Theor. Appl. Genet. 64, 169–175 (1983)

Selection for Egg Production on Part Records

Part 2. Correlated Response to Selection

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Summary. Response in the selected and the correlated traits from five generations of index selection (I.D.S. method) for egg production to 40 weeks of age in four White Leghorn populations have been presented. The correlated traits measured included: Age at first egg, egg weight, body weight and also derived traits such as egg mass, survivors' rate of lay, efficiency index and ratio of egg weight to body weight. Response realized for the selected trait was significant in three out of the four selected lines. Predicted and realized genetic gains were comparable in magnitude for most of the traits studied. The significance of these findings in selection experiments is discussed.

Key words: Direct response – Correlated response – Predicted genetic gains – Realized genetic gains – Egg production – Part records – White Leghorn

Introduction

Estimates of correlated response to selection are of interest as they provide a basis for the improvement of economic traits in farm animals and poultry. The theory of correlated response has been discussed by Falconer (1960). Genetic correlation between selected and unselected traits resulting either from pleiotropy and/or linkage is assumed to be the cause of such response. Direct and correlated responses to selection for traits of economic importance in chickens have been reported by a number of workers. Recent reports that deal with correlated responses to egg production selection are those of Abplanalp et al. (1964), Nordskog et al. (1967), Craig et al. (1969), Kinney et al. (1970), Mohapatra and Ahuja (1971), Gowe et al. (1973), Nordskog et al. (1974) and Poggenpoel and Erasmus (1978). Results realized from these studies indicated that selection for egg production not only yielded positive response (except Nordskog et al. 1967) in the selected trait but also invariably produced concommitant changes in other traits like age at sexual maturity, egg mass, egg weight and body weight at different ages and their ratios in different combinations.

In a recent paper Ayyagari et al. (1980) reported the direct response to 4 generations of selection for egg number to 40 weeks of age in four White Leghorn populations. In this paper the progress made in the criterion of selection is updated with the addition of results from the 5th selected generation and the response in the correlated traits for 5 generations of selection for egg number in the same populations is given.

Materials and Methods

The history of the genetic stocks used, selection procedure adopted, origin and other details regarding the control population and husbandry practices followed have been described previously (Ayyagari et al. 1980). However, a brief description of the populations is given here even though this repeats some of the details given earlier.

The criterion of selection in the selected populations was a family index (Osborne 1957a, b) for egg number to 40 weeks of age. The number of effective sires and dams and the progeny measured, averaged over generations, are shown in Table 1 along with the average selection differential, phenotypic standard deviation and intensity of selection for each line.

A pedigreed randombred control with a sire base comparable to the selected lines was used to measure the environmental trend. To minimize the genetic drift in the control line, as far as possible, each sire contributed a sire and each dam contributed a dam as breeders in succeeding generations.

The unselected traits measured, both observed as well as derived, were as follows:

Egg Weight: The average weight in grams of all the eggs laid during two weeks at 39 weeks of age.

Egg Mass: The product (in grams) of the number of eggs to 40 weeks of age with average egg weight.

0040-5752/83/0064/0169/$ 01.40

Table 1. Population size, selection differential, phenotypic standard deviation and intensity of selection for different lines [a]

Line	No. of sires	No. of dams	No. of progeny	Selection differential		Phenotypic standard deviation	Intensity of selection
				Expected	Effective		
L33	37.2	174.8	727.8	11.66	11.81	16.41	0.719
L55	37.2	171.4	749.0	9.15	9.32	13.24	0.703
L77	37.0	163.0	636.3	9.28	9.41	14.02	0.671
L99	36.8	165.0	649.5	9.18	9.13	14.51	0.629
Control	34.0	160.0	526.3	–	–	–	–

[a] All parameters averaged over generations

Age at First Egg: The age in days at which the first egg was laid.

Survivors' Rate of Lay: The ratio of survivors' egg number to the functional days converted to percentage.

Body Weight: Body weight at 20 and 40 weeks of age to the nearest 10 g.

Ratio of Egg Weight to Body Weight: The ratio of egg weight in grams to body weight at 40 weeks, in kilograms.

Efficiency Index: Egg mass per functional day in grams divided by body weight at 40 weeks in kilograms (Nordskog et al. 1974).

Statistical Analysis: Preliminary analysis revealed substantial differences among hatches. Hence data were corrected for hatch effects by fitting least square constants (Harvey 1966). All subsequent analyses were done on hatch corrected data.

Heritabilities and genetic correlations were computed from variance and covariance component analysis. Heritabilities for the various unselected traits were calculated as $4\hat{\sigma}_S^2/\hat{\sigma}_P^2$ where $\hat{\sigma}_S^2$ is the estimated sire component of variance and $\hat{\sigma}_P^2(\hat{\sigma}_S^2+\hat{\sigma}_d^2+\hat{\sigma}_e^2)$ is the estimated phenotypic variance.

Genetic correlations were estimated as

$$r_G = \frac{\hat{\sigma}_{XY}}{\sqrt{\hat{\sigma}_X^2 \cdot \hat{\sigma}_Y^2}},$$

where $\hat{\sigma}_{XY}$ is the estimated sire component of covariance between traits X and Y, $\hat{\sigma}_X^2$ and $\hat{\sigma}_Y^2$ are the estimated sire components of variance for traits X and Y, respectively.

Heritabilities and genetic correlations were estimated initially on intrageneration intrapopulation basis and then pooled over generations within population by weighting each estimate with the inverse of its variance to provide combined estimates, as shown below.

$$\frac{\sum_{i=1}^{n}\left[\frac{h_i^2}{(S.E._i)^2}\right]}{\sum_{i=1}^{n}\frac{1}{(S.E._i)^2}} = \text{Pooled heritability}$$

$$\sqrt{\frac{1}{\sum_{i=1}^{n}\frac{1}{(S.E._i)^2}}} = \text{S.E. of the pooled estimate}$$

Genetic correlations were also pooled similarly.

Environmental trend in the control was measured from the regression of generation means on generation number. The realized gains for different traits in the selected lines were calculated as deviations from the control line in each generation and were regressed on generation number to obtain average response per generation. The predicted response in the criterion of selection and the predicted gains in the correlated traits were estimated utilizing the following procedure (Falconer 1960).

$$E(R)_x = h^2\, i_X\, \sigma P_X$$

$$E(CR)_Y = h_X \cdot h_Y\, r_{G_{XY}}\, i_X \cdot \sigma P_Y$$

where

h = square root of h^2
$r_{G_{XY}}$ = genetic correlation between the selected trait, egg number (X) and correlated trait (Y)
σP_Y = phenotypic standard deviation of the trait denoted by the subscript
i_X = intensity of selection in the selected trait, egg number (X), in standard deviation units.

The predicted gains in different traits were then corrected upwards by multiplying with a factor "K", which is the expected relative gain over mass selection because of a family index selection used in the selected lines (Nordskog et al. 1967). The theoretical efficiency of index selection over mass selection (K) was obtained from multiple correlations between breeding value of the individual and the criterion of selection.

Results and Discussion

Control Population

The environmental trend per generation due to random selection in the control line for different traits are presented in Table 3.

Regressions of all traits, except for egg number to 40 weeks, body weights at 20 and 40 weeks and egg mass to 40 weeks were negative. In all cases the regression coefficients were non-significant. Keeping in view the size of the breeding population maintained and the mating procedure adopted to minimize the genetic drift and inbreeding (Ayyagari et al. 1980) these non-significant regressions provided little evidence of genetic change in the control population during the years of random selection. Consequently it was assumed that the deviations of the selected and correlated traits in the selected lines from control to be unbiased estimates of genetic change resulting from selection for part period egg number, that is egg number during a portion of the period of egg laying (part period).

Phenotypic Responses in Selected Lines

The means for various traits averaged across the lines within each generation were regressed on generation number to obtain phenotypic responses and are presented in Table 2 along with the realized genetic responses obtained in a similar manner except that the generation means were corrected to control level. As expected the magnitude of phenotypic responses were inflated in most of the traits. On comparing the two sets of regressions, there is a good agreement in the direction of responses as well as their significance for most of the traits. The difference in the magnitude of variance about the regressions obtained for the averaged generation means of the selected lines, with and without control correction, on generation number (Table 2) indicated some evidence for the useful functioning of the control in eliminating the environmental fluctuations between generations that are common for both selected and control population (Hill 1972).

Realized Genetic Responses in Selected Lines

The responses due to selection for number of eggs to 40 weeks of age are presented in Table 3 and Figs. 1–3. The regressions for traits other than egg number to 40 weeks, are estimates of the correlated responses to selection for egg number to 40 weeks. In view of the high standard error of the genetic responses for some traits in separate populations (Table 3) the response was also obtained as an average across all populations assuming them as replicates, because the procedure of selection was the same in these four selected populations in all the generations. The variance of such mean response across the selected lines is expected to be 1/4 times that of an individual line. The mean responses are presented in Table 2.

Table 2. Average phenotypic and genetic responses for selected and correlated traits averaged over selected lines

Trait		Uncorrected	Corrected to control
Egg number to 40 weeks of age	(n)	4.41 ± 1.26*	3.15 ± 0.75*
Egg weight	(g)	− 0.89 ± 0.24*	− 0.52 ± 0.38
Egg mass to 40 weeks of age	(g)	177.60 ± 79.10	133.00 ± 58.45
Age at first egg	(d)	− 5.70 ± 1.76*	− 2.67 ± 0.93*
Survivors' rate of lay	(%)	0.45 ± 0.77	1.13 ± 0.43
Body weight at 20 weeks	(g)	20.67 ± 18.97	22.47 ± 8.79
Body weight at 40 weeks	(g)	− 1.91 ± 19.88	− 3.78 ± 18.48
Ratio of egg weight to body weight	(g/kg)	− 0.52 ± 0.36	− 0.26 ± 0.29
Efficiency index	(g/day/kg)	− 0.22 ± 0.21	0.18 ± 0.25

* $P \leq 0.05$

Table 3. Regressions indicating the time trend in the pedigreed randombred control population and the average realized genetic response to selection for egg number in selected lines

Traits		Random control	Selected populations deviation from control			
			L 33	L 55	L 77	L 99
Egg number to 40 weeks of age	(n)	1.24 ± 1.77	4.55 ± 0.63[b]	3.2 ± 0.67[b]	2.89 ± 0.87[a]	2.03 ± 0.93
Egg weight	(g)	− 0.36 ± 0.18	− 1.15 ± 0.48	− 0.23 ± 0.30	− 0.46 ± 0.39	− 0.23 ± 0.44
Egg mass	(g)	44.57 ± 95.53	169.23 ± 62.62	152.85 ± 53.87[a]	122.64 ± 55.72	84.35 ± 70.21
Age at first egg	(d)	− 3.03 ± 2.36	− 4.42 ± 1.14[a]	− 2.31 ± 0.71[a]	− 1.88 ± 1.14	− 2.08 ± 1.05
Survivors' rate of lay	(%)	− 0.68 ± 0.99	1.23 ± 0.36[a]	1.47 ± 0.39[a]	1.46 ± 0.51[a]	0.36 ± 0.65
Body wt. at 20 weeks	(g)	− 1.80 ± 21.58	13.14 ± 7.37	9.95 ± 11.08	31.87 ± 8.21[a]	27.49 ± 6.64[a]
Body wt. at 40 weeks	(g)	1.67 ± 20.95	−19.47 ± 13.38	−15.78 ± 18.44	12.67 ± 17.34	16.04 ± 21.79
Ratio of egg wt. to body weight	(g/kg)	− 0.26 ± 0.43	− 0.29 ± 0.25	0.30 ± 0.34	− 0.56 ± 0.38	− 0.49 ± 0.34
Efficiency index	(g/day/kg)	− 0.41 ± 0.41	0.19 ± 0.17	0.70 ± 0.29	0.08 ± 0.30	− 0.24 ± 0.28

[a] $P \leq 0.05$; [b] $P \leq 0.01$

Direct Response to Selection

Egg Number to 40 Weeks of Age: Average realized genetic gain per generation was positive in all the lines and was significant in 3 of them (Table 3 and Fig. 1). With the inclusion of results from the fifth selected generation the magnitude of responses in separate lines increased and was significant in two additional lines than reported previously for 4 generations (Ayyagari et al. 1980). The response of 3.15 eggs ($P \leqq 0.05$), averaged across lines, was comparable with the results reported in other egg number selection experiments (Poggenpoel and Erasmus 1978) and suggested the effectiveness of part record egg number as a selection criterion in these lines. This significant improvement for egg number seen in the selected lines could be due to the positive improvement seen in rate of lay coupled with the decline

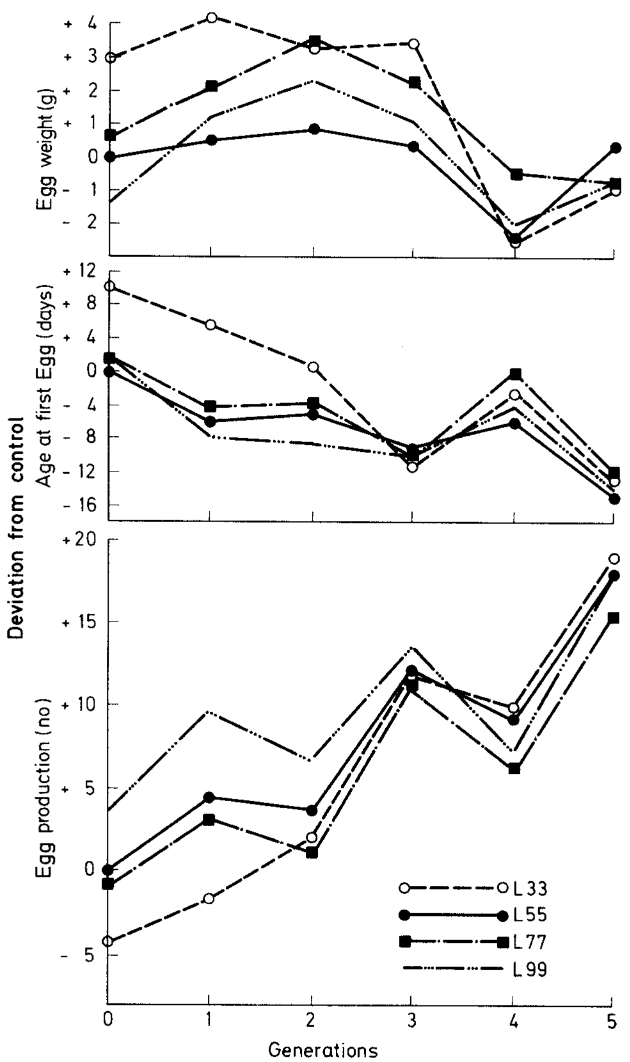

Fig. 1. Direct response to egg number and correlated responses in age at first egg and egg weight

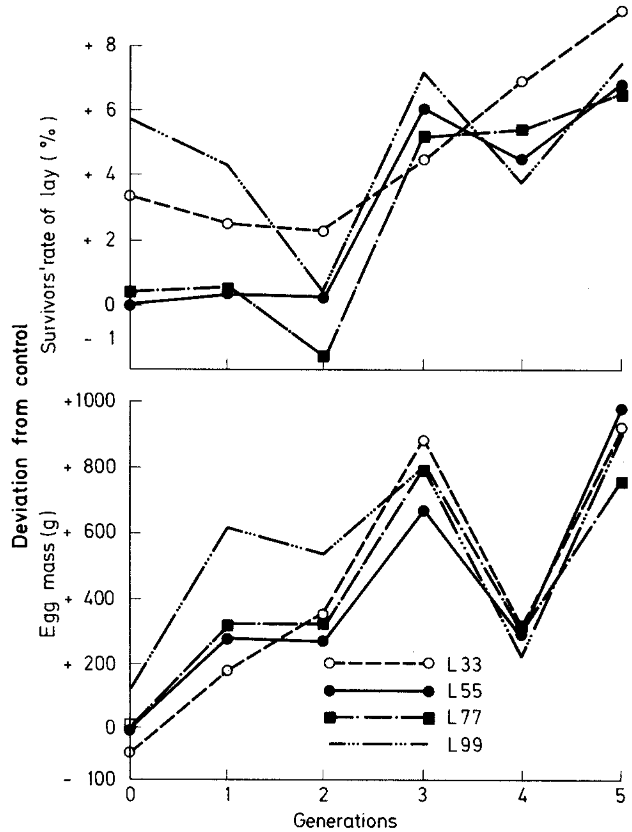

Fig. 2. Correlated responses in egg mass and survivors' rate of lay

in age at maturity (Table 3) because the egg number selection is also a positive selection for rate of lay and a negative selection for age at first egg.

Correlated Response to Selection

Egg Weight: Egg weight declined in all the lines (Fig. 1) as has been observed in egg number selection experiments reported by other workers. The magnitude of decline, however, varied in different lines (Table 3). A decline in egg weight has been consistently observed in all selection experiments whether based on part period rate of lay or number of eggs (Craig et al. 1969; Kinney et al. 1970; Mohapatra and Ahuja 1971; Nordskog et al. 1974; Poggenpoel and Erasmus 1978). The decline of 0.52 g averaged across lines (Table 2), was not significantly different from zero.

Egg Mass: The egg mass improved consistently in all the four lines studied as a correlated response to selection for egg number but was significant only for L 55 (Fig. 2 and Table 3). A positive gain in egg mass due to selection on part period egg production was observed also by Nordskog et al. (1974). The positive genetic gain seen in egg mass was primarily due to a significant increase in egg number which was large enough to offset the decline in egg weight. This suggested a positive genetic association between egg number and egg mass as reported by Waring et al. (1962).

Age at First Egg: The trend of response was towards early maturity even though this trait was not selected directly (Fig. 1). The regression was negative in all the selected lines and was significant in two of them (Table 3). The response of −2.67 days, averaged over lines, was also significant (Table 2). That the egg number selection, as stated above, is also a negative selection for age at first egg is evident from the results and other reports (Abplanalp et al. 1964; Mohapatra and Ahuja 1971; Gowe et al. 1973 and Poggenpoel and Erasmus 1978) where the selection criterion was number of eggs laid to a fixed age.

Survivors' Rate of Lay: Eggs laid to 40 weeks by surviving hens improved in all the lines and the response was significant in three of them (Table 3 and Fig. 2). The mean response averaged across lines was also positive (Table 2). This observation was consistent with the findings of Gowe et al. (1973) that continuous selection for egg number to a fixed age increased the rate of egg production in that period even after 20 generations of selection, in spite of some selection emphasis placed on other traits of secondary importance.

Body Weight: Figure 3 shows the correlated response in body weight at 20 and 40 weeks of age after selection for egg number. Twenty week body weight showed a positive trend in all the lines, consistent with a very high positive genetic correlation of this trait with egg number, and was significant in two of them. The response pooled over lines was also positive.

Forty week body weight, while decreased in two lines, improved in the other two lines resulting in a marginal decrease in the averaged response (Tables 2 and 3). The response in individual lines in the opposite direction could be attributed to the prevailing genetic correlations in the opposite direction in these two sets of lines. From the standard error associated with the response averaged across lines it may be said that body weight at 40 weeks did not change significantly due to the selection for egg number. A decline in mature weight has been observed in many of the selection studies based either on number of eggs to a fixed age or rate of lay (Nordskog et al. 1967; Craig et al. 1969; Kinney et al. 1970; Nordskog et al. 1974). It has been shown in mice that correlated responses in body weight traits increased as the selection intensity

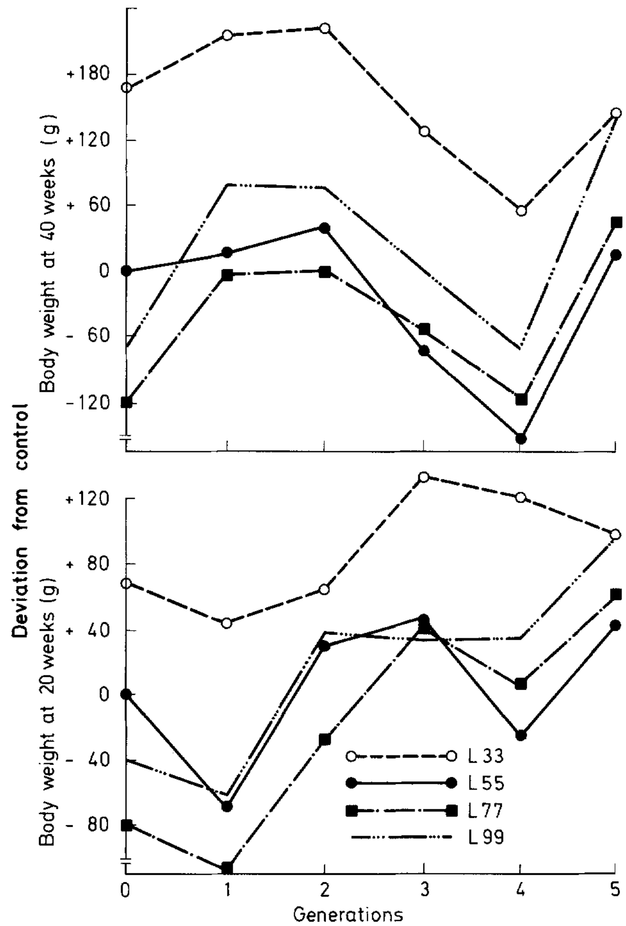

Fig. 3. Correlated responses in body weight at 20 weeks and 40 weeks of age

increased (Eisen et al. 1973). If the same situation were to hold good in chickens the lack of agreement could be due to low intensity of selection coupled with interesting differences in genetic correlations prevailing in different lines of this trait with egg number.

Efficiency Index: The efficiency index has been shown to be a useful indirect measure of feed efficiency for egg production (Nordskog et al. 1974). The correlated response in the index although positive in most cases does not suggest, except in case of L 55, any real change in these lines due to selection for egg number because of the high standard errors associated with the responses.

Egg Weight to Body Weight Ratio: No definite trend emerged in the ratio of egg weight to body weight in the individual lines. Averaged over the lines it was small, negative and not significantly different from zero. This was contrary to the observation of Nordskog et al. (1974) who reported a positive improvement in

Table 4. Estimates of parameters utilized in the prediction of direct and correlated responses along with the predicted and realized genetic responses

Trait		h^2_S	$r_{G(S)}$	σ_P	i	Predicted response		Realized response
						Mass selection	Index selection[a]	
Egg number to 40 weeks of age	(n)	0.188 ± 0.028	–	14.54	0.681	1.862	2.476	3.15 ± 0.75 *
Age at first egg	(d)	0.324 ± 0.040	-0.658 ± 0.010	13.11	–	– 1.957	– 2.603	-2.67 ± 0.93 *
Egg weight	(g)	0.407 ± 0.017	-0.562 ± 0.024	3.62	–	– 0.383	– 0.509	-0.52 ± 0.38
Body wt. at 20 weeks	(g)	0.438 ± 0.052	0.980 ± 0.010	112.92	–	21.60	28.73	22.47 ± 8.79
Body wt. at 40 weeks	(g)	0.494 ± 0.056	-0.238 ± 0.065	200.78	–	– 9.90	–13.16	-3.78 ± 18.48

* $P \leq 0.05$

[a] to obtain the predicted response to index selection, the predicted response to mass selection was multiplied with a factor K (1.33), which is the average expected relative gain of index selection over mass selection

h^2_S = heritability of the trait from sire component of variance

$r_{G(S)}$ = genetic correlation of the trait with egg number from sire component of covariance

σ_P = phenotypic standard deviation of the trait

i = intensity of selection in the selected trait (egg number)

this ratio in their lines selected for rate of lay. Small negative change in egg weight with more or less constant body weight due to selection for egg number might have contributed to this sort of response in the present study.

Unlike the other egg number selection experiments, the results in the present study, particularly correlated responses in egg weight and body weight, were not significantly different from zero, while the criterion of selection has shown significant improvement. Although this is not a proof, it could be evidence that moderate intensity of selection may not adversely affect the ancillary traits that have a bearing on the net economic merit of the populations involved.

Comparison of Predicted and Realized Gains

The prediction was confined only to those traits where parameter estimates were available and are presented along with the realized responses in Table 4. The parameter estimates pooled over generations and lines were used to predict the average responses for the combined lines.

There appeared to be good agreement between predicted and realized gains (Table 4). This could be due to the averaging of the responses across all lines each generation as well as due to pooling of parameter estimates. Kinney and Shoffner (1967) have suggested that predictions with the pooled parameter estimates would be more accurate than with the estimates from a single year. The results of other selection experiments indicate that the prediction of selection response remains fairly valid for short term experiments. Since only 5 generations of selection are covered in this report a close agreement between the predicted and realized responses is in agreement with literature reports.

Literature

Abplanalp, H.; Lowrey, D.C.; Lerner, I.M.; Dempster, E.R. (1964): Selection for egg numbers with X-ray induced variation. Genetics **50**, 1083–1100

Ayyagari, V.; Mohapatra, S.C.; Venkatramaiah, A.; Thiagasundaram, T.; Choudhuri, D.; Johri, D.C.; Renganathan, P. (1980): Selection for egg production on part record. Part 1. Evaluation of short term response to selection. Theor. Appl. Genet. **57**, 277–283

Craig, J.V.; Biswas, D.K.; Saadeh, H.K. (1969): Genetic variation and correlated responses in chickens selected for part-year rate of lay. Poult. Sci. **48**, 1288–1296

Eisen, E.J.; Hanrahan, J.P.; Legates, J.E. (1973): Effect of pupulation size and selection intensity on correlated responses to selection for post-weaning gain in mice. Genetics **74**, 157–170

Falconer, D.S. (1960): Introduction to quantitative genetics. Edinburgh, London: Oliver and Boyd

Gowe, R.S.; Lentz, W.E.; Strain, J.H. (1973): Long term selection for egg production in several strains of White Leghorns. Performance of selected and control strains including genetic parameters of two control strains. 4th European Poultry Conference. pp. 225–245. London

Harvey, W.R. (1966): Least squares analysis of data with unequal subclass numbers. U.S.D.A., A.R.S.20,8. pp. 1–157

Hill, W.G. (1972): Estimation of genetic change. 2. Experimental evaluation of control populations. Ann. Breed. **40**, 193–213

Kinney, T.B. Jr.; Bohren, B.B.; Craig, J.V.; Lowe, P.C. (1970): Response to individual, family or index selection for short term rate of egg production in chickens. Poult. Sci. **49**, 1052–1064

Kinney, T.B., Jr.; Shoffner, R.N. (1967): Phenotypic and genetic responses to selection in a meat-type poultry population. Poult. Sci. **46,** 900–910

Mohapatra, S.C.; Ahuja, S.D. (1971): Selection for egg production in a flock of White Leghorn. II. Response in the secondary traits and their heritabilities. Indian J. Poult. Sci. **6,** 17–22

Nordskog, A.W.; Festing, M.; Verghese, M.W. (1967): Selection for egg production and correlated response in the fowl. Genetics **55,** 179–191

Nordskog, A.W.; Tolman, H.S.; Casey, D.W.; Lin, C.Y. (1974): Selection in small populations of chickens. Poult. Sci. **53,** 1188–1219

Osborne, R. (1957a): The use of sire and dam family averages increasing the efficiency of selective breeding under a hierarchical mating system. Heredity **11,** 93–116

Osborne, R. (1957b): Family selection in poultry. The use of sire and dam family averages in choosing male parents. Proc. R. Soc. Edinburgh, Sect. B **66,** 374–393

Poggenpoel, D.G.; Erasmus, J.E. (1978): Long term selection for increased egg production. Br. Poult. Sci. **19,** 111–123

Waring, F.J.; Hunton, P.; Maddison, A.E. (1962): Genetics of a closed poultry flock. 1. Variance and covariance analysis of egg production, egg weight and egg mass. Br. Poult. Sci. **3,** 151–160

Received August 26, 1982
Communicated by H. Abplanalp

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