THE CORRELATION BETWEEN BODY PIGMENTATION AND EGG PRODUCTION IN THE DOMESTIC FOWL

J. ARTHUR HARRIS and A. F. BLAKESLEE
Station for Experimental Evolution, Cold Spring Harbor, New York
and
D. E. WARNER
Connecticut Agricultural College, Storrs, Connecticut

in consultation with
WM. F. KIRKPATRICK
Connecticut Agricultural College, Storrs, Connecticut

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INTRODUCTORY REMARKS

Many poultry breeders have criteria by which they feel able to distinguish the laying from the non-laying birds in their flocks at any time without recourse to trap-nesting.[1]

It is perhaps not surprising that with the introduction into agricultural investigations of the exact methods of laboratory experimentation these indirect and scientifically untested criteria should receive but little credence or attention.

Nevertheless it must be admitted that in extended and deep-rooted popular belief there is frequently a minimum of substance as well as a maximum of superstition. We therefore decided to test various popular beliefs against the facts of actual controlled experiments, with a view to

[1] KENT (1916) has recently outlined the criteria employed.

eliminating the mass of superstition and differentiating the kernel of truth if existent.

Such a course seemed to have a two-fold justification.

First, it is perhaps self evident that for many practical breeders trap-nesting is an unattainable ideal. Any method which makes possible the selection of the heaviest layers without the expense of trap-nesting should—providing selection itself is worth while—be of practical value.

Second, egg production in the domestic fowl is a remarkable example of the chemical efficiency of an organism. During the year the 150-egg bird stores in her eggs an amount of fatty and nitrogenous substances which in comparison with her body weight is relatively enormous. It would be highly remarkable if these processes could be carried on without affecting, and perhaps profoundly, the visible somatic features of the organism. If this be true, a study of the correlation between the extent of reproductive activity and somatic characters may have its value from the purely physiological side.

Early in these studies two of us (BLAKESLEE and WARNER, 1915 a, b, BLAKESLEE 1915, WARNER 1916) showed that in certain breeds of poultry, such as Leghorns and the so-called American breeds, including Plymouth Rocks, Wyandottes and Rhode Island Reds, there is in fact a close connection between the amount of yellow pigment to be seen in a bird and her previous laying activity.

Since these observations were published, various comments, criticisms, notes of earlier fragmentary observations, and preliminary notes on work in progress elsewhere have appeared, chiefly in the poultry journals. We shall not, we hope, be considered unfair to other writers if in the present technical treatment of the subject we omit all reference to discussions unaccompanied by quantitative data.

It is our purpose in this place to analyze more minutely, by means of the modern biometric formulae, the data upon which the former conclusions were based and other supplementary series.

In doing this we shall not attempt a comprehensive investigation of all the problems presented by the series of data at our disposal, but shall limit ourselves as strictly as possible to one specific problem, that of the relationship between body pigmentation and egg production. In doing this we are also restricting ourselves to one measure only of pigmentation—the percentage of yellow occurring in the ear lobe of White Leghorns as determined by the color top. This measure is selected because it is probably the most accurate of those available and the most suitable for quantitative expression.

It is, therefore, best fitted for a purely physiological study. The results obtained with this character are substantiated by the results of observations on pigmentation of leg, beak and vent, which will be discussed in detail in a forthcoming bulletin of the STORRS AGRICULTURAL EXPERIMENT STATION.

MEASUREMENTS TAKEN

The amount of yellow in the ear lobe can be conveniently measured quantitatively by means of the Milton Bradley color top. In matching ear lobes against the blend produced by the spinning disk, only yellow and white sectors were used. The matching is not perfect, especially in the lower grades, since a certain amount of blue is often present. The amount of yellow has, however, probably been more accurately measured than if the other color components had been considered. Under proper illumination, it appears possible for an observer to repeat observations with a divergence of not over 5 percent.[2] In analyzing the results statistically, we have recorded in classes of 5 percent range.

Pigmentation determinations were made October 19-21, 1914 and October 17-18, 1915.

The egg records were taken as a part of the regular routine of the egg laying contest. Such details as are essential concerning this feature of the work will be given below.

ACCURACY OF DATA AND SOURCES OF ERROR

Our data were drawn exclusively from the egg laying competitions conducted for the past four years at Storrs, Conn. The method of procedure in these competitions has been described elsewhere (KIRKPATRICK and CARD 1915).

Pullets enter the competition November 1 and remain for one year. They are housed in pens of 10 birds each, are fed the same ration, and so far as possible are treated exactly alike.[3] The influence of environmental factors can therefore be disregarded.

[2] Tests in the use of the top indicate that some observers have a constant tendency to read higher or lower than others, but that an individual observer tends to estimate consistently. Accordingly, all the color determinations upon which constants are based were taken by the same observer (BLAKESLEE).

[3] In 1913-'14 four pens, and in 1914-'15 one pen, belonging to the EXPERIMENT STATION, had sour milk substituted for certain ingredients in the normal ration, but since they showed no apparent difference in color that could be attributed to the change in the feed, they are included in the tabulations.

That the use of such data for physiological studies will be criticized by some we have little doubt. Such criticisms will fall into three principal categories:

1. That the birds entered in these competitions constitute a relatively heterogeneous group of organisms.

The fact that these birds were submitted by a large and widely scattered series of breeders may not, we think, be considered altogether, if at all, a disadvantage. The variety of origin of the birds makes certain that the results are typical of the breeds as a whole, not characteristic of and determined by some peculiarities of a particular experiment station flock.

A certain disadvantage of the materials may possibly lie in the fact that while all the birds were in their pullet year when placed in the competition the exact hatching date of the different lots and the number of eggs which may have been laid by the individuals before they were placed in competition on November 1 is unknown.

The absence of these data is far less important (if of any significance at all) in the kind of problem with which we are dealing in this paper, than they would be in studies involving the records of the total egg production of the first and second year.

2. That the records of egg laying competitions lack the accuracy demanded by scientific investigation.

This we doubt. Relatively large economic importance attaches to the results of these competitions, and every reasonable precaution has been taken to secure trustworthy results.

3. Finally, the objection may be made that the pigmentation determinations by means of the color top could not be carried out with the degree of accuracy necessary for quantitative work.

This objection is not supported by the results of our experience of the past two years, which has shown that it is possible to repeat determinations with a fair degree of consistency, and that experimental errors in matching colors are not great enough to materially influence results when the experiments are carried out on a large scale.

Any objections on these grounds would be equally pertinent to any physiological studies in which the same technique was necessary. The extent of the experiment presents certain great advantages as compared with the usual experimental studies. The number of birds involved was relatively very large. As a result, errors of observation, if not of a systematic nature, will tend to average out.

The smoothness of our results and the remarkable agreement of the constants for the two years seems to us the strongest *a posteriori* reason to consider the technical details of the work—both those of the egg laying competition, properly so called, and the measurements of pigmentation—as having been carried out with a relatively high degree of consistency and exactness.

PRESENTATION OF DATA AND BIOMETRIC CONSTANTS

As explained above, we shall in this paper limit ourselves as strictly as possible to a consideration of the problem of the relationship between ear lobe pigmentation and egg production. For this purpose it is necessary to know the frequency distribution and the physical variation constants of the characters dealt with.

Type and variation of characters

The frequency of the different percentages of pigmentation in the two years are shown in tables 5 and 6 below, and graphically on a percentage basis in diagrams 1 and 2.

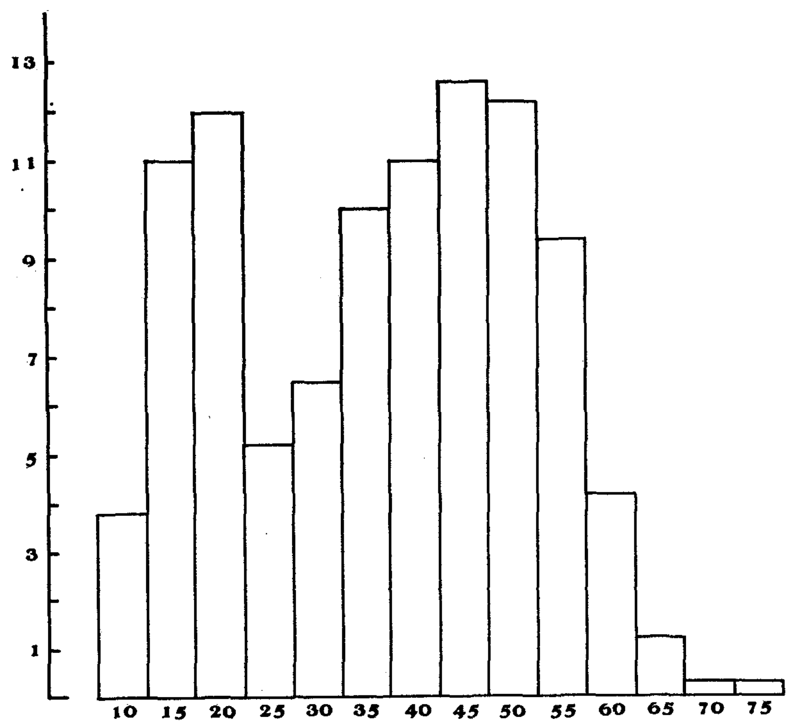


DIAGRAM 1.—Distribution of yellow in five percent classes in ear lobes of White Leghorn hens, 1913-'14. Frequencies are reduced to percentages.

These show a highly interesting bimodal condition. The frequency of birds with given percentages of yellow increases from the lowest recorded class, 10 percent, up to 20 percent, beyond which there is a decline in the number of birds observed which reaches its lowest point at 25 or 30 percent. The frequency then rises to a maximum at 45 or 50 percent, after which it again falls. The variation constants in terms of individual percents are as follows:

	Mean	Standard deviation	Coefficient of variation
1913-'14	36.408 ± .579	15.090 ± .409	41.45 ± 1.30
1914-'15	40.640 ± .560	16.079 ± .396	39.56 ± 1.12
Difference	4.232 ± .805	.989 ± .569	1.89 ± 1.72

The difference in the percentage of yellow in the two years is about 5 times as large as its probable error. Such a difference, considered

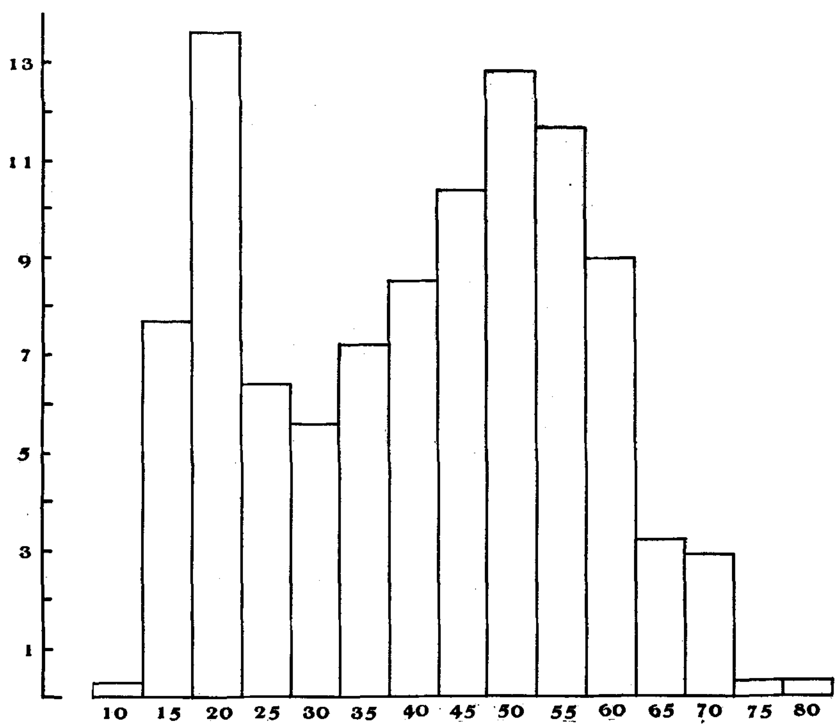


DIAGRAM 2.—Distribution of yellow in five percent classes in ear lobes of White Leghorn hens, 1914-'15. Frequencies are reduced to percentages.

from the purely statistical side, would be looked upon as probably significant. The difference is, however, less than one working unit. When the great difficulties in matching color series under the best conditions are borne in mind, it is not surprising that a difference at least as great as that shown here should be found between the results of two sets of observations separated by an interval of a year.

The variation in the percentage of yellow pigment, measured in the absolute terms of standard deviation or in the relative terms of the coefficient of variation, cannot be said to differ significantly in the two years, when probable errors are taken into consideration.

The variation in number of eggs laid per year is very wide, ranging from 16 to 255 in 1913-'14, and from 0 to 255 in 1914-'15. We give merely the means and variation constants for annual production. These are:

	Mean	Standard deviation	Coefficient of variation
1913-'14	151.63 ± 1.45	37.85 ± 1.03	24.96 ± 0.72
1914-'15	154.48 ± 1.51	43.22 ± 1.06	27.98 ± 0.74
Difference	2.85 ± 2.09	5.37 ± 1.47	3.02 ± 1.03

The mean annual production differs by less than three eggs, or by less than two percent. The birds in the competition in 1914-'15 were perhaps significantly more variable in annual egg production than those studied in 1913-'14.

Notwithstanding the fact that certain differences between the constants for pigmentation and for annual egg production in the two years must be considered statistically significant, the impression which any impartial observer must gain from these constants is that the experiment has been carried out in the two different years with a surprisingly high degree of consistency of results.

For number of eggs laid per month the range is narrow enough that the frequency of birds laying from 0 to 29 eggs, the maximum observed number, may be given for each month individually. Table 1 gives the results for 1913-'14. Table 2 presents those for 1914-'15.

The average number of eggs laid per month by all birds irrespective of their somatic characters are given for the two years in table 3.

TABLE I

Distribution of birds according to number of eggs laid per month in 1913-1914.

Eggs laid	November	December	January	February	March	April	May	June	July	August	September	October	Annual total
0	126	157	158	21	—	—	—	2	4	9	88	184	749
1	26	9	23	12	—	1	—	2	—	5	26	14	118
2	9	5	6	12	—	1	1	—	2	4	14	10	64
3	21	7	16	12	1	—	—	—	1	4	6	4	72
4	13	3	15	3	2	—	1	1	3	—	6	6	53
5	9	9	10	11	1	—	—	1	2	5	4	4	56
6	13	14	9	21	4	1	—	2	1	3	6	3	77
7	10	9	14	19	1	—	—	2	3	3	8	2	71
8	12	14	5	18	1	—	—	2	2	2	6	7	69
9	9	5	15	24	3	2	—	2	3	4	3	8	78
10	10	7	8	17	2	3	—	4	10	8	4	5	78
11	9	7	5	22	7	4	4	8	8	9	5	8	96
12	12	7	4	16	7	6	3	8	6	4	5	2	80
13	6	5	5	17	14	4	2	6	5	6	6	5	81
14	4	5	7	17	17	8	5	8	9	6	5	3	94
15	10	7	1	22	16	8	3	7	5	8	7	3	97
16	7	6	3	15	26	17	5	7	10	16	11	5	128
17	1	6	2	17	25	15	9	7	11	9	12	10	124
18	1	5	2	8	33	22	15	17	13	17	16	9	158
19	—	7	1	3	32	32	16	19	17	11	18	5	161
20	1	7	—	1	40	47	22	27	27	30	19	8	229
21	—	—	—	1	26	44	27	32	21	24	17	2	194
22	—	5	—	—	27	43	48	31	35	32	11	2	234
23	—	3	—	—	15	31	50	47	38	36	3	—	223
24	—	—	—	—	7	16	41	25	31	36	2	—	158
25	—	—	—	—	1	3	24	24	13	9	1	—	75
26	—	—	—	—	1	1	18	10	21	7	—	—	58
27	—	—	—	—	—	—	10	6	6	1	—	—	23
28	—	—	—	—	—	—	5	2	1	—	—	—	8
29	—	—	—	—	—	—	—	—	1	1	—	—	2
Totals	309	309	309	309	309	309	309	309	309	309	309	309	3708

The differences show how closely the results of the two competitions agreed in their results for mean egg production month by month. Absolutely the differences are small, but relatively they are rather large in comparison with the average egg production of either of the two years, which is of course itself low in the winter months.

It does not seem worth while in this place to consider the magnitudes of these differences in comparison with that of the absolute values upon which they are based or to offer any theories concerning the causes of the observed discrepancies.

That the differences are statistically trustworthy may be seen from the fact that they are often several times as large as their probable errors, as is shown by the final column, in which the ratios have been obtained

TABLE 2

Distribution of birds according to number of eggs laid per month in 1914-1915.

Eggs laid	November	December	January	February	March	April	May	June	July	August	September	October	Annual total
0	152	103	133	47	8	4	3	11	12	25	69	190	757
1	20	14	12	18	1	1	2	2	5	9	16	23	123
2	10	12	16	16	1	—	—	—	1	5	6	14	81
3	16	17	22	15	2	1	1	4	6	3	3	12	102
4	13	13	13	19	2	1	1	—	2	4	5	12	85
5	7	18	15	24	5	4	2	3	2	9	5	13	107
6	18	23	11	21	5	—	1	6	2	1	3	10	101
7	9	17	14	18	8	3	3	4	2	4	4	7	93
8	14	13	15	30	10	2	6	—	3	4	2	8	107
9	14	10	10	18	3	5	8	4	6	8	5	7	98
10	15	15	14	21	13	9	3	5	5	1	6	7	114
11	12	16	11	12	14	7	3	5	5	5	10	4	104
12	18	8	16	20	8	5	2	7	9	7	6	6	112
13	10	11	12	12	16	10	7	7	7	8	12	6	118
14	7	7	8	17	21	25	9	4	9	11	11	7	136
15	13	16	8	21	27	19	6	5	9	8	17	7	156
16	6	12	5	14	23	26	10	4	6	10	20	8	144
17	3	17	14	12	22	30	7	4	11	17	23	8	168
18	4	9	8	12	29	32	13	12	16	24	24	7	190
19	5	12	8	2	39	43	25	12	17	14	25	7	209
20	1	5	6	5	42	39	22	17	22	29	29	6	223
21	6	5	3	1	33	40	45	45	23	36	32	4	273
22	—	1	1	—	15	23	39	41	41	50	16	1	228
23	1	—	—	—	18	25	50	50	36	40	13	1	234
24	—	1	—	—	8	13	42	53	39	25	6	—	187
25	1	—	—	—	1	5	29	33	41	10	6	—	126
26	—	—	—	—	1	2	23	23	25	5	—	—	79
27	—	—	—	—	—	1	10	11	10	3	—	—	35
28	—	—	—	—	—	—	2	2	2	—	1	—	7
29	—	—	—	—	—	—	1	1	1	—	—	—	3
Totals	375	375	375	375	375	375	375	375	375	375	375	375	4500

by dividing the differences by their probable errors.[4] Thus the performance of the birds at any stated time differed significantly in the two years. Just such differences should be expected. It is perhaps rather surprising that they are not larger. The birds are entirely different series of individuals. The conditions under which the birds were maintained prior to their installation in the contest probably differed somewhat. Finally, while conditions in the two years of the contest are intended to be as nearly as possible the same, it is quite clear that homologous months in two successive winters will rarely be identical in climatic conditions.

[4] Probable errors have been calculated by the conventional formulae, notwithstanding the abnormal nature of the frequency distributions.

TABLE 3

Mean number of eggs, and probable error of mean number of eggs, laid by all birds for each month.

Month	Mean eggs laid			
	1913-1914	1914-1915	Difference	Diff./E. Diff.
November	4.282 ± .197	5.368 ± .214	+1.086 ± .291	3.73
December	5.217 ± .262	7.219 ± .231	+2.002 ± .349	5.74
January	3.294 ± .178	6.056 ± .223	+2.762 ± .285	9.69
February	9.456 ± .204	8.104 ± .198	—1.352 ± .284	4.76
March	17.702 ± .155	16.125 ± .188	—1.577 ± .244	6.46
April	19.405 ± .140	17.701 ± .162	—1.704 ± .214	7.96
May	21.712 ± .141	20.339 ± .187	—1.373 ± .234	5.87
June	19.874 ± .198	20.080 ± .223	+ .206 ± .298	.69
July	19.379 ± .224	19.267 ± .239	— .112 ± .327	.34
August	17.919 ± .259	16.848 ± .263	—1.071 ± .369	2.90
September	9.133 ± .330	12.904 ± .291	+3.771 ± .440	8.57
October	4.262 ± .256	4.467 ± .223	+ .205 ± .339	.60

Table 4 gives the variation constants for number of eggs laid per month. Comparisons between the results of the two years may again be made by means of the difference column. Many of the differences are several times as large as their probable errors. Thus the variation in

TABLE 4

Standard deviations and probable errors of standard deviations of number of eggs laid per month by all birds.

Month	Standard deviation of eggs laid			
	1913-1914	1914-1915	Difference	Diff./E. Diff.
November	5.134 ± .139	6.140 ± .151	+1.006 ± .205	4.91
December	6.822 ± .185	6.644 ± .164	— .178 ± .247	.72
January	4.639 ± .126	6.408 ± .158	+1.769 ± .201	8.80
February	5.316 ± .144	5.687 ± .140	+ .371 ± .201	1.85
March	4.028 ± .109	5.399 ± .133	+1.371 ± .172	7.97
April	3.640 ± .099	4.660 ± .115	+1.020 ± .152	6.71
May	3.671 ± .100	5.360 ± .132	+1.689 ± .166	10.17
June	5.151 ± .140	6.392 ± .157	+1.241 ± .210	5.91
July	5.847 ± .159	6.874 ± .169	+1.027 ± .232	4.43
August	6.751 ± .183	7.556 ± .186	+ .805 ± .261	3.08
September	8.597 ± .233	8.365 ± .206	— .232 ± .311	.75
October	6.678 ± .181	6.397 ± .158	— .281 ± .240	1.17

egg production in the individual months must be considered to differ significantly in the two experiments. Such differences should be expected for the reasons set forth in the discussion of the means above. The question of the differences between the variabilities at comparable times in the two years or at various times in the same year requires no more detailed discussion here, where the chief value of the standard deviations is to furnish one step towards the correlation coefficients.

Correlation of pigmentation and egg production

Table 5 for 1913-'14 and table 6 for 1914-'15 give the frequency with which birds of different pigmentation classes occur in the two years and the total number of eggs laid by birds of these classes in each month and for the entire year of the two contests. From these totals the mean

TABLE 5

Frequency of birds showing various percentages of yellow and total number of eggs laid by them in each month and during the whole year 1913-1914.

Percent yellow	Number of birds	Total eggs												Annual total
		November	December	January	February	March	April	May	June	July	August	September	October	
10	12	75	108	64	140	234	257	278	247	275	265	224	202	2369
15	34	215	279	176	378	606	665	747	710	746	749	622	456	6349
20	37	220	304	172	402	707	710	848	818	811	759	624	426	6801
25	16	70	68	55	130	261	312	357	345	317	342	262	129	2648
30	20	56	105	86	203	340	342	422	379	390	377	205	64	2969
35	31	94	150	94	329	536	592	638	588	557	548	171	14	4311
40	34	127	134	90	295	591	680	725	634	673	593	219	5	4766
45	39	134	175	72	300	702	766	852	801	730	658	202	9	5401
50	38	132	135	83	327	653	726	808	713	679	597	150	9	5012
55	29	129	120	82	262	521	565	643	572	546	463	107	2	4012
60	13	71	34	44	119	213	264	273	218	203	151	31	—	1621
65	4	—	—	—	35	72	79	83	75	58	35	5	1	443
70	1	—	—	—	—	15	19	12	21	3	—	—	—	70
75	1	—	—	—	2	19	19	23	20	—	—	—	—	83

egg production of birds of a given class may be computed for any period, or data for the determination of the correlation between pigmentation and egg production may be deduced (HARRIS 1910).

Consider first the correlation for October pigmentation and egg production for the entire year.

The nature of the relationship between the concentration of yellow pigment in the ear lobe and the annual egg record of the bird may be most clearly exhibited to the statistically untrained reader by means of

TABLE 6

Frequency of birds showing various percentages of yellow and total number of eggs laid by them in each month and during the whole year 1914-1915.

Percent yellow	Number of birds	Total eggs												Annual total
		November	December	January	February	March	April	May	June	July	August	September	October	
10	1	11	20	3	20	20	19	25	24	22	18	23	10	215
15	29	186	284	241	278	483	551	619	614	622	542	591	409	5420
20	51	332	461	384	449	837	930	1141	1124	1087	1021	975	616	9357
25	24	136	228	192	225	401	417	511	539	515	464	447	270	4345
30	21	116	184	183	168	365	363	452	450	466	420	365	114	3646
35	27	165	203	219	261	469	467	525	534	529	487	428	122	4409
40	32	196	179	158	255	476	525	644	591	564	549	452	48	4637
45	39	182	280	195	317	648	745	798	832	792	728	554	44	6115
50	48	289	296	271	388	769	836	940	919	932	793	455	25	6913
55	44	199	267	193	293	655	748	864	794	682	634	360	4	5703
60	34	118	155	100	237	514	586	629	677	620	395	94	2	4127
65	12	44	70	62	67	188	208	231	226	237	192	67	1	1593
70	11	35	68	70	66	184	199	206	185	157	75	28	—	1273
75	1	—	5	—	8	18	22	19	—	—	—	—	—	72
80	1	4	7	—	7	20	22	23	21	—	—	—	—	104

TABLE 7

Mean number of eggs per year laid by birds showing different percentages of yellow in the two years. The number of birds upon which the averages are based is also shown.

Percent yellow	1913-1914		1914-1915	
	Birds	Mean eggs	Birds	Mean eggs
10	12	197.4	1	215.0
15	34	186.7	29	186.9
20	37	183.8	51	183.5
25	16	165.5	24	181.0
30	20	148.5	21	173.6
35	31	139.1	27	163.3
40	34	140.2	32	144.9
45	39	138.5	39	156.8
50	38	131.9	48	144.0
55	29	138.3	44	129.6
60	13	124.7	34	121.4
65	4	110.8	12	132.8
70	1	70.0	11	115.7
75	1	83.0	1	72.0
80	—	——	1	104.0

the averages of the annual egg production of birds of different pigmentation grades. The results are given in table 7.

The average number of eggs laid per year decreases rapidly from about 200 in birds with 10 percent of yellow to less than 150 in those with over 40-45 percent of yellow in the ear lobes.

The great practical value of the relationship as a means of selecting the best birds may be best seen by grouping these records.

The results are shown in table 7A. Here the birds with 10, 15 and 20 percent yellow are clubbed together, those with 25, 30 and 35 percent form a second group, and so on.

TABLE 7 A

Percent yellow	1913-1914		1914-1915	
	Birds	Mean eggs	Birds	Mean eggs
10—20	83	187.0	81	185.1
25—35	67	148.2	72	172.2
40—50	111	136.7	119	148.4
55—65	46	132.1	90	126.9
70—80	2	76.5	13	111.5

Neglecting the few birds recorded as possessing an unusually high percentage of yellow, i.e., 70-80 percent, it is clear that there are differences of the highest practical significance in the birds constituting the four groups which are sufficiently large to give trustworthy averages. By selecting in October for breeding purposes birds with 10-20 percent yellow, the poultryman will secure a group which have averaged over 30 eggs above the flock as a whole and over 50 eggs above the average of the class with 55-65 percent of yellow. It is to be noted that these differences are not merely very great indeed, but that the group of high-laying birds (10-20 percent yellow) is sufficiently large for economic purposes. Surely eighty birds out of every three or four hundred ought to be a sufficiently liberal number in practical selection operations.

The results may now be expressed in terms of correlation. Summing the products of the total annual egg production, E, by the grades of percentage of yellow, y, for the individual birds, we have

$$\text{For } 1913\text{-'}14,\ \Sigma\,(yE) = 1{,}603{,}225$$
$$\text{For } 1914\text{-'}15,\ \Sigma\,(yE) = 2{,}216{,}875$$

whence by the formula used (HARRIS 1910),

$$r_{yE} = \frac{\Sigma\,(yE)/N = \bar{y}\bar{E}}{\sigma_y\ \sigma_E}$$

where the bars denote the means and the sigmas the standard deviations as given above, we find numerically[5]

For 1913-'14, $N = 309$

$$r = \frac{\Sigma\,(yE)/N - 36.407769 \times 151.134306}{15.090082 \times 37.853644} = -.5816$$

For 1914-'15, $N = 375$

$$r = \frac{\Sigma\,(yE)/N - 40.640000 \times 154.477335}{16.078673 \times 43.222447} = -.5271$$

Thus the relationship between the October ear lobe pigmentation as measured in units of 5 percent range and the annual egg production of the domestic fowl is surprisingly high.

The differences for the two years in the intensity of the relationship is

For 1913-'14, r_{yE}	$= -.5816 \pm .0253$
For 1914-'15, r_{yE}	$= -.5271 \pm .0252$
Difference	$.0545 \pm .0358$

The difference is only about fifty percent larger than its probable error, and cannot be considered statistically significant. Conversely, the results for the two years may be considered practically identical.

The correlation coefficients show on the uniform standard scale of -1 to $+1$ the degree of interdependence of two variables, in this case the percentage of yellow in the ear lobe and the egg record of the domestic fowl. For many purposes measures on such a standard scale are of the highest value. For other comparisons it is desirable to determine not merely the relationship between percentage yellow and egg production on a *relative* scale but also to know just how much birds with different percentages of yellow differ in terms of actual mean number of eggs laid. Such absolute measures have the disadvantage that they are not comparable with measures of the same or other characters taken on the same or any other organism at any other place or time. Thus the two methods supplement each other. Fortunately it is possible to pass at once from relative measures in terms of correlation to absolute values in terms of regression.

[5] In the calculations involved in this paper all the operations have, of course, been carried to a larger number of places than are given in the tables.

The conventional formula, in terms of the present notation, is

$$E = (\bar{E} - r\frac{\sigma_E}{\sigma_y})\bar{y} + r\frac{\sigma_E}{\sigma_y}y$$

where E = eggs laid, y = percent yellow, the bars denote the mean values of the characters and the sigmas their standard deviations in the population as a whole.

The actual equations are

For 1913-'14, $E = 204.754 - 1.459\ y$
For 1914-'15, $E = 212.058 - 1.416\ y$

The second term of the equation shows the *decrease* in annual mean number of eggs laid for each *increase* of one percent of yellow in the ear lobe. Since determinations of yellow are recorded in units of 5 percent range, the second term may be multiplied by five to obtain the actual difference in egg production associated with a difference of one working unit in pigmentation. This will be noted to be about 7 eggs in both years.

These absolute changes may be represented graphically by the slope of a straight line. The points at which such a line cuts the ordinates erected upon the various percentages of yellow, mark off the theoretical mean number of eggs laid by birds of this grade of pigmentation. By theoretical mean number is to be understood merely the mean number which has been calculated from the trend of the data as a whole, on the assumption that the rate of change may be satisfactorily represented by the slope of a straight line. How satisfactorily it can be thus represented is most conveniently determined by a comparison of the theoretical, or smoothed, and the empirical means calculated directly from the data available for the particular class alone.

Such lines are shown for the two years in diagram 3. The actual means from table 7 above are also represented. The agreement of the empirical and theoretical means is not as good as might be wished, but it does not seem desirable on the basis of the present data to consider in any greater detail the precise form of the theoretical line which would best smooth these empirical averages.

Turn now to the interrelationship for the individual months.

The correlations between the percentages of yellow observed in October and egg production for the individual months are given for the two years in table 8.

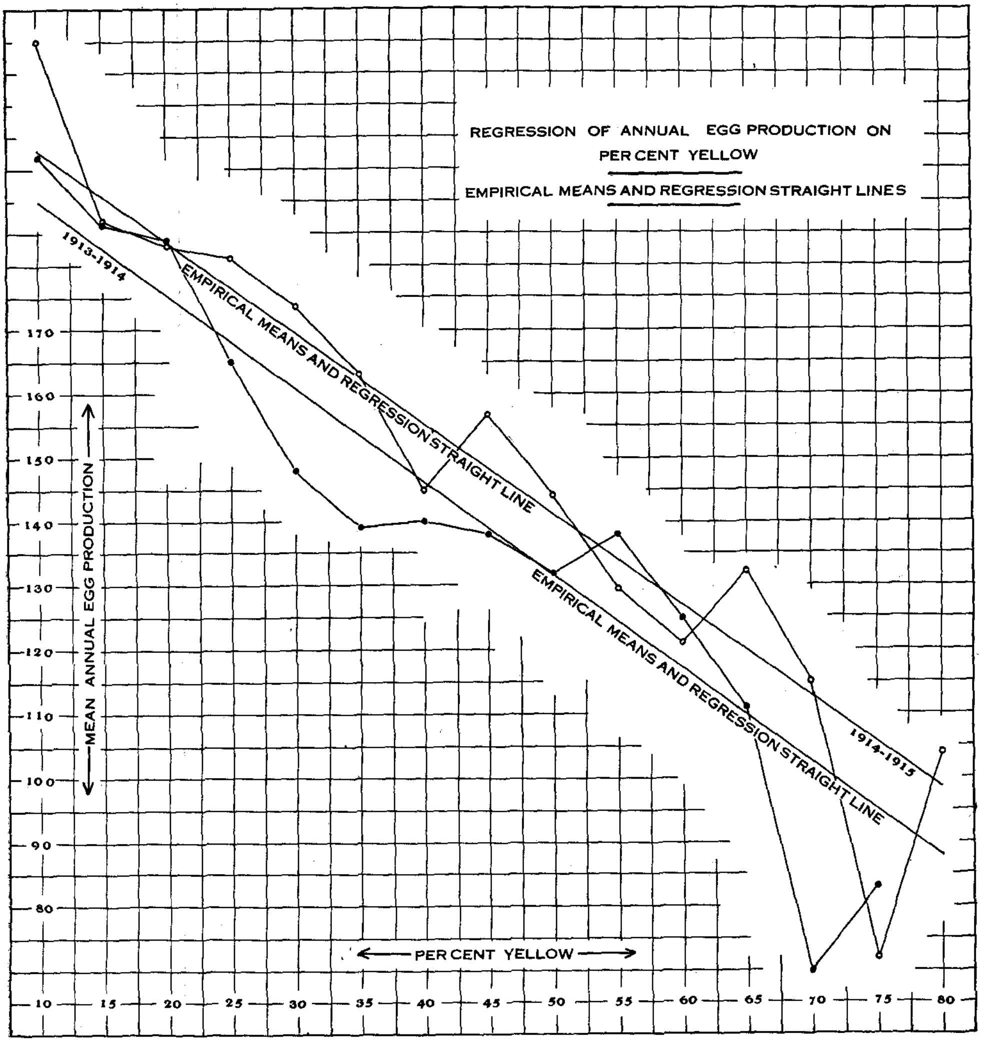


DIAGRAM 3.—Relationship between percent yellow in ear lobes in October and annual egg production. The closed and open circles show the observed mean numbers of eggs laid by birds with varying percentages of yellow. The straight lines represent the equations for the regression of egg production on percent of yellow. They show, on the same ordinates as the empirical averages, the smoothed (theoretical) means calculated from the data as a whole.

Before discussing the absolute magnitudes or the statistical significance of the constants for the individual months, we may draw attention to the consistency of the results for the two years. First of all, it is clear at a glance that although many of the coefficients are low, they are

TABLE 8

Correlations and probable errors of correlations between percent yellow in ear lobes in October and egg production for the individual months of the years, 1913-1914, 1914-1915, and their differences.

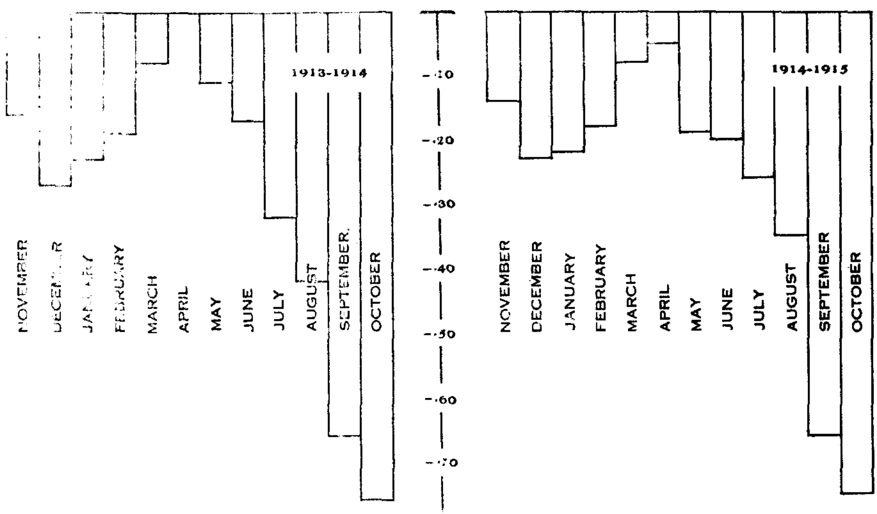
Month	Correlation 1913-1914	r/Er	Correlation 1914-1915	r/Er	Difference in correlation 1913-1914, 1914-1915	Diff./E. Diff.
November	—.167 ± .037	4.51	—.148 ± .027	5.48	—.019 ± .046	0.41
December	—.271 ± .036	7.53	—.230 ± .033	6.97	—.041 ± .049	0.84
January	—.229 ± .036	6.36	—.228 ± .033	6.91	—.001 ± .049	0.02
February	—.193 ± .037	5.22	—.176 ± .034	5.18	—.017 ± .050	0.34
March	—.086 ± .038	2.26	—.080 ± .035	2.29	—.006 ± .052	0.12
April	—.000 ± .038	0.00	—.056 ± .035	1.60	+.056 ± .052	1.08
May	—.114 ± .038	3.00	—.194 ± .034	5.71	+.080 ± .051	1.57
June	—.170 ± .037	4.60	—.202 ± .033	6.12	+.032 ± .050	0.64
July	—.324 ± .034	9.53	—.267 ± .032	8.34	—.057 ± .047	1.21
August	—.429 ± .031	13.84	—.354 ± .030	11.80	—.075 ± .044	1.70
September	—.663 ± .022	30.14	—.663 ± .020	33.15	+.000 ± .030	0.00
October	—.761 ± .016	47.56	—.751 ± .015	50.07	—.010 ± .022	0.45

negative throughout. Comparison of the results for the individual months is facilitated by the column giving the differences and their probable errors. In 8 cases the correlation for 1913-'14 is numerically larger than that for 1914-'15, in 3 cases it is smaller and in one month the coefficients are identical for the first three figures. The absolute magnitude of the differences is of relatively little importance if they are not statistically significant. By dividing these absolute differences by their probable errors, as has been done to obtain the values in the final column of the table, comparable measures of the significance of the differences are obtained. By common consent among statisticians a difference should be at least 2 or 2.5 times as large as its probable error to be regarded as significant—i.e. to be considered to be due to some other cause than the errors of random sampling merely. Of the ratios in this final column not a single one indicates a difference between the coefficients of the two years as much as twice its probable error, only 4 out of the 12 ratios are larger than unity, and the average value is only 0.70. In the discussion of the correlation *for the entire year* it has been shown that the coefficients are, *within the limits of the errors of random sampling,* identical. The results just given show that *in not a single instance can the correlations for the same individual months in the two years be considered to differ significantly.*

We must confess that this result is a matter of some surprise, as well as of gratification to ourselves. Knowing the difficulties of the work and realizing the possible sources of error we were quite prepared to find coefficients distributed with great irregularity and differing by many times their probable errors in the two series of observations. Instead we find results of a higher degree of consistency than are often secured in cases in which theoretically the most refined measurements may be made. A stronger proof of the general accuracy and trustworthiness of our work could not, we believe, be adduced.

As a further means of comparison of the results of the two years, and as a first introduction to the subject of the magnitude of the coefficients for the individual months, diagrams 4 and 5 have been prepared. The two graphs show that the coefficients for the same month in the two years are sensibly identical. They also show that the correlations differ widely from period to period, increasing from the earlier to the later months of the test.

The rate of increase from the first to the last month of the experiment is not, however, uniform. The correlation increases in numerical magnitude from November to December, then it diminishes until it is



DIAGRAMS 4 and 5.—Magnitude of correlation between October ear lobe pigmentation and egg production in the individual months of the two competitions. Distance which the bars extend below the zero line indicates the magnitude of the negative correlations.

practically non-existent in April, after which time it rises rapidly to its maximum value in October. Were there but a single series of data one might suspect the bimodal distribution observed, to be due to chance, but the remarkable agreement of the results for the two years at once throws out this possibility. Furthermore the relation of the constants to their probable errors is such as to leave little doubt concerning the reality of the bimodal nature of the distribution which as a whole shows pronounced skewness. With the exception of the months of March and April only, the constants are three or more times as large as their probable errors. Thus only in April may the correlations be said to be sensibly zero.

Before discussing in detail this question of the differences between the correlations for the various months of the year it seems better to express the results in terms of regression.

The equations appear in table 9. Since yellow is measured in units of five percent range, the amount of change to be expected for a deviation of one working unit has been added in the column headed "change per unit of yellow."

The empirical means for the individual months are calculated from the frequencies and total egg productions recorded in tables 5 and 6. The results are shown for the first three months, November, December

TABLE 9

Straight line equations showing the regression of number of eggs laid per month upon October ear lobe pigmentation.

Month	1913-1914		1914-1915	
	Regression equation	Change per unit* of yellow	Regression equation	Change per unit* of yellow
November	$E= 6.355-.057\ y$	.29	$E= 7.664-.057\ y$	.29
December	$E= 9.677-.122\ y$	.61	$E=11.083-.095\ y$	.48
January	$E= 5.860-.070\ y$	.35	$E= 9.755-.091\ y$	.46
February	$E=11.937-.068\ y$	.34	$E=10.628-.062\ y$	.31
March	$E=18.543-.023\ y$	.12	$E=17.219-.027\ y$	.14
April	$E=19.405-.000\ y$	.00	$E=18.359-.016\ y$	.08
May	$E=22.723-.028\ y$	.14	$E=22.965-.065\ y$	.33
June	$E=21.987-.058\ y$	.29	$E=23.343-.080\ y$	.40
July	$E=23.942-.125\ y$	.63	$E=23.902-.114\ y$	.57
August	$E=24.907-.192\ y$	.96	$E=23.605-.166\ y$	.83
September	$E=22.890-.378\ y$	1.89	$E=26.923-.345\ y$	1.73
October	$E=16.527-.337\ y$	1.69	$E=16.612-.299\ y$	1.50

* Unit = 5 percent.

and January, in diagram 6, for the months February, March and April in diagram 7, for the months May, June and July in diagram 8, for August in diagram 9, for September in diagram 10, and for October in diagram 11.

In these graphs the varying slope of the lines indicates the amount of change in egg production associated with variations of the amount indicated in the percentage of pigment. Since all are drawn to the same scale direct comparisons between them are possible. It is clear, for example, that the rate of change decreases from the first winter months of the experiment to April, when the line shows practically no slope and that it again increases until, in the late summer and early autumn months of August, September and October, the slope of the lines is very steep indeed. All this may be seen from the tables. The diagrams further show—and this is their greatest value—that for all the months excepting October, a straight line furnishes as good a graduation as could be expected from any curve of a higher order. To be sure there is great irregularity in the distribution of the empirical means about the theoretical means given by the straight line, but such discrepancy is regularly and necessarily found as a result of random sampling when

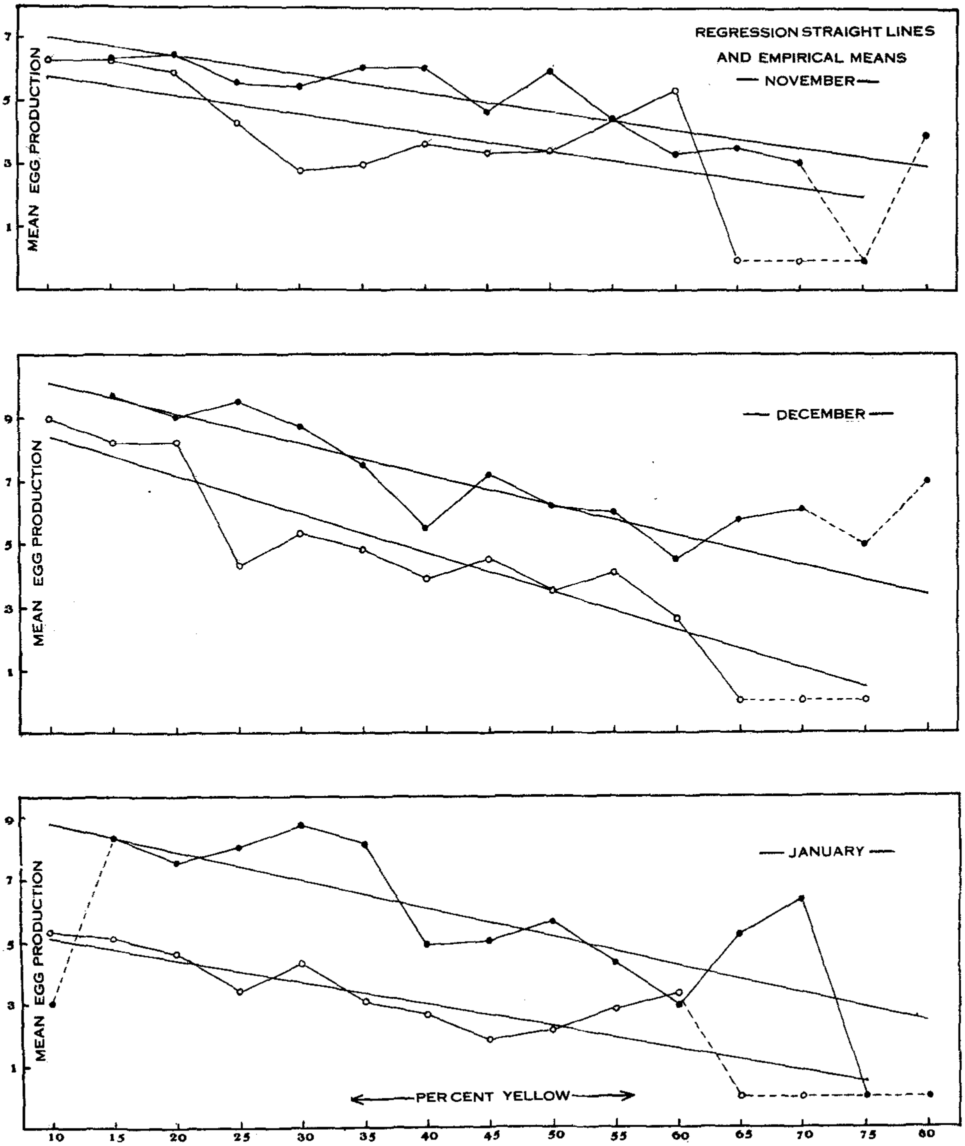


DIAGRAM 6.—Regression of egg production on percent yellow in ear lobes in October for the individual months November, December and January. Compare explanation of diagram 3.

the number of observations is not large and correlation is of a low order of magnitude.

To the exception to the rule of a sensibly linear relationship between

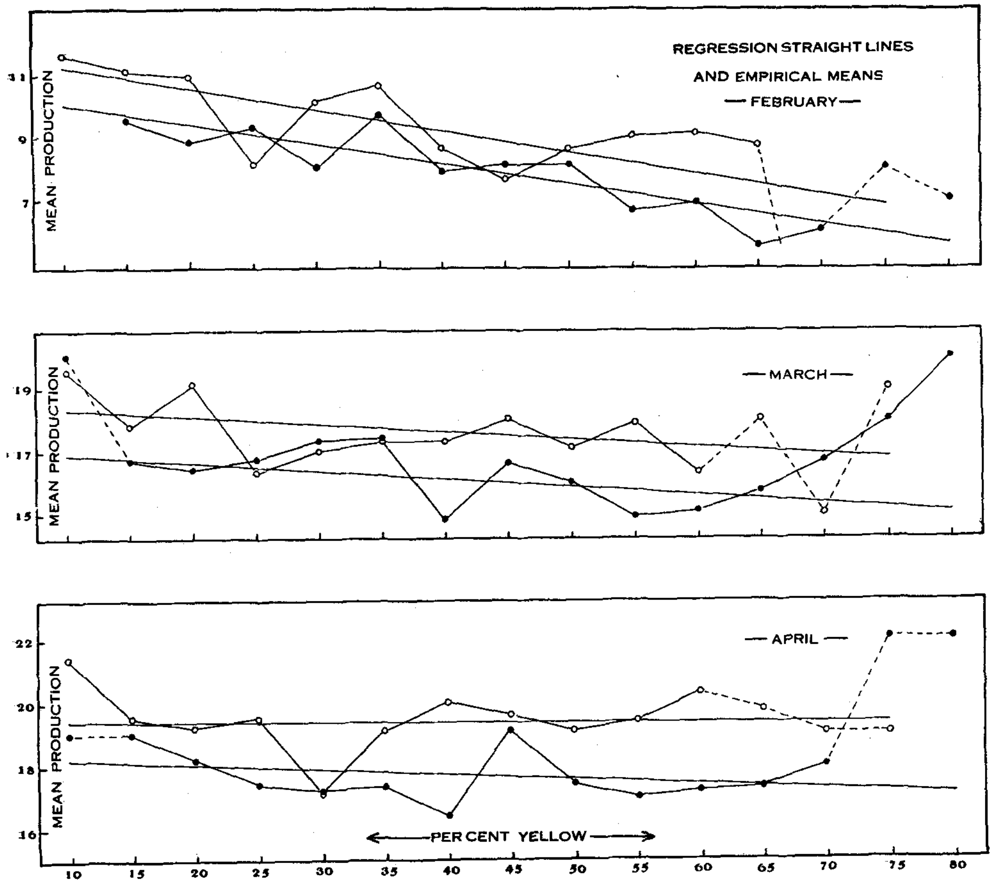


DIAGRAM 7.—Regression of egg production on percent yellow in ear lobes in October for the individual months February, March and April.

percentage of yellow and egg record we shall return in a subsequent section.

The maximum rates of change are found in the winter and autumn months. Thus in December there is a decrease of about half an egg for each increase of 5 percent in October pigmentation. In August, September and October the change is much greater. In March, April and May it is at a minimum.

ATTEMPTED ANALYSIS OF OBSERVED INTERRELATIONSHIPS

In this section we shall attempt by the means of further analysis to interpret certain of the relationships established in the foregoing pages.

One of the most suggestive peculiarities of the measures of inter-

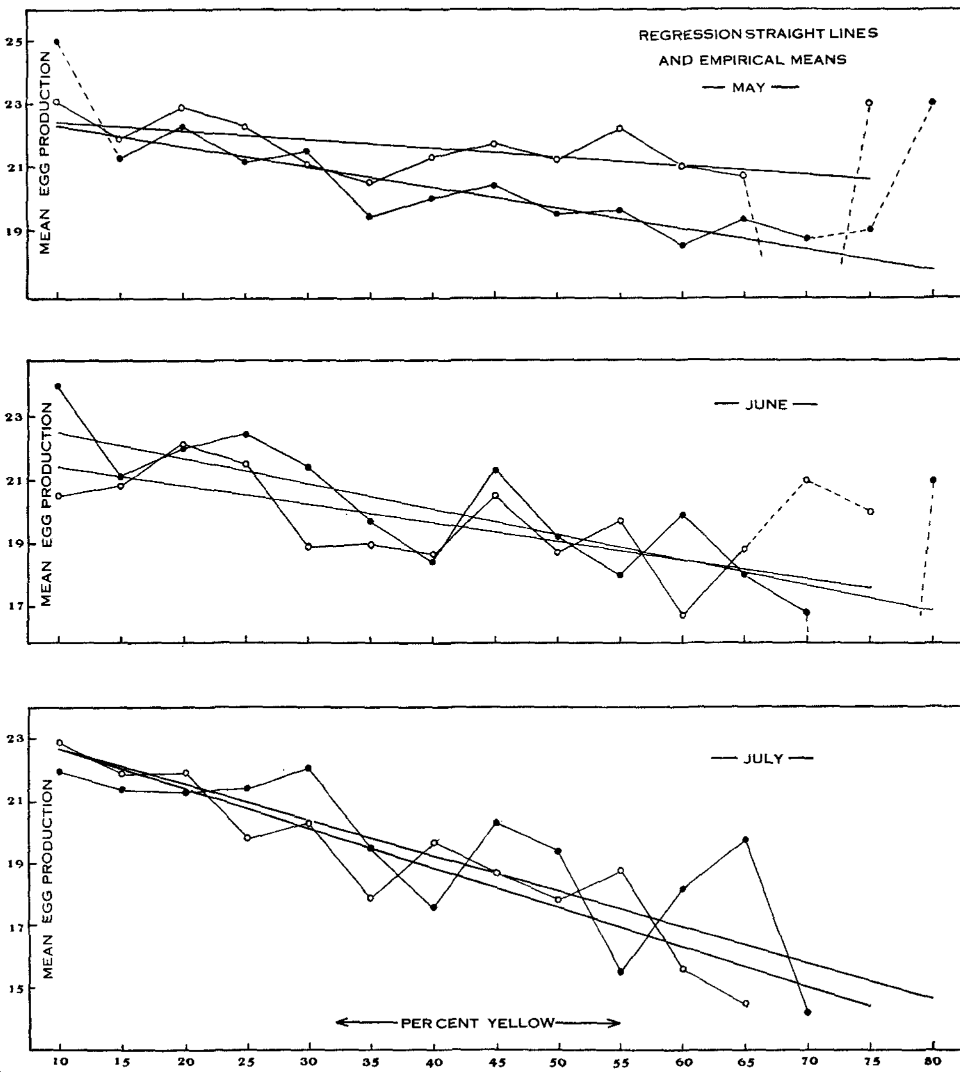


DIAGRAM 8.—Regression of egg production on percent yellow in ear lobes in October for the individual months May, June and July.

dependence of pigmentation and egg production is the difference in the intensity of this relationship exhibited by the several months of the year. If the relationship between pigmentation and egg production be a purely physiological one, at least in some of its essentials, one might expect that the highest correlations would be those determined when the two variables are closely associated in time. This has been shown to be, roughly speaking, the case. It is perfectly clear from the correlations

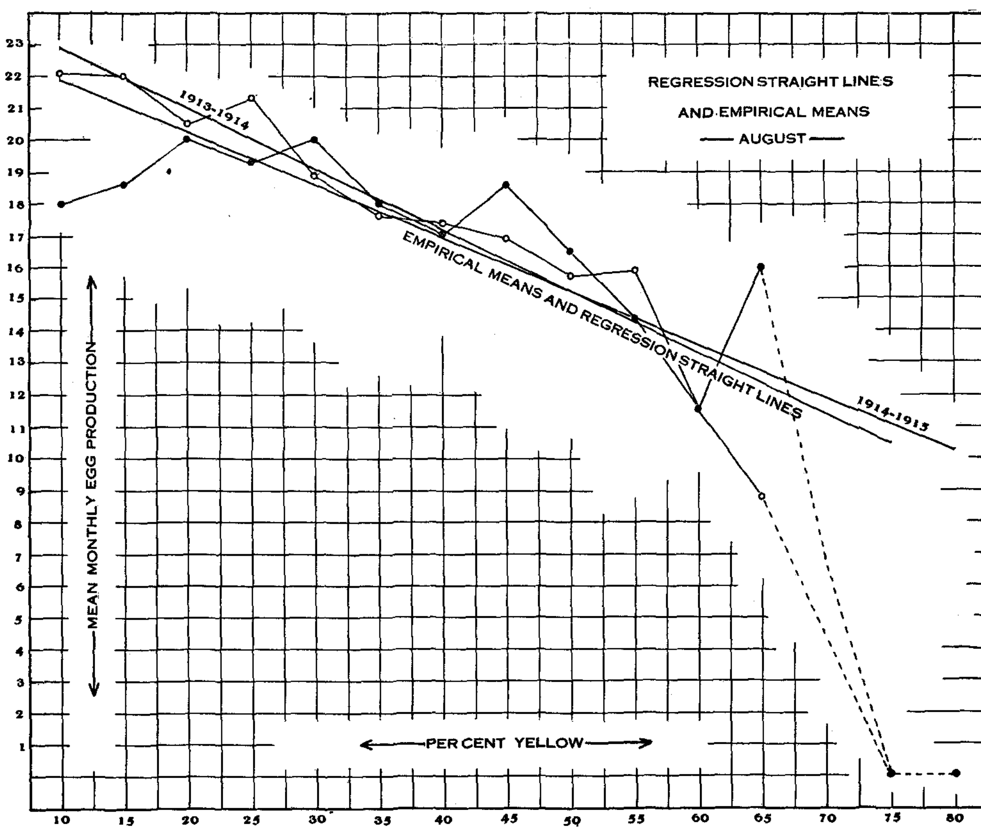


DIAGRAM 9.—Regression of egg production on percent yellow in October for the month of August.

given in table 8, from the regressions shown in table 9, or from the correlations represented in diagrams 4 and 5, or the regressions shown in diagrams 6 to 11, that the numerical magnitude of the interdependence increases toward the end of the experiment. To avoid any possible confusion the reader must always bear in mind that the pigmentation determinations were taken at the end, and (unfortunately) only at the end, of the egg-laying contest.

A priori the most logical hypothesis to account for the relationship observed would seem to be that the growth of the egg abstracts certain substances—in the present case the pigment—from the body tissues with a resulting negative correlation between egg production and quantity of pigment present. This would at once account for the generally

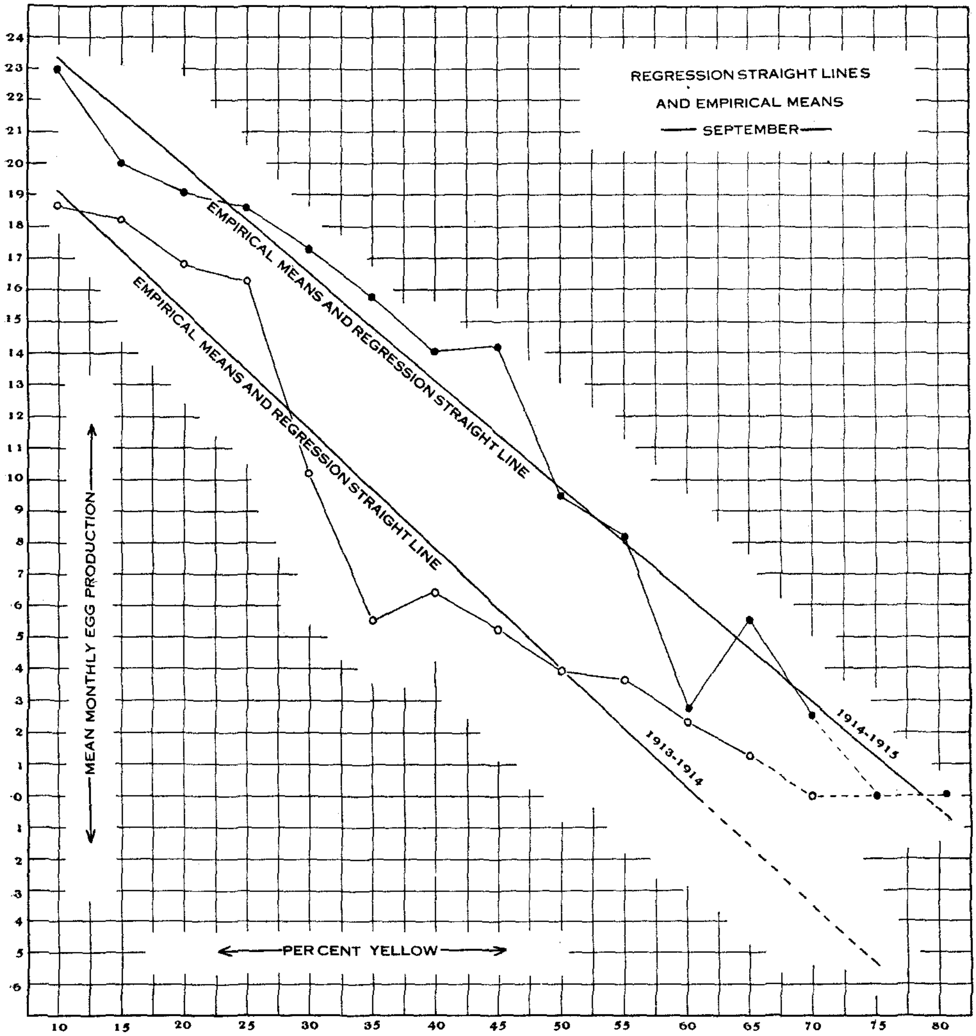


DIAGRAM 10.—Regression of egg production on percent yellow in October for the month of September.

higher correlation between measures made at more closely associated periods of time. If this hypothesis be true, one would expect the maximum correlation to come in or near whatever month the pigment determinations were made.

If this view be the correct one, the (relatively) independent variable would be egg production, the dependent variable would be pigmentation. Egg production would then be looked upon, provisionally at least, as the

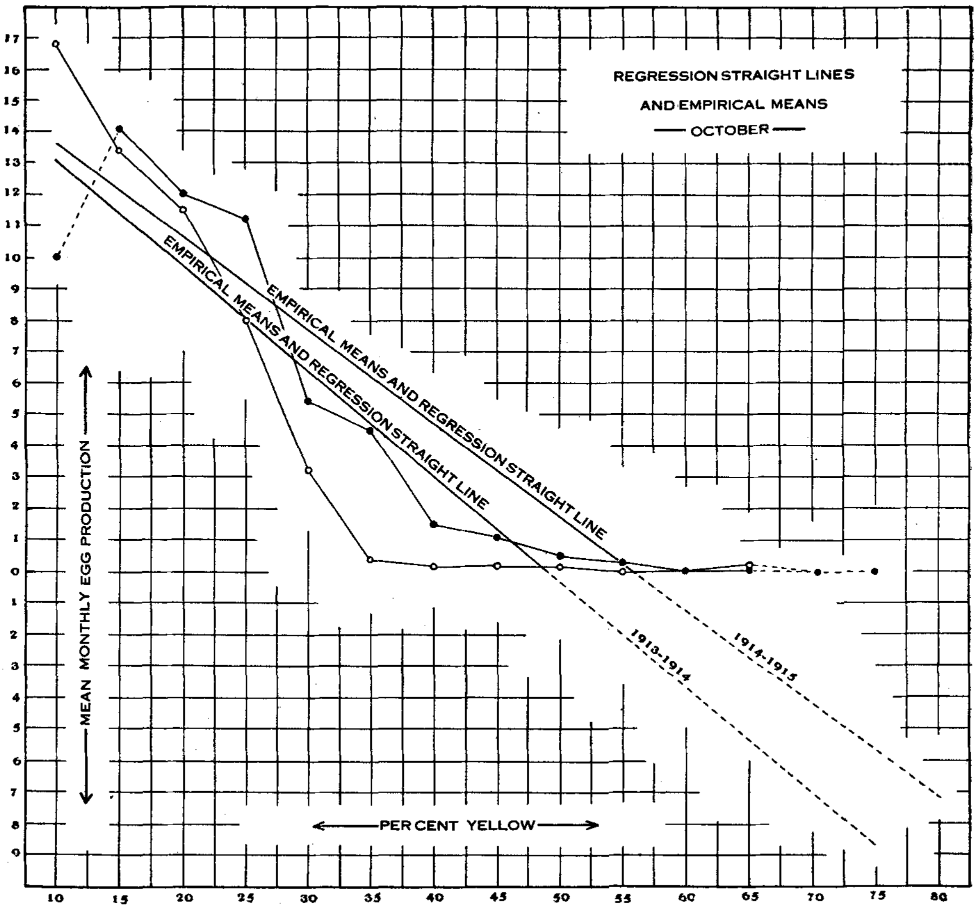


DIAGRAM 11.—Regression of egg production in October on the percent yellow in the ear lobes in the same month.

(chief) proximate cause of the observed intensity of pigmentation. Heretofore in this paper pigmentation has apparently been taken as the more fundamental character. This was not because we believed it to be so *physiologically*, but because we have been seeking to determine the prediction value of a somatic character for use in the selection of birds with a high egg record without actually determining that record by trap-nesting.

Bearing these considerations in mind it is most instructive to compare the distribution of yellow among the birds with different egg records when the egg records are taken in the same month as the pigmentation

TABLE 10

Percent yellow in October 1914 and egg production in November 1913.

November, 1913, egg production	October, 1914, pigmentation: 10	15	20	25	30	35	40	45	50	55	60	65	70	75	Totals
0	3	12	8	4	9	17	14	17	21	13	2	4	1	1	126
1		2	7	2	3	1	3	2	3	1	2				26
2	3	1		1		2			2						9
3			2	3	3	3	4	3	2		1				21
4			1				2	6	1	1	2				13
5			2	1			1	1		2	2				9
6		2	1	2	1	1	2	1		1	2				13
7		1	1			3	1	2		2					10
8		3	2		1			2	2	2					12
9	1	1			2		3			2					9
10		2	4	1				2		1					10
11	1	2				1	1	1	1	2					9
12	3	2	2	1	1	1	1	1							12
13	1		3						1	1					6
14			1			1	1		1						4
15		3	2					1	3	1					10
16		3				1	1		1		1				7
17			1												1
18				1											1
19															0
20											1				1
Totals	12	34	37	16	20	31	34	39	38	29	13	4	1	1	309

determinations and when the two determinations are separated by a wide interval of time.

The tables for November egg production and October pigmentation represent the most widely separated records. Those for October egg production and October pigmentation represent the most closely associated measurements of the two characters. These two months are, furthermore, particularly suited to our present purposes because in each case a very high and fairly similar percentage of the birds laid no eggs at all. The percentages of birds which laid no eggs are:

	November	October
1913-'14	40.78	59.87
1914-'15	40.53	50.67

For the remaining fecundity classes, the range of variation and the distribution of the frequencies as shown by the total columns are very similar.

TABLE 11

Percent yellow in October 1914 and egg production in October 1914.

October egg production	October pigmentation 10	15	20	25	30	35	40	45	50	55	60	65	70	75	Totals
0			2	3	10	25	32	34	33	28	13	3	1	1	185
1			1	2		2	1	3	3			1			13
2		1	1		3	2		1	1	1					10
3			1		1	1			1						4
4		1	1	1	1		1	1							6
5		1	2			1									4
6			2		1										3
7			1	1											2
8		2	2	1	2										7
9		3	4	1											8
10	1	2	1	1											5
11		4	2	2											8
12		1	1												2
13	2	1		1	1										5
14		3													3
15	1		2												3
16		2	1	1	1										5
17	2	3	5												10
18	2	5	1	1											9
19	2	2	1												5
20		3	4	1											8
21	1		1												2
22	1		1												2
Totals	12	34	37	16	20	31	34	39	38	29	13	4	1	1	309

The distribution of the birds in the bodies of tables 10 and 11 for 1913 and of tables 12 and 13 for 1914-'15, is however very different. In the case of the November production for each year the birds of all the different fecundities are scattered with a fair degree of uniformity over the whole range of pigmentation. In October, however, the birds which have laid no eggs at all show a distribution of yellow pigmentation which is far more heavily represented in the higher classes of yellow than are those which are laying. Furthermore it is quite evident from these tables that in October, pigmentation decreases very rapidly as one passes from birds which have laid no eggs to those which have laid 1, 2, 3 or more eggs, but that this decrease soon falls off so that birds which have laid over about 6 or 7 eggs are apparently sensibly alike in the amount of yellow which they exhibit.

The same point may of course be shown by computing the average percent yellow for birds of each class with respect to egg production. These are shown in diagrams 12 and 13.

TABLE 12

Percent yellow in October 1915 and egg production in November 1914.

November, 1914, egg production	October, 1915, pigmentation: 10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	Totals
0		10	16	8	6	11	12	17	19	20	21	7	4	1		152
1			1	2	3		2	2	3	2	1	1	3			20
2		1	1	1	2			1	1	1	1		1			10
3		1	3	2	1	2	2	3	1		1					16
4			2		1	1	1	1	1	3		1	1		1	13
5			3			1		1		1	1					7
6		2	2	2	1		3	1	2	4	1					18
7			3			2	1		1	1	1					9
8		2	3	2		1		3	1	2						14
9		2	2			1	2	2	4	1						14
10		4	2	1	1			1	2	2	2					15
11	1	2	1	1			1	1	3		1	1				12
12		1	2		2	3	2	1	3	3			1			18
13		1	4	1	1					1	1	1				10
14						2	1	1	1		1		1			7
15		2	1	1	1	2		2	1	1	1	1				13
16			1	2	1		1		1							6
17				1			1	1								3
18		1			1		1	1								4
19			1						2	2						5
20							1									1
21			2				1		2		1					6
22																0
23			1													1
24																0
25						1										1
Totals	1	29	51	24	21	27	32	39	48	44	34	12	11	1	1	375

The straight lines in these diagrams are calculated from the equations:

For November, 1913, $y = 38.514 - 0.492\ e$
For October, 1914, $y = 43.740 - 1.720\ e$
For November, 1914, $y = 42.720 - 0.388\ e$
For October, 1915, $y = 49.073 - 1.888\ e$

The minus quantities in these equations show that *if the rate of change in pigmentation were uniform from the lowest to the highest layers*, which it is not in October, the yellow decreases less than half a percent for each additional egg laid by a bird in November, but about one and three quarters percent for each egg laid in October.

It is quite clear that in the case of the November egg records the percent yellow changes but slowly and irregularly with egg production.

TABLE 13

Percent yellow in October 1915 and egg production in October 1915.

October egg production	October pigmentation 10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	Totals
0			3	2	5	10	19	22	35	37	33	11	11	1	1	190
1					2		4	8	5	3		1				23
2			1			1	2	1	6	2	1					14
3			1			4	1	4	1	1						12
4		1	1	2	2	4		1		1						12
5		1	3		4	2	1	1	1							13
6			3	1	1	1	3	1								10
7			1		3		2	1								7
8		5	1	2												8
9		1	2	3		1										7
10	1	1	3	1	1											7
11			3	1												4
12		1	2	2	1											6
13		2	3	1												6
14		3	2	2												7
15		3	2	1		1										7
16			4	2	1	1										8
17		1	5	1		1										8
18		2	5													7
19		3	2		1	1										7
20		1	4	1												6
21		3		1												4
22				1												1
23		1														1
Totals	1	29	51	24	21	27	32	39	48	44	34	12	11	1	1	375

whereas in the October series the yellow pigment falls very rapidly at first, but thereafter remains practically uniform up to the highest egg classes.

The biological inference to be drawn from this result would seem to be that the egg production of a recent period influences very profoundly the concentration of yellow pigment, so that there is a very rapid decrease in yellow pigment for each additional egg laid, up to a certain point, beyond which the body pigment is relatively little reduced by extra egg production. Thus for October the change in pigmentation is to be described by a curve, not by the slope of a straight line. The change in pigmentation is not proportional to egg production, but at first is very rapid and then falls off.

The point has been investigated in a somewhat different manner in our preliminary paper (BLAKESLEE and WARNER 1915 a, b). There a table is given showing the distribution of 932 records made on 317

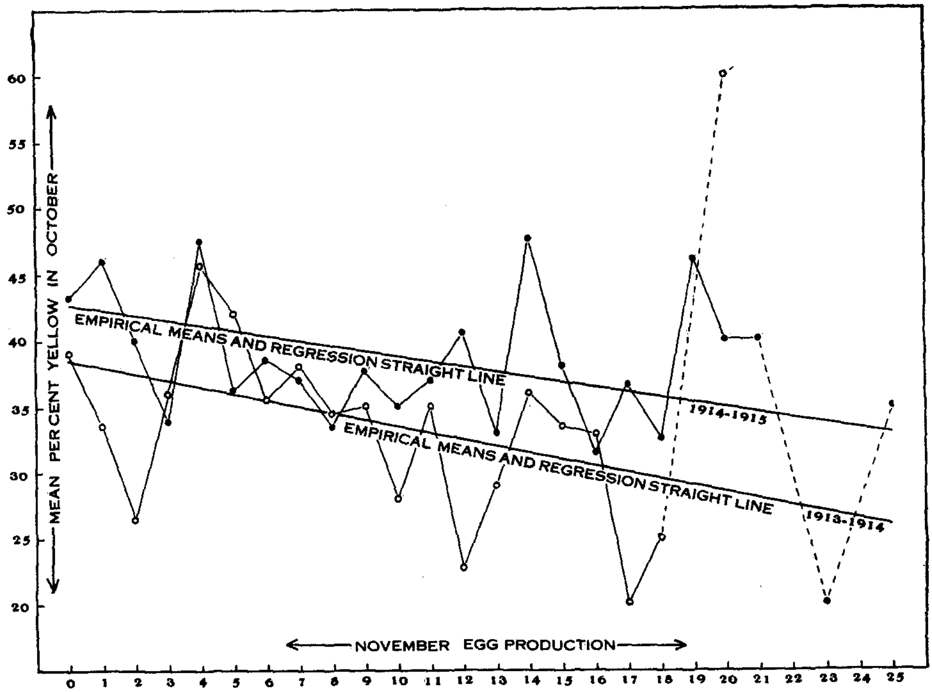


DIAGRAM 12.—Regression of percent of yellow in ear lobes in October on egg production of the *preceding* November. The closed and open circles show the mean percentage of yellow in October for birds laying various numbers of eggs in November. Note the very gentle slope of the lines and the great irregularity in the distribution of the empirical means. Compare diagram 13.

White Leghorns in three series of observations in October of the 1913-'14 competition. The records summarized in this table were made to show the length of time since laying for birds of the various pigment grades. In collecting these data a bird which laid on the day the pigment determination was made or on a later day within the month was considered to be laying, and was recorded in the zero class, i.e., no days since laying. If she laid on the day before the record was taken but not later she is recorded as one day since laying, and so on.

In the table, the results of which are represented graphically in diagram 14, the data are treated in two ways. First of all, the percentage of the birds of various pigmentation classes which are "laying" or "not laying" at the time the color determinations were made, is given. These are represented by the ordinates connected by the light line in the diagram. The percentage of the birds which are laying falls precipitously

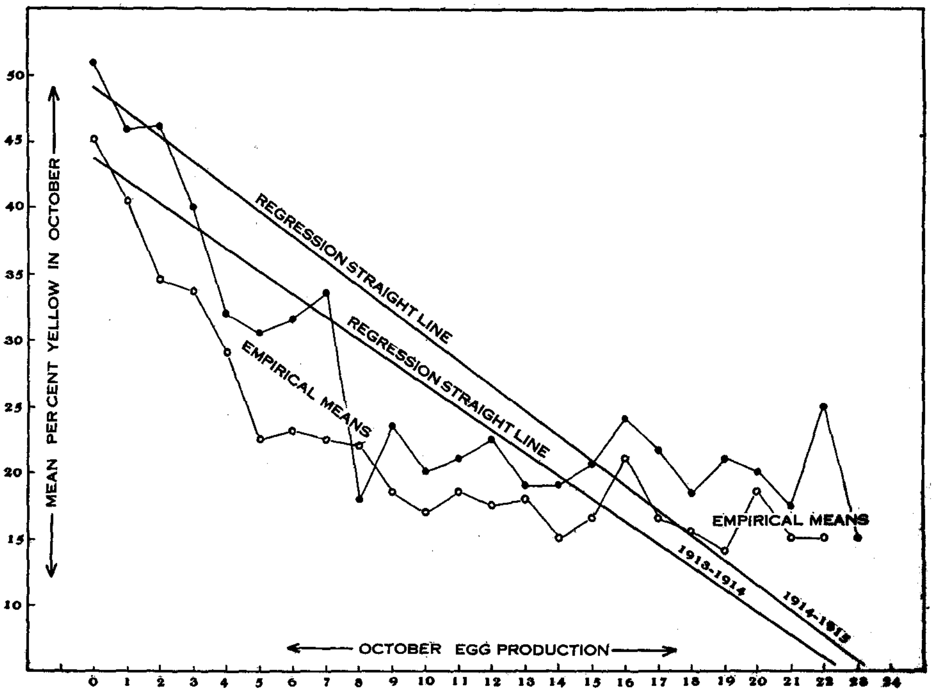


DIAGRAM 13.—Regression of percent of yellow in ear lobes in October on egg production for the same month. Note that as egg production increases the mean percentage of yellow decreases very rapidly, not slowly as in the case of the regression of October pigmentation on the egg production of the preceding November as shown in diagram 12. Note also that the change in percent of yellow is not a uniform one, as is approximately true in the case of the relationship shown in diagram 12, but that the rate of decrease falls off as the heavier-laying classes of birds are reached.

from 87.8 percent among those showing only 6-10 percent yellow, to practically zero for all grades of yellow above 30 percent.[6]

The average number of days since laying has also been computed. This is shown by the heavy line in the diagram. Beginning with an average of only .4 day since laying, in the 6-10 percent color class, the average length of time since laying increases rapidly. Probably the irregularity just before the upper limit of 71 days is due to the small number of records.

[6] The three cases of laying, among 557 records, in the grades above 30 percent yellow were for sporadic layers. The one in the 40 percent group laid October 18, but at no other time in October or September. This case may perhaps be an error in the egg record. One of the two in the 50 percent grade laid during October only on the 2nd, 4th and 25th, though she laid 18 eggs in September; the other laid during October only on the 16th and 19th and had no eggs to her credit in the second half of September.

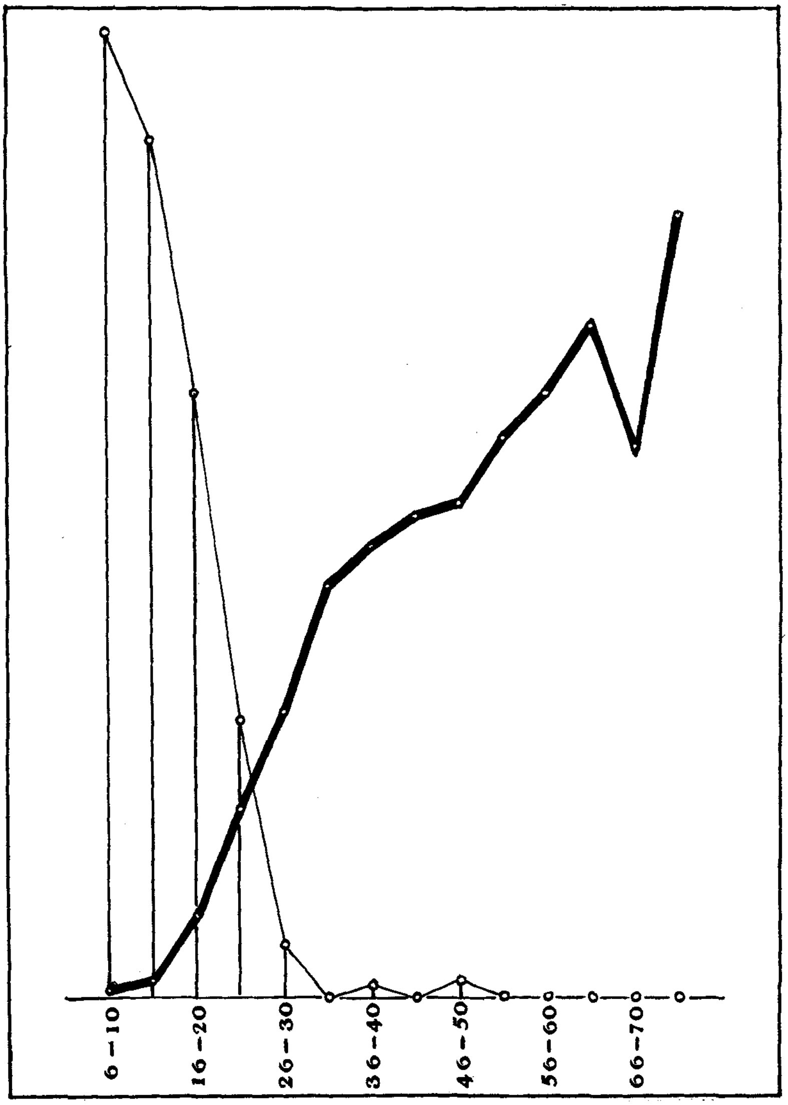


DIAGRAM 14.—Percentage of birds which are laying (light line) and mean number of days since laying (heavy line) in birds with different grades of ear lobe pigmentation.

We now turn to a different aspect of the problem.

If the relationship between percentage of yellow and egg production be chiefly of a physiological nature, it is quite conceivable that the correlations between the October percentage of yellow and egg production during the earlier months of the experiment, may be largely the resultant of other interrelationships. Let us consider this possibility in detail.

Yellow pigment is closely correlated with October egg production. Inspection of the values of the correlation coefficients for percentage yellow and egg production of the individual months shows that the correlation decreases as the monthly egg record becomes farther distant in time from the date of color determination. The decrease is not a uniform one.

If the October egg production of a bird be correlated with her egg production for each of the preceding months of the experiment, then these two interrelationships would tend to bring about a correlation between October pigmentation and the egg production of every other month in the year.

A quantitative measure of the influence of this factor may be secured as follows:

Let r_{ye_1}, r_{ye_2}, $r_{ye_3} \cdots r_{ye_{12}}$ be the correlations between percent yellow in the twelfth month of the contest and egg production in the first, second, third ... twelfth months respectively. Further let $r_{e_{12}e_1}$ $r_{e_{12}e_2}$, $r_{e_{12}e_3} \cdots r_{e_{12}e_{11}}$ be the correlations between October and November, October and December, October and January ... October and September egg productions. If now the values of r_{ye_1}, r_{ye_2}, r_{ye_3} $\cdots r_{ye_{11}}$ be in large part the resultants of $r_{e_{12}e_1}$ and $r_{ye_{12}}$, $r_{e_{12}e_2}$ and $r_{ye_{12}}$, $r_{e_{12}e_3}$ and $r_{ye_{12}} \cdots r_{e_{12}e_{11}}$ and $r_{ye_{12}}$, material reductions in the values of r_{ye_1}, r_{ye_2}, $r_{ye_3} \cdots r_{ye_{11}}$ should result from the rendering constant of the variable e_{12}. Hence applying the well known partial correlation formula for one variable, e_{12}, constant we have:

$$_{e_{12}}r_{ye_1} = \frac{r_{ye_1} - r_{ye_{12}} r_{e_{12}e_1}}{\sqrt{1 - r_{ye_{12}}^2}\sqrt{1 - r_{e_{12}e_1}^2}},$$

$$_{e_{12}}r_{ye_2} = \frac{r_{ye_2} - r_{ye_{12}} r_{e_{12}e_2}}{\sqrt{1 - r_{ye_{12}}^2}\sqrt{1 - r_{e_{12}e_2}^2}},$$

$$_{e_{12}}r_{ye_3} = \frac{r_{ye_3} - r_{ye_{12}} r_{e_{12}e_3}}{\sqrt{1 - r_{ye_{12}}^2}\sqrt{1 - r_{e_{12}e_3}^2}},$$

$$\vdots \qquad \qquad \vdots$$

$$_{e_{12}}r_{ye_{11}} = \frac{r_{ye_{11}} - r_{ye_{12}} r_{e_{12}e_{11}}}{\sqrt{1 - r_{ye_{12}}^2}\sqrt{1 - r_{e_{12}e_{11}}^2}}.$$

The evaluations of these equations require merely the calculation of 24 new correlations, the values of $r_{e_{12}e_1}$, $r_{e_{12}e_2}$, ... $r_{e_{12}e_{11}}$ for the two years. These constants are given in table 14. They are positive throughout, indicating that birds which excelled in egg production in October gave on an average higher productions in every other month of the year. The intensity of the correlations, however, varies greatly from the first to the eleventh month. This point does not, however,

TABLE 14

Correlation between October egg production and the egg production of the other eleven months of the year.

Correlation between October and:	1913-1914	1914-1915	Differences	Diff./E. Diff.
November	.219 ± .037	.139 ± .034	—.080 ± .050	1.60
December	.333 ± .034	.253 ± .033	—.080 ± .047	1.70
January	.255 ± .036	.236 ± .033	—.019 ± .049	.39
February	.219 ± .037	.207 ± .033	—.012 ± .050	.24
March	.139 ± .038	.130 ± .034	—.009 ± .051	.18
April	.043 ± .038	.116 ± .034	+.073 ± .051	1.43
May	.207 ± .037	.217 ± .033	+.010 ± .050	.20
June	.265 ± .036	.170 ± .034	—.095 ± .050	1.90
July	.326 ± .034	.271 ± .032	—.055 ± .047	1.17
August	.365 ± .033	.305 ± .032	—.060 ± .046	1.30
September	.694 ± .020	.579 ± .023	—.115 ± .030	3.83

especially concern us in this place. The results for the two years are very closely similar. In only one case is the difference between the coefficient obtained for the 1913-'14 and the 1914-'15 competition twice as large as its probable error. The results are generally lower in 1914-'15 than in the first of the two competitions.

Inserting these values (kept to a larger number of decimal places) in the above equations, we find the results set forth in table 15.

The results are also represented graphically in diagrams 15 and 16. Here the bars on the negative side of the zero bar indicate by their lengths the magnitude of the (negative) correlation between October pigmentation and egg production for the 12 individual months of the year. In this feature the diagram is merely a repetition of diagrams 4 and 5, above. The shaded areas superimposed upon these are the partial correlation coefficients from table 15.

The magnitudes of the interrelationships have been very greatly reduced by correcting for variable egg production in October. Since the correlation so nearly disappears in the early months when correction is made for October egg record, it seems reasonable to conclude that the correlation between yellow pigment in October and egg production in the earlier months of the year cannot be looked upon as indicating that there are strains of birds characterized by lighter pigmentation that are better layers, and that a mixture of all these strains in the flock results in correlations of the kind which we have demonstrated. The indications are rather that egg production in the earlier months is related to October pigmentation because the birds which are better layers in the early months are also better layers in the fall months, and because October egg production is closely correlated with October pigmentation.

TABLE 15

Partial correlations and probable errors of October pigmentation and egg production in remaining eleven months for constant October egg production.

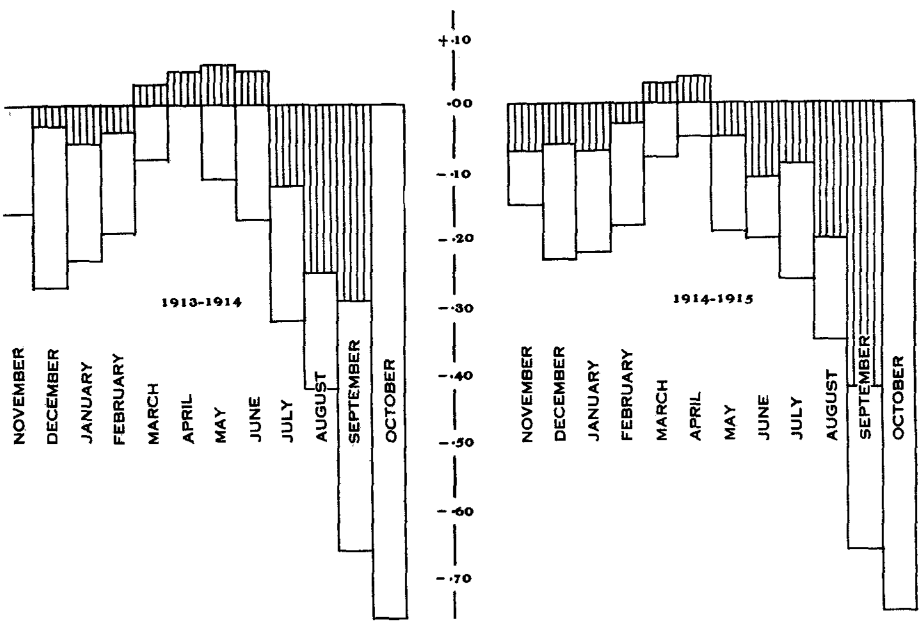
Month	Partial correlation and probable error	
	1913-1914	1914-1915
November	—.001 ± .038	—.067 ± .035
December	—.029 ± .038	—.064 ± .035
January	—.056 ± .038	—.079 ± .035
February	—.042 ± .038	—.031 ± .035
March	+.030 ± .038	+.027 ± .035
April	+.051 ± .038	+.048 ± .035
May	+.068 ± .038	—.048 ± .035
June	+.051 ± .038	—.114 ± .034
July	—.123 ± .038	—.099 ± .035
August	—.251 ± .036	—.199 ± .033
September	—.289 ± .035	—.424 ± .029

That the correction for October egg production should not so nearly eliminate the correlation between October pigmentation and the egg production of the immediately preceding months, say August and September, is perhaps due to the fact that eggs developed and laid in these months or developed in these months and laid in a subsequent month, must—if the purely physiological theory be the correct one—influence profoundly the pigmentation measured in October.

BIOLOGICAL HYPOTHESES IN EXPLANATION OF THE OBSERVED CORRELATIONS

While the primary purpose of this paper has been the presentation of data and the statistical constants showing the relationship between body pigmentation (ear lobe pigmentation only, in the present paper) and egg production deduced from them, it is proper to refer briefly to the underlying physiological causes of the demonstrated relationships.

The simplest hypothesis is, as pointed out above, that in heavy laying the large quantity of yolk substance produced removes the yellow pig-



DIAGRAMS 15 and 16.—Correlations between October pigmentation and egg production for individual months (unshaded polygon) and partial correlations between October pigmentation and egg production for the individual months (shaded polygon). In the partial correlations, the influence of the correlation of the egg production of November to September with that of October upon the correlation of the egg record for November to September with October pigmentation is eliminated.

ment from the somatic tissue more rapidly than it can be replaced. This is the suggestion offered in an anonymous press letter (1914) from the MAINE AGRICULTURAL EXPERIMENT STATION and by BLAKESLEE and WARNER (1915 a, b).

Since we have been unable to contribute purely chemical data to the problem, it will be sufficient to point out merely that such observations as have been reported by others from the field of physiological chemistry are quite consistent with the above view.

The nature of the pigment of the ear lobe of the domestic fowl has not been directly demonstrated, but BARROWS (1914) finds that the yellow shank color is due to yellow fat deposits in the Malpighian layers of the epidermis. It seems most reasonable to consider the color of the ear lobe due to an identical fat-soluble pigment.

While concerned primarily with the problem of fat deposition in, and fat absorption from, the egg, RIDDLE (1911, pp. 475-476) in discussing the mechanism of pigment deposition, says:

"As a concluding word on the rôle of the partition coefficient we record our belief that it alone accounts for the presence of the yolk coloring matter—vitello-lutein and vitello-rubin—in the yellow yolk and not in the white. These are lipochrome pigments, soluble only in fat and fat solvents and are abundant in the large yolk spherules, probably because, as we have shown by comparative analyses, these spherules abound in fat."

Turning now to the more purely chemical literature it is important to note that SCHENCK (*fide* PALMER 1915) as early as 1904 indicated that the pigment of the yolk of the egg and of the blood serum of the hen is identical with one of the forms of xanthophyll,—L-xanthophyll,—which he had isolated from plant tissue. More recent work by WILLSTÄTTER and ESCHER (*fide* PALMER 1915), who have isolated the pigment from the yolks of 6000 hen's eggs, leads them to the conclusion that the principal coloring material of the fowl's egg is isomeric with the crystalline xanthophyll of the chloroplast. PALMER (1915) from his chemical and feeding studies holds that xanthophyll is the principal natural pigment of the egg yolk, body fat and blood serum of the hen, just as he and one of his associates (ECKLES) earlier showed that carotin is the natural pigment in the corpus luteum, body fat, blood serum and milk fat of the cow.

The chief interest of these studies in the present connection is that they indicate *the identity of body and yolk pigment,* thus supporting the view that the correlations here demonstrated rest primarily upon physiological phenomena of the migration of fat-soluble yellow pigment.

The best source of information concerning the mechanism of pigment redistribution is work on feeding of Sudan III and other substances capable of staining fat in the living organism initiated in the investigation of the physiology of the bird by RIDDLE (1907, 1908, 1910, 1911) and continued by GAGE and GAGE (1908), MENDEL and DANIELS (1912), ROGERS (1912) and others. Those who are interested in the details of this subject from the standpoint of the physiological chemist must turn to the original papers. For the purposes of the present paper it is sufficient to point out that in the later rapidly developing stages of the yolk of the fowl's egg Sudan III will be taken up from the alimentary canal in large quantities. Indeed, RIDDLE has shown that, with heavy feeding, perceptible amounts of the stain will appear in the egg at the end of two or three hours. As the studies of GAGE and GAGE (1908) and others have shown, the Sudan III may be transferred from the yolk fat to that of the young chick.

The generalization to be drawn from the many varied experiments with Sudan III is that while in the animal body it clings at all times to the fats or their constituent fatty acids, and so goes quite mechanically wherever these particles go. This does not, however, preclude the possibilities of differential distribution of the pigment throughout the body. Nor does it preclude the possibility that the fat of the egg may withdraw pigment from the fat of the body tissues.[7] The ovum of the fowl has not merely the capacity of taking up the fat (and with it the Sudan III stain) from recently injected food, but of developing at the expense of body (stored) fat as well.

For the purposes of the present discussion nothing need be said concerning the manner in which either the fat or the fat-soluble pigment which goes along with it, is carried in the blood, or concerning the mechanism of its distribution throughout the body, or of its translocation from body tissues to the yolk. For all such data, which are as yet far from complete, the reader must consult the original physiological literature.

RECAPITULATION

The present paper is a contribution to the general problem of the relationship between somatic characters and fecundity. Specifically it presents and analyzes by means of the modern higher statistics, data bearing upon the relationship between the concentration of yellow pigment in the ear lobe of White Leghorn hens and their egg records of the preceding months.

The data comprise pigmentation evaluations and egg records for 309 and 375 birds entered in the 1913-'14 and 1914-'15 International Egg-Laying Contest held at Storrs, Connecticut.

[7] A quite analogous case of the withdrawal of the pigment from the tissues by the developing egg is furnished by the natural pigment of the egg of salmon. It is practically certain that here the natural coloring matter is derived from the muscles of the fish, from which the fat in which most if not all the coloring matter resides, is transferred to the ovary and to the growing eggs.

The egg records cover a period of one year, November to October, inclusive, of the pullet year. Pigmentation determinations were made in October, that is at the close of the laying period considered. The measures of yellow pigment concentration were obtained by the use of the white and yellow sectors of the color top. The ear lobe was selected for measurement because it presented the least practical difficulty in the quantitative measurement of pigmentation. The results here presented will be confirmed by more qualitative determinations made for these and other birds on the leg, beak and vent.

Incidental to the discussion of the main problem, considerable series of constants for mean fecundity and for variation and correlation in fecundity in the White Leghorn are given. For these the reader must refer to discussions in the body of the paper. With regard to the central problem, the statistical analysis of the data leads to the following conclusions:

There is a very close interdependence between October ear lobe color and the egg production of the year. Numerically the correlation, measured on the universally applicable scale of -1 to $+1$, is expressed by a constant of the order $r = -.550$. The negative sign indicates that *higher* concentrations of yellow pigment are associated with *lower* annual egg record. The results for the two years are in close agreement.

Expressed in absolute instead of relative terms, the correlations determined indicate that on an average birds differing by 5 percent in the amount of yellow in the ear lobe will differ by about 7 eggs in their annual production. Thus the difference is one of very real practical significance. For example, birds showing only 10-20 percent of yellow in their ear lobes in October will have laid on an average about 185 eggs each, whereas, birds exhibiting 55-65 percent of yellow will have an average annual production of only about 130 eggs.

The correlations between October pigmentation and the egg production of each month of the year have also been determined for the two years. All of these coefficients are negative in sign. Thus they show that a high percentage of yellow in October indicates lower egg production not merely in the year as a whole, but in each individual month of the year as well. Almost without exception these coefficients may be considered significant in comparison with their probable errors. The results for the individual months are in remarkably good agreement in the two years. In not a single case can the differences between the constants for the same month in the two competitions for which data are available be considered greater than those to be attributed to experimental errors.

While all the correlations between October pigmentation and the egg production of the individual months are negative in sign, they differ greatly in magnitude. Beginning with a correlation of about —.150 in November, the intensity of the relationship increases numerically to about —.250 in December, after which it falls to practically zero in March and April, and then increases in (negative) intensity rapidly to about —.750 in October.

The fact that roughly speaking the correlation increases in intensity as the two variables become more closely associated in time, suggests that the correlation demonstrated is of a purely physiological nature. The hypothesis that the growth of the egg abstracts certain substances—in the present case, yellow pigment—from the body tissue, or precludes its being deposited there, would at once account for the generally higher correlation between measures made at more closely associated periods of time.

If this view be the correct one, egg production must be regarded as the (relatively) independent variable, and intensity of pigmentation as the dependent variable. Egg production would then be looked upon as the chief proximate cause of the observed intensity of pigmentation.

For a detailed discussion of a number of lines of evidence for this view, the reader must consult preceding pages.

The fact that pigmentation has throughout this paper apparently been taken as the more fundamental character must not suggest that it has ever been considered by the authors to be such *physiologically*. Any such emphasis results merely from the fact that we have been seeking to determine the prediction value of a somatic character for use in the selection of birds characterized by high egg production without actually determining their record by trap-nesting.

Finally those who may be interested in the practical application of the results here secured must bear in mind the fact that the flocks from which our data were obtained represent a selected class of birds. Only groups of birds which are supposed to be the most promising are placed in the competition. The birds in the contest show, because of better breeding, better feeding and care, or both, a far higher annual egg production than those of the average flock. Unfortunately data of the kind presented here are not as yet available for the unselected class of layers.

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