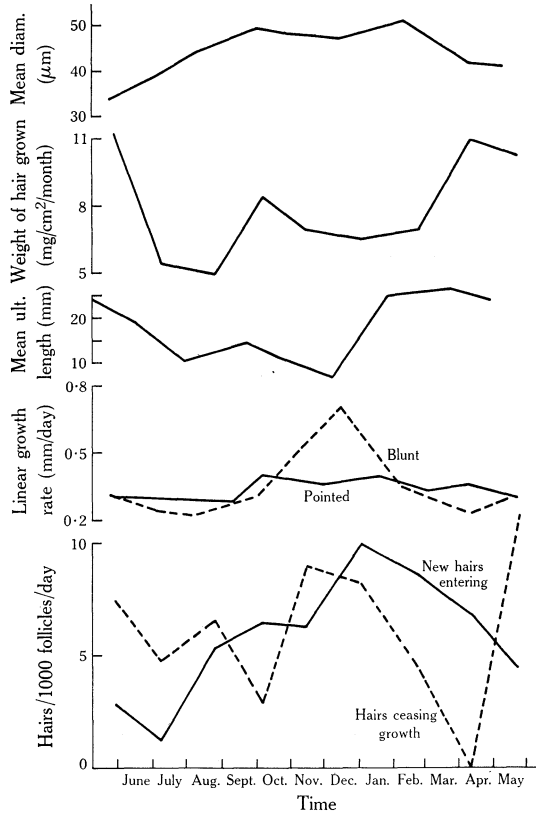

Fig. 2.—Various parameters of hair growth in British breed untreated males. The parameter "mean diameter" refers to the diameter of growing hairs, and the parameter "mean ultimate length" refers to the ultimate length of hairs commencing growth at the given dates.

A curve of the number of growing hairs is shown in Figure 1 by displacing the number of blunt hairs per 1000 follicles at each sampling date one sampling date to the left. Number of growing hairs ranged from 74% of follicles in April to 16% in December, and followed a smooth curve except for a subsidiary rise in October.

The broken curve in Figure 1 represents, for purposes of illustration, the cumulative number of new hairs appearing after June 1. The cumulative number of new hairs equals the number of growing hairs when these two curves cross, on August 24. The oldest of these new hairs, those initiated on June 1, are therefore due to cease growing on August 24, i.e. 84 days after commencing. Similar estimates of the mean growth life of hairs initiated on any date are plotted in the upper part of Figure 1.

The cumulative curve of new hairs per 1000 follicles from June 1 reaches 1000 on December 21, when, on average, hairs initiated on June 1 are due to be replaced by new hairs; i.e. the mean length of the total follicle cycle for hairs initiated on June 1 was 203 days. Similar estimates of the mean cycle length for hairs initiated on any date are shown as the top curve in Figure 1.

TABLE 2

MEAN NUMBERS OF NEW HAIRS PER 1000 FOLLICLES AT EACH SAMPLING AND MEAN TOTALS ±S.E. FOR EXPERIMENTAL PERIOD

Number of animals of each sex given in parenthesis

Month	Interval (days)	British Breed, Clipped		British Breed, Untreated		Africander Cross, Clipped		Africander Cross, Untreated
		Male(11)	Female(8)	Male(8)	Female(12)	Male(9)	Female(11)	Male(10)
June	40	39	95	114	117	76	157	127
July	43	20	28	57	83	51	80	85
Sept.	54	358	242	281	254	233	174	334
Oct.	28	271	262	184	193	235	176	238
Dec.	51	223	343	309	291	322	403	279
Jan.	48	370	277	474	338	454	346	431
Mar.	55	379		494		416		441
Apr.	37	207		254		205		218
June	48	202		206		206		307
				Mean totals				
May–Jan.	264	1280	1247	1419	1276	1371	1336	1493
		±72	±67	±57	±54	±37	±93	±47
May–June	404	2068		2372		2198		2460
		±96		±57		±55		±79
				Adjusted to 365 days				
		1966		2230		2074		2268

The growing phase was 80–100 days for hairs initiated between the end of January and the end of May, whereas hairs initiated in mid-December grew for only 20 days. Similarly, total cycle length was about 200 days for hairs initiated in February–May, but 110 days for hairs initiated in mid-December. The quiescent phase between cessation of growth and replacement by a hair, determined by difference, was about 120 days for hairs initiated in February–June and about 90 days for hairs initiated in September–December.

Because clipping level is the reference point for commencement of growth, the true growing phase is underestimated by about 10 days, total cycle length is unbiased, and the quiescent phase is overestimated by about 10 days. Although total cycle length varied considerably with season, it averaged about 6 months. The total number of new hairs collected in 12 months was equivalent to 2·2 times the number of follicles (Table 2).

The number of hairs per 1000 follicles ceasing growth per day can be calculated as $[B-(b-P)]/I$, using the notation defined previously, and this is plotted in the lower

part of Figure 2. In February–April very few hairs ceased growing but many hairs completed growth in May and also about November.

The mean linear rate of growth of hairs, calculated by the equations given previously, is shown in the middle of Figure 2. Separate curves are plotted for new (pointed) hairs and old (blunt) hairs. The growth rate of new hairs showed little seasonal variation, averaging $0 \cdot 3$–$0 \cdot 4$ mm per day. Growth rate of blunt hairs showed a peak of $0 \cdot 7$ mm per day in midsummer but was in the range of $0 \cdot 2$–$0 \cdot 3$ mm per day from April to September.

From the length of the growth phase (Fig. 1) and mean growth rates, the mean ultimate length attained by hairs initiated on any date can be calculated and this is shown as the middle curve in Figure 2. Its seasonal variation is much more a function of the length of the growth phase than of mean growth rate. The mean length of 7 mm for hairs initiated in December is a minimum because of the short growth phase and despite the high growth rate. Hairs initiated in February–May were estimated to reach an ultimate mean length of 25 mm.

The two uppermost curves in Figure 2 show two characters which were directly measured. The weight of hair grown, in the range 5–11 mg/cm²/month, followed a seasonal trend similar to that of the number of growing hairs (Fig. 1). Mean diameter of growing hairs was a minimum (33 μm) in June 1958, but was about 20% higher in May 1959. Peak mean diameters of about 50 μm occurred in October and February, corresponding to the peaks in rate of entry of new hairs.

(b) Differences between Animals in the Parameters of Hair Growth

(i) Entry of New Hairs

Effects of sex, breed, treatment, and individuality of animals upon the total number of new hairs in the year and on their seasonal pattern of appearance were examined.

The total numbers of new hairs produced in 13 months (males only) and in the samplings from June to January (males and females) are shown at the bottom of Table 2. In all comparisons, numbers were greater in Africander cross than in British-breed animals, and in males than in females, but these differences were not statistically significant. Clipped animals produced about 12% fewer hairs in a year than unclipped groups and this difference was significant ($P < 0 \cdot 01$) statistically, but there is some doubt about its implications as the difference was greater in the period following cessation of treatment in January and was only just significant over the period of actual treatment.

Interactions between breed and treatment, sex and treatment, and breed and sex were not significant.

Analysis of variance does not reveal overall significant differences in the total number of new hairs between individual animals of the same breed, sex, and treatment, though they are just significant in pooled results for the three female groups and in one of the four male groups. These differences are tested against animal × month interaction which, as an error term, is inflated by real differences between animals in the seasonal pattern of appearance of hairs (see below). That there are animal

differences in the total number of new hairs is suggested by the following correlations
with coat scores:

Total number of new hairs June–June (males only): $r = -0.311$ (d.f. 33, $P < 0.10$)

Total number of new hairs June–January (both sexes): $r = -0.395$ (d.f. 61, $P < 0.01$)

The results indicate that sleeker-coated animals produced more hairs per 1000
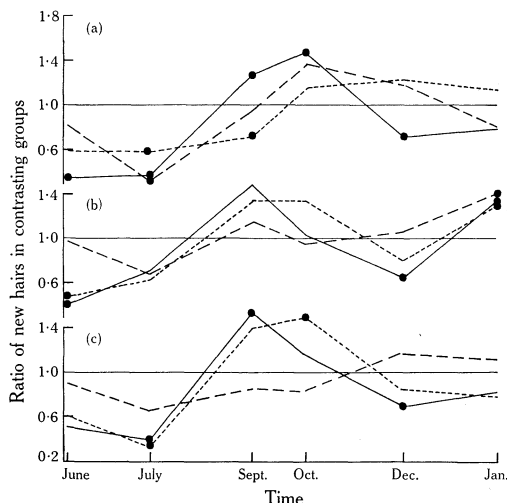follicles over a year.

Fig. 3.—Treatment (a), sex (b), and breed (c) effects on mean number of new hairs at each
sampling from June to January. In (a) groups are compared by plotting the ratios clipped/
unclipped for British breed males (———), British breed females (— —), and Africander cross
males (- - - - -). In (b) groups are compared by plotting the ratios males/females for British breed
clipped (———), British breed unclipped (— —), and Africander cross clipped (- - - - -) animals.
In (c) groups are compared by plotting the ratios British breed/Africander cross for clipped male
(———), unclipped male (— —), and clipped female (- - - - -) animals. At points marked ●, the
ratio differs significantly from unity, i.e. the groups representing numerator and denominator
differ significantly in number of new hairs (see Table 2).

Analysis of the numbers of new hairs recorded at the various sampling dates
reveals significant interactions between months on the one hand and breed, treatment
and sex, on the other. These effects are illustrated in Figure 3, where the ratio of the
number of new hairs per 1000 follicles in one group to the number in the contrasting
group is plotted. In each case, the numerator of the ratio is that class of animal
expected to have longer coats and the denominator that with sleeker coats. Thus the
ratios are of British to Africander cross, of males to females (Turner and Schleger
1960), and of clipped to unclipped, the latter because other responses of the clipped
groups (numbers of new hairs and growing hairs) were characteristic of animals
growing longer coats. Various significant differences between groups are shown and
the pattern is fairly consistent. In June and July, and to some extent again in
December, the number of new hairs was less in clipped than in unclipped animals, in
males than in females, and in British-breed animals than in Africander cross. In

September and October, and possibly in January, these differences tended to be reversed.

The same phenomenon of differences in pattern of appearance of new hairs is shown with results covering the full year in Figure 4. The animals of each of the seven groups (or four groups from March to June) have been divided into those with high and low coat scores, and the mean rates of entry of new hairs have been plotted for each of these two classes. Although the weighted mean difference between high and low scorers is significant only for the samplings of June ($P < 0.05$) and December ($P < 0.01$), it appears that the sleeker-coated (lower scoring) animals show some anticipation of the spring renewal of hairs as early as June and July, and the summer peak of renewal also occurs earlier in these animals.
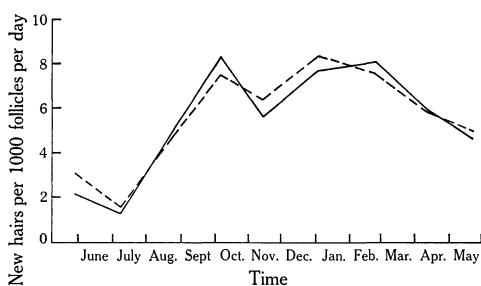

Fig. 4.—Number of new hairs per 1000 follicles per day, averaged over all groups. The two curves represent division of the animals in each group into those of higher (———) and those of lower (— —) coat scores.

(ii) Number of Growing Hairs

The mean number of growing hairs per 1000 follicles for each group of animals is shown in Table 3. Analyses of variance show significant effects of treatment ($P < 0.01$), breed ($P < 0.05$), and sex ($P < 0.05$). The effect of treatment (clipping) is of course seen only during the period May–December when the relevant groups were clipped, not during the following months when all groups were untreated. During the period of clipping, mean number of growing hairs was about 20% higher in clipped than in control groups.

The mean number of growing hairs was significantly higher in British than in Africander cross. The sex difference is surprising in that females had more growing hairs than males, although they had lower scoring (shorter) coats, as is generally true (Turner and Schleger 1960).

None of the interactions between breed, sex, treatment, and months are significant.

Within groups, there are highly significant differences between animals ($P < 0.01$); this arises from results for males ($P < 0.01$), differences between animals in the female groups being non-significant.

The correlation between coat score and mean number of growing hairs of animals within the same group is 0.673 (d.f. 33, $P < 0.01$) for males, 0.146 (d.f. 27) for females, and 0.470 (d.f. 61, $P < 0.01$) pooled. A correlation between coat score and the mean length of the growth phase of hairs could be expected. The number of growing hairs indicate mean length of the growth phase only to the extent that numbers of new hairs do not differ. The ratio of blunt (growing) hairs to pointed (new) hairs has therefore been calculated as an index of the relative length of the growing period. This

ratio is highly significantly correlated with coat score in both male ($r = 0\cdot523$) and female ($r = 0\cdot512$) individuals of the same group.

TABLE 3

MEAN NUMBERS OF GROWING HAIRS PER 1000 FOLLICLES AT EACH SAMPLING AND MEANS $\pm$ S.E. FOR EXPERIMENTAL PERIOD

Number of animals of each sex given in parenthesis

Date	British Breed, Clipped		British Breed, Untreated		Africander Cross, Clipped		Africander Cross Untreated
	Male(11)	Female(8)	Male(8)	Female(12)	Male(9)	Female(11)	Male(10)
May 8	682	861	596	650	639	647	543
June 17	436	479	432	419	470	550	303
July 30	263	254	256	224	271	290	266
Sept. 22	253	252	194	217	250	184	222
Oct. 20	348	369	258	308	348	332	234
Dec. 10	195	258	151	249	199	271	168
Jan. 27	229		244		202		265
Mar. 23	444		468		390		333
Apr. 29	628		747		532		545
Mean:							
May–Dec.	363	412	315	344	363	379	289
	±18	±12	±19	±15	±20	±13	±13
May–Apr.	387		372		367		320
	±17		±20		±15		±10

(iii) *Linear Growth Rate*

The typical seasonal trend in growth rates has been shown (Fig. 2) and group means are given in Table 4. In all groups of animals mean rates were higher in pointed than in blunt hairs, in all months except December and January; in January rates

TABLE 4

MEANS AND STANDARD ERRORS FOR VARIOUS PARAMETERS OF HAIR GROWTH IN BRITISH AND AFRICANDER CROSS BREEDS

Results for June–January samplings only, common to all groups

Parameter	British Breed, Clipped		British Breed, Untreated		Africander Cross, Clipped		Africander Cross, Untreated
	Male	Female	Male	Female	Male	Female	Male
Mean growth rate (μm/day)							
Pointed hairs	323 ± 14	278 ± 9	334 ± 15	308 ± 8	297 ± 7	295 ± 5	335 ± 8
Blunt hairs	293 ± 13	263 ± 9	327 ± 21	285 ± 12	249 ± 8	230 ± 10	303 ± 12
Mean hair diameter (μm)	$42\cdot2\pm1\cdot0$	$45\cdot5\pm0\cdot9$	$44\cdot0\pm1\cdot0$	$47\cdot7\pm1\cdot0$	$52\cdot9\pm1\cdot7$	$58\cdot5\pm1\cdot4$	$54\cdot4\pm0\cdot5$
Mean No. of medullated hairs (%)	53 ± 5	53 ± 5	52 ± 7	64 ± 3	75 ± 2	74 ± 2	77 ± 2
Mean weight of hair grown per month (mg/cm^2)	$7\cdot06\pm0\cdot34$	$6\cdot86\pm0\cdot30$	$6\cdot61\pm0\cdot33$	$6\cdot49\pm0\cdot28$	$7\cdot47\pm0\cdot44$	$7\cdot07\pm0\cdot34$	$6\cdot62\pm0\cdot31$
Mean weight of skin sample (mg)	332 ± 12	363 ± 12	344 ± 16	363 ± 10	416 ± 9	449 ± 10	407 ± 16

were considerably higher in blunt hairs. Growth of blunt hairs represents a later stage of growth of hairs previously measured as pointed. Growth rates of both types of hair were higher in untreated than in clipped animals, and in males than in females. All these differences were highly significant. Growth rate of blunt hairs was very significantly higher in British than in Africander cross, but in pointed hairs there was no significant breed difference.

(iv) *Weight of Hair Grown*

The total weight of hair grown in 12 months (data for males only) averaged 94 mg/cm^2. The weights, exemplified in Table 4 as monthly rates for part of the experimental period, did not differ between breeds and, although they were slightly higher in males than in females, the sex difference was not significant. During the period of treatment, but not subsequently, clipped animals yielded a higher weight of hair per unit area from the sampling site than did untreated animals ($P < 0.05$).

Differences between animals within groups were highly significant. Weight of hair was correlated with coat score in males ($r = 0.552, P < 0.01$), but not significantly in females ($r = 0.203$).

(v) *Skin Thickness*

Skin sample weight, as a measure of skin thickness, is shown in Table 4. It was 22% higher ($P < 0.01$) in Africander cross than in British-breed animals, and 8% higher ($P < 0.01$) in females than in males, but did not differ between clipped and untreated animals. No consistent pattern of seasonal change was discernible. Differences between animals within groups were highly significant. In all British groups correlations between skin thickness and coat score were negative (sleek coat associated with thick skin), and in Africander cross groups they were positive, but the correlations were not significant, and not quite significantly different.

(c) *Joint Relationships of Hair Growth Parameters to Differences between Animals*

Differences between animals within groups in coat score, weight of hair per unit area, and body weight gain are shown as functions of hair growth parameters in Table 5. The parameters used as independent variates in the multiple regression model are (1) total new hairs per 1000 follicles, (2) mean number of growing hairs per 1000 follicles, (3) mean linear growth rate of new hairs, (4) mean diameter of growing hairs, and (5) mean percentage of medullated hairs. Each parameter was totalled or averaged over the whole period of observation of each animal.

The multiple correlation between coat score and covariates was 0.657 ($P < 0.01$). Animals with the sleeker coats (lower coat scores) had more new hairs ($P < 0.05$), fewer growing hairs ($P < 0.01$), and hairs of higher diameter ($P < 0.01$).

The multiple correlation between weight of hair grown and the covariates was 0.782 ($P < 0.01$), very significantly higher than the simple correlation between hair weight and coat score ($r = 0.325$, $P < 0.01$). Number of growing hairs had the greatest effect on weight of hair, whereas number of new hairs had no significant independent effect. While diameter and medullation were closely correlated, their independent effects on hair weight were of opposite sign and both significant. Thicker

hairs increased hair weight but, at the same diameter, medullated hairs, being hollow-cored, reduced hair weight.

Body weight gain was significantly correlated with the hair growth covariates ($R = 0\cdot418$, $P<0\cdot01$) and this correlation was higher, though not significantly, than the simple correlation between coat score and gain ($r = 0\cdot342$, $P<0\cdot01$). Almost all the variance of gain accounted for was associated with the number of new hairs produced during the total period of observation. The mean number of growing hairs and their diameter were important determinants of coat score, but neither had any significant independent effect on gain.

Differences in the linear growth rate of hairs were of no significance in relation to any of the dependent variates studied.

TABLE 5

MULTIPLE REGRESSIONS OF MEAN COAT SCORE, WEIGHT OF HAIR PER UNIT AREA, AND BODY WEIGHT GAIN ON PARAMETERS OF HAIR GROWTH

Variation analysed is between animals within groups

Independent Variates	Standard Partial Regression Coefficients for following Dependent Variates:		
	Coat Score	Hair Weight per 1 cm^2	Body Weight Gain
New hairs	$-0\cdot24$*	$-0\cdot13$	$0\cdot39$**
Growing hairs	$0\cdot40$**	$0\cdot72$**	$-0\cdot12$
Growth rate of new hairs	$-0\cdot11$	$0\cdot17$	$-0\cdot17$
Diameter of growing hairs	$-0\cdot37$**	$0\cdot21$*	$-0\cdot02$
Percentage medullated hairs	$-0\cdot01$	$-0\cdot27$**	$-0\cdot09$
R^2†(d.f. = 57)	$0\cdot431$**	$0\cdot611$**	$0\cdot175$**

* $P<0\cdot05$.   ** $P<0\cdot01$.

† R^2 = fraction of variance of dependent variate accounted for by independent variates.

(d) Effects of a Pathological Condition

Effects of a pathological depression of thrift are shown in Figure 5. One animal, whose results have been eliminated from the main data, showed clinical symptoms of ingestion of *Lantana camara*, a hepatotoxic plant, in May. Between June and September its body weight declined 140 lb while other members of the same group (Africander cross, untreated males) gained nearly 100 lb, and its weight remained low until December but very rapidly recovered by January. Similarly its coat remained woolly until December but then shed rapidly and became sleek by January. The number of new hairs per 1000 follicles per day was only $0\cdot9$ in October when its mates were producing $8\cdot5$, and new hairs were still low up to December but approximately normal from then on. Number of growing hairs may have been slightly increased in

September, and were reduced in October–December as a consequence of failure of entry of new hairs, but in general direct effects on number of growing hairs were less marked than on entry of new hairs. There was no indication that the temporary inhibition of new hairs was compensated by an increased rate of entry after recovery. Indeed the new hairs per 1000 follicles of this animal during 12 months numbered only 1784, 79% of the number produced by its mates and well below two hairs per follicle.
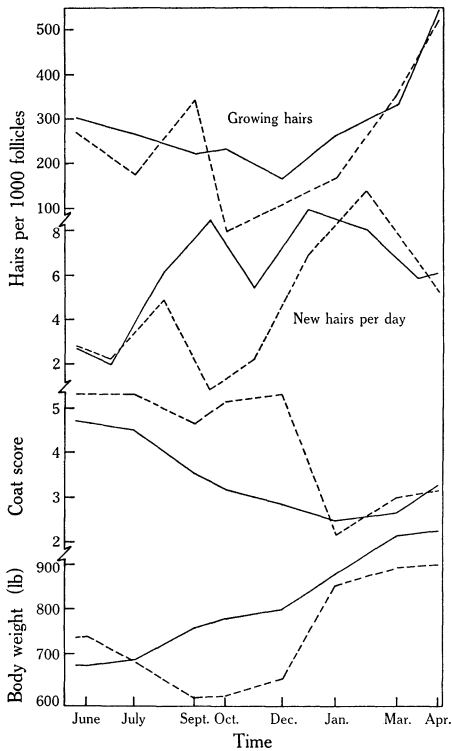

Fig. 5.—Body weight, coat score, and numbers of new hairs per day and growing hairs of an animal affected by *Lantana* poisoning (— — —) and mean values for unaffected animals of the same group (——).

VI. DISCUSSION

The cyclic behaviour of follicles, which is the main determinant of seasonal variation in coat type, is represented in an integrated form in Figure 6. Herein, the left-hand boundary of each shaded section is a plot of cumulative number of new hairs, and its slope represents the number of new hairs per 1000 follicles per day. The right-hand boundary is a plot of cumulative number of hairs completing growth, and its slope represents the number of hairs ceasing growth per 1000 follicles per day. Any horizontal line through the graph represents the presumed successive phases of growth and quiescence, succeeded by shedding and regrowth, undergone by an individual follicle. Any vertical line through the graph indicates the proportions of follicles which are active or resting at a given date.

In the period February–April, new hairs appear at a high rate and have a long growth phase. Three-quarters of the follicles produce new hairs during this period, and

at the end of April these are all actively growing. This activity causes the build-up of a long, dense, winter coat. All these hairs remain in the coat (or, strictly, are not replaced by new hairs) at least until August. During May–July, the remaining 25% of follicles which were carrying relatively short hairs grown in January, produce new hairs but their rate of entry is relatively slow and their growth phase becomes progressively shorter. The long hairs grown during autumn are replaced between August and November at a fairly high rate, particularly in September–October. The new hairs have a short and progressively decreasing growth phase. In December–January, particularly December, there is a very high rate of entry, two-thirds of the follicles producing new hairs in 2 months. Their growth phase is very short and at any time very few hairs are growing. Total cycle length is short, the hairs being replaced as early as March. At the end of January there is a sudden change, hairs initiated at this time having a long growth phase and cycle length.
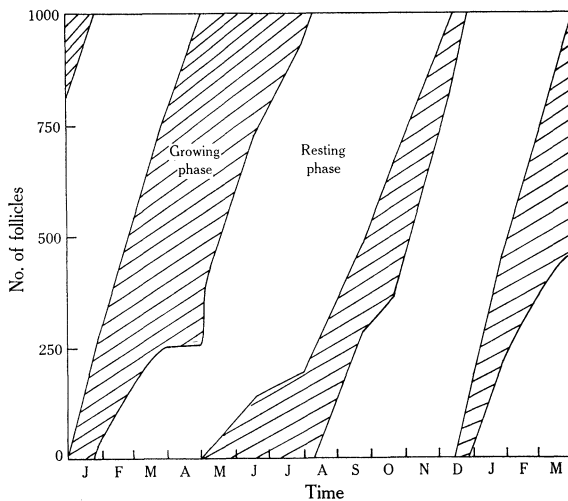

Fig. 6.—A representation of the successive phases of activity and quiescence through which each of a representative 1000 follicles pass during the year in untreated British breed male animals.

Thus seasonal changes in coat length arise mainly from the fact that hairs initiated during February–May have a measured growth phase (about 10 days shorter than the true growth phase) of 80–100 days, compared with 20–40 days for hairs initiated during August–January. Total cycle lengths vary correspondingly so that entry of new hairs occurs in two peaks which are not 6 months apart but fall in spring and summer.

The assumption in Figure 6 that individual follicles follow each other in the same order in successive cycles, coupled with the fact that the number of cycles (new hairs) per follicle per year was not exactly two but slightly greater, leads to the picture of each follicle coming into activity slightly earlier each year. Whether in fact different types of follicle tend to be triggered at characteristic times each year and the number of cycles per follicle is either exactly two, or is two in the majority and three in a

minority as suggested by Hayman and Nay (1961), cannot be determined in the present study. Long, thick "guard" hairs are characteristically the first to be shed from the coat at the beginning of spring, and they are presumably always produced by the same "giant" follicles (Hayman and Nay 1961), so these follicles at least appear to be in fixed phase with the seasons. The spring and summer peaks in diameter of growing hairs suggest that large follicles predominate during the periods of peak production of new hairs. To weigh against the possibility that the number of cycles is exactly two are the indications that the number of new hairs per 1000 follicles in approximately 12 months differed between groups (Table 2) and between animals within groups (Table 5). (Table 5 shows combined results for all animals, of which the females were not observed for a full year, but separate analyses of males only attach similar significance to number of new hairs.) The observations of two seasonal peaks of hair shedding and of follicle activity by Dowling and Nay (1960) and Hayman and Nay (1961) suggested to them that the majority of follicles grow two hairs per year but did not quantitatively establish the number of cycles.

The question of the value of the procedures adopted for study of the dynamics of hair growth must be raised. Quantitative collection of regrowth by clipping at exactly the same level at each sampling is subject to some variation, and subsampling of hair samples, though carefully executed to avoid bias, also introduces error variation. The standard errors of difference between different samplings from the same animals, cited in Section IV, correspond to standard deviations of about 110 for numbers of new hairs and growing hairs per square centimetre. Results from a single sampling therefore have low precision, but results from sampling a number of animals each on a number of occasions have been adequate to establish various significant features about hair growth. There remains the possibility that the very clipping of the sampled area itself affected hair growth at this site. The fact that clipping of the whole animal had some effects on hair growth at the sampled site lends weight to the possibility that clipping of the site alone also affected hair growth. In fact it was observed that the shade of colour of the hair grown on the site was sometimes perceptibly different from that adjacent to the site. While the parameters of hair growth derived are therefore not necessarily quite normal, it is believed that they give a useful indication of normal seasonal variation and the relative importance of animal differences in the various parameters.

The counts of active follicles made by Dowling and Nay (1960) and Hayman and Nay (1961) should be comparable with our results on number of growing hairs. They show a peak of about 70% of active follicles in March, essentially the same value as our number of growing hairs near the end of April. Both types of study show a second, lower peak in spring, but theirs reached about 50% and ours (October) reached only 26–37%. Their summer minimum of 30–40% was also higher than our December value of 15–27%. They found a minimum in July of 20–30% comparable to our values of 18–25% which were recorded in September, though the actual trough could have occurred in August. The general pattern is similar in each study, and differences in animals and locations and the incomplete representations of sampling times make precise comparisons difficult. Any suggestion that our counts were lowered by the clipping associated with sampling is contraindicated by the fact that clipping of the whole body increased counts of growing hairs.

It has been shown that animal differences in the mean rate of entry of new hairs and in its seasonal variation, in the time for which they grow (indicated by relative number of growing hairs), and in hair diameter, are important determinants of differences in coat type. The evidence in Table 5 is that gain in body weight, while related to coat type as has been more extensively shown by Turner and Schleger (1960), is related to the total number of new hairs produced in a year and not significantly to other components of coat type. In particular, the number of growing hairs, such an important component of coat type, is not significantly related to gain in body weight.

These contrasts are of interest in relation to the possibility, discussed by Turner and Schleger (1960) and Turner (1962), that some component of coat type, not necessarily related to the coat's insulating properties, may be particularly correlated with gain and significant as an index of growth potential even in the absence of heat stress. Total production of new hairs fits this specification. Whereas it is a relatively minor component of coat type as scored, it is the only component revealed as accounting for the correlation between coat score and gain. It is also implicated as the component strongly affected by a pathological depression of thrift. Furthermore, we have found (unpublished observations) that the main effect of topical application of the adrenal corticoid analogue Fludrocortone (Merck, Sharpe, & Dohme) to the skin is a profound depression in the number of new hairs. This suggests one possible link between this aspect of hair growth and general thrift of the animal.

VII. Acknowledgments

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