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The Incidence of Double-Yolked Eggs in Relation to Improvement in Egg Production*

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Summary. The production of double-yolked eggs and its relation to other egg production traits has been summarized over a period of thirty years for a closed flock selected for gains in total egg production.

The number of double-yolked eggs per pullet as well as the percentage of pullets laying at least one double-yolked egg have increased rather steadily, although it is evident that the trait possesses no selective advantage. Pullets which laid double-yolked eggs showed earlier sexual maturity and superiority in egg production but it is clear that the corresponding genetic correlations are low or negligible.

The heritability of the trait increased with its level of incidence and is sufficiently high that selection should increase the incidence to a level permitting further study of multiple ovulation.

Introduction

One of the phenomena observed in flocks of chickens under selection for higher egg production has been the appearance of occasional eggs containing more than one yolk. By and large, up to 1940 the literature was descriptive; little attention had been paid to the frequency of occurrence of double-yolked eggs in the improvement of flocks. CURTIS (1914) reported that 18% of 189 pullets laid one or two double-yolked eggs but only 1.5% laid more than two. However the length of the period of lay is not clear, nor is the number of single-yolked eggs in the period given. LACASSAGNE and JACQUET (1963 and 1965) presented data from which one can infer that the proportion of double-yolked eggs observed under normal conditions was roughly .125 and .035 respectively in two experiments for the first three months of lay. (These figures are based on samples of 232 and 40, respectively, Rhode Island × Wyandotte pullets, but the higher is surprising to the writer.) In the University of California White Leghorn flock at Berkeley, which has been selected for increased egg production continuously since 1932 (LERNER, 1958; ABPLANALP et al., 1964), the proportion of eggs with two (and occasionally more) yolks appears now to be of the order of .03 during the first four months of lay. An investigation as to whether the tendency to lay double-yolked eggs has increased concurrently with egg production was undertaken. The summaries presented here for a sample of years pertain to the change in incidence of double-yolked eggs and to its relation to the behavior of some other traits. Some analyses were made in an attempt to identify possible genetic mechanisms underlying this trait.

Material and Methods

A long-term selection program for greater egg production has been carried on in a flock of Single-Comb White Leghorns since 1932. Concomitant selection against low egg weight has been practiced in order to maintain a spring egg weight of about 56 grams and hen-housed average production, rather than production of survivors, has been used in an attempt to maintain or increase viability. Until 1949, records for a full year's production (to October 1) comprised the basis of combined family and individual selection for females; since 1954, hen-housed egg production to January 1 only has been the primary selection criterion.

Chicks were hatched over a four-week period beginning early in March; thus they have been (since 1954) about fifty weeks of age at the time of selection of parents of the next generation. From 1932 to 1955 all eggs were candled and eggs with double-yolks were recorded; thereafter double-yolks were diagnosed merely from the abnormally large size and elongated shape usually associated with them. The error resulting from this change is believed to be primarily an underestimate in the number of pullets laying only one double-yolked egg, since the appearance of at least one double-yolked egg on the daily production record of a pullet would have increased the likelihood that the person recording would check (by candling) any subsequent doubtful double-yolked eggs laid by the pullet. For the purpose of this study only double-yolked eggs laid before December 1 were counted since it was obvious that their number was exceedingly small after that date. For Tables 1 and 4 tabulations for one of the earliest years and for ten of the subsequent years were thought to be sufficient to show the trends. The interval between the years chosen is not constant because years with known disease outbreaks between time of hatch and Decem-

* Dedicated to Professor HANS STUBBE on the occasion of his 65th birthday.

Table 1. *Characteristics of the egg-production line.*

Pullet yr. of hatch	No. of pullets laying at least one egg	Mean age at first egg	Jan. 1 Prod. Index	July 1 Prod. Index	% DY* pullets	No. d-y eggs per pullet	No. d-y eggs per DY pullet	No. d-y eggs per pullet selected as dam	Previous generation, no. d-y eggs per dam of DY* pullets
1934	651	196	40	138	14	0.23	1.64	0.32	0.33
1940	412	177	62	164	26	0.55	2.11	0.59	1.06
1942	411	170	70	175	31	0.56	1.78	0.52	0.21
1945	430	165	74	178	40	0.89	2.24	0.79	0.15
1948	539	157	75	184	48	1.16	2.38	1.50	0.72
1951	319	162	76	187	83	1.99	2.39	1.34	1.17
1953	555	153	85	186	77	2.08	2.70	2.11	1.72
1955	509	146	84	172	62	2.19	3.50	2.23	2.20
1957	641	145	90	193	45	1.37	3.04	—	—
1959	291	143	82	170	55	1.69	3.06	—	—
1962	294	142	92	189	74	3.17	4.26	—	—

* DY designates pullets which laid at least one double-yolked egg.

Table 2. *Percentage of pullets laying the specified number of double-yolked eggs.*

Pullet yr. of hatch	0	1	2	3	4	5	6	7	8	9	10	More than 10
1934	85.7	8.8	2.9	1.7	0.5	0.2	0.1	0	0	0	0	0
1940	74.1	12.9	7.0	2.6	1.6	0.9	0.2	0	0	0.2	0	0.5
1942	69.3	18.2	6.6	3.1	1.9	0	0.7	0.2	0	0	0	0
1945	60.0	17.0	12.1	3.5	3.5	2.1	0.9	0.2	0.2	0.2	0.2	0
1948	51.3	22.5	10.2	6.9	3.5	1.5	2.0	0.7	0.4	0.4	0.2	0.4
1951	16.9	40.1	14.7	10.7	6.6	5.3	1.9	1.3	1.2	0.3	0	0.9
1953	22.7	33.0	16.2	10.6	4.5	4.7	2.9	1.6	0.9	0.5	0.7	1.6
1955	37.2	21.5	10.1	9.7	5.5	4.7	2.8	1.0	2.6	0.6	1.2	3.2
1957	54.8	17.2	9.8	5.9	3.4	3.1	1.7	0.8	0.6	0.8	0.3	1.6
1962	25.5	19.4	12.6	9.5	8.8	5.8	3.4	2.0	2.7	1.7	2.0	6.5

ber 1 were avoided. The basis of selection of the five years for which the more extensive analyses of the other tables were carried out was simply that the time interval between years analyzed should be six or seven years. 1957 was included because the population in that year was very large.

Results

The data of Table 1 show a more or less steady gain in the production indexes[1] (for example, from 40 eggs in 1934 to 92 eggs in 1962 for the January 1 index). Concurrently the number of pullets laying at least one double-yolked egg (designated as "DY" pullets) increased as well as the average number of double-yolked eggs such pullets laid (see also Table 2). Meanwhile the age at first egg decreased by some 50 days. The last four columns (several of which were completed only for the years of egg candling) suggest that artificial selection for increased egg production was not operating to the advantage of those phenotypes higher than the mean in double yolked egg production. Table 2 indicates the changes in the distribution of double-yolked eggs for the sampled years.

Table 3 shows superiority in the means of several production traits for those pullets laying at least one double-yolked egg in comparison with those which laid none. The DY pullets also seem consistently to be a more homogeneous group with respect to age at first egg. Table 4 indicates the relation between age at first egg and number of double-yolked eggs over all the years of Table 1. The most provocative aspect of the table is the fact that although the most early maturing pullets each year show a higher incidence of double-yolked eggs, the actual age at first egg of these classes of pullets has declined considerably over generations. Thus Table 4 shows that although an age at first egg of 154 days, for example, may have been associated with more than four double-yolked eggs in 1943, by 1953 it was associated with regularity of ovulation (no double-yolked eggs); similarly, an age at first egg of 144 days was associated with more than four double-yolked

[1] The production indexes of Table 1 are averages over all birds housed while the sexual maturity average of that table and all averages of Tables 2, 3 and 4 are over only those birds which laid at least one egg.

Table 3. *Averages and their standard errors for several production traits for pullets laying at least one double-yolked egg and for other pullets.*

Pullet yr. of hatch	Class of pullet	No. of pullets	Age at 1st egg		July 1 Prod. Index	
			Mean	Std. Error	Mean	Std. Error
1942	non-DY	281	178	1.63	173	3.52
	DY	130	161	1.19	197	4.93
1948	non-DY	276	163	1.83	176	3.93
	DY	262	151	0.76	200	2.97
1955	non-DY	191	155	2.07	168	5.93
	DY	318	142	0.65	185	4.13
1957	non-DY	351	148	1.45	185	3.72
	DY	290	141	0.61	205	3.36
1962	non-DY	75	143	1.29	180	9.68
	DY	219	142	0.62	198	4.29

Table 4. *Association of age at first egg and number of double-yolked eggs.*

Pullet yr. of hatch	Number of double-yolked eggs					
	0	1	2	(3 or more)	(4 or more)	5 or more
1934	199	172	159	(166)	—	—
1940	183	161	160	155	(154)	—
1942	175	161	159	164	(155)	—
1945	170	159	159	157	155	155
1948	163	153	149	151	146	145
1951	160	158	151	152	156	152
1953	154	149	148	149	145	144
1955	153	143	143	140	140	139
1957	148	141	142	143	139	141
1959	145	144	142	144	137	138
1962	143	143	143	145	141	139

eggs in 1948 but in 1959 with regularity of ovulation. These observations suggest that incidence of double-yolked eggs is less a function of the average genetic change in age at first egg effected over generations than of the peculiar interaction of genotype and environment responsible for early maturity of individual pullets within each generation. In other words, one might predict that a low genetic correlation obtained between the two traits. Thus, it is possible that improvement in overall rate of production rather than early maturity may have been responsible for the genetic increase in double-yolked eggs.

Table 5. *Offspring averages for dams classed according to number of d-y eggs laid.*

Pullet yr. of hatch	No. of dams	Dam class*	Offspring average			
			No. of pullets	No. d-y eggs per pullet	Age at 1st egg	July 1 P.I.
1942	63	0	373	0.53	172	173
	10	1	48	0.64	158	125
	1	> 1	3	0	197	158
1948	48	0	341	1.10	157	184
	15	1	114	1.22	156	193
	13	> 1	84	1.33	159	189
1955	25	0	138	1.61	146	184
	27	1	125	1.73	150	168
	54	> 1	246	2.75	144	180
1957	42	0	255	0.90	145	193
	26	1	160	1.45	146	185
	41	> 1	225	1.87	144	201
1962	5	0	27	2.29	143	183
	9	1	71	2.52	141	216
	33	> 1	196	3.54	143	182

* Dams which laid 0 d-y eggs, 1 d-y egg or more than 1 d-y egg, respectively.

Low or negligible genetic correlations between the incidence of double-yolked eggs and age at first egg and between the former trait and egg production (as measured by the production index to July 1), respectively, are also indicated by the results in Table 5. In this case the dams of a given generation of pullets were classified as having laid none (0), one (1), or two or more (> 1) double-yolked eggs. Neither production characteristic of pullets from each of these three classes showed a consistent association with the respective incidence of double-yolked eggs in their mothers' class. In contrast to the appearance of low genetic correlation (or none) with egg production, the evidence that double yolk incidence in daughters was strongly correlated with that of the dams is consistent and suggests high heritability of the trait. (The heritability of a trait is measured by that proportion of the total phenotypic variance of the trait which is additively genetic. Discussion of this parameter of a population and of the statistics by which it may be estimated may be found in LERNER (1958) or in FALCONER (1960)). It is of interest in this connection to refer to the estimates of heritability for the number of double-yolked eggs which are presented in Table 6, as h_s^2 and h_d^2 and $2\,b_{\bar{o}d}$. The first two estimates were obtained from the sire and dam components of variance, respectively, while $b_{\bar{o}d}$ represents the intrasire regression of daughters' mean on dam, an estimate of one-half the heritability. The heritability of the number of double-yolked eggs appears to be quite high and increasing with the incidence over the years, which might be expected for a threshold trait with incidence increasing over generations from an initially low level. The behavior of the heritability of such traits has been discussed by DEMPSTER and LERNER (1950) from a statistical point of view. Another explanation might be that genes for a high production index or for low age at first egg may have had pleiotropic effects for a greater number of double-yolked eggs. If such genes were present in the population at low frequency initially, one would expect an increment in their average (additive) effects as their frequency increased under selection. Clearly only genes with relatively large effects could be expected to show this phenomenon in sufficient magnitude to be detectable in a quantitative study. (See FALCONER, 1960, pp. 119—120.)

Table 6. *Estimates of heritability of the tendency to lay d-y eggs.*

Pullet yr. of hatch	h_s^2	h_d^2	$2b_{\bar{o}d}$
1942	.10	.30	—.02
1948	.28	.24	.18
1955	.40	.18	.42
1957	.47	.32	.36
1962	.63	.79	.76

Discussion

CURTIS (1914 and 1915) inferred several physiological causes for the formation of double-yolked eggs. Attacking this general problem, CONRAD and WARREN (1940) undertook to estimate the relative frequencies of the following three ways in which the formation of double-yolked eggs may occur: (1) one of the pair of ova may be ovulated at the normal time and the other nearly a day prematurely; (2) one of the ova may not be ovulated at the normal time and may be held in the body cavity and released later along with the ovum which was to follow it and (3) two ova may develop concurrently for some time before both are simultaneously ovulated. They concluded that these relative frequencies were about 0.25, 0.10 and 0.65, respectively, on the basis of pauses in egg production observed immediately before and after double-yolked eggs were laid and immediately before and after single-yolked control eggs.

The genetic mechanisms affecting the formation of the various types of double-yolked eggs may be different; thus it appears quite clear that a study of the kind made here, in which the types of double-yolked egg were not separable, can only be a preliminary guide to the study of multiple ovulation in fowl, that is, the tendency to produce more yolks than the number of days in a given interval of time. So far as the genetics of this trait is concerned one might expect more clear-cut answers from a selection experiment. We have undertaken to select for increased double-yolked egg production in the hope of establishing a flock of chickens in which multiple ovulations are numerous and persistent. Physiological observations appropriate for distinguishing the postulated modes of double-yolked egg production may then clarify which of these is the most important genetically. Endocrine mechanisms responsible for superovulation must also be examined, such as that reported by FRAPS and RILEY (1942). These workers demonstrated that hens pretreated with FSH but prevented from ovulating would release numerous yolks, not necessarily simultaneously, upon injection with anterior pituitary extract rich in luteinizing hormone. Inadequate timing of hormone releases in young pullets subsequently well-coordinated is an attractive hypothesis which might explain the high incidence of double-yolked eggs in exceptionally, and perhaps abnormally, early maturing pullets. The "abnormality" of earliness may well be relative to the length of day encountered at the onset of lay. Over the years the change in the length of day prevailing at this critical time in the fall can be inferred from the decreasing age at first egg shown in Table 1 (since the hatching time of the chicks remained constant each year). Thus from year to year the photoperiod was increasing as the rate of egg production was increasing. This might have posed a conflict among the high-rate pullets which only the more adaptable were able to resolve.

LACASSAGNE and JACQUET (1963 and 1965) conducted two experiments in which age at first egg was retarded by restricting the number of hours of light, and consequently the amount of feed consumed, during the growing period. (In the second experiment these two effects were separately estimated.) They observed significantly greater percentages of double-yolked eggs in the records of the pullets raised under normal conditions. They noted that the parts played by the significantly earlier maturity and greater intensity of lay of these pullets could not be separately evaluated in their effects on the increased frequency of double-yolked eggs.

Perhaps the most encouraging finding of this study for the future understanding of multiple ovulation in the fowl is the fact that the heritability of this trait has reached a high level in our population. Either an increase in the frequency of genes favorable to multiple ovulation under selection for high egg production, or a more precise measurement of genetic variation underlying double-yolked eggs accompanied by a lowering of a hypothetical threshold for their occurrence may be involved. The heritability estimates based on variation between half-sister averages, h_s^2 (the estimate least likely to be biased by non-additive gene effects) may be presumed to be conservative. This is due to the fact that the mating system which has been followed in our egg production lines has excluded matings of close relatives with the result that the sire contribution to the variance in such a population tends to be somewhat underestimated.

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Zusammenfassung

An einer für eine Steigerung der Ei-Produktion ausgewählten Herde Weißer Leghornhühner wurde der Anfall von Eiern mit zwei Dottern und ihre Beziehung zu anderen Merkmalen der Ei-Produktion für einen Zeitraum von 30 Jahren zusammengestellt.

Die Anzahl doppeldottriger Eier je Hühnchen und der Prozentsatz Hühnchen, die wenigstens ein doppeldottriges Ei legten, ist ziemlich konstant geblieben, wenn auch dieses Merkmal offensichtlich keinen Selektionswert hat. Hühnchen, die Eier mit zwei Dottern legten, zeigten eine frühere Geschlechtsreife und eine höhere Ei-Produktion, aber es ist klar, daß die entsprechenden genetischen Korrelationen niedrig sind.

Die Erblichkeit des Merkmals stieg mit seinem Auftreten, sie ist hoch genug, daß eine Selektion das Auftreten noch steigern könnte, um eine weitere Untersuchung der mehrfachen Ovulation zu ermöglichen.

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