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A Replicated Single Generation Test of a Restricted Selections Index in Poultry* **

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Summary. Predicted and realized responses in a single generation of mass selection for an index and for its component traits were compared. The index included the log transformed traits determining egg mass in chickens to 40 weeks of age (days tested from sexual maturity, egg weight, rate of lay). The index was restricted to allow no increase in log days tested. Other traits measured were egg mass, age at first egg, egg weight, rate of lay, number of eggs and body weight. When averaged over replicates, realized and predicted responses were in close agreement for index values and for the component traits. Significant corresponding correlated responses were obtained for egg mass and weight. The restricted trait, log days tested, and the correlated trait age at first egg did not change. Egg mass was increased solely through change in egg weight.

Key words: Poultry – Genetics – Index selection – Egg mass

Introduction

The theoretical concept of the restricted selection index was developed by Kempthorne and Nordskog (1959). The validity of the theory has been tested biologically in a number of studies involving several species (Abplanalp et al. 1963; Scheinberg et al. 1967; Okada and Harding 1967, 1970; Eisen 1976; McCarthy and Doolittle 1977). The reports have generally confirmed the effectiveness of the restricted index, but all authors have pointed out discrepancies between predicted and realized results. The discrepancies generally involved responses in the selected traits which were less than expected, and the responses in the restricted trait tended to be negative, or the effect of the restriction was greater than expected.

Several of the experiments cited were unreplicated, and all were of a multigeneration type. The problems involved in testing genetic theory in multigeneration experiments with minimal replication have been discussed by Bohren (1975) and the value of highly replicated single generation experiments for this purpose was emphasized. In experiments with these properties, the observed responses should be comparable with those predicted because of minimization of the effect of random genetic drift, inbreeding and sampling errors.

The economic importance of the negative genetic correlation between egg weight and egg production in chickens is well known and has stimulated interest in egg mass as a useful criterion of selection (Waring et al. 1962; Hicks 1963). Interpretation of the effects of selection for egg mass is complicated by the negative genetic correlation existing between number of eggs to a fixed age and age at sexual maturity. The latter, however, appears not to be correlated with rate of lay, the third component trait of egg mass (Kinney et al. 1970; Garwood and Lowe 1975). The problems arising from these interrelationships among the component traits involved in selection for egg mass were discussed by Bohren (1970) who proposed that selection for egg mass might be effective through use of an index formed from a linear combination of the logarithmic functions of the component traits but restricted so as to allow no change in age at first egg.

The purposes of this experiment were (1) to test the ability of a restricted selection index, including the component traits age at first egg, egg weight and rate of lay, to increase egg mass while maintaining age at first egg constant and (2) to compare the predicted and realized responses in a single generation of selection for an index and for its component traits.

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Materials and Methods

Traits of primary interest were the index and its component parts, log days of testing, log egg weight and log arc sin rate of lay to 40 weeks of age. Correlated traits also of interest were the untransformed variables egg mass, age at first egg, egg weight, rate of lay, number of eggs and body weight. Annual rate of lay was also measured.

The Regional Cornell Randombred White Leghorn served as the base population for the experiment. The establishment and maintenance of this population has been reported by King et al. (1959) and the inbreeding that has accumulated was reported by Lowe and Garwood (1973). The effective population size has been about 167, and the present inbreeding level is about 4%.

Genotypic and phenotypic parameters necessary for the derivation of the index were calculated from data collected on the population from 1957 through 1965. Details of the data collection were given by Kinney et al. (1968). Two pedigreed hatches were made yearly. The first hatch was obtained by equally randomizing 250 females to 50 sires for mating. After eggs for this hatch were collected, the males were shifted to different pens of females. After 2 weeks, eggs were saved for the second hatch. Nested analyses of variance and covariance were performed on both the raw and transformed data for each hatch, and the parameter estimates derived were averaged over hatches for each particular variance or covariance (Table 1). The index derived from the parameter estimates was $I = 0.023D + 0.117E + 0.41R$ where D is log days tested to 40 weeks of age, E is log egg weight at 40 weeks, R is log arc sin rate of lay to 40 weeks. The relative genotypic weights (a_i) of the above traits for derivation of the index were taken as $a_1 = a_2 = a_3 = 1$.

For the zero generation, 2226 pullets of the base population were randomized to 14 replicates of 159 pullets each and housed in 20-x 40-cm individual cages. Within each replicate, the 12 females with the highest index values were selected and mass mated to 3 random males of the base population to produce the first selected generation progeny group. Concurrently, 12 random females of the base population were mass mated to another sample of 3 males to produce a random selected control group for each replicate. In each selected and control group, 40 female progeny were sought. All pullets were individually caged for the laying period at 18 weeks of age. The part period egg records were ended when the flock was 40 weeks old, at which time body and egg weights were measured. Annual egg records were ended at 70 weeks.

Table 1. Estimates of genetic and phenotypic variances and covariances used for index development[a]

Log days tested (D)	Log egg weight (E)	Log arc sin rate of lay (R)
0.00604763	−0.00017108	0.0011244
0.00211280		
−0.0051128	0.00116649	−0.00004099
	0.00059864	
0.00027356	−0.00036998	0.005598
		0.00057034

[a] Genetic values are below the broken lines

Disproportionate subclass numbers existed. Consequently analyses of variance were based upon unweighted means according to the following model:

$$\bar{Y}_{ij} = \mu + S_i + R_j + SR_{ij} + \bar{E}_{ij}$$

where $\bar{Y}_{ij}$ is the mean measurement on progeny in the i^{th} group and the j^{th} replicate.

Realized gains in the index and in each component trait were calculated from the data. Expected gain from the index was calculated as $\hat{h}^2\ \bar{\imath}\ \sigma_I/2$, where $\hat{h}^2$ is the estimated heritability of the index in the base population, and $\bar{\imath}$ and σ_I, respectively, are the mean standardized selection differential and phenotypic standard deviation of the index over replicates in the initial or zero generation. Expected gains (ΔG_i) for the component traits were calculated as $\Delta\ G_i = \sum_j b_j G_{ij}\ \bar{\imath}/2\sigma_I$ where b_j are the coefficients in the index for the component traits and G_{ij} the genetic covariances between the i^{th} and the j^{th} component traits.

Results

The number of pullets available for selection in each replicate in the initial generation, the proportion selected, the number of progeny tested in the selected and control groups, the standardized selection differential and the standard deviation of the index for each replicate are given in Table 2.

A constant selection intensity over replicates was intended by selecting 12 out of 159 tested pullets, or 7.5%. However, the replicates varied in numbers of pullets available for selection because of differential mortality, nonlayers and availability of eggs for weighing at 40 weeks of age. These losses reduced the average number of birds available for selection to 138. By keeping the number selected at 12 from each replicate, the average percentage of birds saved increased to 8.7 and varied from 8.2 to 9.2.

Table 2. Number of females in the initial generation (G_0), proportion selected (P), number of progeny tested in the selected (G_1) and control (C_1) groups, selection intensity ($\bar{\imath}$) and observed standard deviation of the index (σ) for each replicate

Replicate	G_0	P	G_1	C_1	$\bar{\imath}$	σ
1	136	8.8	43	34	1.43	0.0046
2	139	8.6	40	41	1.71	0.0042
3	146	8.2	35	39	1.42	0.0046
4	137	8.8	42	38	1.45	0.0048
5	144	8.3	37	38	1.15	0.0052
6	136	8.8	40	38	1.75	0.0053
7	141	8.5	40	33	1.61	0.0045
8	141	8.5	36	37	1.37	0.0046
9	139	8.6	41	39	1.46	0.0053
10	134	9.0	38	35	1.42	0.0058
11	139	8.6	37	26	1.39	0.0053
12	130	9.2	36	10	1.22	0.0062
13	137	8.8	40	29	1.53	0.0055
14	132	9.1	39	40	1.71	0.0046

Intensity of selection averaged 1.47 standard deviations, which is about 19% lower than expected on the basis of the percentage saved for breeding.

In general, the numbers of progeny tested in the selected and control groups within replicates were similar, except for replicates 11, 12 and 13 in which the numbers in the control group were reduced. This reduction was a consequence of reduced rates of lay and hatchability.

The responses to selection by replicates are given in Table 3 for the index and component traits of the index, as well as the untransformed measures for egg mass, age at first egg, egg weight, rate of lay, egg production and body weight. The corresponding analyses of variance are given in Table 4. Mean performances over replicates of the control progeny group (C_1) are presented in Table 5, along with the overall responses to selection (S_1-C_1). Significant differences between selected and control groups were found for the index and egg mass. The response to selection was 24 x 10^{-4} index units which resulted in a 246 g increase in egg mass. Significant group differences were also found for log egg weight and 40-week egg weight but not for log arc sin rate of lay or rate of lay. The difference for log egg weight was translated into a significant increase of 3 grams in the untransformed egg weight. No significant change due to the selection occurred in log days tested, and none was reflected in the number of days at first egg. The significantly increased body weight (124 g) would be expected as a correlated response to the gain in egg weight. Neither annual rate of lay or the residual period rate of lay changed significantly.

The realized heritability and its standard error for the index, as calculated from the replicate gains and selection differentials, was 0.60 ± 0.08. The estimated heritability of the index based on parameter estimates from the base population was 0.59 ± 0.0002. This unusually close agreement between two such estimates resulted in good agreement between the predicted and realized total gains in index units (0.0023 *vs.* 0.0024, Table 5). The results in Table 5 show that the response in the index was entirely due to an increase in egg weight because egg weight was

Table 3. Response to selection by replicate

Replicate	Index x 10^4	Log days tested x 10^4	Log egg weight x 10^4	Log rate of lay x 10^4	Egg mass	Age first egg	Egg weight	Rate of lay	Egg production	Body weight	Annual rate of lay
1	33	– 4	258	74	536	– 8	2	1	– 6	64	5
2	8	–616	267	–196	–234	8	4	–2	9	78	–3
3	13	– 7	160	–143	–109	5	5	–4	10	190	–4
4	23	227	205	–151	13	– 3	1	–5	3	155	–3
5	32	707	159	– 52	537	– 6	1	3	– 8	339	–2
6	54	139	370	183	424	– 7	3	–3	– 3	– 16	–3
7	15	– 49	57	204	610	– 4	4	1	– 5	290	7
8	16	38	203	–203	666	–10	0	4	–11	– 97	0
9	35	270	178	214	–270	6	1	–1	6	139	3
10	38	– 73	437	–284	796	– 9	4	2	– 9	– 42	6
11	13	–283	185	– 35	176	4	6	–2	6	332	0
12	10	363	98	–230	–252	5	4	–5	11	– 37	–3
13	25	36	259	–131	482	– 5	3	0	– 3	153	–3
14	23	23	216	– 62	62	– 4	2	–6	3	182	–4

Table 4. Mean squares from the analyses of variance of selected traits and correlated variables

Source	df	Index x 10^7	Log days tested x 10^4	Log egg weight x 10^4	Log rate of lay x 10^4	Egg mass	Age first egg	Egg weight	Rate of lay	Egg production	Body weight	Annual rate of lay
Groups (G)	1	410*	2.1	33*	2.8	421646*	28.0	57.1*	10.3	.3	106889*	0.6
Reps (R)	13	29*	3.7	1.9*	1.9*	70643*	17.6*	2.1*	7.2*	19.4*	4820*	7.5*
G x R	13	8.5	4.6*	4.9*	1.2	70416*	19.5*	1.5*	5.0*	28.3*	9785*	7.6*
Error	851	7.3	2.6	3.9	0.9	30444	9.0	.6	2.6	9.0	1861	3.6
	k†	28.5	27.8	31.9	31.9	31.8	31.9	31.9	31.9	31.9	31.4	28.2

† Harmonic mean no. of observations per cell

* $P \leqslant 0.05$

the only component trait with a response significantly different from zero. The response in egg weight was greater than predicted, but the decrease in rate of lay was less than predicted. Because the small response that occurred in log days tested (55×10^{-4}) was not significant, it is considered to be in agreement with the imposed restriction of no change. Thus, the conclusion that selection based on the index was successful in increasing the index values and indirectly increasing egg mass without reducing age at maturity, the restricted trait, seems valid.

Discussion

The similarity of the predicted and realized responses to selection in this experiment is a result of accurate estimation of parameters in the base population and the replicated single generation design. Although the outcome of a single replication cannot be predicted accurately because of the cumulative random drift, the expected value over replicates can be predicted accurately, but only for a single generation. The only other experiment involving single generation selection is that of Wilson (1974) in which the relative gains from individual, family and index selection were compared in *Tribolium castaneum* in 10 single generation replicates as well as in a multigeneration test. In contrast to the present study Wilson (1974) concluded that the realized responses did not agree with the predicted values.

In view of the emphasis in the present study placed on egg weight by the index used, it of interest to compare the coefficients used with those derived without any restrictions and without transformation of the component traits. The comparative coefficients are as follows:

	Traits		
Type of index	Days tested	Rate of lay	Egg weight
Transformed, restricted	0.2	0.4	1
Untransformed, restricted	0.2	0.7	1
Transformed, unrestricted	1.5	0.1	–1
Untransformed, unrestricted	1.6	0.3	–1

The log transformation had little effect except to slightly reduce the weightings on rate of lay. But removing the restriction resulted in a dramatic shift of emphasis, the major weighting was placed on days of testing, and that for egg weight became negative. The predicted response ($\times 10^3$) in the component traits from selection on an unrestricted index of the log transformed variables would be log days tested = 1.07, log egg weight = -1.95 and log arc sin rate of lay = 0.24. Here, in contrast to the index used, egg mass would be increased in spite of a reduction in egg weight by both decreased age at first egg and increased rate of lay.

Table 5. Mean performance over replicates of the test generation control (C_1), gain from selection ($S_1 - C_1$) and predicted gain ($\hat{G}$)

Trait	C_1	$S_1 - C_1$	$\hat{G}$
index $\times 10^4$	3241	24*	23
log days of testing $\times 10^4$	20189	55	0
log egg weight $\times 10^4$	17374	218*	58
log arc sin rate of lay $\times 10^4$	18091	–58	–82
egg mass, g	4730	246*	
age at first egg, days	176	–2	
egg weight, g	55	3*	
rate of lay, %	81	–1	
number of eggs	86	0	
body weight, g	1834	124*	
annual rate of lay, %	74	0	

* Significantly different from zero ($P \leqslant 0.05$)

An idea of the importance of the genetic drift in interpreting responses to selection can be obtained by examining the replicate by group interaction. Of 11 analyses of variance (Table 4), all but two had significant interactions and even those two had F values greater than one. Although the analysis of the index criterion was one instance in which the interaction was not statistically significant, the interaction component is estimated as 1.2×10^{-7}, which is only 0.6% as large as the within replicate-group error variance. On the other hand, the interaction component from the body weight analysis is 7924 which is 15% of the within cell error variance. Although these drift variances are small in any one generation, their accumulation over generations could lead to serious errors in interpretation of the response to selection. The consistency and magnitude of the estimates of the random drift variance emphasize the need for random replication of any selection experiments.

The theoretical drift variances for the index and for its component parts were estimated by equation (3) of Hill (1972). The ratios of the theoretical drift values to the values estimated from the interaction components were: index (130:12); log egg weight (0.55:1.00); log days trapped (2.3:2.0) and log arc sin rate of lay (86:24). The two traits for which the interaction components are significant are in reasonably close agreement with the theoretical values, but the very small and non-significant interaction component for rate of lay is low relative to the theoretical value and makes the interaction component for the index also low.

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