ON THE SIGNIFICANCE OF SOME CHARACTERISTICS OF EGG PRODUCTION IN BREEDING UTILITY BREEDS OF POULTRY [1] [2]

M. VAN ALBADA
(State Poultry Institute, Beekbergen, the Netherlands)

SUMMARY

A statistical investigation was instituted among White Leghorn chickens, to examine the correlations between some characteristics of egg production, and again between them and total production in the first production year. This investigation concerned successively a random sample from a specific breeding establishment and the entire White Leghorn breeding stock of the State Poultry Institute for the years 1947 to 1952. The investigation showed that productivity as a whole was influenced considerably not only by the length of the production year (and this, in particular, in so far as it was dependent on the age at which laying ceased), but also by the average length of the laying cycle.

In addition to the interrelation of the various production characteristics, their heritability, and consequently their significance in breeding for egg production, were also studied with reference to the Institute's White Leghorn stock, already referred to. In this connection, it was found that selection of the dams for the characteristics of age at first egg, age at last egg, and average length of laying cycle (even when the last-mentioned factor was measured only in the first two months of production) was bound to be considerably more effective in the case of this material than selection for egg production, expressed in numbers of eggs or weight of eggs in kg, over a period extending to 1st. February or 1st. October of the year following year of birth.

As regards the practical side of trapnesting, it follows from this that, if it is desired to apply a partial check during the first laying year, a daily check throughout some months at commencement of production, followed by checking on a limited number of days per week throughout the rest of the year, is greatly to be preferred to intermittent trapnesting carried on indefinitely.

In statistical treatment of the data, indications were obtained to the effect that, when selective mating is applied — as was done in breeding from the stock described, and as will frequently occur in breeding practice — a variance analysis is not a reliable method to use in the selection work, owing to the fact that such mating has a levelling influence on hereditary variance.

INTRODUCTION

In the course of the years a great deal of literature has been published concerning the value of certain characteristics of egg production in fowls for estimation of productivity as a whole and for breeding for egg production. Detailed surveys of this literature have been given recently, for instance by HUTT (1949), LERNER (1950), JULL (1952), and HAYS and KLEIN (1952).

The results of statistical investigations carried out at the State Poultry Institute in 1944, for purposes of experimental technique, led to a renewed interest in this subject.

INVESTIGATION FOR CORRELATIONS BETWEEN PRODUCTION AT THE BEGINNING OF THE FIRST PRODUCTION YEAR AND SUBSEQUENT PRODUCTION

The object of this investigation, which was carried out in 1944, was to ascertain whether any advantages might accrue, from the point of view of

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experimental technique, by inserting a preliminary period when carrying out fodder tests with laying hens in the first laying year.

The experimental material

The birds on which this investigation was carried out were 478 White Leghorn hens, obtained from a random sample of hatching-eggs from one breeding establishment, and all with the same date of birth, viz., 17th May. The birds were accommodated in 19 compartments of identical laying houses, and they were trapnested throughout the whole of the first laying year. In the course of that year none of the fowls were removed, except on account of sickness. No artificial lighting was used in the winter.

From this experimental material those birds which began to lay before reaching the age of 7 months, i.e. not later than 15th December, and which completed the entire production year, terminating on 30th September, were chosen for the statistical investigation to be discussed here. In all, 329 birds were concerned.

Significance of early maturity, production and length of laying cycle before the age of 7 months, in calculating subsequent production

In the case of the 329 hens which began to lay before reaching the age of 7 months, correlations were calculated between the following quantities:

1 Age, in days, at which the first egg was laid.
2 Number of eggs laid up to and including 15th December.
3 Average length of laying cycle up to and including 15th December.
4 Number of eggs laid from 16th December up to and including 30th September in the following year.

By "average length of laying cycle" throughout a certain period is understood the number of eggs laid in complete cycles in that period, divided by the number of cycles. Cycles which fall only partly in the relevant period are also allocated in their entirety to that period, provided at least half the cycle concerned falls within the period.

In view of the fact that, when plotting the correlations in a points diagram, it was found that the connection between age at time of laying the first egg, or average length of laying cycle, on the one hand, and production after 15th December on the other hand, more or less followed a logarithmic pattern, the logarithm was taken for the correlation calculations of the values named under 1 and 3. The correlations found are shown in Table 1.

In the case of these hens, which began to lay on time, the age at the first egg is only weakly correlated with later production. The number of eggs laid by the hens up to the age of seven months (15th December) is distinctly correlated with subsequent production; and the length of cycle measured in the same period is slightly more so.

The partial correlation coefficients show that neither the age at first egg, nor the number of eggs laid by the hens up to the age of seven months, constitutes a real measure of the later productivity of the birds. Only the length of cycle in the first seven months is still distinctly correlated with subsequent production even when the influence of age at first egg and number of eggs laid in the first seven months is eliminated.

Table 1. Correlations between some characteristics of production in a preliminary period, and between them and production in the rest of the first production year.

Correlated quantities	Total correlation coefficient	Partial correlation coefficient on eliminating the influence of:			
		Number of eggs up to and including 15th Dec.	Logarithm of average length of cycle up to and including 15th Dec.	Logarithm of age at first egg	Remaining two characteristics
Number of eggs up to and including 15th Dec. – number of eggs after 15th Dec.	+0.378	–	+0.067	+0.387	+0.113
Logarithm of average length of cycle up to and including 15th Dec. – number of eggs after 15th Dec.	+0.433	+0.237	–	+0.413	+0.192
Logarithm of age at first egg – number of eggs after 15th Dec.	–0.145	+0.169	+0.023	–	+0.093
Number of eggs up to and including 15th Dec. – logarithm of average length of cycle up to and including 15th Dec.	+0.788	–	–	+0.784	–
Number of eggs up to and including 15th Dec. – logarithm of age at first egg	–0.685	–	–0.679	–	–
Logarithm of average length of cycle up to and including 15th Dec. – logarithm of age at first egg	–0.378	+0.361	–	–	–

In view of the importance of length of laying cycle in evaluating productivity, it seemed important to investigate whether the greater or lesser regularity of length of cycle, expressed as the coefficient of variation in the length of cycle in the case of one particular bird, is of significance in evaluating the productivity of that bird. At the same time, the question was examined as to whether the average length of the intervals between the cycles can constitute a measure of the bird's productivity. To this end, the correlations of these quantities with each other, and with later production, were scrutinized in respect of those hens which had completed at least two full cycles, with immediately subsequent interval, on or before 15th December. The results of this calculation, which concerned 273 hens in all, are given in Table 2.

It has been found that the average length of the interval between the cycles is of minor importance in judging the subsequent productivity of the bird. When the influence of length of cycle has been eliminated, the negative correlation with subsequent production is no longer significant. As the length of cycle increases, the average length of interval decreases, while the variability in the length of cycle then increases. In itself, however, the coefficient of variation in the length of cycle is of no value in judging the subsequent productivity of the bird.

The importance of length of laying cycle in estimating productivity has

Table 2. Correlations between average length of cycle, coefficient of variation in length of cycle, and average length of the intervals between the laying cycles in a preliminary period, and between these factors and production during the rest of the year.

Correlated quantities	Total correlation coefficient	Partial correlation coefficient after elimination of the influence of: Logarithm of average length of cycle up to and including 15th Dec.	Coefficient of variation in length of cycle	Average length of interval	Remaining two characteristics
Logarithm of average length of cycle up to and including 15th December – number of eggs after 15th December	+0.327	–	+0.303	+0.287	+0.240
Coefficient of variation in length of cycle up to and including 15th December – number of eggs after 15th December	+0.130	–0.018	–	+0.160	+0.016
Average length of interval up to and including 15th December – number of eggs after 15th December	–0.194	–0.106	–0.216	–	–0.106
Logarithm of average length of cycle up to and including 15th December – coefficient of variation in length of cycle up to and including 15th December	+0.444	–	–	+0.514	–
Logarithm of average length of cycle up to and including 15th December – average length of interval up to and including 15th December	–0.304	–	–0.410	–	–
Coefficient of variation in length of cycle up to and including 15th December – average length of cycle up to and including 15th December	+0.135	+0.316	–	–	–

been repeatedly stressed in the literature of the subject, where it has been remarked that the length of cycle, in its turn, is determined by the average length of time elapsing between two successive ovipositions. This lapse of time, all according to the length of day, determines the length of cycle. It would probably be better to measure the average lapse of time between two ovipositions, but this is impossible in practice. The significance of the measured length of cycle may perhaps be increased by also taking into account the day-length in the period of measurement.

Where length of cycle is mentioned in the literature of the subject, it is always taken as a standard of production intensity. In the handbooks on poultry breeding little attention has been paid to the specific character of the cycles, except by Hays et al. (1952). For practical reasons, the percentage of laying over a certain period, with or without previously deducting the larger intervals, is usually taken as an adequate standard of productivity.

It would be preferable to use the *average length of cycle* (with or without transforming it as described above) only as a standard for the *production rhythm;* the *average interval length* for the length of the *production pauses;* and the *percentage of laying* for the total intensity.

AN INVESTIGATION OF THE SIGNIFICANCE OF SOME CHARACTERISTICS OF EGG PRODUCTION IN CONNECTION WITH PRODUCTIVITY OVER THE WHOLE OF THE FIRST YEAR OF PRODUCTION

In consequence of the findings stated above with regard to the importance of length of laying cycle in judging the productivity of laying hens, the length of cycle was determined in respect of the State Poultry Institute's own breeding material. This and other data were subjected to various statistical processes, the results of which will be discussed in the following pages.

Material

Since the poultry stock of the Institute is only of limited extent, and comprises different breeds, while, for reasons of experimental technique, the birds used for feeding experiments are kept separate from the breeding stock proper, which is subject to a uniform treatment, the number of birds available for breeding purposes, per breed, is rather small. Accordingly, for the calculations set out below, it was necessary to collect material for six years running. It consisted of White Leghorns born in the years 1947 to 1952 inclusive.

Since 1943 this material has been bred in a closed flock, avoiding close inbreeding. Owing to war conditions only a small number of birds could be raised in the years 1944, and fewer still in 1945.

On account of this, too little serviceable information was gathered during the years 1944 to 1946 inclusive, while the difficulties then experienced in obtaining food also impaired the usefulness of material collected in these years.

After exterior evaluation at the age of 20 weeks, the birds did not undergo any further culling during the whole of the first laying year, which ended on 30th September. Until that date they were trapnested daily, from commencement of laying onwards. Artificial illumination was not applied. The calculations were made in respect of those birds which were present at the end of the first laying year and so produced complete data in all 203 hens.

Characteristics examined

As regards the material described above, the following data were used in our calculations.

1 *Earliness of maturity,* expressed in: age at first egg.

(Owing to the fact that the period of observation of this characteristic was not terminated at the end of seven months, logarithms are not used here, in contrast to procedure in the foregoing investigation).

2 *Persistency,* expressed in:
  a age at last egg during control period (ending 30th September) and
  b length of production year, meaning period from first registered egg to last registered egg.

3 *Winter production,* expressed in: number of eggs from commencement of production to February 1st.

4 *Production rhythm,* measured in:
  a average length of cycle up to the age of 7 months, and
  b average length of cycle over whole laying year.

In contrast to the foregoing, instead of the logarithm of these two averages, $I = 1 - \frac{1}{s + 1}$ was derived and used, in which s represents the average length of cycle and I may be called the maximum production intensity in a cycle of average length with a constant interval of one day between the cycles. This transformation, which ignores the real variations in the intervals, has the advantage, as compared with the average length of cycle as such, of establishing a practically rectilinear connection between this derived function and the (year's) production, besides making it possible to include in the average length of cycle up to the age of 7 months those birds which only started laying after 7 months, taking $s = 0$ in that case. When $s = 0$, the formula $I = 1 - \frac{1}{s + 1}$ also $= 0$. The formula $I = 1 - \frac{1}{s + 1}$ is a special form of the formula for the real intensity, namely $I = 1 - \frac{p}{s + p}$, in which p represents the average length of interval (pause in laying). $I = 0$ when $s = 0$; $I = 1$ when $p = 0$.

5 *Mean egg weight.* This was determined by taking the mean weight of all eggs laid on Mondays throughout the whole production year.

6 *Year's production.* This was defined as
 a the total number of eggs laid in the first production year;
 b the total weight of the eggs laid in the first production year, calculated by multiplying the number of eggs sub 6a by the mean egg weight as determined sub 5.

Correlations between some production characteristics and year's production

Table 3 represents the correlation coefficients calculated for the above-mentioned production characteristics. In determining average length of cycle up to 7 months, the difficulty presents itself that, if the average length of cycle in the case of birds not yet in lay at the age of 7 months is assumed to be 0, part of the natural correlation between the length of cycle at commencement of production and the other characteristics disappears. In order to eliminate this difficulty to some extent, the correlations with average length of cycle up to 7 months have also been calculated excluding all birds not yet in lay at the age of 7 months. These correlations too have been entered in Table 3.

Examination of the correlation coefficients represented in Table 3 gives rise to the following remarks.

Age at first egg. The earlier the birds start, the more they exhibit a slight tendency to keep on laying longer, which helps to bring about an additional increase in length of production year. At the same time there is an increase in winter production, average length of cycle and year's production, while mean egg weight tends to decrease.

Age at last egg. A long-continued lay naturally means a long production year, besides being accompanied by higher all-round production and a tendency to a somewhat greater egg weight. The correlation with year's production is a little more pronounced than in the case of age at first egg.

Length of production year. This has a positive correlation with winter production, average length of cycle and year production, but shows no connection

Table 3. Correlations between some production characteristics and their relation to year's production.

Characteristics	1 Age at first egg	2 Age at last egg	3 Length of production year	4 Winter production	5 Average length of cycle up to 7 months	6 Average length of cycle over whole year	7 Mean egg weight	Year's production number	Year's production kg
1 Age at first egg ..	–	–0.204	–0.761	–0.573	–0.793	–0.176	+0.221	–0.459	–0.432
2 Age at last egg ...	–0.204	–	+0.789	+0.326	+0.262	+0.343	+0.127	+0.604	+0.596
3 Length of production year	–0.781	+0.789	–	+0.574	+0.670	+0.337	–0.054	+0.688	+0.664
4 Winter production .	–0.573	+0.326	+0.574	–	+0.619	+0.321	–0.170	+0.757	+0.718
5 Average length of cycle up to 7 months	–0.793	+0.262	+0.670	+0.619	–	+0.280	–0.256	+0.532	+0.489
6 Average length of cycle over whole year	–0.176	+0.343	+0.337	+0.321	+0.280	–	–0.148	+0.666	+0.606
7 Mean egg weight ..	+0.221	+0.127	–0.054	–0.170	–0.256	–0.148	–	–0.033	+0.108
Only for birds already in lay at 7 months:									
Average length of cycle up to 7 months	–0.237	+0.201	+0.273	+0.701	–	+0.490	–0.154	+0.594	+0.531

with mean egg weight. As in the case of age at first egg, correlation with average length of cycle up to 7 months is considerably more pronounced than with average length of cycle over whole year. This indicates that, as regards both age at first egg and length of production year, a factor connected with the fact of part of the hens not laying before 7 months makes itself felt, beside the correlation with the production rhythm of those birds already in lay before that age.

Winter production, which forms an essential part of the year's production, will evidently be strongly correlated with the latter. In addition, there exists a pronounced correlation with average length of cycle, showing the same features as the correlation of age at first egg and length of production year with average length of cycle.

Average length of cycle up to 7 months. This is strongly correlated with age at first egg; but, when the birds not yet in lay at 7 months were excluded, this correlation appeared to be largely due to assumption of a length of cycle = 0 for these late-maturing hens. The same holds good for correlation with length of production year, but not for that with age at last egg. The correlation with winter production appears to be rather a question of production rhythm than of an earlier or later start of laying, as this correlation is even somewhat more pronounced in the case of birds that start laying early. The same applies to correlation with year's production and, of course, to that with average length of cycle over the whole year. The correlation with mean egg weight is negative and of little importance.

Average length of cycle over the whole year. A great length of cycle, i.e. long sustaining of the cycles, or a quick succession of eggs in a cycle, appears to be generally accompanied by a great persistency in egg production, result of an early start as well as of a late cessation of laying. In addition, there is a positive correlation with winter production and a very pronounced positive correlation with year's production.

Mean egg weight is but slightly correlated with other characteristics of egg production, and even has only a minor influence on year's production of eggs, in kilogrammes.

In order to get a better impression of the significance of each separate characteristic for productivity as a whole, the partial correlations of each separate characteristic with year's production in kilogrammes have also been calculated, excluding the influence of each of the other characteristics in turn. These partial correlations are represented in Table 4. The corresponding partial correlations with year's production in number of eggs have not been shown separately, as they present about the same picture.

Table 4. Correlations of some production characteristics with year's production in kilogrammes of eggs, eliminating the influence of each of the other characteristics in turn.

Characteristics correlated with year's production in kg / Characteristics the influence of which has been eliminated	1 Age at first egg	2 Age at last egg	3 Length of production year	4 Winter production	5 Average length of cycle up to 7 months	6 Average length of cycle over whole year	7 Mean egg weight
None	–0.432	+0.596	+0.664	+0.718	+0.489	+0.606	+0.108
1 Age at first egg	–	+0.575	+0.573	+0.635	+0.266	+0.597	+0.231
2 Age at last egg	–0.394	–	+0.394	+0.690	+0.430	+0.533	+0.040
3 Length of production year	+0.151	+0.157	–	+0.550	+0.079	+0.542	+0.193
4 Winter production	–0.037	+0.550	+0.442	–	+0.082	+0.571	+0.335
5 Average length of cycle up to 7 months	–0.083	+0.556	+0.519	+0.606	–	+0.560	+0.276
6 Average length of cycle over whole year	–0.416	+0.519	+0.614	+0.695	+0.418	–	+0.252
7 Mean egg weight	–0.471	+0.590	+0.675	+0.752	+0.538	+0.633	–

A closer inspection of the figures in Table 4 suggests the following remarks concerning the importance of the various production characteristics.

Age at first egg. The correlation between age at first egg and year's production is apparently due to the accompanying prolongation of the production year. If the influence of length of production year is excluded, early maturity will even tend to be associated with lower year's production. If early maturity does not go together with greater autumn and winter production (influence of winter production or average length of cycle up to 7 months excluded), correlation with year's production will obviously also disappear. On the other hand, elimination of the influence of age at first egg has little effect on the correlations of the other characteristics with year's production, except in the case of average length of cycle up to 7 months, which seems obvious. The particular conclusion to be drawn from the latter feature is that, as regards this material, which, on an average, was mature at 188 days, the degree of maturity did not greatly influence productivity, once laying had started.

Although the correlation of mean egg weight with year's production becomes quite twice as great, the connection between these two quantities is of little importance.

Age at last egg. This characteristic likewise owes its influence on year's production chiefly to the prolongation of the production year resulting from a long continuance of the lay. It is striking that the correlation between length of production year and year's production is affected more strongly by excluding the influence of age at last egg than by excluding the influence of age at first egg. This may indicate that long continuance of laying does more to increase productivity than an early start. This might possibly be even more conspicuous if the control year were not closed on 30th September.

Length of production year. Further to what has already been said on this topic, it may be remarked that other factors have little influence on the correlation between length of production year and year's production. Evidently the length of year is an important factor in itself.

Winter production. Since winter production forms an important part of the year's production, it is understandable that it will, under all circumstances, exhibit substantial correlation with year's production. Elimination of the influence of length of production year lessens this correlation most of al.

Average length of cycle. There is a distinct difference in conduct between the correlation of average length of cycle up to 7 months and that of average length of cycle over the whole year. Elimination of the influence of any other characteristics will not affect the correlation of average length of cycle over the year with year's production, and this correlation is always very pronounced. On the other hand, the correlation of average length of cycle up to 7 months with year's production is not only weaker, but practically disappears when the influence of length of production year or winter production is eliminated, while elimination of the influence of age at first egg also results in a considerable decrease in this correlation. This proves that average length of cycle up to 7 months is not a reliable standard of production rhythm, owing to the lack of data and, consequently, assumption of a length of cycle = 0 for birds which do not begin to lay before 7 months. The above will easily be understood from the fact that, in the case of this material, the average age at first egg was 188 days, so that, at the beginning of the lay, the length of cycle was only calculated over 3 or 4 weeks on an average, and, for some of the birds, not at all. Observation over a constant period after the first egg will undoubtedly give better results as regards evaluation of the production rhythm at commencement of laying. It will be desirable to see whether, and, if so, by how much, the exactness of this observation will increase with the length of the period, and what corrections for length of day might successfully be applied in the period of observation.

Mean egg weight. The partial correlations, too, show that, in the case of this material, mean egg weight had but little influence on the total weight of eggs in kilogrammes.

The connection is strongest on elimination of the influence of winter production, as will be self-evident.

On the whole it seems clear, from the foregoing, that average length of cycle has a predominant influence on total production, while at the same time length of production year, and more especially the moment of cessation of laying, i.e. when the moulting period begins, is of considerable importance. This predominant significance of average length of cycle is not so self-evident as superficial observation would suggest, considering that measurements have extended over the whole year. For a correlation of such strength would not exist if great average length of laying cycle had not been present together with a great number of cycles. The results of the 1944 experiments mentioned in the first part of this paper, which were conducted with material of quite different origin, warrant the supposition that this preponderance of average length of cycle is of general validity.

The heritability of some characteristics of production

If poultry are to be bred for egg production, importance must be attributed not only to the extent to which certain production characteristics are correlated with the total production, but likewise to the extent to which these characteristics, as well as the total production, are determined by heredity or can be improved by selection based on genetic factors. In the literature of the subject various methods are described for obtaining information on these points by statistical means, of which methods two have been mainly followed here.

1 Lush (1945, p. 93) describes a method of calculating heritability from the relation to each other of dam and daughter production in respect of dams which have been mated with the same sire. The method given by him may be indicated by the following formula:

$$h^2 = \frac{2(\overline{D}_1 - \overline{D}_2)}{\overline{M}_1 - \overline{M}_2}$$

in which h^2 denotes heritability; $\overline{M}_1$ and $\overline{M}_2$ the weighed average productions of groups of dams of high and low productivity, respectively, both types of dams in each group being mated with the same sire; and $\overline{D}_1$ and $\overline{D}_2$ the corresponding averages of the relevant daughter groups. Here, h is actually a factor indicating the connection between genotype and phenotype, while, moreover, it has been assumed that sire and dam have an equal influence on the genotype and phenotype of the daughter. Furthermore, it should be assumed that a difference in the case of the dams, irrespective of its position in the scale in which production has been expressed, invariably corresponds with the same difference in the case of the daughters, while the heritability should be what is called "additive". If epistatic or sex-linked factors are involved, the result will be too low, while the presence of a special influence on the part of the dam will definitely give too high a result.

2 Heritability can also be calculated on the basis of a variance analysis, viz.:

a from the contribution to the variance provided by difference in dams (D);
b from the contribution to the variance provided by difference in sires (S);
c by averaging a and b.

The method described under 2 and followed here has been derived from Lerner (1950, p. 121). Just as in the previous case, the presence is assumed of additive heritability, epistatic and sex-linked factors being considered as absent; sire and dam are also assumed to exert an equal influence on the productivity of the daughters. For the rest, the method can only be applied when there is no interaction of genotype and environment, while, finally, the material must be distributed in a statistically normal manner. This method is superior to that mentioned under 1 in that it is less dependent on the number of dams, (which is sometimes comparatively small), as, in fact, the averages of the daughter groups are used. On the other hand, the effect on the daughters obtained by selection of dam groups is expressed more directly by the figures found by applying 1.

As a disadvantage of the method mentioned under 2, the fact can be adduced that the differences in variance, which necessarily form the basis of the calculation, are not always all significant, in which case the results become very unreliable.

In order to meet this objection, the formulas and methods evolved by LERNER (1950) were elaborated. Using these new formulas, the variance caused by hereditary factors could be calculated from the really significant differences in variance in the following three ways:

$$\alpha.\ \sigma_G^2 = \frac{4 \times (\text{variance between sires—variance between dams})}{yz}$$

$$\beta.\ \sigma_G^2 = \frac{4 \times (\text{variance between sires—variance within dams})}{z\,(y + 1)}$$

$$\gamma.\ \sigma_G^2 = \frac{4 \times (\text{variance between dams—variance within dams})}{z}$$

in which formulas y = number of dams per sire; z = number of daughters per dam. The heritability was obtained by dividing the hereditary variance, thus calculated, by the total variance.

Since, owing to the nature of the material, most of the sires were used in one and the same year, the variance "between sires" has been confounded with the environment variance "between years", which might have resulted in calculation of too high a heritability. To eliminate this drawback, these values have been recalculated by means of the variance "between sires within years" instead of the variance "between sires". All the calculated values have been entered in Table 5. If, in using one of the methods mentioned under α, β and γ, a non-significant value should be found, it will not be calculated, and consequently does not appear in the table. For purposes of comparison some values have been included which have been taken from LERNER & TAYLOR (1943), and from LERNER & TAYLOR (1943) as quoted in LERNER (1950). The first have been defined as "heritability between families", the second have been derived from them as "heritability between individuals".

On scrutinizing the figures in Table 5, the first thing that meets the eye is that the variance differences between "dams minus within dams" have had no significance in any case whatever (column 7). From this it follows that the values given in column 2 are of no importance, while, as a result, the reliability of the values in columns 3 and 4 has also been more or less impaired.

As regards the various individual characteristics, the following can be deduced from the figures.

Age at first egg

The figures calculated from the significant variance differences, and according to LERNER, should give an indication that sex-linked factors are involved here. The abnormally high values found by LUSH (> 100) tend, on the other

Table 5. Heritability (h^2) of some production characteristics of own material, either calculated by various methods or taken from the literature of the subject, expressed in percentages.

Characteristics	Calculated according to LUSH *) (1945) p. 93	Calculated according to LERNER (1950) p. 121			Calculated from significant variance differences					From LERNER & TAYLOR (1943)	
		$h^2 = \frac{4D}{Q+D+S}$	$h^2 = \frac{4S}{Q+D+S}$	$h^2 = \frac{2(D+S)}{Q+D+S}$	between sires minus within dams	between sires minus between dams	between dams minus within dams	between sires within years minus within dams	between sires within years minus between dams	Original	Quoted in LERNER (1950)
Age at first egg	109	17	60	38	53	60	—	24	25	21.5	6
Age at last egg	93	–17	26	4	—	26	—	—	—	4.7 **)	1 **)
Length of production year	62	32	16	24	18	—	—	19	—	—	—
Winter production	23	–18	82	32	67	84	—	64	81	—	—
Average length of cycle up to 7 months	–24	14	14	14	—	—	—	—	—	—	—
Average length of cycle over whole year	77	10	24	17	22	—	—	—	—	—	—
Mean egg weight	48	– 8	25	8	20	25	—	—	—	45.9	12.5
Year's production in number of eggs	20	9	51	30	44	51	—	49	57	22.5	5.5
Year's production in kgs of eggs	18	13	54	33	47	54	—	52	60	—	—
	1	2	3	4	5	6	7	8	9	10	11

*) Only for those cases in which more than one dam was mated with one sire.
**) Date at last egg; value not significant.

hand, rather to indicate a greater effect on the part of the dams. For the rest, the difference between the sires proves partly to be based on differences in environment between years (columns 5 and 6, opposite 8 and 9).

Age at last egg

According to the figures calculated from the significant variance differences, there is no hereditary influence of importance. As opposed to this, a high heritability is found by applying LUSH's method.

Length of production year

Here, the sire's influence on age at first egg seems to be partly having its effect. According to LUSH, considerable heritability can be detected here as well.

Winter production

Here, the variance differences show pronounced heritability, with strongly predominant influence on the part of the sire which is not affected by differences between years. Heritability as calculated by LUSH's method also points to a secondary influence on the part of the dam.

Average length of cycle up to seven months

No hereditary influences of any importance can be found here.

Average length of cycle over whole year

Here again, a difference in results is revealed, all according to the method followed. The differences in variance do not point to hereditary factors, but LUSH's method indicates very considerable heritability.

Mean egg weight

Here, too, there is only a difference between sires that proved to be due to a difference in environment between years. According to LUSH, however, substantial heritability was again found.

Year's production in number and kg of eggs

These two characteristics present almost the same picture as "winter production", apart from the fact that the heritability found is, on the whole, rather lower.

The question should be asked as to what significance can be attached to the figures found, and what the consequences are of the contradictions established.

To answer this, it is necessary first of all to remember the conditions binding the methods applied. In brief, these are as follows :

1 The heritability must be polygenic and (at any rate, predominantly) additive, therefore : no epistasis,
no sex-linked factors.
No particular influence of the dam is observable on either the genotype or the phenotype.
2 The values found are applicable only to an (infinitely) large population under conditions of "random breeding", i.e. non-selective mating.

If we proceed to examine the extent to which these conditions are fulfilled, an interrogation mark must be placed after point 1, for the time being, since one of the very objects of the whole investigation is to answer the question as to whether the phenomena mentioned under 1 occur at all.

If we first confine our attention to point 2, it must be admitted that the condition imposed therein has not been satisfied. In the first place, the population is limited, and owing to this a certain degree of inbreeding has taken place. An average inbreeding coefficient of 0.175 has been calculated for the whole body of material. If a correction were to be applied for this, all the computed values would become rather higher, but the error thus made is of no great importance. It must be considered of more moment that a certain amount of selective mating has taken place, namely, by:

1 Excluding from propagation birds which are less suitable for it on the grounds of their own production or that of members of their family. The hereditary variance will be artificially reduced in this way.
2 When forming combinations,
   a avoiding close inbreeding,
   b choosing the combinations in such a way that weak qualities in one breeding bird are compensated for by strong qualities on the part of the mate, in order to reduce the risk of minus variants occurring.

The last point, in particular, is bound to lead to a certain levelling-out of differences, including the occurrence of a reduction of the chance of extremely favourable variants.

This breeding method, which, as a rule, will be followed where the material is too limited in quantity for rigid selection to be applied, will result in slower progress, but fewer culls, than would be the case in forming preferential combinations between extremely good birds. As regards the calculated values, however, it will end by making entirely unreliable the degree of heritability calculated from variance differences (according to LERNER's method, or one based on it).

This disadvantage applies much less to the figures calculated by LUSH's method. In calculations according to LERNER's principle, strong correlation between genotype and phenotype will lead to pronounced equalization of differences, and consequently to low heritability values. In calculations by LUSH's method, the combination as such plays no part, because, there, comparison is always made of daughter groups from dams mated with the same sire. At the most, the differences between dams mated with the same sire will be slightly reduced, with, consequently, a lesser degree of accuracy of the values obtained, but without a systematic error necessarily arising.

If, bearing in mind the above, we review the figures in Table 5, we can expect that, in cases in which strong correlation is present between genotype and phenotype (high heritability according to LUSH), selective mating will have been more perfectly accomplished, with, as a result, less heritability, calculated from the variance differences. In actual fact, this *is* largely the case. According to LUSH, high heritability is found for:

Age at first egg (109) and, as opposed to this, from the significant variance differences: 24,25.

Age at last egg (93) and, as opposed to this, from the significant variance differences: nil.

Length of production year (62) and, as opposed to this, from the significant variance differences: 19.
Average length of cycle over whole year (77) and, as opposed to this, from the significant variance differences: nil.
Mean egg weight (48) and, as opposed to this, from the significant variance differences: nil.

Moderately great heritability is found by LUSH for:

Winter production (23) and, as opposed to this, from the significant variance differences: 64 and 81.
Year's production in number of eggs (20) and, as opposed to this, from the significant variance differences: 49 and 57.
Year's production in kg (18) and, as opposed to this, from the significant variance differences: 52 and 60.

Accordingly some heritability still is found in such cases when applying LUSH's method of calculation but the correlation between genotype and phenotype is evidently considerably less than in the case of the first-named characteristics. This correlation will therefore have had but little influence on the selective matings, with, in consequence, higher heritability values when calculating from the variance differences. Here, for instance, it would be possible for sex-linked factors to be involved; like epistatic factors, these give too low values when LUSH's method is applied.

In conclusion, as regards the average length of cycle up to seven months, no heritability was found by any of the methods – a fact which, of course, can also be reconciled with the above line of reasoning.

The foregoing raises the question of the extent to which, in comparing groups of progeny, it will really be possible to rely on a variance analysis when dealing with a body of material of such a composition – which will, of course, frequently be encountered in poultry-breeding practice. There are three possible ways of obtaining an answer to this:

a) comparison of daughter groups from different dams, mated with the same sire. The basis of the effectiveness of this comparison is the variance ratio: "between dams within sires"/"within dams";

b) comparison of daughter groups from different sires, each of them mated with a number of different dams. The basis of the effectiveness of this comparison is the variance ratio: "between sires within years"/"within sires";

c) comparison of daughter groups with different sires and dams. The basis of the effectiveness of this comparison is the variance ratio: "between families"/"within families (dams)".

In case a) we have a comparison of progeny between dams, in case b) a comparison between sires, in case c) a comparison of combinations of sires and dams.

The "F" values of the variance ratios for the three cases have been entered in Table 6.

Table 6. Variance ratio (F) for the separate production characteristics.

Characteristics	a comparisons of dams	b comparisons of sires	c comparisons of combinations
Age at first egg	1.13	2.02 [1]	1.51 [1]
Age at last egg	< 1	1.28	1.02
Length of production year	1.23	1.69	1.33
Winter production	< 1	4.08 [2]	1.36
Average length of cycle up to 7 months	1.10	1.14	1.18
Average length of cycle over whole year	1.07	1.57	1.21
Mean egg weight	< 1	1.02	1.08
Year's production in number of eggs	1.07	3.10 [2]	1.37
Year's production in kgs of eggs	1.10	3.26 [2]	1.43 [1]

1) $P < 0.05$ 2) $P < 0.001$ remaining values $P > 0.05$

From the figures in Table 6 it can be seen that, on the basis of the variance analysis, in dealing with this material it is only possible to effect successful selection for progeny, except in one exceptional case, in respect of those characteristics which, according to Lush, possess only a moderate degree of heritability – in other words, a heritability which is not so great as largely to eliminate the essential differences when selective breeding is carried out. This applies to winter production and to the year's production of eggs, in numbers and in kg. In these cases, it is almost true to say that only the comparisons of sires can yield results. Sometimes, it will also be possible to find another combination which is better than others, but comparison of the daughter groups of the dams is usually rather pointless in such material. The number of dams per sire and the number of daughters per dam will probably both be too small for that. Dams with a particularly large number of daughters might form an exception to this.

Of the characteristics with a high degree of correlation between phenotype and genotype, it would only be possible for progeny investigation of sires and comparison of combinations to produce a reasonable effect with regard to age at first egg.

In the light of the above considerations, it is important to investigate the effect on the year's production in kgs of eggs of the daughters, produced by selection of the dams according to various production characteristics. For this purpose, in conformity with procedure according to Lush's method, the dams have been classified per sire in two groups, viz. high and low (favourable and unfavourable), with reference to the characteristic concerned. In doing this, care was taken to ensure that, both per sire and as a whole, the number of dams, as well as the relevant number of daughters, in each of the two groups was as nearly equal as possible. In this way, both dams and daughters were classified in approximately equal numbers of "good" and "less good" birds. The difference in year's production in kg was calculated, both in absolute terms and expressed as percentages of the average production, between the daughter groups belonging to each of the two dam groups. The figures are given in Table 7. Beside them is shown the ratio of the differences found in the daughters, after selection of the dams on the basis of a certain characteristic, to the differences found in the daughters on selection of the dams on the basis of number of kg of eggs. Multiplication of these ratio figures by the heritability of the year's production in kg (calculated by LUSH's method) yields a measure of the genetic connection between the specific characteristic of the dams and the year's production in kg of the daughters. Finally, for purposes of comparison, the heritability (calculated by LUSH's method) of the selected characteristic is shown again. In addition, some data are given which might provide an idea of the level of production as a whole and in the individual dam and daughter groups.

Scrutiny of the figures in Table 7 reveals unmistakably that, when dams are selected on the basis of the less complicated characteristics, the differences between the daughters are greater than when dams are selected on the basis of number of eggs. The only possible explanation of this is that the influence of environment on the expression of the hereditary factors promoting production is less in the case of these less complex characteristics than in that of production measured in number of eggs. The small difference in numbers of kg of eggs per year between the daughter groups, when the dams are selected for mean egg weight, must naturally be attributed to another cause, namely, the slight degree of correlation between mean egg weight and year's production in kg.

Accordingly, it has been found that age at first and last egg, and average length of laying cycle, are better criteria of hereditary productivity than winter production and year's production expressed in either numbers of eggs or in kgs of eggs. The characteristics concerned are those which, in addition to possessing high intrinsic heritability, exhibit substantial correlation with the year's production in kg.

A special position is occupied by the average length of laying cycle up to the age of seven months, which, in spite of low intrinsic heritability, has nevertheless proved to be effective in selection for year's production in kg. This apparent contradiction can probably be explained by the influence of the greater or lesser earliness of maturity embodied in the length of cycle up to the age of seven months, and which (inter alia in connection with differences in length of day) *is* effective in selection for total production, but not in selection for length of cycle in these first months of the laying period.

POSSIBILITIES OF SELECTION FOR PRODUCTION AT COMMENCEMENT OF LAYING

As regards both selection of sires for progeny and selection of young dams for their own production, it is important to have available good standards of hereditary productivity, which standards can be applied from the very beginning of the laying period.

Bearing this in mind, and on the basis of the considerations described above, the question has been investigated as to what correlations exist between some production characteristics at the beginning of the laying period on the one hand, and the year's production on the other.

The calculated correlations are given in Table 8.

Table 7.

Dams selected in two groups according to the characteristic :	Average production of dam groups			Average production of groups of daughters from dams in		
	"High" group	"Low" group	Average	"High" group	"Low" group	Average
Age at first egg	161.7	181.7	171.9	183.2	194.1	188.8
Age at last egg	543.0	512.9	527.9	525.2	511.2	518.2
Length of production year	378.5	334.3	357.0	335.6	321.8	328.9
Winter production	82.8	57.7	69.2	53.7	50.8	52.1
Year's production in number of eggs	244.0	195.3	219.8	184.3	179.5	181.9
Average length of laying cycle over 7 months	0.761*)	0.656*)	0.708*)	0.565*)	0.590*)	0.577*)
Average length of laying cycle over whole year	0.779*)	0.709*)	0.742*)	0.736*)	0.709*)	0.722*)
Mean egg weight	63.01	58.86	61.18	60.70	59.71	60.26
Year's production in kg of eggs	15.05	12.18	13.53	11.11	10.85	10.97
No. of eggs in first two months of production	42.4	33.2	37.9	30.5	31.5	31.0
Average length of cycle in first two months of production	0.765*)	0.692*)	0.729*)	0.695*)	0.689*)	0.692*)

*) Transformed values : $I = \frac{1}{s+1}$. The averages correspond with an actual length of cycle of:

up to age of 7 months	3.184	1.907	2.425	1.299	1.439	1.364
over the whole year	3.525	2.436	2.876	2.786	2.436	2.597
first two months	3.255	2.247	2.690	2.279	2.215	2.247

Table 8. Correlations between, on the one hand, the number of eggs at commencement of laying and the average length of cycle, measured in periods of varying duration, and on the other hand the year's production, expressed in number of eggs.

Characteristics	Periods	Correlation with year's production
Number of eggs	First 2 months of production	+0.556
,, ,, ,,	,, 4 ,, ,, ,,	+0.625
,, ,, ,,	,, 6 ,, ,, ,,	+0.693
Average length of laying cycle	First 2 months of production	+0.618
,, ,, ,, ,, ,,	,, 4 ,, ,, ,,	+0.574
,, ,, ,, ,, ,,	,, 6 ,, ,, ,,	+0.597
Average length of laying cycle	Entire production year	+0.666

Difference in egg production between groups of daughters, expressed in kg of eggs per year		Ratio of difference between groups of daughters to difference when dams are selected for year's production in kg	Heritability, deduced from the heritability of the year's production in kg and the ratio figures in the previous column	Heritability of the selected characteristic, calculated by LUSH's method
absolute	as a percentage of the average production			
+0.81	+7.38	+3.12	56	109
+0.97	+8.84	+3.73	67	93
+0.67	+6.11	+2.58	46	62
+0.38	+3.46	+1.46	26	23
+0.23	+2.10	+0.88	16	20
+0.97	+8.84	+3.73	67	−24
+0.72	+6.56	+2.77	50	77
−0.13	−1.19	−0.50	−9	48
+0.26	+2.37	1	18	18
−0.05	−0.46	−0.19	−3	−22
+0.97	+8.84	+3.73	67	16

It can be seen that the correlation between number of eggs and year's production exhibits a gradual increase as the period of measurement becomes longer. This is to be expected, because the characteristic measured forms an increasing part of that year's production.

In the case of the average length of cycle, no increase in the correlation is seen as the period of measurement lengthens. The values remain almost constant, and only slightly lower than the correlation values of the average length of cycle measured over the whole year with the year's production. The average length of cycle measured over only two months forms a standard of the year's production which is just as reliable as the number of eggs laid in four months.

With the object of also ascertaining its significance in the selection of breeding stock, the effect of number of eggs and average length of cycle in the first two months of laying on the year's production in kg of daughters was determined in the case of selection of dams for the characteristics concerned. These data, like those for the characteristics previously discussed, are given in Table 7. From this it can be seen that the average length of cycle in the first two months of laying, inspite of low intrinsic heritability, is a good standard for the selection of dams. The number of eggs laid in the same period, on the other hand, is of no importance in selection.

Accordingly, we have arrived at the conclusion that the following characteristics have a predominant influence in breeding for egg production in the case of the material discussed:

a age at first egg;
b age at last egg;
c average length of laying cycle, measured in the first two months of production or over a longer period.

From this it follows that trapnesting on a certain limited number of days per week is attended by a formidable drawback. For, when this procedure is adopted, it is impossible to determine the lengths of laying cycle. The results of the present investigation have shown that, in order to limit the work involved in trapnesting, it is advisable to carry it out daily throughout a certain period at commencement of laying, and subsequently to trapnest on a limited number of days per week during the rest of the year or part of it. This part of the year should, in any case, include the summer months, to enable the age at which the last egg is laid to be approached as closely as possible. Naturally, errors will also occur in determining length of cycle even when trapnesting is carried out every day, since it will always be found that certain fowls will lay their eggs more or less regularly outside the trapnest. Owing to this, a cycle which is actually uninterrupted can be split into shorter cycles. This source of errors was also present in the case of the material discussed here. However, such errors can only result in the correlations found and the selection results being given too low a value, along with the length of cycle.

Further research will be necessary, in order to test the results obtained by reference to other breeding material, and to ascertain what can actually be achieved by selection for the three important characteristics named.

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