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Selection response for part period egg number and egg mass in chickens – a comparison

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Summary. Two sublines from each of four flocks of White Leghorn were subjected to two cycles of selection for part year egg number and part year egg mass. A family index (combined selection) was the selection criterion for each of the two traits. The generation means of an unselected pedigreed randombred control, bred and maintained along with the selected sub-lines, were used for correcting short term environmental trends. The sublines selected for a common selection criterion were considered as replicates. The control corrected generation means, when averaged over replicates, gave the mean direct and correlated responses for the selected and different unselected traits. The average genetic change per generation was 2.16 eggs in egg number selected sublines and 146 g of egg mass in egg mass selected sublines. The direct response marginally exceeded the correlated response for both part period egg number and egg mass seen in the corresponding sublines. Except for egg weight the correlated responses for different unselected traits were in the same direction in both egg number and egg mass selected sublines. While the egg weight in egg number lines did not change, its response was positive in egg mass selected lines. A comparison between the lines revealed that the egg mass selected lines matured later and laid heavier but slightly less numerous eggs than the egg number selected sub-lines.

Key words: Selection response – Part period egg number and egg mass – White Leghorn

Introduction

Responses observed in most selection experiments with egg number as selection criterion suggested a negative genetic correlation between egg number and egg weight.

Since simultaneous improvement in both these traits is desirable in commercial stocks, the potential value of egg mass as a selection tool has stimulated interest (Waring et al. 1962; Hicks 1963). Bohren (1970) proposed egg mass as a selection criterion to improve both egg number and egg weight. Like egg number, egg mass has also been reported to be lowly heritable, the magnitude of the estimates being more or less similar to those of egg number and much lower than those of egg weight (Waring et al. 1962; Arboleda et al. 1976; Quadeer et al. 1977). For low heritability traits, the accuracy of selection can be increased by combining the information of sire and dam family averages with the individual's performance (Lush 1947; Osborne 1957a, b). Garwood et al. (1978); Marks (1981) and Craig et al. (1982) reported positive responses to selection for egg mass in chickens using different selection criteria (but not a family index). A simultaneous comparison of selection response for egg number and egg mass, using the same base population, does not seem to have been attempted to assess their relative superiority as selection criteria for improving both egg number and egg weight.

This study reports the responses realised for both selected and unselected traits in four White Leghorn populations from two generations of selection in their sublines selected separately for egg number and egg mass by using a family index. Also reported is the relative efficiency of egg number and egg mass as selection criteria for improving traits of economic importance in egg type chickens.

Materials and methods

Genetic stocks and mode of selection

Chicks hatched from four different closed flocks of White Leghorn (L 33, L 55, L 77 and L 99) constituted the base population (S_0). For all available birds of the base generation (S_0), a family index (Osborne 1957a, b) that included individual performance and dam and sire family averages for pullets, and dam and sire family averages for cockerels, was computed separately for egg number (EN) and egg mass (EM). Within each flock those pullets and cockerels with higher index values for egg number constituted the parents of the egg number subline (EN) and those with higher index values, for egg mass constituted the parents of the egg mass sublines (EM) of the S_1 generation. Birds that were found eligible for inclusion in both EN and EM sublines on the basis of their index values were randomly allotted to either EN and EM sub-lines. Among the progeny of each subline of the S_1 generation a second cycle of selection was practised for the respective selection criterion. The progeny from these selected parents of each sub-line constituted the second selected generation (S_2). In both generations the selected females were allotted at random to selected males except that the full and half-sib matings were intentionally avoided to minimise inbreeding. The selection criteria and the mode of selection remained the same in the corresponding sub-lines of all four flocks. The sublines for the four flocks are referred to hereafter as the egg number and egg mass sub-lines.

A pedigreed randombred control population, developed from one of the selected lines (L 55) of the base generation, was hatched and reared simultaneously along with the selected lines in order to make the necessary corrections in the selected line for short term environmental fluctuations. Origin and other details of this control have been described by Ayyagari et al. (1980). The number of sires and dams used and the progeny measured in each sub-line are given in Table 1.

The S_0 and S_1 generations were hatched in 4 to 6 weekly hatches and the S_2 generation in 3 to 4 hatches each spaced 10 days apart. Chicks belonging to the same hatch from different sub-lines were grown intermingled. At the time of sexing, only two cockerels per dam were saved for subsequent selection. At the age of 18 weeks all available healthy pullets were housed in 3-tier individual cages in open type houses. While the S_0 and S_1 generation birds had only natural day light, the S_2 generation were given additional artificial light to give a total of 16 hours a day. Feeding and other management practices were kept similar as far as was possible for all generations of both the control and selected lines.

Traits measured

1. Egg number – number of eggs to 40 weeks of age; 2. egg mass – computed in grams as a product of egg number at 40 weeks and egg weight as defined in 3 below (Bohren 1970); 3. egg weight – average weight in grams of all the eggs laid during the 39th and 40th week; 4. age at first egg – age in days at which the first egg was laid; 5. body weight – obtained in grams at the age of 20 and 40 weeks.

Statistical analysis

The data from the selected as well as the control line were all corrected for hatch effects. The generation means for the selected and unselected traits in different sublines were corrected to the control level by subtracting the improvement or adding the decline that was observed for different traits in the control line. The control corrected mean differences between S_2 and S_0 gave an estimate of cumulated direct response for the selected traits and correlated response for the unselected traits in the intervening two generations of selection. As two generations were involved, the cumulated response was halved to obtain average direct and correlated responses per generation. The control corrected generation mean differences (S_2-S_0) were statistically tested against SE (S_2-S_0) for significance by a *t*-test.

The hatch corrected data of each subline in each generation were also subjected to variance and covariance component analysis in order to estimate the genetic correlations among the different traits studied.

Results and discussion

The number of sires and dams used and the individuals measured in each generation are shown in Table 1.

Control correction

The generation means of the controls suggested that the environment, particularly the introduction of artificial light to supplement the natural light during S_2 generation, contributed to an inflationary environmental trend notably for age at first egg and, consequently, for the egg number. In two generations, the control line showed a cumulative improvement of 18 eggs, 935 g of egg mass, 160 g in body weight at 20 weeks and 115 g in body weight at 40 weeks and a decline of 19 days in age

Table 1. The number of individuals measured in each generation and the average selection differentials

Lines	S_0			S_1			S_2			Criterion of selection	Average selection differentials[a]		
	Sires	Dams	Progeny measured	Sires	Dams	Progeny measured	Sires	Dams	Progeny measured		Expected	Effective	Standardized (I)
L33	30	136	438	25	115	495	30	154	665	Egg number	11.47	11.67	0.73
			–	25	110	432	30	135	662	Egg mass	622.58	671.45	0.71
L55	27	119	319	25	113	630	30	154	821	Egg number	10.38	10.02	0.74
			–	25	107	589	30	156	758	Egg mass	528.83	507.57	0.64
L77	29	120	329	25	115	492	30	163	774	Egg number	9.08	9.32	0.68
			–	25	113	480	30	163	770	Egg mass	536.27	545.88	0.70
L99	30	121	360	25	110	432	30	150	567	Egg number	10.28	9.83	0.68
			–	25	111	433	30	152	575	Egg mass	510.57	482.34	0.59
Control	27	119	319	30	136	339	30	217	663	Random Selection	–	–	–

[a] The selection differentials are number of eggs in egg number selected lines and grams of egg mass in egg mass selected lines

Table 2. The control corrected generation means of egg number and egg mass selected sublines for egg number, egg mass and age at first egg

Trait	Line	Selection criterion	Generation means corrected to control			$(S_2-S_0)\pm SE$	Average response
			S_0	S_1	S_2		
Egg number (no.)	L33	EN	54.33± 0.85	57.30± 0.65	61.81± 0.56	7.48± 0.96**	3.74
		EM	54.33± 0.85	57.71± 0.71	60.66± 0.59	6.33± 1.00**	3.16
	L55	EN	58.54± 0.80	62.98± 0.51	62.57± 0.39	4.03± 0.80**	2.01
		EM	58.54± 0.80	63.25± 0.54	62.25± 0.40	3.71± 0.81**	1.85
	L77	EN	57.68± 0.80	62.80± 0.58	59.65± 0.42	1.97± 0.83*	0.98
		EM	57.68± 0.80	61.49± 0.58	59.41± 0.42	1.73± 0.83*	0.86
	L99	EN	62.19± 0.77	67.64± 0.69	66.01± 0.50	3.82± 0.88**	1.91
		EM	62.19± 0.77	68.63± 0.70	64.86± 0.52	2.67± 0.90**	1.33
Egg mass (g)	L33	EN	3,202.81±48.88	3,394.17±37.99	3,611.76±33.32	408.95±57.09**	204.47
		EM	3,202.81±48.88	3,417.78±41.54	3,571.88±34.42	369.07±58.06**	184.53
	L55	EN	3,202.04±45.09	3,470.49±29.33	3,461.09±22.56	259.05±45.82**	129.52
		EM	3,202.04±45.09	3,519.54±31.46	3,515.50±23.86	313.46±46.99**	156.73
	L77	EN	3,272.31±45.24	3,556.41±33.10	3,503.11±26.07	230.80±49.68**	115.40
		EM	3,272.31±45.24	3,525.40±33.42	3,548.14±22.00	275.83±49.56**	137.91
	L99	EN	3,493.53±43.74	3,782.68±38.71	3,762.60±30.43	269.07±51.70**	130.76
		EM	3,493.53±43.74	3,834.57±38.21	3,755.05±31.40	261.62±52.62**	130.76
Age at first egg (days)	L33	EN	201.42± 0.92	198.31± 0.68	192.68± 0.47	−8.74± 0.94**	−4.37
		EM	201.42± 0.92	198.45± 0.74	193.36± 0.50	−8.06± 0.97**	−4.03
	L55	EN	192.91± 0.87	187.02± 0.49	187.81± 0.27	−5.10± 0.69**	−2.55
		EM	192.91± 0.87	186.47± 0.51	187.78± 0.30	−5.13± 0.73**	−2.56
	L77	EN	192.90± 0.76	187.67± 0.56	188.80± 0.38	−4.10± 0.76**	−2.05
		EM	192.90± 0.76	187.52± 0.56	189.29± 0.37	−3.61± 0.75**	−1.80
	L99	EN	191.04± 0.82	185.61± 0.69	184.08± 0.37	−6.96± 0.80**	−3.48
		EM	191.04± 0.82	185.67± 0.70	184.33± 0.37	−6.71± 0.80**	−3.35

* $P \leqq 0.05$; ** $P \leqq 0.01$

Table 3. The control corrected generation means of egg number and egg mass selected sublines for egg weight and body weights at 20 and 40 weeks of age

Trait	Line	Selection criterion	Generation means corrected to control			$(S_2-S_0)\pm SE$	Average response
			S_0	S_1	S_2		
Egg weight (g)	L33	EN	59.16±0.19	58.85± 0.16	57.82±0.16	−1.34± 0.25**	−0.67
		EM	59.16±0.19	58.86± 0.18	58.27±0.16	−0.89± 0.25**	−0.44
	L55	EN	54.84±0.17	55.14± 0.12	55.37±0.12	0.53± 0.22**	0.26
		EM	54.84±0.17	55.63± 0.13	56.22±0.12	1.38± 0.22**	0.69
	L77	EN	56.81±0.18	56.67± 0.16	57.97±0.14	1.16± 0.24**	0.58
		EM	56.81±0.18	57.25± 0.16	58.74±0.13	1.93± 0.23**	0.96
	L99	EN	56.22±0.18	56.10± 0.17	56.27±0.15	0.05± 0.24	0.02
		EM	56.22±0.18	56.15± 0.17	57.32±0.16	1.10± 0.25**	0.55
Body weight at 20 weeks (g)	L33	EN	1,050.28±5.37	899.56± 5.37	1,001.01±4.57	−49.27± 7.12**	−24.63
		EM	1,050.28±5.37	898.97± 5.72	1,000.28±4.56	−50.00± 7.11**	−25.00
	L55	EN	940.83±4.57	865.16± 4.11	972.35±3.52	31.51± 6.32**	15.76
		EM	940.83±4.57	869.83± 4.37	973.54±3.60	32.71± 6.29**	16.35
	L77	EN	901.22±4.71	828.03± 4.28	906.48±3.47	5.26± 6.14	2.63
		EM	901.22±4.71	826.45± 4.31	921.07±3.51	19.85± 6.19**	9.92
	L99	EN	981.87±5.20	874.70± 5.58	973.52±4.21	−8.53± 6.71	−4.17
		EM	981.87±5.20	880.33± 5.54	980.14±4.27	−1.73± 6.79	−0.86
Body weight at 40 weeks (g)	L33	EN	1,784.86±9.84	1,774.15± 9.85	1,780.57±9.70	−4.29±14.37	−2.14
		EM	1,784.86±9.84	1,763.63±10.16	1,770.45±9.55	−14.40±14.21	−7.20
	L55	EN	1,547.68±9.01	1,550.35± 6.49	1,591.86±7.85	44.18±13.79**	22.09
		EM	1,547.68±9.01	1,560.33± 7.07	1,600.67±7.86	52.99±13.45**	26.49
	L77	EN	1,496.45±7.12	1,536.84± 7.45	1,542.27±7.04	45.82±12.61**	22.91
		EM	1,496.45±7.12	1,528.00± 7.14	1,575.50±7.47	79.05±12.34**	39.52
	L99	EN	1,616.58±9.01	1,617.32± 8.45	1,621.59±9.45	5.01±13.86	2.50
		EM	1,616.58±9.01	1,631.72± 8.18	1,628.99±9.30	12.41±13.75	6.20

* $P \leqq 0.05$; ** $P \leqq 0.01$

at maturity and 0.8 g in egg weight. The size of the breeding population and the mating procedure followed to minimise the genetic drift and inbreeding in the control line, by representing each sire by a sire and each dam by a dam in succeeding generations, lead us to assume that the improvement or decline in different traits could have occured more because of the environment than a genetic change. Marks (1981) observed a large environmentally induced increase for egg mass in the control line of the S_1 generation. Such positive trends in the control line, as observed in this study, in spite of a random selection, are commonly mentioned in the literature.

Realized response

Two generations of selection resulted in a substantial phenotypic improvement for egg number in the egg number selected line and for egg mass in the egg mass selected lines. To discount the environmental trend from the total change observed for different traits in the selected lines, their generation means were corrected to the control level. The control corrected generation means in the egg number and egg mass selected sub-lines for different selected and unselected traits are presented in Tables 2 and 3. The difference between the control corrected means of generations S_2 and S_0 was assumed to be the genetic response resulting from the two intervening selection cycles. Such genetic gains in selected and unselected traits appear in Tables 2 and 3 along with the control corrected generation means in the egg number and egg mass selected sublines.

Although the selection was carried out on index values, the selection differentials were obtained for egg number only as number of eggs and for egg mass only as grams of egg mass from the actual trait values of the individuals selected as parents. These are given in Table 1. It is apparent that the differences between expected (unweighted) and effective (weighted) selection differential averaged over the two generations were small. The standardized selection differentials ($\bar{i}$) varied from 0.68 to 0.74 σ_P in egg number selected lines and from 0.69 to 0.71 σ_P in egg mass selected sub-lines. The average intensity of selection for egg number selected lines (0.70 σ_P) was close to that of egg mass selected lines (0.66 σ_P).

Because of the similarity in genetic material (White Leghorns) and the selection procedure followed, the individual sub-lines selected on a common selection criterion were considered as replicates. However, the number of individuals measured in each sub-line, was adequate enough to minimise the measurement sampling error. The genetic changes in different traits were also obtained as an average of all the replicates belonging to each of the selection criterion and are presented in Table 4. The genetic and phenotypic correlations were initially estimated on an intra-subline and generation basis, and their pooled estimates are shown in Table 5.

Response in selected traits

The direct as well as the correlated responses in different traits are shown for each of the sublines in Tables 2 and 3.

Egg number. The direct response in the egg number selected lines varied from 0.98 to 3.74 eggs per generation and the correlated response for this trait in the egg mass selected lines varied from 0.86 to 3.16 eggs. When averaged over all the sublines for part period egg number, the direct response was marginally more than the correlated response (Table 4). In spite of the moderate intensity of selection and for only two-generation, the average response of 2.16 eggs is in the range of responses reported in the literature for other egg number

Table 4. A comparison of responses for egg mass and egg number as selection criteria after two selection cycles

		L33	L55	L77	L99	Average of all lines	EM–EN
Egg number (no.)	EN	3.74	2.01	0.98	1.91	2.16	
	EM	3.16	1.85	0.86	1.33	1.80	– 0.36
Egg mass (g)	EN	204.47	129.52	115.40	134.53	145.95	
	EM	184.53	156.73	137.91	130.76	152.48	6.53
Age at first egg (days)	EN	– 4.37	– 2.55	– 2.05	– 3.48	– 3.11	
	EM	– 4.03	– 2.56	– 1.80	– 3.35	– 2.93	+0.18
Egg weight (g)	EN	– 0.67	0.26	0.58	0.02	0.04	
	EM	– 0.44	0.69	0.96	0.55	0.44	+0.40
Body weight at 20 weeks (g)	EN	– 24.63	15.76	2.63	– 4.17	– 2.60	
	EM	– 25.00	16.35	9.92	– 0.86	– 0.10	+2.50
Body weight at 40 weeks (g)	EN	– 2.14	22.09	22.91	2.50	11.34	
	EM	– 7.20	26.49	39.52	6.20	16.25	+4.91

Table 5. Estimates of genetic (sire component) and phenotypic correlation amongst different economic traits in four sublines of White Leghorns

Lines		Egg no.		Egg mass		Egg weight		Age at maturity		Body wt at 20 weeks		Body wt at 40 weeks	
		r_G	r_p	r_G	r_p	r_G	r_p	r_G	r_p	r_G	r_p	r_G	r_p
L33	EN[a]	–	–	0.960*	0.964	–0.638*	–0.116	–0.914*	–0.709	0.353*	0.307	–0.123	–0.037
	EM[a]	0.958*	0.956	–	–	–0.186	0.179	–0.912*	–0.703	0.511*	0.372	0.112	0.068
L55	EN	–	–	0.931*	0.958	–0.296	0.025	–0.768*	–0.640	0.362*	0.256	0.309	0.110
	EM	0.928*	0.960	–	–	0.388*	0.360	–0.973*	–0.592	0.567*	0.321	0.451*	0.229
L77	EN	–	–	0.907*	0.956	–0.210	–0.051	0.483*	–0.639	0.370	0.327	0.185	0.106
	EM	0.917*	0.948	–	–	0.607*	0.315	–0.140	–0.583	0.739*	0.457	0.543*	0.246
L99	EN	–	–	0.917*	0.956	–0.515*	–0.026	–0.895*	–0.704	0.897*	0.330	–0.191	0.092
	EM	0.979*	0.956	–	–	0.818*	0.309	–0.999*	–0.670	0.676*	0.408	0.126	0.215
Control	EN	–	–	0.938*	0.951	–0.385*	0.024	–0.640*	–0.665	0.492*	0.274	0.384*	0.123
	EM	0.938*	0.951	–	–	0.079	0.344	–0.503*	–0.626	0.579*	0.363	0.547*	0.212

[a] EN and EM for L33 to L99 refers to egg number correlations with other traits in egg number subline and egg mass correlations with other traits in egg mass selected subline. In the control EN and EM refers to egg number and egg mass traits' correlation in the control line with other traits

* The estimate exceeded twice SE. All phenotypic correlation estimates were significant

selection experiments. An average correlated genetic change of 1.8 eggs per generation in the egg mass selected sublines is not unexpected because by selecting for egg mass, selection pressure was indirectly imposed on both egg number and egg size. Marks (1981) and Craig et al. (1982) observed substantial correlated changes in hen day and hen housed egg production to egg mass selection.

Egg mass. Both egg mass and egg number as selection criteria have produced significant direct and correlated responses for egg mass in the different sublines (Table 2). While the direct responses ranged from 130 g to 185 g. The correlated response ranged from 115.4 to 204.47 g.

An exception is L33 where the direct response for egg mass was found to be 20 g less than the correlated response for egg mass in the egg number selected subline. This may have happened because in the egg mass selected subline of L33 egg weight showed a negative response unlike in the egg mass selected sublines of the other three lines. The averaged direct response for egg mass over the four selected sublines was found to be 152 g per generation and did not differ much from the averaged correlated response for this trait (146 g) seen in the egg number selected sublines.

The close similarity of direct and correlated responses for egg number as well as for egg mass suggests that with either trait as a selection criterion more or less similar responses can occur in these two traits. The positive and high genetic association between egg number and egg mass both observed here in different lines (Table 5) and cited in other reports (Waring et al. 1962) should account for a greater similarity in direct and correlated responses, for these two traits.

Response in unselected traits

Age at first egg. The trend of response was towards early maturity in both egg number and egg mass selected sublines. The decline in age at first egg was of the same order in both the egg number and egg mass selected sublines of different flocks. Averaged over the sublines the correlated responses in egg number and egg mass selected sublines did not differ much (Table 4). Since egg number selection, particularly the early part period, is a positive selection for rate of lay and negative selection for age at maturity, the correlated decline in age at first egg to egg number selection or to egg mass selection, in which the egg number is also a component, is not unexpected. In several egg number selection experiments correlated decline in age at maturity was consistently observed. Craig et al. (1982) realised a sizable correlated decline in age at maturity to egg mass selection. Except in one line (L77), the genetic correlation (from sire component) of age at maturity with egg number and egg mass were of the same sign and more or less of the same magnitude (Table 5). This may explain the reason for obtaining a similar correlated responses in egg number and egg mass selected sublines for age at first egg.

Egg weight. It can be seen from Table 5 that while the genetic correlations of egg weight with egg number were negative and low they were positive and high with egg mass at least in three of the four lines. In the fourth line (L33) the egg mass, although negatively correlated with egg weight, its magnitude was considerably less when compared to that of egg number with egg weight. As expected from the correlations seen in L33, egg weight declined in both egg number and egg mass selected sublines, the decline being greater in the former. While the positive genetic correlation in the other three egg mass selected lines adequately reflected in positive egg weight responses, the low magnitude negative genetic correlations did not bring about any marked decline in egg weight as a correlated response. Responses averaged over the sublines revealed that egg mass as a selection criterion produced positive correlated responses in egg weight compared to egg number as a selection criterion.

Genetic selection pressure aimed at increasing egg mass can force changes in egg number or egg size or both. The available genetic variation of the traits and their genetic association in the base population may govern the relative degree of changes in egg number and egg size. Similar to the positive egg weight response to egg mass selection observed in this study, Marks (1981) also observed that the mean egg size of his egg mass selected lines was larger than the egg weight mean in the control. In addition, Craig etal. (1982) observed that the egg mass selected pullets laid heavier eggs than the unselected control.

Body weight. Body weight at 20 weeks of age, although it declined in the S_1 generation, recovered to the base generation level in the S_2 generation in both egg number and egg mass selected sublines (Table 3). The response in individual lines varied. It was positive in two lines and negative in the other two. The response averaged over the four lines suggested that body weight at 20 weeks of age did not change much in egg number or egg mass selection. The estimated genetic correlations from the sire component were all positive and in most cases low in magnitude (Table 5). On the other hand, body weight at 40 weeks showed a tendency to increase during the two selected generations in at least 3 of the 4 lines for both egg number and egg mass selection. The positive response found in two of them was significant (Table 3). The estimated genetic correlations were low and negative in two of the egg number selected sublines and although positive in the remaining line, were low in magnitude. Averaged over the four sublines the response for 40 week body weight was 11.34 g and 16.25 g in egg number and egg mass selected sbulines.

The lack of a correlated change in 20 week body weight and only marginal correlated changes in 40 week body weight could be due to low genetic correlations prevailing in different lines between the body weights and the selection criteria. Also, the intensity of selection for either selection criterion was not more than 0.7 σ_P in this study. Eisen et al. (1973) showed that the correlated response in body weight increases with increased intensity of selection in mice.

Comparison between egg number and egg mass selected sublines

The sublines selected for egg number and egg mass of a given line had the same genetic background in the base generation. Also, the average intensity of selection was not much different between them. Therefore, differences, if any, between selection responses in subsequent selected generations may be assumed to have occurred primarily as a result of differences in the effectiveness of the selection criterion. The difference (EM–EN) in the average responses shown in Table 4 are the reflection of the effectiveness of EM over EN in bringing about responses in different traits for one generation of selection. Notable among them is that all the egg mass sublines had higher egg weight than was observed in the egg number selected sublines. When the differences were averaged over the lines it was found that the egg mass selected lines laid marginally, fewer eggs which were heavier. They matured more or less at the same age and weighed the same at 20 and 40 weeks of age compared to those selected for egg number.

The positive difference in egg mass in favour of egg mass lines could have resulted from the increase in egg weight of the egg mass selected lines in spite of the fact that they laid fewer eggs than the egg number selected lines.

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