

RESPONSE TO SELECTION FOR BODY WEIGHT AND EGG WEIGHT IN CHICKENS

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WELL conducted selection experiments are useful in testing the validity of modern selection theory. Observed genetic changes from selection frequently show poor agreement with expectation. The relationship of selection to the genetic variance composition of a population, to correlated responses, to plateaued populations and to selection limits are problems not yet well understood.

This study reports the results of a 2-way selection experiment for both body weight and egg weight in White Leghorns. Body weight is highly responsive to selection in chickens (SIEGEL 1962a; MALONEY, GILBREATH and MORRISON 1963) and in turkeys (ABPLANALP, OGASAWARA, and ASMUNDSON 1963) but evidently not in Coturnix quail (COLLINS and ABPLANALP 1965). Egg weight is also highly heritable in chickens (OLSON and KNOX 1940; SNYDER 1945; SHULTZ 1953) and is correlated with body weight (SIEGEL 1963a, b; MALONEY *et al.* 1963; SHULTZ 1953).

Although correlated responses in reproductive traits are of special interest to us in our over-all selection experiment, we will report on that separately. This report is confined to changes in body weight and egg weight over 7 years from 2-way selection for each of these traits. Changes in genetic parameter estimates over generations are also given. As experimental checks, both a randombred control line and a companion line of common origin, but selected exclusively for high egg production, are included. NORDSKOG and FESTING (1962) gave a preliminary report of the first 4 years of the experiment.

MATERIALS AND METHODS

The base population was derived from reciprocal crosses between four commercial Leghorn strains in 1956. Table 1 specifies the lines originating from the base population and the randombred control population. In the body weight lines, B and C, both sires and dams were selected on their own phenotypes. In the egg weight lines, D and E, the sires were selected on their full sister records.

Line A, selected for high rate of egg production, is included in the study as a supplementary "quasi-control" line. It has the same origin as the other selection lines and has responded little, if any, to selection for high rate of egg production (NORDSKOG, FESTING and WEHRLI VERGHESE 1967). Because of limited population number the inbreeding per generation, estimated from $F = 1/(8N_m) + 1/(8N_f)$ (WRIGHT 1940) was about 1.6% in each line except Line A, where F was about 1% per generation. In the formula, N_m and N_f are the number of males and females

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TABLE 1
White Leghorn selection and control populations

Line	Year started	Selected for:	Number of breeders	
			Male	Females/male
A	0(1956)	High egg production (\hat{X})	16	9-14
B	0(1956)	High 32 week body weight (\hat{W})	8	8-10
C	0(1956)	Low 32 week body weight (\check{W})	8	8-10
D	0(1956)	High 32 week egg weight (\hat{Z})	9	8-10
E	0(1956)	Low 32 week egg weight (\check{Z})	8	8-10
RCC	2(1958)	Randombred	50*	5*

* Maintained at the North Central Regional Laboratory, Purdue University.

having progeny selected as breeders in the following generation. Because full-sib and half-sib matings were avoided the amount of inbreeding would be less than estimated from the formula.

Not all birds had complete records for the December and March body weights and egg weights. For this reason, the number of records per trait varied typically (except for Line A) from 150 to 200 per line (Table 2). All records available were included in the study in order to avoid a possible bias from selectivity. Because Line A was carried in more breeding pens and was more highly reproductive than the other lines, the number of records were generally three or four times larger.

Chicks were produced from three hatches between January and March. They were reared intermingled under infrared brooders and at 8 weeks of age were transferred to a summer range. After the third generation the lines were quartered separately, more or less according to body size. At 20 to 24 weeks of age the birds were housed in pens of 200 to 400 birds each with control birds in each pen.

Hatching eggs from the Regional Cornell Leghorn Control strain (KING, CARSON and DOOLITTLE 1959; KING, VAN VLECK and DOOLITTLE 1963) produced by the North Central Regional Poultry Breeding Laboratory, Lafayette, Indiana, were shipped to Ames each year.

Eggs were collected for weighing over a 4-day trapnest period in December and March. Hence, the number of weighed eggs per pullet varied from 0 to 4.

Notation, definitions and statistical procedure: The traits are body weight (W) and egg weight (Z) as shown in Table 1. Lines selected upwards are indicated with a hat (^) and lines selected downwards with an inverted hat (check). The March records are primed (W' and Z') to distinguish them from the December records.

TABLE 2
Mean number of body weight (W) and egg weight (Z) records per generation

Line	December (32 weeks)		March (55 weeks)	
	W	Z	W	Z
A	756	666	699	578
B	184	138	154	118
C	219	180	181	158
D	225	198	170	154
E	222	189	195	170
RCC*	157	135	128	119

* Not available in generations 0 and 1.

In accordance with FALCONER (1960), we define a *primary trait* as the criterion on which selection is made. Any other trait is a secondary trait. Direct responses to selection in the B and C lines are $DR(\hat{W})$ and $DR(\check{W})$ and in the D and E lines are $DR(\hat{Z})$ and $DR(\check{Z})$. The correlated response, for example, in trait Z from selection on \check{W} in the B line, is represented by $CR(Z, \check{W})$. The refression of the response on generation number is the estimator of the realized response per generation to selection. The linear regression of the response on the cumulative selection differential per generation is the estimator of the "realized" heritability.

The letter E in place of R in the above notation designates the expected response from selection estimated from population parameter estimates. Thus, for December body weight, $DE(W) = h^2_w \delta \sigma_w$, where

h^2_w = heritability of W estimated from the population.

δ = selection differential in standard deviation units.

σ_w = phenotypic standard deviation of W.

In general, for any amount of selection applied, δ , we are interested in, for example, how well $DE(W)$ predicts $DR(W)$. Likewise for a correlated response, we are interested in, say, how well $CE(Z, W)$ predicts $CR(Z, W)$.

Most of the data were examined on both the arithmetic and logarithmic scales with the results on either scale leading to essentially the same conclusions. Only the analyses using the arithmetic scale are presented here.

The selection differentials were calculated as a simple average of the difference between the mean of the population and the mean of the selected parents for each sex of the body weight lines and for females of the egg weight lines. The selection differentials for males of the egg weight lines were estimated from the weighted deviation of their sister's mean egg weight from the line mean. The weighting factor was $k = \frac{(1/2)n}{1 + (n-1)t}$ where n is the number of full sisters in a sire's family and $t = .3$ is the assumed phenotypic correlation between full sisters. It can be shown that k is, in fact, the regression of the sire's genotype on the mean of his n sisters' phenotype and hence k is the appropriate correction for the variable number of sisters per family.

Heritabilities and genetic correlations were estimated from an hierarchial analysis of variance within lines and years using twice the fraction of sire and dam variance as the estimate (FALCONER 1960). Although such an estimate is inflated by various unknown amounts of non-additive, sex-linked and maternal effects (KEMPTHORNE 1957), its sampling error is only half as large as that from heritability estimated separately from the sire or dam component.

RESULTS

Selection intensity: The selection intensity varied from about one half to one third of all the records. The total selection applied in cumulative standard deviation units (Table 3) was greater in the body weight lines than in the egg weight

TABLE 3
Cumulative selection differentials in standard deviation units
over seven generations of selection

Line	Trait	Cumulative sires	Cumulative dams	Cumulative Average	Average/generation
B	\hat{W}	10.24	5.67	8.02	1.146
C	\check{W}	-8.60	-5.14	-6.88	-0.983
D	\hat{Z}	6.36	6.41	6.40	0.914
E	\check{Z}	-5.31	-6.03	-5.66	-0.809

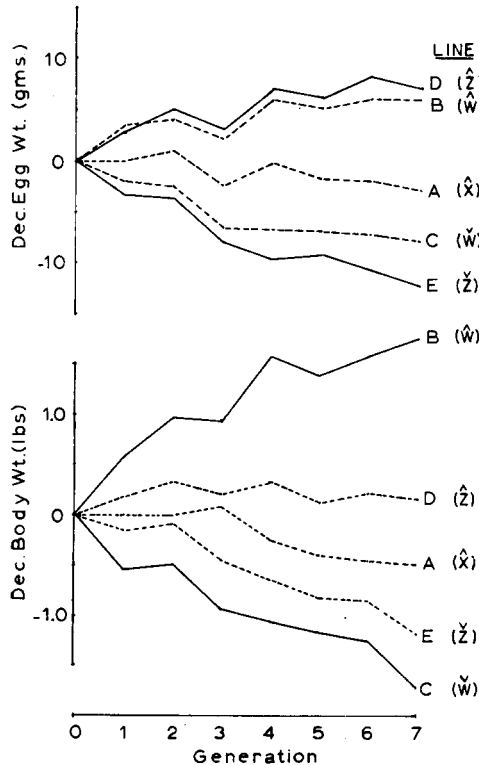


FIGURE 1.—Response to selection for December body weight and egg weight relative to the RCC control line. Solid lines are direct responses and dotted lines are correlated responses.

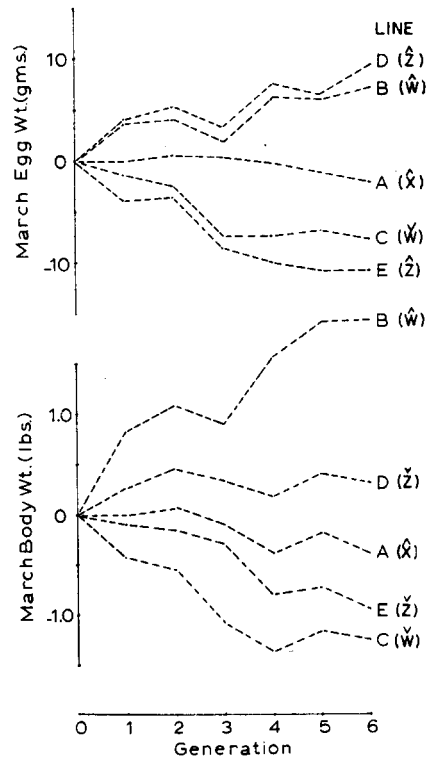


FIGURE 2.—Correlated selection responses in March body weight and egg weight relative to the RCC control.

lines because the former is measurable in both sexes but for the latter only in females. Consequently, the selection differential for males was about 70 to 80% larger than the females in the body weight lines but about the same in the egg weight lines.

Realized gains from selection: The body weight and egg weight deviations of the selected lines from the control are shown in Figure 1 (December records) and in Figure 2 (March records). The generation means of the selected lines were adjusted to the RCC randombred control except for the zero and first generations in which the A line was used because the RCC was not available until the second generation. Solid lines are direct responses to selection, and dotted lines are correlated responses of the secondary traits. The highly significant direct responses to selection were regarded as essentially linear because the fitting of a second degree polynomial did not significantly reduce the variation due to deviations from regression. The greater divergence of the 2-way selection body weight lines again reflects the use of individual records for both sexes. In generation 7, the spread between the extremes was about 75% greater in the body weight than

in the egg weight lines. An unexpected asymmetry is shown in Figure 1. The correlated response in egg weight, $CR(Z\hat{W})$ in the B line is strong while that for body weight, $CR(W\hat{Z})$ in the D line is weak. Thus, upward selection on body weight moves egg weight strongly with it but upward selection on egg weight does not move body weight correspondingly. In the down lines, the correlated responses were both fairly strong.

The response curves for the selection criteria plotted against cumulative selection differentials, shown in Figures 3 and 4, are essentially linear. The least squares linear regression coefficients fitted to each of these is an estimate of the realized heritability. For body weight, the heritability for up selection is .34 and for down selection is .52. For egg weight, the heritability for up selection is .24 and for down selection about .55. On a logarithmic transformed scale the difference was essentially unchanged for body weight but was slightly greater for egg weight.

Heritability estimates from the population: Generation trends in population parameter estimates of heritability (full-sib correlations) for body weight (Figure 5) and for egg weight (Figure 6) are based on the combined average of the December and March records to reduce sampling error. Neither trait shows clear-cut trends, but the body weight fluctuations from generation to generation (Figure 5) are considerably less than for egg weight fluctuations (Figure 6). The results give no indication of a loss in additive genetic variance from selection.

An analysis of variance of the line-generation heritability means is given in Table 4. Differences between lines selected upwards and downwards and differences between generations were statistically significant for body weight heritability but not egg weight heritability.

The parameter estimates of heritability are compared with the realized estimates in Table 5. In general, the realized heritability estimates are smaller than the parameter estimates for lines selected upwards but larger for lines selected downwards. The parameter estimate of .64 for Line E body weight is significantly

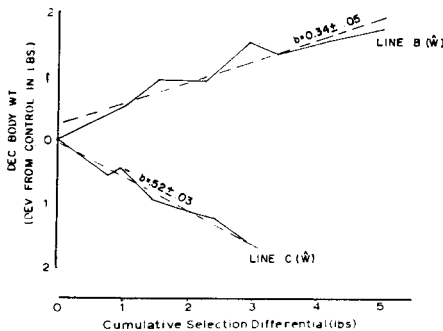


FIGURE 3.—Regressions of response on cumulative selection differentials (realized heritability) for the body weight lines.

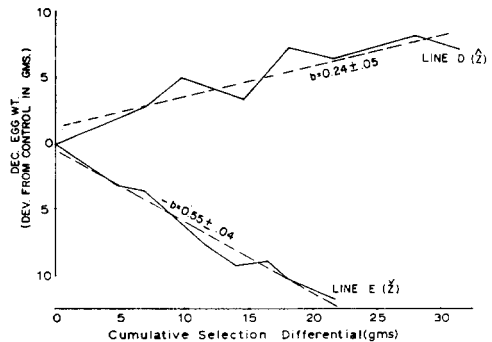


FIGURE 4.—Regressions of response on cumulative selection differentials (realized heritability) for the egg weight lines.

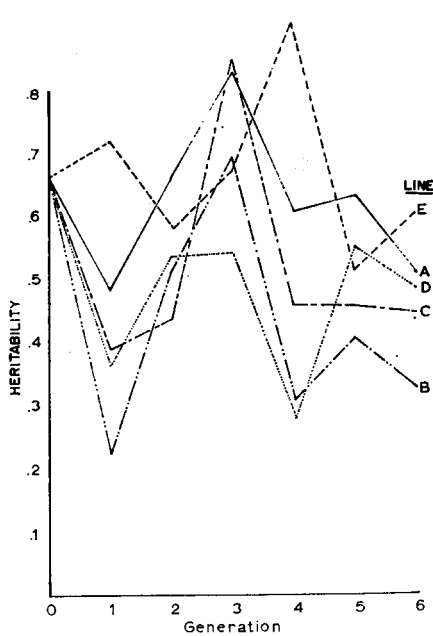


FIGURE 5.—Population parameter heritability estimates of body weight by lines and generations.

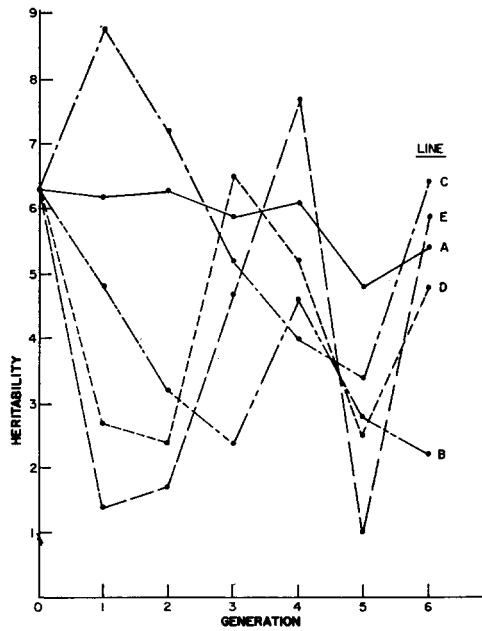


FIGURE 6.—Population parameter heritability estimates of egg weight by lines and generations.

higher than the other lines. The realized heritability of .52 for Line C is significantly higher than the .34 for Line B. The difference between the parameter estimates and the realized heritability estimates for Lines B and C are not statistically significant.

For egg weight the population parameter estimates in Table 5 are not statistically significant based on the F variance ratio test. The difference in the realized heritabilities (.24 for Line D and .55 for Line E) is statistically significant.

TABLE 4

Analysis of variance of heritability estimates for body weight (W) and egg weight (Z) from full-sib correlations

	d / f	Mean squares	
		$h^2 w$	$h^2 z$
Lines	4	.0611*	.0850
Up vs. down	1	.1188*	.0722
Body wt. vs. egg wt.	1	.0580	.0591
Generations	6	.0551*	.0643
Linear	1	.0411	.1423
Quadratic	1	.0059	.0168
Remainder	24	.0136	.6404

* P < .05.

TABLE 5

Comparison of realized heritability estimates (R) with population parameter heritability estimates (E) for body weight and egg weight

	Line	E	R	E-R
Body weight (W)	B (\hat{W})	.44	.34	.10
	C (\check{W})	.43	.52	-.09
	D (\hat{Z})	.42
	E (\check{Z})	.64
	Av. SE	$\pm .06$	$\pm .04$	$\pm .072$
Egg weight (Z)	B (\hat{W})	.40
	C (\check{W})	.58
	D (\hat{Z})	.37	.24	.13
	E (\check{Z})	.42	.55	-.13
	Av. SE	$\pm .07$	$\pm .05$	$\pm .086$

Again, the parameter estimates are not statistically different from the realized heritability estimates, but the interaction difference, $.13 - (-.13) = .26$ is statistically significant.

Correlated responses, regressions and correlations: The regression coefficients of the secondary traits on the primary traits, given in Table 6, all differ significantly from zero, except for Line D. The regressions of egg weight on body weight are in fair agreement for the up (\hat{W}) and the down (\check{W}) lines; i.e., for the body weight lines, the regression response in egg weights is symmetrical. This seems not to hold for the egg weight lines: the regression of body weight on egg weight in Line D is significantly lower than that in the Line E; i.e., body weight increase in Line D is less than expected. Thus, the correlated response to selection for body weight is weak upward but strong downward. The regressions of March records on December records are symmetrical and, being close to unity, demonstrate that these correlated responses are substantially equivalent to direct responses from selection.

TABLE 6

Regression of secondary on primary traits

Traits regressed*	Up selection		Down selection	
	Line	Regr.	Line	Regr.
Z (W)	B	$.52 \pm .05^{**}$	C	$.37 \pm .04^{**}$
Z' (W)	B	$.34 \pm .06^{**}$	C	$.44 \pm .06^{**}$
W (Z)	D	$.19 \pm .22$	E	$1.25 \pm .22^{**}$
W' (Z)	D	$.47 \pm .27$	E	$1.22 \pm .22^{**}$
W' (W)	B	$1.11 \pm .16^{**}$	C	$1.10 \pm .11^{**}$
Z' (Z)	D	$0.97 \pm .05^{**}$	E	$0.96 \pm .07^{**}$

* Primary trait in parenthesis.

** $P < .01$.

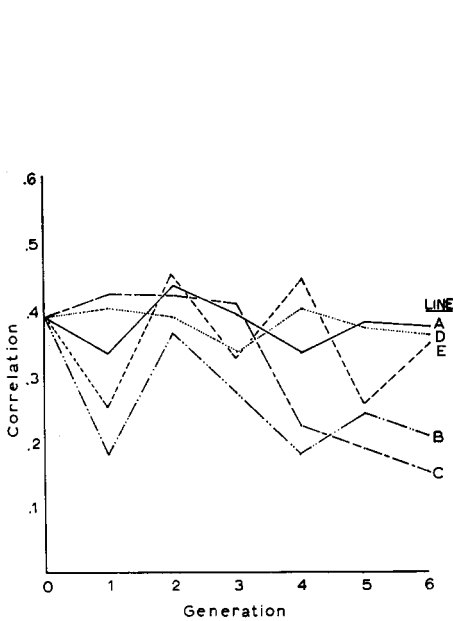


FIGURE 7.—Phenotypic correlations between body weight and egg weight by lines and generations.

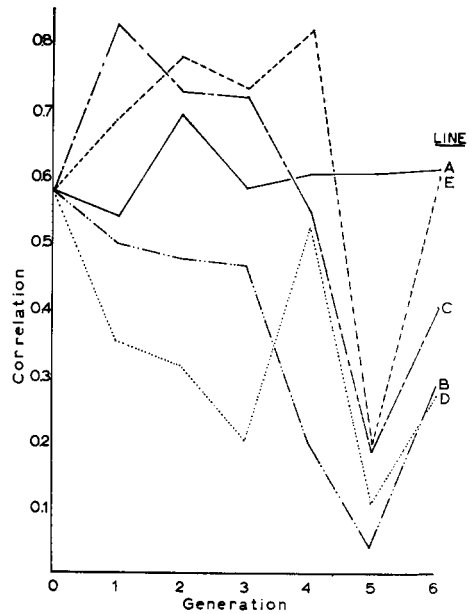


FIGURE 8.—Genetic correlations between body weight and egg weight by lines and generations.

The population parameter estimated correlations were computed by lines and generations. The phenotypic correlations (Figure 7) show no clear-cut trend but the genetic correlations (Figure 8) indicate a loss in covariance over successive generations of selection. The genetic correlations for the selection lines B, C, D and E declined sharply in generation 5, but those in Line A, regarded here as a

TABLE 7

*Analysis of variance of phenotypic and genetic correlations
(population parameter estimates)*

	d / f	Mean squares	
		Phenotypic correlation	Genetic correlation
Lines	4	.0167*	.1317**
Up vs. down	1	.0018	.4207**
Body wt. vs. egg wt.	1	.0401**	.0012
Generations	6	.0117*	.0863*
Linear	1	.0371**	.2390**
Quadratic	1	.0024	.0156
Remainder	24	.0046	.0270
	34		

* P < .05
** P < .01.

TABLE 8

Comparison of realized genetic correlations (R) with population parameter estimates (E) between body weight and egg weight

Lines	Phenotypic correlation	E	R	E-R
B (\hat{W})	.25	.31	.60	-.29*
C (\check{W})	.31	.58	.57	.01
D (\hat{Z})	.39	.30	.10	.20
E (\check{Z})	.38	.68	.78	-.10
Av. SE	$\pm .03$	$\pm .07$	$\pm .09$	$\pm .11$

(\wedge) UP selection. (\checkmark) Down selection.

* $P < .05$.

control, tended to remain unchanged. The decline in the B, C, D and E lines was statistically significant; thus, selection in these lines may have reduced the genetic covariance between body weight and egg weight. An analysis of variance of the line-generation means of Figures 7 and 8 is given in Table 7. The linear declines of both phenotypic and genetic correlations were highly significant, statistically.

The population parameter estimated correlations are compared with the realized genetic correlations in Table 8. Line differences among the phenotypic correlations as well as for each type of genetic correlation are statistically significant. The phenotypic correlations are symmetrical with respect to 2-way selection but not the genetic correlations. The parameter estimated correlations in the up lines are lower than in the down lines. The realized genetic correlations agree reasonably well in the downward selected lines (C and E) but not in the upward selection lines.

Comparison of expected and observed response to selection: Approximately 95% confidence intervals for the expected response to selection for body weight and egg weight were calculated from the usual prediction equation, $\Delta G = h^2 \delta \sigma$, where ΔG is the expected genetic change per generation, and δ is the cumulative selection differential in units of σ . Standard errors of the heritability estimates were calculated by the method of OSBORNE and PATTERSON (1952) using the selection differentials realized in the experiment. Heritability estimates obtained from the base population were $h^2 = .67 \pm .07$ for W and $h^2 = .68 \pm .087$ for z .

The confidence intervals and the observed responses to selection are shown in Figure 9. The predictions tended to overestimate genetic change, but observed responses in the body weight lines were within the confidence intervals up to about generation 4 after which the response in the B line was less than predicted from the parameter estimates. The observed response in the C line remained within the confidence intervals through generation 7.

The predicted responses considerably overestimated the genetic change in the D line; the observed values fell within the confidence interval only in generations 1 and 2. On the other hand, the response in the E line has stayed within the confidence interval throughout the experiment.

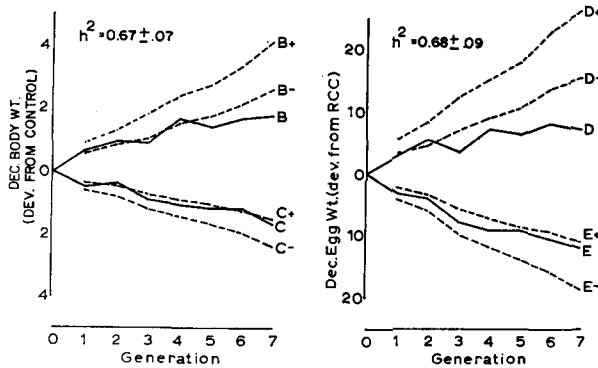


FIGURE 9.—Upper (+) and lower (—) 95% confidence intervals for selection response expected from base population heritability estimates. Solid lines are observed responses.

DISCUSSION

Selection efficiency: Two-way selection for body weight and for egg weight resulted in marked changes in these traits both as direct and correlated responses. After eight generations of selection in the Leghorns (1965 test year) the deviations between the 2-way body size lines (B vs. C) were 8σ in body weight (W) as a direct response and 3.7σ in egg weight (Z) as a correlated response to selection. In the egg size lines, Z differed by 5.6σ as a direct response and W by 3.3σ as a correlated response to selection.

Indirect selection for W was equal to 45% of the efficiency of direct selection (SEARLE 1965), i.e. $CR(W:Z)/DR(W) = .45$, while for Z, indirect selection was 55% as efficient as direct selection, i.e., $CR(Z:W)/DR(Z) = .55$.

Asymmetry of response: FALCONER (1960) has pointed out that when the variance is correlated with changes in the mean resulting from selection, then the selection differential and the response to selection will change accordingly. This is called a scale effect. It follows that progress in the upward direction should increase while progress in the downward direction should decrease. Consequently, the response to 2-way selection would be asymmetrical.

This study revealed several forms of asymmetry in connection with 2-way selection including not only direct and correlated responses but also population parameter estimates of heritability and genetic correlations. The higher realized heritability of the down compared with the up selection lines persisted even after a log transformation on the data. According to FALCONER (1960) differences in realized heritability are very little influenced by scale effect. Hence, the asymmetry would seem to require a genetic interpretation. If the initial gene frequencies, for example, for large egg size, were high in the base population then selecting for lower egg size should increase the additive genetic variance while selecting for larger egg size should lower the additive variance further. Yet, this interpretation is not too well substantiated by the results: the estimates of the genetic components of variance of the downward selected lines were larger than the upward selected lines in less than half of the comparisons.

Both the phenotypic and genetic correlations between body weight and egg weight declined with selection. This supports the theory that the genetic covariance tends toward zero during the course of selection for one of the covariables. Evidently body weight and egg weight are controlled by both independent and pleiotropic genes.

BOHREN, HILL and ROBERTSON (1966) studied the conditions necessary for the development of asymmetrical correlated responses using simulated selection in a simple genetic model. They found that loci influencing two traits independently contributed little to asymmetry while pleiotropic loci producing negative covariance with frequencies differing from $\frac{1}{2}$ contributed most. Of less importance were contributions from unequal numbers of loci, and unequal effects of pairs of loci, influencing the two traits. Also the rate of development of asymmetry was inversely related to the number of genes influencing the traits. Since, in our work, asymmetry was evident in the early generations of selection, we might deduce that the number of genes contributing negatively to the covariance between body weight and egg weight should be relatively few.

Decline in egg production from selection: An important practical consequence of selection for a metric trait is the decline in egg production and other components of reproductive fitness. This aspect of the present experiment will be considered in a separate report. Suffice it to say here that for the body weight lines, rate of egg production declined 1.4σ in high body weight Line B and 0.8σ in low body weight Line C compared with the control. For the egg weight lines, rate of egg production declined 0.9σ for large egg Line D and $.06\sigma$ for small egg Line E. Thus, in each case, egg production declined up to the eighth generation, but for Line E the decline was not statistically significant from zero. In general, up selection lowered rate of egg production more than down selection.

One might raise the question whether genes for high egg production may become lost when selection is directed exclusively towards body size or egg size. For example, will the cross, say, between Lines B and C selected in opposite directions for W return to the original level of egg production in the base population? Experiments carried out over the past 3 years comparing reciprocal crosses between the high and low body weight and egg weight lines with the mid-parent, show no evidence of loss in high egg production genes. Essentially, the original egg production level has been recovered but with no indication for heterosis above the A line.

Replication: One shortcoming of the present experiment is the lack of replication. The results from two other lines of a different breed (Fayoumi) also selected for high body weight and high egg weight are, therefore, worth mentioning here. Fayoumi Line K selected exclusively for high body weight has increased by 4σ in 8 generations and egg production has declined 1.4σ , which is similar to the large body Leghorn Line B. In the Fayoumi Line L selected for high egg weight, the primary trait has increased 2.4σ in 8 generations with a loss of $.4\sigma$ in egg production. Thus, selection progress in the Fayoumi lines was similar, although somewhat less than in the Leghorn lines; in both cases, the decline in egg pro-

duction rate was considerably more than can be explained by inbreeding depression.

SUMMARY

Four lines of Leghorns, of common origin, were each selected for a single quantitative trait. These consisted of a 2-way set (Lines B and C) selected for body weight (W) high and low, respectively, and another set (Lines D and E) selected for egg weight (Z) high and low, respectively. The selected breeders consisted of eight sires each mated to eight to ten females per line per year. The Cornell White Leghorn Randombred was the control population used each year. In addition Line A, selected for high rate of egg production, served as a quasi-control population. This line responded little to selection, and its origin was in common with the other selected lines. Selections were based on measurements at approximately 32 weeks of age.—Responses to selection over seven generations were immediate, large and essentially linear. Mean December body weight in the seventh generation was: Line B 6.1 lb, C 2.7 lb, D 4.5 lb and E 3.1 lb. Mean December egg weight was: Line B 57 g, C 43 g, D 58 g and E 39 g.—Realized heritabilities calculated from the regression of the selected trait on the cumulative selection differential were asymmetrical with respect to the direction of selection. These were, high W .34, low W .52, high Z .24 and low Z .55. In contrast, variance component heritabilities estimated from sire and dam analysis of variance were symmetrical and intermediate. The variance component heritabilities were largest in the upward selected lines but smallest in the downward selected lines.—The estimation of genetic correlations from variance components and from realized selection response between W and Z paralleled those for the estimation of heritabilities. The realized genetic correlations, were, Line B .60, C .57, D .10 and E .78. A weak correlated response in body weight from selection for large egg size indicated for Line D was unexpected. The genetic correlations from variance components were, Line B .31, C .58, D .30 and E .58. Thus, the agreement between realized and variance component correlations was good in the downward selected lines (C and E) but poor in the upward selected lines (B and D).—Generation trends in variance (covariance) estimates of heritabilities and genetic correlations were tested by a factorial analysis of variance. The trends in the heritabilities were not statistically significant, but both the phenotypic and genetic correlations declined significantly over generations. In the upward selected lines (B and D), the variance component genetic correlations declined from 0.6 to .2–.3 in generation 6. In the downward selected lines (C and E), they declined less (to .4–.5). In the control A line no decline was observed. The rates of decline between the lines were statistically significant. Body weight and egg weight are evidently controlled by both independent and pleiotropic genes.

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