THE INFLUENCE OF AGE ON EXPRESSION OF GENES CONTROLLING RATE OF CHICK FEATHERING

by

MERRITT IRA DARROW

B. S., Michigan State College
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INTRODUCTION

It is only in more recent years that emphasis has been placed upon rate of feathering in chickens. The differences which exist in rate of feathering of various breeds has become a major problem in production of high quality broilers. Because of the discrimination of the market against "bare backs", the practical breeder has endeavored to develop strains of heavy breeds that will be well feathered at broiler age. In the early stages of production of early feathering breeds, most investigators have found that the incorporation of the gene for sex-linked early feathering largely but not entirely solved the problem of poor broiler feathering. The observed variations among sex-linked early feathering birds have formed a basis for this investigation.

The twofold purpose of this study is to investigate: (1) the relationship of day-old chick wing feather development to degree of broiler feathering, and (2) the nature of the heritable factors involved in bringing about differences in degree of feathering.

REVIEW OF LITERATURE

Research workers have considered both the physiological and genetic nature of differences in rate of feathering. Danforth (1929) observed that there is considerable difference 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. He further stated that these differences tend to be associated with breeds.

Juhn (1931), working with Brown Leghorns, stated that the feathers in the posterior breast show the most rapid growth; next in order is the growth rate in the anterior breast. The back and saddle show relatively low growth rate, which is more rapid posteriorly than anteriorly. Martin (1929) found that Barred Plymouth Rock chicks show dimorphism with respect to rate of feather growth, the males feathering slower than the females. He also found that rate of development of feathers over the back is closely related to rate of growth, the heavier chicks feathering more rapidly.

Jaap and Morris (1937) have shown very little, if any effect of hybrid vigor on rate of feather growth. They also found that when both poor and well feathered individuals were in a population at eight weeks of age, 51 per cent of the variability was due to differences of varieties, sires, dams, and sex and 49 per cent was not inherited. Therefore they conclude that more rapid progress in improving broilers could be expected by selecting for weight than for feathering.

Observation of the growing chick has shown two genetic types of feathering; namely early and late feathering. Serebrovsky (1922) reported evidence for a sex-linked gene affecting the rate of feathering. Later, Warren (1925) described the factors responsible for differences in rate of feathering as an allelomorphic pair of genes which are sex-linked. The dominant gene is slow feathering which is typical

of most heavy breeds, and its recessive allelomorph, early feathering, is found in the Mediterranean breeds. This gene controls the rate of feathering from day-old chicks through the growing period, but is not discernible in the adult.

Warren (1933) described another type of feathering, retarded feathering, in the chick which is expressed only in the juvenile plumage and it behaves as a simple autosomal recessive factor. Its expression is to modify the number of secondaries of the day-old chick and inhibit appearance of tail feathers for several weeks.

Hadi and Warren (1938) studied the feathering of a strain of Rhode Island Reds known to be homozygous for late feathering. By selection, they established two strains which as broilers differed genetically in degree of feathering. The one strain which was better feathered at broiler stage was incompletely dominant to the other strain which was less well feathered. The results indicated that this genetic difference is probably the expression of a relatively few genes acting as modifying factors on the sex-linked late feathering condition.

STOCK USED

The stock used in this study consisted primarily of early feathering strains of heavy breeds. The breeds studied were Barred Plymouth Rocks, Rhode Island Reds and White Plymouth Rocks and are those which are being developed for early feathering at Kansas State College. The term "early" is applied to birds having the sex-linked recessive gene for early feathering

as found in the Leghorn, the chick expressing this factor by being well covered with feathers at an early age. This gene was incorporated into these larger breeds by out crossing and then inbreeding and backcrossing to purify the breed for its original characteristics with the addition of the gene for early feathering.

Throughout this investigation, the chicks referred to as experimentals include both purebreds and crossbreeds from matings of various types, made for the purpose of studying the inheritance of modifying factors influencing the expression of the early feathering gene. In addition to the stock mentioned, a number of White Leghorns and Barred Plymouth Rocks were classified for rate of feathering for purposes of comparison.

Approximately 3000 pedigreed chicks were utilized in this investigation. All chicks were kept under study for the first six weeks. In addition, two hatches were also studied as to degree of feathering at eight weeks. The chicks were removed from the incubator on the twenty-second day. They were taken directly to a battery room and brooded at a temperature of 95° F. for the first week and 85° F. for the next two weeks. At the end of the third week, they were placed in a large permanent brooder house with electric hovers. Throughout the experiment, all chicks were fed the standard college ration.

METHODS AND MEASUREMENTS

Differences in degree of feathering are not discernible in the adult; therefore, a critical study of the chick was

made during the early growing period. Each chick was described at one-day, ten-days, and six-weeks of age. The following classifications were made at these ages.

One-Day Descriptions

The one-day age was chosen as it was believed to be the earliest age at which all chicks could be accurately classified. Chicks at this time were dry and well fluffed out and more easily handled. One hatch was classified at 21 days of incubation and again (approximately 24 hours later) at one-day of age as a check on the growth that had occurred in wing feathers during that period.

All chicks were classified into three arbitrary groups in an endeavor to predict and study the rate of feathering. Early feathering chicks, referred to as earlies, were those that had primary feathers longer and larger in diameter than their covert feathers. Late feathering chicks, classed as lates, were those that had wing feathers shorter and of about the same diameter as their coverts. Intermediates were a group of chicks that had rather long primary and secondary feathers; however, these feathers were of about the same length and diameter as their covert feathers.

The primary wing feathers were studied for the following:

Number -- total number of well developed feathers

Length -- maximum length measured in millimeters

Coverts -- relative length of coverts to primaries (Scored as 5/8, 6/8, 7/8, 1, etc.).

Secondary wing feathers were described for the following:

Number of well developed feathers -- total number of feathers which are at least one-half the length of the longest secondary. Number of secondaries is difficult to determine in the day-old chick since they gradually become shorter, virtually disappearing in the proximal portion of the wing. (Figure 1).

Length -- maximum length measured in millimeters

Coverts -- relative length of coverts to primaries (Scored as 5/8, 6/8, 7/8, 1, etc.).

Ten-Day Descriptions

Ten-day age was selected for the second description as the widest differences in tail and wing development between early and late feathering chicks appear at this time.

These five arbitrary scores as to degree of feathering were established for the tail.

0 -- No tail

1 -- Tail showing in sheath

2 -- Tail showing, some feathers developed

3 -- Short feathers, well developed but webbing not well formed

4 -- Long well developed feathers.

The length of wings were scored as to relative length of body (5/8, 6/8, 7/8, 1). This is largely a measure of length of primaries since they are the most conspicuous feathers showing in the folded wing.

Explanation of Figure 1

(A) The detached wing from an early feathering chick with at least five well developed secondaries shown in the proximal (lower) portion of the wing. Note the thick sturdy appearance of the feathers.

(B) The wing of an early feathering chick with few well developed secondaries. Only two or possibly three are shown; however, others which are short and small in diameter are masked by the down. Also note that the primaries of this wing are as well developed as those of the other wing.

(A) (B)

Fig. 1

Four arbitrary grades as to the relative length of secondaries to primaries at the ten-day age were set up as follows:

0 -- Very short, less than ½ length of primaries

1 -- One-half or slightly more than ½ the length of primaries

2 -- Ranging from 5/8 to 7/8 as long

3 -- Approximately as long as primaries.

Six-Week Descriptions

Six-weeks of age was chosen as the time for description of broiler feathering. While it is recognized that this is much too early for broilers, it is at this age that the greatest variation in degree of feathering is expressed. Radi (1937) working with slow feathering found seven weeks as the most advantageous age for description of degree of feathering; however, with sex-linked early feathering, a somewhat earlier age should be used.

The back region was scored as the index of broiler feathering. This region was selected because it was known to be the last feather tract to become clothed with feathers.

All chicks were scored for the back feathering utilizing the following five grades which are also illustrated in Figure 2:

0 -- No fully developed feathers, but having pin feathers or a few poorly developed feathers

Explanation of Figure 2

The standards for back scores established for chicks at six-weeks of age.

4 3 2 1 0

Fig. 2

1 -- Few well developed feathers extending down the median line of the back region

2 -- Back region having several rows of well developed feathers

3 -- Back fairly well covered by feathers

4 -- Back region completely covered.

The tail development was classed into four groups as a means of observing whether the ten-day relationship followed on through to the broiler age. Since no significance was found for this measurement, it is omitted from further discussion.

0 -- No tail feathers developed; may have pin feathers

1 -- Few short tail feathers in addition to considerable number of pin feathers

2 -- Tail feathers well developed but of medium length or may be few in number

3 -- Tail feathers relatively long and abundant.

RELATIONSHIP STUDIES

In the previous work on rate of feathering, there has been no critical examination of the factors which might be used as a means of predicting degree of feathering at broiler age in chicks carrying sex-linked early feathering. Radi and Warren (1938) were the first to make an analysis on late feathering Rhode Island Reds. It is common knowledge that birds which tend to be well feathered at an early age may be observed to have long, well developed primary and secondary flight feathers at one-day of age and a well developed tail at ten-days of age.

At the present time, the degree of development of the tail has been the factor used primarily as a means of selection for early feathering.

This phase of the study was an endeavor to disclose relationships between factors that might be used in a basis for prediction of differences in degree of feathering. All chicks were classified into three arbitrary groups, namely: Early, Intermediate, and Late.

Normal White Leghorn chicks have long, well developed primary and secondary feathers at one-day of age. Six or seven well developed primaries are usually present and are all of about the same length. The maximum lengths of primaries has been found to range from 12 to 20 mm. Associated with each primary is a covert feather which tends to be smaller in diameter and from two-thirds to three-fourths the length of the primary feather. The secondaries in White Leghorns tend to range from long distal feathers to short proximal ones. Numbers recorded in Table 1 are well developed numbers and a feather to be considered well developed had to be at least one-half of the length of the longest secondary as shown in Figure 1. In Leghorns were found five to eight well developed secondaries which ranged in length from 7 to 14 mm. Paired with each secondary is a covert feather which is smaller in diameter and is about two-thirds the length of the secondaries. The earlies described from heavy breed matings varied from the Leghorns by having slightly shorter wing feathers and in some instances a fewer number of secondaries.

Table 1. Measurements at one-day age of White Leghorn and early chicks

Stocks	Primaries				Secondaries			
	Number		Length in mm.		Number		Length in mm.	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Males								
Leghorn	6.5	6-7	15.8	13-19	6.6	5-8	11.1	8-13
Early	6.4	5-8	14.4	10-20	5.2	2-8	10.2	4-15
Females								
Leghorn	6.6	6-7	16.0	12-18	6.5	5-8	11.2	8-14
Early	6.5	5-8	14.5	9-20	5.3	2-8	10.4	4-15

Lates are those chicks that had no well developed wing feathers, in fact, they are seldom extended beyond the down of the wing. Upon close examination, primary and secondary feathers were usually visable; however, they were very short. The covert feathers tended to have about the same diameter but were longer than the primaries and secondaries.

Intermediates are those chicks which had fairly long primary and secondary feathers; however, they were not considered well developed as described in the earlies. The flight feathers were observed to be approximately the same length and diameter as their coverts and have the general appearance of lates with lengthened flight feathers.

One-Day Measurements

One-day measurements of the early, late and intermediate groups show rather different pictures as to wing feather growth. The late and early feathering chicks differ quite widely; however, the intermediates seem to behave at one-day of age more like the slow feathering group than the early chicks. The late feathering chicks produced from these matings tended to measure approximately the same as the Barred Plymouth Rocks which were known to carry the sex-linked gene for late feathering. The results of measurements on early feathering chicks are summarized on Table 1.

The Leghorns were apparently pure for sex-linked early feathering and were classified as a control. The chicks from early feathering heavy breed matings that were classified as

early, (Table 1) appeared about the same as Leghorns only that there was more variability in the range in number of secondaries.

The number of secondaries given is the number of well developed feathers. The data from a group of 339 male and 443 female earlies were summarized to make a comparison of the total number and the number of well developed secondaries. In the males, means of 7.4 was obtained for total number and of 5.2 for number of well developed secondaries; the females gave slightly higher means of 7.5 and 5.4 respectively.

The earlies, intermediates and lates may be compared as to degree of wing feather development at one day of age by lengths of primary and secondary feathers. The lengths given are the means from measurements of maximum length in millimeters. The means obtained from measurements of secondaries for males were 10.2 for early, 5.4 for intermediate, and 2.7 for late; the means for females were 10.4, 5.4, and 3.9 respectively. Measurements of primaries gave means in millimeters for males of 14.4 for early, 10.6 for intermediate, and 6.5 for late; the means for females were 14.5, 10.6, and 6.8. This shows that as an average the wing feathers are very short in late feathering chicks and much longer in early feathering. The intermediate group tended to behave as the name implies.

There is a question as to the effect of length of time a chick has been hatched on feather development at one-day descriptions. To answer this question, one hatch was removed at noon of the twenty-first day and chicks classified, and measured. These chicks were again handled from 20 to 24

hours later which was the time at which most day-old descriptions were made. In the earlies, 115 males showed an increase of 0.39 in number of secondaries or 7.8 per cent, 0.01 in number of primaries or 0.2 per cent, 2.10 mm. in length of secondaries or 21.7 per cent, and 2.55 mm. in length of primaries or 18.1 per cent. In 123 females of the same group, an increase was observed of 0.37 in number of secondaries or 7.1 per cent, 0.02 in number of primaries, or 0.3 per cent, 2.12 mm. in length of secondaries or 20.6 per cent, and 1.82 mm. in length of primaries or 12.9 per cent. There were only six intermediates and five lates obtained in this hatch and they in general showed the same tendencies as the earlies. It can be concluded that variations in time of hatching has only a slight effect upon number of flight feathers but does influence the feather lengths recorded in the day-old descriptions.

Ten-Day Measurements

The three arbitrary groups as established at one-day of age were maintained throughout the study. The factors considered at ten-days of age were amount of tail development, the relative length of the wing to that of the body, and relative length of secondaries to primaries. Length of wing shows little or no correlation to broiler feathering score. However, it should be brought out that the relative wing lengths varied but little in the early feathering chicks. Since the tail score was found to be highly correlated with six-week back score, it will be used for comparison of one-and ten-day measurements.

Observations on 60 male and 66 female Leghorn chicks have shown all chicks to have very well developed tails as mean scores of 3.8 were obtained for both sexes. The earlies, including 954 males and 1133 females had a mean score of 2.0 and 2.3 respectively. This indicates that the tails were somewhat shorter and less developed than those of the Leghorns, the females having the better developed tails. Those of the intermediate group appear to be just developing tails as is shown by a mean score of 0.4 for 145 males and 0.3 for 74 females. The lates, including 96 males and 48 females, were lacking tails as were the Barred Plymouth Rocks.

In the latter part of the experiment chicks were also classified for relative lengths of secondaries and primaries at ten-days of age. Observations at this age showed that the secondaries were almost as long as the primaries in the earlies, about two-thirds as long in the intermediates, and half as long in the lates. The conclusion might be drawn that better feathered broilers have secondaries and primaries of approximately the same length at ten days of age.

Six-Week Measurements

Analysis of the same three groups at six weeks of age was made for degree of back feathering. It was found that chicks having a back score of either three or four were satisfactorily feathered. It appeared that the health of the chick had some influence on the back feathering. Analysis of the back score of 55 male and 58 female White Leghorn chicks at six weeks of age

gave means of 3.2 and 3.3. The earlies, including 871 males and 1040 females, averaged 2.0 and 2.3, which was a fairly well covered back at this age. These results indicate that rate of development of body feathers in Leghorns is somewhat faster than in the early feathering heavy breeds. In the intermediate group, 135 males had a score of 1.8 and females had a mean of 1.7, and a bird with this score would have several rows of feathers down the median line of the back. The lates showed a distinct sexual dimorphism in back feathering. The mean score of 86 males was 1.1 and for 40 females was 1.6, the females being almost as well feathered as the intermediates. The Barred Plymouth Rocks showed even a greater sex difference; mean scores of 0.2 and 1.4 were recorded for 39 males and 43 females. The males were virtually bare-backed at six weeks of age except for a few pin feathers.

The broiler feathering score, which was in this study the score of the back region at six-weeks, was checked by re-describing two hatches for this factor at eight weeks. This was to determine whether variations observed at the six-week age were maintained at later stages. In the earlies, 111 males showed an increase in mean score from 2.1 to 2.7 with a correlation value of .855 between back scores; 161 females gave an increase in means from 2.4 to 2.9 and a correlation coefficient of .905. It was found that in addition to chicks with back scores of 3 or 4 at six weeks, 50 per cent of those scoring 2 at six weeks were also well feathered at eight weeks. This indicates that part of those birds considered poorly

feathered at the six-week age would be fairly well feathered at the broiler age. These results indicate that six-week descriptions are fairly accurate basis for measurement of feathering.

Correlation Values of Measurements of Earlies

Radi and Warren's (1938) conclusion that solution to broiler feathering would depend upon detection and propagation of sex-linked early feathering gene has laid the basis for the detailed study on the earlies. They have made a rather careful study of late feathering chicks and this investigation was made with early feathering chicks. Because the degree of development of the tail at ten days of age is found to give the highest correlation to back score at six weeks, it is probably the best ten-day measurement for purposes of prediction.

Relationship of Ten-Day Tail Score to Six-Week Back Score. Analysis of earlies has been made upon birds which appeared to have the sex-linked gene for early feathering. The study includes three breeds and experimentals, many of which were crosses between these breeds. Data given in Table 2 on tail score at ten days of age show a wide range of variability in mean scores. The low mean tail score of 1.4 for the males of the 1940 experimentals may be explained by the fact that these matings were for the study of inheritance and included extreme variants of early feathering.

The mean scores for back ranged from 1.5 to 2.8. It was found that the Rhode Island Red males were much more poorly

Table 2. Measurements and correlations of ten-day tail score and six-week back score

Stocks	Number	Mean ten-day tail score	Mean ten-day back score	r
Males				
Experimentals '40	133	1.4	2.4	.557
Experimentals '41	183	1.9	1.8	.636
White P. Rocks	342	2.1	2.7	.387
Barred P. Rocks	96	2.7	2.2	.576
R. I. Reds	117	2.1	1.5	.629
All Chicks	871	2.0	2.0	.517
Females				
Experimentals '40	122	1.8	2.5	.561
Experimentals '41	220	1.9	2.1	.668
White P. Rocks	421	2.5	2.8	.377
Barred P. Rocks	179	2.5	2.6	.600
R. I. Reds	98	2.5	2.0	.637
All Chicks	1040	2.3	2.4	.527

feathered than those of any of the other breeds; in fact, no Rhode Island Red male was given a score of 4 for the back region at six weeks.

The coefficient of correlations as given in Table 2 are all highly significant and are rather consistant for the various matings with exception of the White Plymouth Rocks. This may be due to the fact that this breed had a higher back feathering score than any other and thus lacked variability in that measurement.

The correlation coefficients obtained between ten-day tail and six-week back scores were the highest correlation values obtained in this study. The correlation value between these two measurements for all males was .517 and for all females was .527. These are weighted values obtained from the individual correlation coefficients. The error curve when plotted appeared very nearly normal. One may conclude that the development of the tail at ten days of age is a valuable characteristic for prediction of broiler feathering in chicks, carrying the sex-linked early feathering gene.

Relationship of Day-Old Secondary Numbers to Ten-Day Tail and Six-Week Back Scores. Day-old wing feathers have been critically observed in an endeavor to find a measurement that would have a prediction value with reference to broiler feathering. As was previously stated, secondary numbers in the earlies, as given in Table 3 refers to well developed feathers and not to total number of secondaries. In each breed studied, a highly significant coefficient of correlation was obtained between

Table 3. Correlation coefficient for relationship of number of well developed secondary feathers in day-old chicks to ten-day tail and to six-week back score

Stocks	No. birds	Mean No. of secondaries	r-Value with tail score	r-Value with back score
Males				
Experimentals '40	137	5.0	.621	.495
Experimentals '41	208	4.9	.523	.528
White P. Rocks	379	5.6	.216	.284
Barred P. Rocks	100	5.2	.568	.339
R. I. Reds	130	4.9	.592	.601
All Chicks	954	5.2	.429	.416
Females				
Experimentals '40	134	5.1	.600	.596
Experimentals '41	242	4.7	.511	.478
White P. Rocks	465	5.8	.337	.152
Barred P. Rocks	186	5.0	.608	.497
R. I. Reds	106	5.4	.636	.661
All Chicks	1153	5.3	.478	.381

number of well developed secondaries and both ten-day tail and six-week back scores. All breeds with exception of the White Plymouth Rocks tended to be rather consistent in their correlation. As previously explained, this strain showed less variability and a somewhat higher mean for broiler feathering. In the 421 White Plymouth Rock chicks measured, 75 per cent had secondary numbers of 5 or 6 and 62 per cent had a back score of 3. The lack of variability would lower the correlation coefficient but would still mean that the well feathered broiler had a rather large number of well developed secondaries.

Including all breeds, 954 males and 1153 females gave correlation coefficients of .429 and .478 respectively, between number of secondaries at one-day and ten-day tail score. Correlation values between number of secondaries and six-week back feathering was .416 for 954 males and .381 for 1153 females. This measurement has possibilities of value for prediction of degree of broiler feathering at one day of age.

Analysis was made on 339 males and 443 females for total number instead of number of well developed secondaries. This measurement when compared to back score gave a correlation coefficient of .472 for 271 males and .511 for 350 females. The total number of secondaries prove equally as efficient for prediction of degree of broiler feathering in the earlies as was the number of well developed secondaries; however, determination takes much longer since the proximal feathers are short and difficult to observe in the down of the chick.

Relationship of Day-Old Primary Numbers to Ten-Day Tail and Six-Week Back Scores. Radi and Warren (1938) studied primary numbers in late feathering chicks and found a significant correlation of 0.2038 in the males and 0.2774 in the females. However, they concluded that this correlation was too low to serve as a practical basis for prediction.

In the earlies, including 954 males and 1133 females, the males had a mean number of 6.4 primaries and the females a mean of 6.5, numbers ranging from 5 to 8. A coefficient of correlation of .136 for males and .202 for females was obtained between number of primaries and ten-day tail score. The primaries correlated to feathering at six-weeks gave values of .100 for 954 males and .220 for 1133 females. While this indicates some association of number of primaries and back feathering score, it is by no means a satisfactory basis for prediction.

Relationship of Day-Old Secondary Lengths to Ten-Day Tail and Six-Week Back Scores. Differences in lengths have long been observed in wing feathers at hatching, and these variations have been recorded in this study by measuring maximum lengths in millimeters. Analysis of 954 males and 1133 females, disclosed the mean length of secondaries to be 10.2 mm. for males and 10.4 mm. for females. The range in lengths being 4 to 15 mm. for both sexes. Correlation coefficient values of .343 for males and .436 for females were obtained between secondary lengths and ten-day tail score. A somewhat lower, but still significant, correlation value was observed with degree of broiler feathering. The coefficient of correlation for 954

males was .221 and for 1133 females was .260. The correlation for lengths is statistically significant in their relation to broiler feathering but a much less dependable factor for prediction than number of secondaries.

Relationship of Day-Old Primary Lengths to Ten-Day Tail and Six-Week Back Scores. Another measurement studied was the length of primaries at one-day of age. In the earlies, including 954 males and 1133 females, the males had a mean primary length of 14.4 mm. and the females a mean of 14.5 mm. The primaries ranged from 10 to 20 mm. in length. Statistically significant correlation coefficients of .207 for males and .321 for females were obtained between one-day primary lengths and ten-day tail score. In 954 males and 1133 females, correlation coefficients of .157 and .185 were observed between primary lengths at one-day and the back score at six weeks. However, from an analysis by breeds it was found that in some instances the values were not statistically significant. Therefore, lengths of primary wing feather in day-old chicks would be unreliable as a prediction of broiler feathering. This is the same conclusion that Radi and Warren (1938) reached in their study of sex-linked late feathering stocks.

Analysis of Intermediates

Intermediates were observed for rate of feathering to determine whether prediction values for feathering in the earlies could be applied.

The number of secondaries found in intermediates is not

comparable to the number reported in the earlies. None of these feathers would be considered well developed and that was the basis of the counts recorded for the earlies. It was found that there was a tendency for correlation between secondary numbers and ten-day tail score. In the relationship between numbers of secondaries and six-week back scores, the mean back scores for each tail classification ranging from 0 to 3, in 135 males were 5.3, 5.2, 6.0 and 6.8 and for 74 females were 5.7, 6.1, 5.8 and 6.4, respectively. This would indicate a relationship exists between number of secondaries and feathering.

Mean back scores were determined for each ten-day tail score ranging from 0 to 3. In 135 males observed, mean back scores of 1.7, 1.9, 2.3 and 2.0 were obtained for the four classifications of increasing tail lengths and for 74 females they were 1.7, 1.9 and 1.8. This indicates that some relationship exists between tail score and back score and that the better the developed tail at ten days, the better the broiler feathering at the later stages. A nonsignificant relationship was found between lengths of both primaries and secondaries at one-day and the six-week back score.

Analysis of Lates

The lates were also studied to determine whether factors found suitable for prediction in the earlies were of value in the late feathering chicks. As in the intermediate, no well developed secondaries were found and little relationship was found between number of secondaries and either ten-day tail or

six-week back scores. No study of relationship between ten-day tail score and broiler feathering was made since all chicks lacked tails at ten days of age.

The wings varied from one-half to seven-eights the length of the body at ten days and it was found that the longer the wing feathers at this age, the better the feathering score.

Conclusions on Relationships

If prediction of degree of broiler feathering is to be successful, the sex-linked gene for early feathering should be present. The highest correlation observed was with ten-day tail score and the next highest coefficient was with number of well developed secondaries at one-day of age. The other one-day measurements were not highly enough correlated with any variations in feathering at later stages to be practical as a basis for prediction of broiler feathering.

It has been found in this study that when chicks were selected with five or more secondaries, 57 per cent of the males and 71 per cent of the females would be well feathered at six-weeks. When chicks were selected with a ten-day tail score of 3 or 4, 65 per cent of the males and 78 per cent of the females were well feathered at the broiler age.

INHERITANCE STUDIES

Hadi and Warren (1938) concluded from their selection in Rhode Island Reds that genetic differences in broiler feathering were probably due to autosomal modifying genes acting upon

the sex-linked dominant late feathering factor. They also concluded that the simplest method for improvement of broiler feathering would be the incorporation of the sex-linked early feathering gene.

It has been found that even in some breeds in which the early feathering gene was present that there is a wide range in degree of feathering at the broiler age. This variability, if heritable would indicate the presence of modifying factors which affect the expression of the early feathering factor.

This phase of the study is an endeavor to determine the genetic nature of the modifying factors. The major variations observed were in the expression of wing feathers at one day of age and in the degree of development of the tail at ten days of age.

It should be emphasized that the parent stock used had not been described in such detail as were the chicks produced in this study. The types of parent stock utilized were Leghorns, earlies, modified earlies, intermediates, and lates. The White Leghorn females used were homozygous for feathering and were probably free from modifying factors. Earlies as previously described were similar to Leghorns in having well developed primary and secondary wing feathers at one day. At ten days of age, they had wing feathers as long as the body and well developed tail feathers.

Modified earlies were those birds that as day-old chicks were described as early but at ten-days had defective tail feather development or lacked tails. They also frequently had

but few well developed secondaries. Intermediates at one-day of age had the appearance of late feathering chicks with elongated flight feathers. They usually had wings about seven-eights the length of the body and poorly developed tail feathers at ten-days of age. Lates were normal chicks carrying the sex-linked dominant late feathering gene, and showed poorly developed flight feathers at one day and short wings and no tail at ten days. All the foregoing types are more fully described under the heading of Relationship Studies.

Inheritance of the Intermediate Type of Feathering

It was observed in the relationship studied that the chicks classified as intermediates had longer wing feathers at one day of age than normal lates but behaved somewhat as lates at the broiler age.

This intermediate condition was first observed in a strain of Rhode Island Reds that had been selected for improvement of broiler feathering. It might be true that by selection for better feathering some factor or factors affecting the length of wing feathers at hatching has been introduced.

Three of the matings established to study inheritance of modifying factors were found to produce intermediates. All of the males listed in Table 4 were believed to be heterozygous for sex-linked late feathering and the results indicate this to be the case since approximately half of the female offspring were early feathering, if one considers those listed as lates and intermediates as late feathering.

Table 4. Results of matings of intermediate males with Leghorn, early and late females

Male No.	Type of female mate	Feathering type of offspring					
		Males			Females		
		Early	Late	Inter-mediate	Early	Late	Inter-mediate
1641M	Leghorn	13	3	6	21	8	6
1641M	Early	33	12	25	28	16	5
1623M	Early	26	6	21	23	12	12
1624M	Early	38	0	23	32	3	26
1641M	Late		13	16	16	3	11
1623M	Late		14	5	7	5	2

Since the intermediate condition appears to be a modification of late feathering the ratio of intermediates to lates shall be considered primarily. The proportion of early feathering chicks will indicate the constitution of the parent stock with respect to sex-linked feathering gene. Since heterozygous sex-linked late feathering males 1641M and 1623M were each described as intermediates, this might lead to the conception that this condition is an expression of heterozygous early feathering. This could not be true since intermediates are found in the female offspring and since the female is heterogametic for the sex-chromosome, thus always being homozygous for late or early feathering. The mating of the intermediate males to late females (Table 4) is the critical test for mode of inheritance since the factor would have to be dominant in

order to be expressed. When male 1641M was mated to lates, the ratio of late to intermediate chicks was 13 to 16 for males and 3 to 11 for females. If the factor is dominant as it seems to be, the lates (Barred Plymouth Rocks) must carry the recessive expression of the factor or in other words lack the modifier; otherwise intermediates would be produced in this pure breed which is not true. When this same male was mated to Leghorns, the ratio of intermediates to lates was 3 to 6 in the males and 8 to 6 in the females or approximately a one to one ratio. This would seem to indicate that the Leghorns like the Barred Plymouth Rocks lack the modifier, intermediate. This factor would not express itself in the presence of early feathering because the wing feathers are already well developed. With this in mind, the earlies, which have resulted from crossings of Rhode Island Reds, could carry either the dominant or recessive expression of the factor. If this assumption is correct, the data indicate that males 1641M and 1623M were heterozygous and male 1624M was homozygous for a dominant factor responsible for the intermediate type of chick feathering.

Matings of the heterozygous males with early females show a preponderance of intermediates among the late feathering male offspring. This would lead to the conclusion that the factor for the intermediate condition might be sex-linked. If any of the early feathering females carried a sex-linked factor for the intermediate type, they would transmit it to their male offspring but not to their daughters since females receive their only sex-chromosome from their father. If the factor is a

dominant sex-linked one, and a dam carrying it is mated to heterozygous males, she would produce only early and intermediate male offspring. An early feathering dam carrying the recessive factor mated to the same male would be expected to produce male chicks in ratio of 2 early: 1 late: 1 intermediate. It was found that eight of the females in these two matings produced 49 earlies and 49 intermediates and no lates; and that five females produced 22 earlies, 17 lates and 15 intermediates. In addition, if this factor were autosomal, the eight dams mentioned would have had to be homozygous in order to produce no late sons. Then the female offspring from these dams should also show no lates; however, there were 13 lates and 9 intermediates observed. The data seem to fit quite closely the hypothesis of sex-linkage.

The results of the mating utilizing 1624M indicates that this male is heterozygous for late feathering and apparently homozygous for the intermediate factor. This male was described as early feathering at both one day of age and ten days of age. Normally the heterozygous late feathering male would be described as late and this might be explained by interaction of genes. It is possible that the interaction between homozygous intermediate and heterozygous late feathering factors is such that the wing feathers were lengthened to the point that the male was described as early feathering. This mating gives results which agree with previous data that the factor is dominant.

The conclusions to be drawn are that the intermediate condition is the result of a dominant modifying factor acting

upon sex-linked late feathering. The indications are that the modifier is a sex-linked factor but that it is not very closely linked to the late feathering gene. Also, there is some evidence of the modifying action of the homozygous intermediate factor upon heterozygous sex-linked late feathering to the degree that it has the appearance of early feathering.

Inheritance of Modified Early Condition

In White Leghorns, the tail was found almost invariably to be well developed, scoring three or four; this being the typical expression of the sex-linked early feathering gene. However, in the heavy breeds which have the early feathering factor incorporated, there was found a wide variability in development of the tail at ten days of age. This would indicate there might be a factor involved which affects the degree of feathering of the tail at ten-days. The factor affects not only feathering at ten-days of age, but also the six-week back feathering.

Many of the variations reported in degree of tail feathering are found in the Rhode Island Reds. With the introduction of early feathering in this breed, modifying factors were found which earlier had not been permitted to express themselves. The majority of the modified early birds used in this study were Rhode Island Reds.

The matings of early feathering heavy breeds are summarized in Table 5. All birds used in these matings carried the recessive sex-linked early feathering gene. The variability in

tail development is probably the result of the action of some modifying factor or factors.

Table 5. Ten-day tail scores of chicks from early feathering strains of heavy breeds

Stocks used	Number of chicks	Tail scores				
		0	1	2	3	4
Males						
White Plymouth Rocks	118	2	40	39	31	6
Barred Plymouth Rocks	98	6	7	15	47	23
Rhode Island Reds	37		9	11	9	8
Females						
White Plymouth Rocks	96	1	16	39	27	13
Barred Plymouth Rocks	103	1	12	21	37	32
Rhode Island Reds	30		8	6	10	6

The tail scores as given represents the range from no feathers to abundant feathers. It should be stressed that the defective tail condition is represented by either a score of 0 or 1 and that score 2 is a somewhat questionable condition but probably should be included with score 3 and 4 as representing well developed tail feathers. It was found that chicks of a late feathering strain, Barred Plymouth Rocks, rarely if ever scored above 1 and that most White Leghorns scored 3 or higher.

The parent stock in Table 5 had well developed tail feathers; however, their offspring varied from having no tail feathers to well developed tails at ten-days of age.

The fact that parents which have well developed tails produced chicks with poorly developed tails is good evidence for a recessive factor being involved. When tail scores 1 and 2 are considered poorly developed, all three breeds produced approximately one-fourth of the chicks with defective tails. The poor tail feathering condition constitutes such a high percentage that it may indicate more than one factor is involved, since a three to one ratio would be obtained only when each parent was heterozygous. It seems improbable that every individual chosen would be heterozygous for this factor.

In order to obtain more critical data on the inheritance of the modified early type, males showing this condition were mated to White Leghorn females which were believed to be free from the supressor of tail development. The same males were also mated to modified early and to late females. The results are summarized in Table 6.

These results show that modified early males mated to Leghorn females produced practically all chicks with well developed tails, only six of 43 males and one of 25 females were defective to any degree. This indicates that poor tail development is recessive to condition found in Leghorns. The mating of the same male to lates (Barred Plymouth Rocks) indicates the affect of the late feathering gene, since here all males lacked tails which is the typical expression of late feathering. The critical data for inheritance of this condition are available from matings of modified early males and females. Of the male offspring, there were 87 defective to 21 with well

Table 6. Results of matings of modified early males with females of various types

Female mates	Number of chicks	Tail scores				
		0	1	2	3	4
Males						
Leghorns	43		6	6	20	11
Modified Barlies	108	34	53	16	5	
Lates	10	10				
Females						
Leghorns	25		1	2	12	11
Modified Barlies	125	43	58	17	6	1
Lates	14	2	4	2	5	1

developed tails and in females 101 defective to 25 well developed. It is also to be noted that very few chicks scored above 2.

These results all point toward the existance of a major recessive factor producing defective tail feathering at the ten-day age. There was no apparent difference between behavior of parents with partial tail development or complete lack of tail feathers and it should be emphasized that both sexes breed like homozygous recessives. This would seem to indicate that the factor involved is a recessive autosomal modifier of sex-linked early feathering; however, presence of some well developed tails in the modified early stock and a few poorly developed tails in matings with Leghorns may also indicate presence of some additional genetic factors or the action of complicating environmental factors.

If the results in the previous matings can be explained by presence of a recessive suppressor of the early-feathering gene, it would seem that the gene involved might be the same as Warren's (1933) retarded found in Leghorns, since chicks very similar to his description of retarded were observed in this study. In order to check upon this a retarded male was mated to modified early females. It was found that in 16 male offspring, 11 were scored defective and five were scored 2, and that in 20 female offspring, 11 were defective, five scored 2, and four had well formed tails. This indicates that the modified early condition observed in the early feathering heavy breeds is the same as the earlier described retarded. The mating of the two stocks produced mostly defective tails when mating of each

to normal Leghorns produced mostly normals.

This defective tail condition has a definite influence on number of secondaries at one day of age and on degree of feather development as measured by back score at six-weeks of age. The mean secondary number and mean back feathering scores for various stocks are given in Table 7 and it is of interest to compare these means with the incidence of defective tails in the same stocks shown in Tables 5 and 6.

The results in Table 7 show that the modified earlies and the mating of retarded male by modified early female tend to have reduced the number of secondaries. Also that the Rhode Island Reds have a lower number of secondaries than the other breeds studied; yet slightly higher number than the special matings. If this factor is recessive, this would indicate the Rhode Island Reds carry the factor to a great extent and it should be recalled that the modified earlies were mostly from this breed. Considering the agreement in data shown in Tables 5, 6 and 7, it seems that the reduction of number of secondaries and defective tail condition are the expression of the same modifying factor. These two same characteristics are found in the retarded stock.

Results of six-week back scores show that the early feathering heavy breeds are not so well feathered as the Leghorns; however, White Plymouth Rocks tended to approximate the same score. The Rhode Island Reds were definitely inferior in feathering; in fact, none of them were scored 4 for back region. The mating of retarded male and modified early females had a

Table 7. Number of secondaries at one-day and back scores at six-weeks in various stocks

	Males			Females		
	Number of chicks	Number of secondaries	Back score	Number of chicks	Number of secondaries	Back score
Leghorns	55	6.6	3.2	59	6.5	3.3
White Plymouth Rocks	114	5.7	2.9	89	6.0	3.1
Barred Plymouth Rocks	95	5.2	2.3	101	5.1	2.6
Rhode Island Reds	33	4.7	1.4	29	4.3	1.5
Modified Earlies	96	3.4	1.3	111	3.8	1.6
Retarded male and Modified early females	15	4.1	1.9	17	4.0	2.1

mean back score of 1.9 for males and 2.1 for females and this is very similar to means of 1.5 for males and 1.6 for females of the modified early stock.

It may be concluded that the modified early condition is the result of a recessive modifier of the sex-linked early feathering gene and probably is the same factor previously described as retarded. This factor acts as a suppressor of early feathering by reducing the number of secondaries at one day of age, delaying the development of tail feathers, and even affecting the degree of feathering at six-weeks of age. There is also evidence that other modifying factors may be present; however, additional matings will have to be made to determine their number and mode of inheritance.

Inheritance of Number of Secondaries

The previous section has shown the effect of different types of matings upon number of well developed secondaries present at one day of age. In order to obtain more critical data on the inheritance of these flight feathers, several matings were made in which the number of secondaries at one day of age were known for both parents. The results summarized in Table 8 are from the Rhode Island Red matings and seem to offer some evidence as to inheritance of secondaries.

Table 8. Inheritance of number of well developed secondary flight feathers in day-old Rhode Island Reds

Number of secondaries:		Distribution of secondary numbers in progeny								
Sire	Dam	0	1	2	3	4	5	6	7	8
					Male offspring					
4	4-5				9	30	14	3		
4	6-7				3	4	11	9	2	
5	3-5				4	1	1			
5	6-7				2	5	3			
6	3-5				4	6	4	5	2	
6	6-7				1	1	3	3	5	1
					Female offspring					
4	4-5				9	14	14	5		
4	6-7				1	7	8	4		
5	3-5			1	1	1	1	1		
5	6-7			1	3	2	3	3	2	
6	3-5				2	4	1	4		
6	6-7					1	1	7	2	

The number of secondaries are given for each sire; however, the females were more numerous and were grouped. Two groups established for females were for numbers ranging from 3 to 5 and 6 to 7. The data obtained indicate that the females of the 6 to 7 group invariably produced offspring that had a higher range in numbers than the 3 to 5 group when mated to the same male.

The results indicate that number of secondaries is definitely inherited. The mode of inheritance is not determined; however, from foregoing data, it seems probable that this is the affect of the retarded factor. At least, it indicates the importance

of number of secondaries as a basis of selection for improvement in degree of broiler feathering.

Conclusions on Inheritance

The studies on inheritance show that the early feathering heavy breeds are not so well feathered as are the Leghorns at six-weeks of age. All the breeds studied, White Plymouth Rocks, Barred Plymouth Rocks, and Rhode Island Reds, show some evidence of modifying factors.

The factor for the feathering condition called "Intermediate" acts as a modifier of sex-linked late feathering and seems to behave as a dominant. The data obtained indicate that the factor if sex-linked, however the evidence for this is not so critical as desired. Intermediate tends to lengthen the day-old chick flight feathers and improves the broiler feathering to a degree.

The evidence indicates that the presence of poor tail development at ten-days of age in early feathering heavy breeds is due to a recessive autosomal modifier of the sex-linked feathering factor. This gene is apparently the same as retarded which was previously reported in White Leghorns. It suppresses the number of secondaries at one-day of age, delays tail feather development, and reduces the rate of feathering at the broiler age.

The number of secondaries is inherited and is probably an expression of the retarded factor. Parents having few secondaries tend to produce similar offspring and the opposite is true of parents having an increased number of secondaries.

SUMMARY

(1) Approximately 3000 chicks, most of which were early feathering, were described at one-day, ten-days, and six-weeks of age to determine the degree of variability in feathering at these ages and to analyze the genetic factors involved.

(2) The sex-linked early feathering gene is necessary if broiler feathering is to be improved to any great extent.

(3) Measurements for prediction were found to be dependable only as long as the gene for sex-linked early feathering was present.

(4) The highest coefficient of correlation obtained was between ten-day tail and six-week back scores. The coefficient obtained was .517 for males and .527 for females.

(5) Variations in length of wing feathers at one-day of age were found to be impractical for predicting degree of feathering at the broiler age.

(6) There was little variation in number of primaries at one-day of age and thus this measurement was of little value as an indication for degree of feathering at six-weeks of age.

(7) The number of well developed secondaries was significantly correlated with ten-day tail and six-week back scores. The correlation coefficients obtained between number of secondaries and ten-day tail score were .429 for males and .478 for females. The values secured between secondary numbers and back scores were .416 for males and .381 for females. This was the only one-day measurement that proved to be practical as a basis for prediction.

(8) The significance of number of secondaries in the day-old chick should be emphasized in any program of improvement in broiler feathering since it was found that variations in number are definitely inherited.

(9) The factor which decreases the number of secondaries at hatching also delays tail feather growth and even body feathers at the broiler age. The early feathering breeds, especially Rhode Island Reds, carry this autosomal recessive modifier for sex-linked feathering. It appears to be the same gene previously described in White Leghorns as retarded.

(10) "Intermediate" is a type of late feathering and is the result of a dominant modifier of sex-linked late feathering.

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