

An Experimental Test of the Efficiency of Family Selection in Chickens*

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Summary. Responses to single trait selection on individual phenotype and sire-family mean phenotype for survivor's egg weight and rate of lay were measured for a single generation in 13 replicates. Each replicate-selection criterion-trait subclass consisted of eight sire families or 72 females measured and was reproduced from the best 25% of the families or individuals. The realized heritability of egg weight was 0.39 and that of rate of lay was 0.31, both of which were significantly greater than zero but not significantly different from the predicted values based on half-sib correlations in the base population.

The standardized response to sire-family selection was less than the response to individual selection for both traits and the difference was significant for rate of lay (0.10; 0.31) but not for egg weight (0.22; 0.39). The predicted responses to sire-family selection were less than those for individual selection for both traits, and the observed responses to sire-family selection were not significantly different from the predicted values for either trait.

These experimental results do not disagree with the theoretical expectations of the relative efficiencies of individual and sire-family selection.

Key words: Genetics – Poultry – Family selection – Individual selection

Introduction

The theoretical relative efficiency of family and individual selection to improve individual performance was devel-

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oped and discussed by Lush (1947). The application of these selection criteria to the improvement of individual performance in poultry was discussed by Lerner (1950). The general conclusion has been that for lowly heritable traits, selection based on full or half-sib family means would be superior to selection based on the individual phenotypes, whereas, for highly heritable traits individual selection would be superior to either full or half-sib family selection.

Kinney et al. (1970) in an unreplicated experiment, compared sire and dam family selection (both half-sib families) with individual selection for the lowly heritable trait, survivor's rate of lay from first egg to 40 weeks of age. The average response over generations from individual selection was intermediate to the average responses from selection on sire family and dam family means. When responses were standardized for selection intensity and differences in the phenotypic standard deviation, individual selection was clearly more efficient than either family-mean criterion of selection.

Wilson (1974) reported that individual selection produced greater response than family selection for both larval and pupal weights of *Tribolium castaneum* in a single-generation replicated experiment and in a multiple-generation experiment, but the differences observed between criteria were not statistically significant. Individual selection for pupal weight was also reported by Campo and Tagarro (1977) to produce greater, but statistically similar, response than family selection in two unreplicated, multiple-generation experiments.

The objective of the present experiment was to further observe the relative efficiencies of half-sib sire family and individual selection in chickens for egg weight at 40 weeks of age, which is generally accepted to have a high heritability, and survivor's rate of lay from first egg to 40 weeks of age, which is generally accepted to have a low heritability.

Materials and Methods

A replicated single generation selection experiment was performed for which females and males were sampled from an unselected synthetic line (NCR). The basis of the line was about 450 random females and 50 random males hatched in 1972 from each of six commercial White Leghorn type strains. All possible crosses between strains were made in 1973 by mating 10 random males of each strain with 30 random females from each of the other five strains. The next year, one random female from each of the 30 strain cross combinations was placed in each of 30 floor pens. Four random males from each strain cross combination were randomized to the pens with the restriction that each pen contain no more than a single male of a given cross. In succeeding years the flock was maintained by mating 60 random males with 360 random females.

In 1975, the NCR line was expanded to 104 males and 624 females which were used to produce the four populations needed in the present experiment. The first and second populations were produced in a single hatch, followed two weeks later by another hatch which produced the third and fourth populations. Each of the 104 males was represented by an average of nine daughters in each of the four populations. In each population, sire families were randomized equally to 13 replicates, each consisting of 72 females. The pullets of each hatch were reared together in floor pens until they were 17 weeks old; they were then randomly distributed to individual laying cages.

The selection criterion in the first population was sire family average for survivor's rate of lay from first egg to 40 weeks of age. Individual selection was practiced in the second population for the same trait. The criteria of selection in the third and fourth population were again sire family average and individual phenotype respectively, but the trait selected was egg weight at 40 weeks of age. An effort was made to keep selection intensity constant. Therefore, in the populations concerned with sire-family selection (1 and 3), the two superior families of the eight in each replicate, or 25%, were saved for breeding. Similarly, in the populations concerned with individual selection (2 and 4), the proportion saved was maintained at 25% by selection of the 18 superior individuals of the 72 tested in each replicate.

The selected 18 females of each replicate-selection criterion-trait subclass were mated to a random sample of three NCR males to produce about 20 daughters for testing. Concurrently, for each subclass, 18 random NCR females were mated to another random sample of three NCR males to produce 20 daughters for controls. All test and control pullets were hatched in a single hatch and housed in individual cages at 17 weeks of age. Traits measured on all pullets included: age at first egg, number of eggs to 40 weeks of age, survivor's rate of lay from first egg to 40 weeks of age (transformed by arc sine to angles in degrees to normalize the distribution), and egg weight at 40 weeks of age. Egg weight was measured as the average weight of eggs collected for three consecutive days near 40 weeks of age.

Response to selection (ΔG) in each replicate-selection criterion-trait subclass was calculated as the deviation from the respective control group. Because selection intensities varied among subclasses in spite of efforts to keep them constant, response for each subclass was standardized by the respective selection intensity (\bar{i}), which was calculated as the expected selection differential divided by the standard deviation. Comparisons of the relative efficiencies of the two criteria of selection were desired, so the response for both criteria were also standardized for the individual phenotypic standard deviation (σ_1) for the trait. The expected standardized response to individual selection (ΔG_{SI}) is then

$$\Delta G_{SI} = \frac{\Delta G_I}{\bar{i}_I \sigma_1} = h_1^2 \quad (1)$$

and the expected standardized response to family selection (ΔG_{SF}) is then

$$\Delta G_{SF} = \frac{\Delta G_F}{\bar{i}_F \sigma_1} = h_1^2 \left[\frac{1 + (n-1)r}{\sqrt{n[1 + (n-1)t]}} \right] \quad (2)$$

where, h_1^2 is the heritability of individual observations, n is the average number of progeny within a family, r is the average genetic relationship between members of a family, and t is the average phenotypic correlation between family members and assumed to be $h_1^2 r$. The ratio $\Delta G_{SF}/\Delta G_{SI}$ is then the usual expression for the relative efficiency of family to individual selection.

Because only two criteria of selection were compared within replicates Student's paired 't' test was used to determine the significance of any differences between criteria within the same replicate. The individual and family criteria of selection in the same replicate were compared on the basis of both the observed and standardized responses. To compare the theoretical responses to family selection with the observed responses to family selection, the predicted standardized responses for each replicate were estimated on the basis of the realized heritability obtained from individual selection and equation (2). Correlated responses resulting from the two selection criteria were also compared for the traits selected, as well as age at first egg, and number of eggs to 40 weeks of age.

Results and Discussion

Direct Responses

The mean performances, by replicate-selection criterion-trait subclass, of the test progeny and controls are given in Table 1, along with the standardized selection differentials, the phenotypic standard deviations, and the gains standardized for selection intensity and phenotypic standard deviation. The mean gains in transformed rate of lay were 1.29° for sire family selection and 3.67° for individual selection which were significantly different ($P < .01$). The mean gains in egg weight were 1.0 g for sire family selection and 2.5 g for individual selection. The difference of 1.5 g was not significantly different from zero ($P > .05$).

When rate of lay was standardized for selection intensity and individual phenotypic standard deviation, the gain for sire family selection (0.10) was still significantly smaller ($P < 0.05$) than that for individual selection (0.31). The ratio of the mean gain for sire family selection to that for individual selection (relative efficiency) was decreased from 35 to 32% as a result of the standardization and reflects the slightly stronger average selection intensity for sire family selection than for individual selection, as seen in Table 1.

After standardization, gain in egg weight for family selection (0.22) was still inferior to, but not significantly

Table 1. Means (\bar{X}) by replicates following a single generation of sire family (F) and individual (I) selection together with the control (C) means, standardized selection differentials (\bar{i}) and responses (ΔG_S) standardized for selection intensity (\bar{i}) and phenotypic standard deviation (σ_{PI}) for two selected traits

Replicate	\bar{X}_F	\bar{X}_C	$\sigma_{PI(F)}$	\bar{i}	ΔG_{SF}	\bar{X}_I	\bar{X}_C	$\sigma_{PI(I)}$	\bar{i}	ΔG_{SI}
Survivor's rate of lay to 40 weeks of age (angles in degrees)										
1	68.26	65.34	12.41	0.84	0.28	67.16	61.01	9.03	1.04	0.65
2	68.91	68.10	9.33	1.19	0.07	66.06	65.74	10.54	1.00	0.03
3	66.95	67.64	7.67	1.09	-0.08	65.85	65.05	9.61	1.01	0.08
4	63.00	62.91	8.94	1.47	0.01	66.91	70.32	8.77	0.92	-0.42
5	67.73	64.26	11.26	0.99	0.31	69.24	65.42	10.92	0.98	0.35
6	69.48	67.65	10.19	1.31	0.13	65.28	62.40	10.44	1.10	0.25
7	65.01	68.89	9.40	0.79	-0.52	69.34	63.59	12.36	0.96	0.48
8	69.56	66.36	10.62	0.85	0.35	66.70	63.82	11.26	0.91	0.28
9	65.65	62.36	10.52	1.08	0.28	72.25	65.11	12.10	0.98	0.60
10	67.69	71.00	7.14	1.26	-0.36	64.54	61.99	8.63	1.05	0.28
11	68.22	66.00	9.15	1.21	0.20	69.90	66.28	10.27	1.06	0.33
12	65.17	61.24	9.03	1.11	0.39	70.07	58.35	8.52	1.15	1.19
13	66.62	63.83	9.42	1.18	0.25	70.32	66.82	10.43	0.93	0.36
Mean	67.10	65.81	9.62	1.10	0.10	67.97	64.30	10.22	1.01	0.31
Egg weight (grams)										
1	59.8	57.8	4.68	1.27	0.33	61.7	60.0	4.20	1.28	0.31
2	59.1	60.1	4.88	1.29	-0.15	58.8	59.3	5.01	1.14	-0.08
3	59.6	60.0	5.78	1.26	-0.05	62.4	57.2	5.51	1.25	0.75
4	59.3	60.4	4.92	1.10	-0.20	62.0	59.5	4.37	1.34	0.42
5	61.5	57.0	4.10	1.24	0.88	60.3	57.6	3.75	1.35	0.53
6	59.6	58.6	4.83	1.14	0.18	61.8	57.2	4.71	1.40	0.69
7	59.8	55.9	4.67	1.04	0.80	63.4	60.3	4.87	1.20	0.52
8	60.9	61.6	4.03	1.08	0.16	62.1	58.2	5.08	1.30	0.59
9	61.4	61.7	4.60	1.44	-0.04	58.9	57.1	4.38	1.23	0.33
10	60.8	60.8	4.32	1.04	0.00	58.6	59.7	4.19	1.36	-0.19
11	61.0	62.3	5.53	1.06	-0.22	62.9	58.1	4.84	1.31	0.75
12	61.2	58.0	4.69	0.94	0.72	60.7	60.4	4.60	1.02	0.06
13	62.1	58.8	4.88	1.36	0.49	63.3	60.3	5.01	1.34	0.44
Mean	60.47	59.46	4.76	1.17	0.22	61.30	58.84	4.66	1.27	0.39

different from, that for individual selection (0.39). The ratio of the gain for sire family selection to that for individual selection (relative efficiency) was increased from 41% to 56% by standardization and reflects the effect of the greater average selection intensity applied to the individual selection for this trait (Table 1).

The standardized responses to individual selection are the realized heritabilities of the traits. The response for egg weight (0.39) is significant and agrees well with the average of such estimates reported by Kinney (1969), but it is not significantly different from the heritability estimate of 0.55 derived from half-sib correlations in the base population. On the other hand, the estimate of the realized heritability for rate of lay (0.31), which is also significant, seems high in relation to the average of 0.11 reported

by Kinney (1969). The population under study resulted from several crosses and would be expected to be genetically heterogeneous. An estimate of the heritability of rate of lay based on half-sib correlations in the base population was 0.22 which is not significantly different from the observed heritability. Therefore, the observed estimate may be reasonable for this population. High estimates of the realized heritability for early rate of lay have also been observed in early generations in some populations by others; for example, an estimate of 0.44 was reported by Yamada et al. (1958).

For derivation of a predicted standardized response to family selection in the two selected traits, the realized heritabilities within replicates were substituted into equation (2) along with values of n and r . The average genetic

relationship between the daughters of a sire was estimated to be $r = 0.27$, and the average number of daughters (n) measured per sire family was 8.43 for egg weight and 9.19 for rate of lay. The average predicted relative efficiencies on this basis were 0.77 for egg weight and 0.80 for rate of lay. These results show that individual selection is more efficient than sire family selection under these conditions as predicted.

The results agree with those of Kinney et al. (1970), Wilson (1974) and Campo and Tagarro (1977) wherein an advantage existed for individual over family selection. Campo and Tagarro (1977) and Wilson (1974) both interpreted the lack of statistical significance between genetic gains by the two criteria as being contrary to the theoretical prediction of Lush (1947). But both Kinney (1970) and Campo and Tagarro (1977) pointed out that in their experiments the effective population size was much larger for the individual selection population than that in which family performance was the criterion. As a consequence, differences in inbreeding depression and losses of genetic variation due to genetic drift were confounded with the differences obtained in genetic gain by selection. This characteristic of multi-generation, single replicate selection experiments led Bohren (1975) to argue that they do not give valid tests of infinite population selection theory and that such tests are best obtained from single generation replicated experiments. The amount of replication is determined by the degree of precision desired.

The observed responses to sire family selection for the two selected traits in this experiment were both less than the predicted responses to family selection but not significantly so. Wilson (1974) also found the response to full-sib family selection for two traits in *Tribolium castaneum* to be less than either the response to individual selection or the predicted response to family selection, but not significantly so. The consistency of the observed response to family selection being less than the predicted might lead one to suspect that some factor in family selection may be reducing the response to selection, in spite of the non-significance of the differences within any one experiment.

Gain in single-generation selection experiments may be measured by either one of two methods. In the first method, gain is based on the difference between the zero and the first generation in the selected population (S) and in the control population (C), or $(S_1 - S_0) - (C_1 - C_0)$. In the second method, gain is based on the simple difference between the selected and control populations in the first generation, or $(S_1 - C_1)$. Although each method yields an estimate of gain, the compositions of the variances associated with the estimates are quite different. The variance of the estimate by the first method contains half as much drift variance as does that of the estimate by the second method. Conversely, the variance of the estimate by the

second method contains half as much measurement error variance as does the variance of the estimate by the first method. Because measurement error variance is likely to be larger than the drift variance in a single generation, the second method was used in the present experiment whereas Wilson (1974) chose to use the first method.

From the data presented by Wilson (1974), estimates of responder comparable to those in the present experiment cannot be obtained. The selection intensities realized were not reported, and responses standardized for the selection intensity were not presented. In a replicated single-generation experiment these omissions may not have been serious, although some differences in selection intensity probably did exist, just as in the present experiment (Table 1). Also, a single control was used in each replicate, therefore the responses resulting from selection on the different criteria in the same replicate are correlated. The correlation between responses should not bias the difference in responses between selection criteria in the same replicate, so the responses in the experiment of Wilson (1974) were re-evaluated from the means (Table 9, page 832) as deviations from the control in the same generation, or $(S_1 - C_1)$. Analysis of variance did not show any differences between the revised responses resulting from the selection criteria, individual phenotype and sire-family mean phenotype. Results of the analysis agree with those of the analysis presented by Wilson (1974). This lack of significant differences between responses to the different criteria of selection was, as mentioned previously, interpreted by Wilson (1974) as being different from theoretical expectations. But with only small predicted differences, the experiments may not have been extensive enough to detect differences of these magnitudes. N differences would be expected with the numbers of observations if $h^2 = 0.46$, which is close to the heritability of pupal weight.

Even though the revised mean responses from selection on the two criteria derived from the data of Wilson (1974) were not statistically different, their rank was quite different from that resulting from Wilson's (1974) estimates. Now the mean responses estimated as $(S_1 - C_1)$ for individual and sire family selection are 11.5 and 13.7 units of gain for larval weight and 9.7 and 10.4 units for pupal weight, as compared to 14.5, 13.4, 12.0 and 9.8, reported respectively by Wilson (1974). The expected and realized efficiencies of family selection in relation to individual selection now are 1.05 and 1.07 units for pupal weight and 1.13 and 1.18 units for larval weight. From this method of estimating response, apparently the realized relative response to family selection has been as great as, or greater than, that expected for both traits.

In view of the data presented in the present experiment as well as that presented by Wilson (1974), a conclusion that observed responses to family selection should be significantly less than the responses predicted seems unjustified.

Correlated Responses

In those populations in which egg weight was the selected trait, no significant differences between selection criteria were found for any correlated trait, and no correlated trait changed significantly. On the basis of previous studies, a negative response in number of eggs and rate of lay might have been expected. But when rate of lay was the selected trait, age at first egg was significantly ($P < 0.05$) reduced (6 days) by family selection. For both criteria, the number of eggs to 40 weeks of age was increased significantly by 8 eggs. Egg weight did not change by family selection but increased significantly (3 g) by individual selection. Although the positive response in number of eggs was expected from selection on rate of lay, the response in age at first egg was not; and the correlated response in egg weight would have been expected to be negative rather than positive.

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