

TWO FACTORS INFLUENCING FEATHERING IN CHICKENS

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INTRODUCTION

The material for this paper has been collected in the course of some studies on transplantation of skin in the fowl. The methods and some of the results have been described by DANFORTH and FOSTER (1927). In these experiments skin of the back was transferred from one chick to another within a few days after hatching and its subsequent reactions followed, in some cases, for as much as fifteen months. For present purposes only a relatively short period of early growth will be considered.

Skin grafting has proved especially satisfactory for analyzing the interaction of genetic and other factors in production of form, color and marking of feathers. It has some disadvantages in studies on the rate of feathering in that certain grafts may at any time begin to regress slowly, necessitating careful and frequent scrutiny of all specimens under observation in order to eliminate abnormal cases. It may be, too, that grafting occasionally causes some modification in the growth rate of feathers on apparently normal skin, but by appropriate methods it seems feasible to detect and evaluate such alterations if they occur. Aside from these possible objections, the method seems to be of considerable value in studying the action of growth factors, and this paper is presented partly as a contribution to the technique of such studies.

There are considerable differences in the time at which feathers first appear in young chicks, and also in the rate at which feathers grow after having made their appearance. These differences tend to be associated with breeds, the so-called American and Asiatic classes being in general more or less retarded, while the Mediterranean and other of the smaller breeds are on the whole precocious in this, as in other respects. Sex also is popularly supposed to be a factor in the rate of feathering, females being said to become feathered more rapidly and uniformly than males.

The observations to be reported relate only to the feathers of a restricted area, the back and anterior part of the rump (the "saddle" or "sweep" of the American Standard of Perfection, 1927). This region will be referred to here simply as the "back." The breeds chiefly considered are the white Leghorn, Rhode Island Red, and barred Plymouth Rock.

NORMAL DIFFERENCES IN THE RATE OF FEATHERING

In all the breeds used in the experiments feathers appear on the back later than they do on a number of other parts of the body. Indeed, the regions immediately in front and behind the one selected are usually more advanced. In the rapidly feathering Leghorns there is ordinarily a good number of pin-feathers along the middle of the back by about the thirtieth day after hatching. Many Plymouth Rocks, on the other hand, do not reach a comparable stage until after the fiftieth day. There are rather pronounced individual differences within the same breed, especially among Plymouth Rocks and Rhode Island reds, but the two classes, slow-feathering and rapid-feathering, are reasonably distinct from each other with very few doubtful cases.

The heredity of these two types of feathering has been studied by SEREBROVSKY (1922) and WARREN (1925). The latter found that in crosses involving white Leghorns and Jersey Black Giants (American class) slow-feathering, as indicated by the age at which tail feathers appear, behaves as a dominant sex-linked trait. His conclusion is supported by consistent evidence from reciprocal and back crosses. Earlier results seem to have been fully confirmed by SEREBROVSKY and WASSINA (1926).

To the records already in the literature may be added the numerically meager results of several crosses made in connection with the present experiment. Banded Plymouth Rock females, known to have been slow-feathering, were mated to a white Leghorn male which as a chick had been rapid-feathering. This cross produced three quick-feathering females and a rather slowly feathering male. The outcome, so far as it goes, is in accord with expectations on the basis of the above hypothesis, except that the male was less retarded than is the average Plymouth Rock male at a corresponding age. This is possibly to be explained on the same basis that SPILLMAN (1909) and COLE and LIPPINCOTT (1919) explain differences in width of bars in feathers of the two sexes, namely that, although dominant, the sex-linked gene is more effective in the homozygous male (ZZ) than in the heterozygous female (ZW). It would seem that the suggestion could be tested in both cases by comparing the rate of feathering and width of bars in an adequate number of F_1 offspring from females of a rapid-feathering black breed mated to an ordinary Plymouth Rock male.

Conversely, a slow-feathering Rhode Island Red male mated to white Leghorn hens gave four chicks, all of which were slow-feathering, but not so slow as are many typical Rhode Island Reds and Plymouth Rocks.

Finally, the same Plymouth Rock females and Rhode Island Red male mated together produced six females, all moderately slow in feathering and nine males which were decidedly slow-feathering. The latter, however, showed considerable variation in the time at which the first feathers appeared. At 47 days of age some of them had no feathers or pin-feathers whatever on the back, while others showed a few scattered pin-feathers, and still others feathers with three or four bars.

While in general the foregoing data are in accord with WARREN's results with Leghorns and Giants and indicate that what is presumably the same dominant sex-linked gene occurs in both the Plymouth Rock and the Rhode Island Red, the diversity found in the F_1 males of Plymouth Rock-Rhode Island Red parentage suggests some additional factor in one or the other of these breeds. The existence of this second factor seems to be established by the results obtained by means of skin grafting.

THE RATE OF FEATHERING ON SKIN TRANSPLANTS BETWEEN RHODE ISLANDS REDS AND WHITE LEGHORNS

In making the transplants, skin from the greater part of the back (as here defined) was taken, most often on the second day after hatching, and sewed in place on the back of the host, from which a piece, preferably somewhat larger, had just been removed. By drenching the backs of chicks to be operated on with alcohol, the use of ether anaesthesia, and reasonable precautions as to asepsis, the procedure was rendered fairly simple. Nevertheless, owing to the loss of many chickens and the failure of some of the grafts on those that lived, the number of individuals that ultimately became available for purposes of the present study was not great. Most of the records were made at weekly intervals, so that dates at which the feathers are first recorded tend to be slightly later than the true dates at which they first appeared. For comparative purposes this is not a matter of importance, since there was no bias in favor of any one group.

Seventeen of the Rhode Island Reds which received white Leghorn grafts survived and produced feathers on the grafted skin. The average age at which the first pin-feathers appeared on the grafts was 33.6 days. This indicates a very slight retardation when compared with the time at which the feathers would have appeared on the Leghorn skin had it not been removed from its original site. In five of these cases both the donors and the hosts were males, and in this group the average age at which pin-feathers appeared was 36 days. In six other cases the donors and hosts were all females and here the average age of pin-feather production

was 32 days. These facts are put on record as suggestive, even though they may not be statistically significant.

The white Leghorn feathers on Rhode Island Red hosts appeared considerably in advance of the host's own feathers and grew more rapidly, so that by the 70th day the grafts bore large white feathers which were surrounded only by small red feathers and pin-feathers. Not until much later did the feathers of the host equal those of the graft in size.

Transplants in the reverse direction presented quite a different picture. Skin from slow-feathering Rhode Island Reds grafted on 23 rapid-feathering white Leghorns showed the first pin-feathers at an average age of 47 days, or about two weeks later than the reciprocal grafts, and after the surrounding feathers of the hosts had become well developed. The average ages of first appearance of pin-feathers with reference to the sex of donors and hosts were as follows: five transplants from male Rhode Island Reds to male Leghorns, 50 days; eight transplants from female to female, 46 days; six from males to females, 46.6 days; three from females to males, 49 days. The sex of one donor was not recorded.

The possibility that the slow feathering of the Rhode Island Red skin grafted on white Leghorns is due to some imperfection of the white Leghorn as a host was tested by eight grafts to white Leghorns from other rapidly feathering strains. These produced feathers at an average age of 32 days, which is comparable to the 33.6 days required for Leghorn skin to produce its feathers when grafted on Rhode Island Reds. This result, in conjunction with the fact that reciprocal grafts between white Leghorns and Rhode Island Reds parallel the unoperated controls in the time at which feathers are produced, seems to leave little room for doubt that in the white Leghorn and Rhode Island Red the genes for slow-feathering and for rapid-feathering act locally in the skin or feather follicles rather than through the intermediation of gonadal or other hormones. At the same time, in both sets there is a suggestion, not adequately supported statistically, that the tendency to slow-feathering is slightly augmented by maleness.

THE RATE OF FEATHERING IN SKIN TRANSPLANTS INVOLVING BARRED PLYMOUTH ROCKS

Barred Plymouth Rock chicks served as donors to chicks of rapidly feathering strains in seven successful cases. The recipients included white and brown Leghorns, black Minorcas and Campines. The average age at which Plymouth Rock feathers appeared on these grafts was 44 days. This agrees very well with what might have been expected in light of

results from the Leghorn-Rhode Island Red combinations. But in the nine cases in which barred Plymouth Rocks served as hosts for grafts from rapidly feathering white Leghorns and Campines, the results were not at all in accord with those obtained in the first series. Here the average age at which the first pin-feathers appeared on the grafts was 47 days. That this late appearance was due to the influence of the hosts and not to the grafts is indicated by results from sixteen cases in which skin was exchanged between other members of these same rapidly feathering breeds,



FIGURE 1.—A barred Plymouth Rock female at the age of 73 days. The white Leghorn graft on its back shows a few pin-feathers whose growth is still considerably inhibited.

the average date of feathering in these cases being 35 days, as would have been expected on the basis of the previous experiments.

This result led to a more critical examination of feather growth in Plymouth Rock chicks and grafts placed upon them. In several cases of grafts to Plymouth Rocks from Campines and Leghorns, the transplanted skin produced a few good feathers early, after which feather-production was seemingly held in abeyance for a while, some of the pin-feathers becoming stunted and even falling out, so that the grafted area assumed the same denuded appearance as other parts of the chick (figure 1). When-

ever any of the first feathers persisted through this period they were of fair size, as they would have been in their normal place, or grafted on a Rhode Island Red, except that some of them were possibly arrested before reaching full development. (see figure 8, a.) During this same period the Plymouth Rock's own feathers appear only sparsely and grow very slowly. In general the whole picture is one suggesting inhibition of feather growth. Later the appearance becomes more normal in both graft and host, the feathers of the former often growing more rapidly at first, after which each type follows its natural course (figure 2).

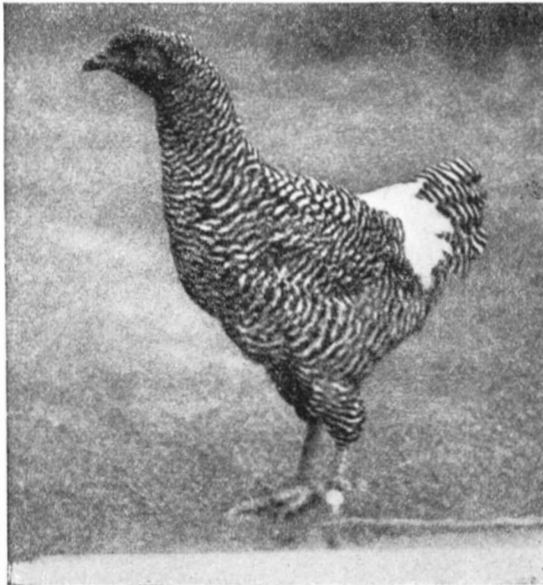


FIGURE 2.—A barred Plymouth Rock pullet with a white Leghorn graft.
This is a later stage of the individual shown in figure 1.

Evidence pointing in the same direction is obtained from cases where the Plymouth Rock serves as donor. When the host is a Rhode Island Red the results are not striking, since both donor and host are slow-feathering (figures 3 and 4). But when the host is of a rapidly feathering breed critical comparisons can readily be made between the feathers of the two individuals involved in any transplant. Two such pairs may be reported in some detail.

1. A barred Plymouth Rock graft on a black Minorca host

Barred Plymouth Rock male no. 71 served as donor to black Minorca male (Mediterranean class) no. 74. The two chicks were hatched on the



FIGURE 3.—A Rhode Island Red cockerel with a barred Plymouth Rock graft.

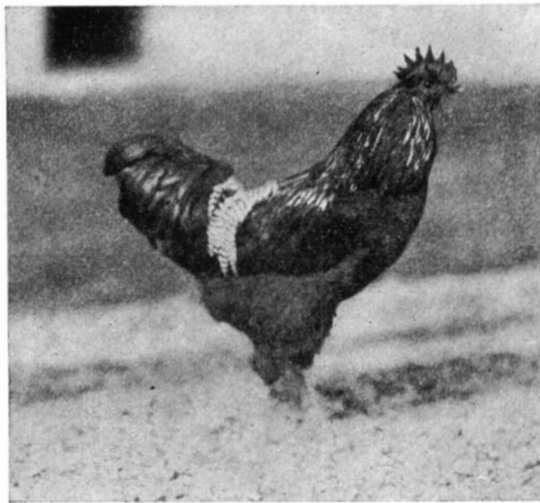


FIGURE 4.—The same bird as shown in figure 3. Both the host and the graft exhibit a parallel development of plumage in this and the preceding figure.

same day and the transplant from the Plymouth Rock to the Minorca was made two days later, enough of the original skin being left on the back of each to produce some feathers characteristic of the individual. Both chicks were kept in the same flock and received similar treatment throughout the experiment. They are shown at the age of 148 days in figures 5 and 6.

No. 71 feathered very slowly but did not pass through a long period in which the body was largely bare, as do many Plymouth Rock males. The Minorca developed his own feathers at the usual rather rapid rate. The graft grew well and showed indications of a few small pin-feathers at the age of 42 days. At 49 days there was one feather. By 75 days the feathers were numerous, most of them showing about three bars.

Representative feathers plucked from the backs of nos. 71 and 74 on the 96th day are shown in the top row of figure 7. The feathers from the grafted skin were larger than those of the donor, but not so large as those of the host. They were slightly constricted, but not of the male type, as perhaps might be inferred from the figures. Feathers of the adult male type began to appear, however, at about this time. The largest of these to be found on the donor at the 110th day is shown as figure 7 d. Figure 7 e, represents, not one of the largest feathers on the graft at this date, but one which, had the skin not been disturbed, would have grown within a few millimeters of 7 d. The bottom row in figure 7 shows two juvenile male feathers from no. 71, and two, somewhat more advanced, from no. 74 plucked at the age of 148 days.

It will be apparent from the records and figures that, while slow as compared with that of the Minorca, the grafted Plymouth Rock skin developed feathers much faster than it would have if it had been left in place. That which remained on the Plymouth Rock showed an initial lag followed by a gradual approach to the rate of growth of that on the graft. Not only the feathers but the whole individual exhibited such a lag. At 96 days no. 71 weighed 820 grams, while no. 74 weighed 1015 grams. At 148 days no. 71 weighed 2080 grams and no. 74 only 1670 grams.

Whether it should be stated that from about the 40th to about the 120th day growth was stimulated by the Minorca soma or inhibited by that of the Plymouth Rock is not evident, but it seems clear that some factor with an origin outside the skin and capable of influencing feather growth was effective during this period.

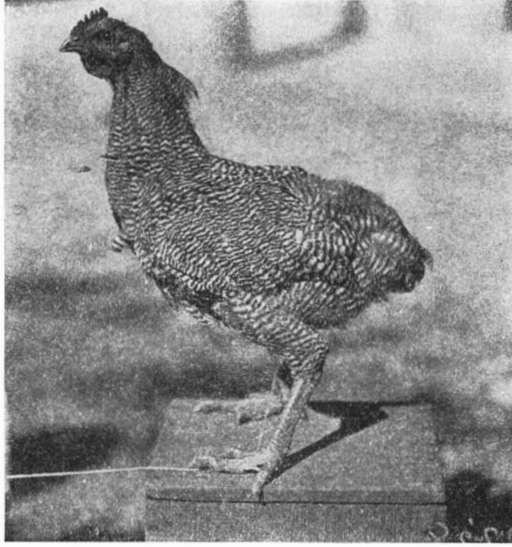


FIGURE 5.—The barred Plymouth Rock male no. 71 at the age of 148 days.

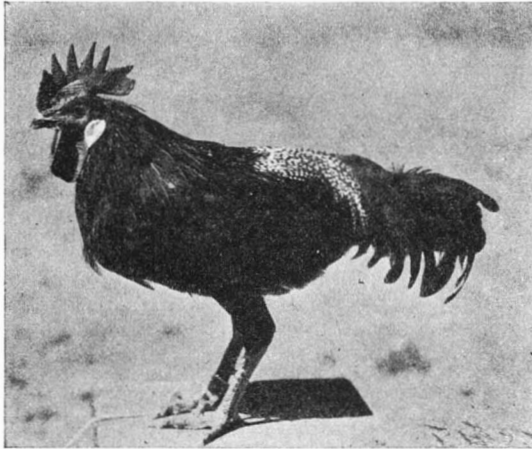


FIGURE 6.—Black Minorca male no. 74 (with graft from no. 71) at the age of 148 days.

2. *A barred Plymouth Rock graft on a brown Leghorn host*

The treatment and results in this case are similar to those described in the preceding section, except that the graft was from a barred Plymouth Rock male to a brown Leghorn female, and the male himself had a graft from another brown Leghorn female. This male was designated as no. 70, the host female as no. 88.

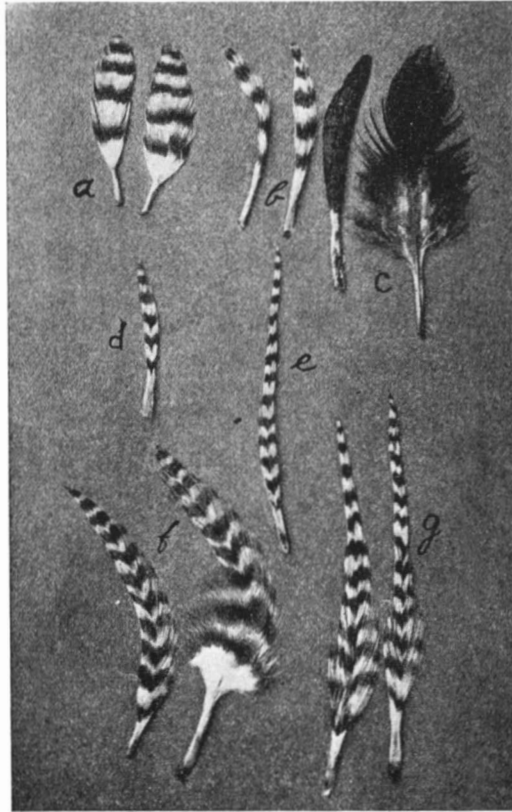


FIGURE 7.—Feathers from nos. 71 and 74 at various ages, arranged transversely according to the age and vertically according to the individual. Top row, 96 days; middle row, 110 days; bottom row, 148 days. a, d, f, feathers from undisturbed skin of no. 71; c, from undisturbed skin of no. 74; b, e, g, from the skin of no. 71 grafted on no. 74.

The graft on no. 70 had produced a few juvenile brown Leghorn feathers by the 34th day, after which it remained more or less quiescent until about the 90th day, during which time the chick as a whole was rather nude. By the 96th day there were many small new feathers like those of a Leghorn male. This is in accord with what is known of the hormonal

control of secondary sexual characteristics in the plumage (GOODALE 1916, DOMM 1927), except that the host at this time had developed no male feathers of his own.

The Plymouth Rock graft (from no. 70) on the brown Leghorn hen no. 88 had one small feather on the 41st day and two on the 48th. By 75 days it had many feathers with five or six bars. These, however, were

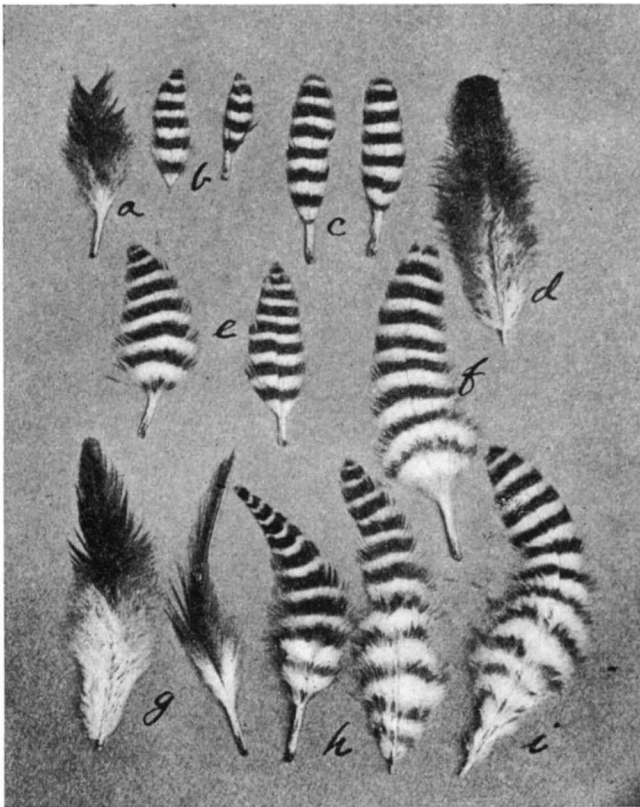


FIGURE 8.—Feathers plucked at different ages from nos. 70 and 88. Top row, 96 days; middle row, 110 days; bottom row, 148 days. a, g, brown Leghorn feathers from the graft on no. 70; b, e, h, feathers from the undisturbed skin of no. 70; c, f, i, from skin of no. 70 grafted on no. 88; d, from the undisturbed skin of no. 88.

recorded as much shorter than those of the host. Figure 8 shows in the top row feathers plucked from no. 70 and no. 88 on the 96th day. Represented by a is one of the residual Leghorn feathers that first appeared on the graft to no. 70. The feathers marked b are the largest that could be found on the back of no. 70 at this time, while those indicated by c are

two average feathers grown on no. 88; *d* is one of 88's own feathers. At the 110th day the discrepancy in size between feathers of the donor, *e*, and those from the graft, *f*, is still very great. By the 148th day some of the feathers of the donor, *h*, have reached a size about equal to that of the grafted feathers, *i*. Some of the former are now of the juvenile male type.

In this case also the host, again of a rapidly feathering breed, proved to be for a time more favorable for the development of Plymouth Rock feathers than the Plymouth Rock donor itself. During the most of this period the Leghorn graft on the Plymouth Rock was greatly inhibited in its feather production. The period in question appears to extend from as early as the 40th day to well past the 100th day.

The body weight followed the same course in this as in the preceding case. At 96 days no. 70 (male) weighed 810 grams, and no. 88 (female), 990 grams. At 148 days, no. 70 weighed 1680 grams and no. 88, 1350 grams. Similar results were obtained in comparisons between Plymouth Rocks and white Leghorns or Campines.

DISCUSSION

Parallel experiments, where in one case Rhode Island Reds, in the other barred Plymouth Rocks serve as the slow-feathering subjects, show interesting points of similarity and difference. But all the results obtained in both sets appear to be consistent and intelligible on the assumption that there are two different factors making for slow feathering, both present in the barred Plymouth Rock, only one in the strain of Rhode Island Reds used in the experiments. The slow-feathering factor which is common to both breeds is apparently conditioned by the sex-linked gene previously known to exist and designated as *S* by SEREBROVSKY. It is apparent that this gene and its allelomorph, *s*, produce their effects by imparting a particular character to the feather follicles themselves, or to the immediately surrounding tissues, thus determining a definite mode of developmental activity during the first few weeks after hatching. Exchange of skin between two individuals whose genotypes differ in respect to *S* and *s* has no marked effect on the manifestation of these genes. It is the genetic constitution of the donor and not that of the host which determines the rate of feathering in so far as it is regulated by this pair of allelomorphs. This experimental finding is in accord with the observation of WARREN (1925) that in white Leghorns the state of nutrition or physical condition of a chick has very little effect on its rate of feathering.

The other factor is apparently of quite a different nature. In this case it is the constitution of the host and *not that of the donor* that exercises

the determining influence in feather growth. In the absence of adequate breeding records nothing can be said of the exact mode of heredity of this factor, or whether it is simple or complex. The most natural inference is that we are concerned here with a hereditary endocrine or metabolic trait. This supposition is strengthened by the parallelism between feather growth and body weight in barred Plymouth Rocks during the critical period under consideration.

The two factors revealed in these experiments are characterized by different modes of expression. The action of one is local and direct, possibly its effect is restricted to the feather follicle. The action of the other is indirect and probably general ("constitutional"). It is of course not improbable that there are other factors of both types which influence the rate of feather production. There is a mere suggestion in the data that sex has a weak effect in both ways; directly, through homo- or heterozygosis, and indirectly through a slight differential effect on the rate of feathering by male and female constitutions. If, as seems not improbable, the second factor is really a combination of several components which happen to be associated in the barred Plymouth Rock, it is possible that more extensive studies will show that certain of these are also present in the Rhode Island Red, but thus far there have been found no indications that this is the case. A few white Plymouth Rocks were observed, and these seemed to agree more closely in their mode of feathering with the Rhode Island Red than with the Barred Plymouth Rock.

It is of passing interest that the factor for indirect production of slow-feathering should appear in one of the races which also has a factor for the direct production of a similar trait. The two factors apparently have no other relation to each other unless there be some as yet undetected endocrine effect in the embryo which sensitizes or imparts some definite character to the skin which determines its future development and responses.

One other point of interest in this connection is the production of cock-feathering on grafts to male hosts. Up to the present time the type of feathering, as regards secondary sexual characteristics, has been believed to be wholly under endocrine control (LILLIE 1927). Nevertheless the graft from a brown Leghorn female to a barred Plymouth Rock male produced cock feathers in advance of the host, and the graft from a Plymouth Rock male to a Minorca male produced cock feathers later than the host but earlier than the donor. Such relations suggest that the production of cock-feathering is in some measure related to the class of phenomena considered in this paper. The time at which a young fowl assumes its adult plumage may depend not alone on the establishment of a certain endocrine balance, but also upon the age at which the feather follicles become re-

sponsive to particular stimuli. Factors for responsiveness to internal stimuli, or for the type of such stimuli produced, may apparently vary independently and become segregated in different strains. (DANFORTH 1928.)

The general inference to be drawn from this study is that activity of a feather follicle, as registered by the feathers which it produces, is regulated by two factors (or sets of factors) which act in quite diverse ways. In genetic or physiologic studies of feather growth both types of factors need to be taken into consideration.

CONCLUSIONS

Transplantation of skin from one newly hatched chick to another has proved to be of value in analysis of factors influencing the rate of feathering.

Evidence obtained by this method indicates that there are two entirely different factors which are capable of producing "slow-feathering" in the young chick.

One of these factors appears as a sex-linked hereditary trait which manifests itself through a direct effect of the gene on the feather follicles.

The other factor produces an indirect inhibitory effect through the intermediation of the soma.

The first of these factors occurs in the Rhode Island Red; both of them are present in the barred Plymouth Rock.

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