

Correlated responses in reproductive fitness to selection in chickens*

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1. INTRODUCTION

Intermediate phenotypes usually have highest reproductive capacity (Fisher, 1930; Lack, 1954). Therefore, artificial selection for extremes of metric traits is expected to lower reproductive fitness. From two-way selection experiments for wing length and body weight in *Drosophila melanogaster* reported by Latter & Robertson (1962) and Sheldon (1963), reproductive fitness declined more in the downward selection lines than in the upward lines.

As a rule, hatchability and egg production in chickens decline with selection for body weight, but this is not always true (Clark & Cunningham, 1953; Lerner, 1958; and Maloney, Gilbreath & Morrison, 1963). Reduction in hatchability from selection for increased shank length may lower the opportunity for artificial selection (Lerner & Dempster, 1951). Natural selection for hatchability may also limit responses to artificial selection for egg weight in chickens (Shultz, 1953). The current fertility and hatchability problems in commercial turkey flocks may very well be a side effect from the intense selection for large body size and extremely broad breast conformation practised in recent years.

The purpose of this study was to evaluate correlated responses in reproductive fitness from selection for body weight and egg weight in Leghorn and Fayoumi chickens and to interpret the results in terms of various genetic models.

2. MATERIALS AND METHODS

Five Leghorn and three Fayoumi lines were selected for single traits over seven generations. Line designations, selection criteria and average number of selected breeders per line are given in Table 1.

The Leghorn base population consisted of a cross-population made between four commercial strains in 1956. The Fayoumi lines were selected from a panmictic-mated flock maintained at Iowa State University for several years. Details of the breeding programme are given elsewhere (Festing & Nordskog, 1967).

Since individual fitness data (fertility, hatchability) were not available in the regular random-bred control populations, two supplementary quasi-control

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populations were used, each of a different breed. These were the Leghorn *A* and Fayoumi *J* lines selected for high rate of egg production. Using them as controls seemed justified since no consistent improvement in rate of egg production was observed in either of the two lines (Nordskog, Festing & Vergheese, 1967).

Body weight was measured at housing time for the males and at approximately 9 months of age for the pullets. Selection in the body weight lines (*B*, *C* and *K*) was based on individual records for both males and females.

Egg weights were taken during six trapnest days when the birds were approximately 9 months old. The females in the egg weight lines (*D*, *E* and *L*) were selected on their individual records, and the males on their full sisters' records (sib test).

Table 1. *Line designations with number (N) of selected breeders*

Leghorn	Fayoumi	Selection criterion	Selected breeders		
			Males <i>N</i>	Females per male	
				Leghorn <i>N</i>	Fayoumi <i>N</i>
<i>A</i>	<i>J</i>	High egg production (\hat{X})	16	10-14	7-10
<i>B</i>	<i>K</i>	High body weight (\hat{W})	8	8-10	7-10
<i>C</i>	—	Low body weight (\hat{W})	8	8-10	—
<i>D</i>	<i>L</i>	High egg weight (\hat{Z})	8	8-10	7-10
<i>E</i>	—	Low egg weight (\hat{Z})	8	8-10	—

The selection intensity varied between 30 and 50% of the records available in the body weight and egg weight lines. The average selection differentials over both sexes per generation were about one σ in the body weight lines and 0.85σ in the egg weight lines (see Festing & Nordskog, 1967). Usually five to six sire families were represented in the breeding pens each year to maintain a reasonably broad genetic base. Also matings between half sibs and full sibs were strictly avoided to minimize inbreeding.

The average inbreeding per generation, estimated from effective population size (Wright, 1940), was about 1.6% per generation in each line except the controls, where it was about 1%, but because half and full sib matings were avoided, inbreeding would be less than indicated from the formula (see Festing & Nordskog, 1967, for further details).

Besides egg weight and body weight, the following four reproductive fitness traits were measured on the selected breeders: percentage egg production for the complete test-year record (*P*), percentage fertility of total eggs set (*F*), percentage hatchability of fertile eggs hatched (*H*), and offspring survival, measured as percentage of pullets surviving from housing to 9 months of age (*S*).

A fitness index (*I*) was then computed as the product of the four fitness traits, i.e. $I = P \times F \times H \times S$. The index *I* estimates the number of offspring surviving to breeding age.

The fitness index was computed on an individual hen basis as well as on a total

population basis. The contribution of each fitness component to the total variation of the fitness index within each line was estimated from a logarithmic transformation so that the fitness index of each individual could be expressed as the sum of the logarithms of the four components. The variance associated with each individual component (neglecting covariances) was then expressed as a percentage of the total variance of the fitness index. Since the logarithm of zero is minus infinity, such values had to be neglected.

Simple linear regression coefficients were computed for the fitness index by using body weight and egg weight as the independent variables.

The trends of the total fitness components, P , F , H and S for each line, were examined by regressing each component on the generation number. Also, the fitness index was regressed on body weight and egg weight within successive generations. The percentage variables of each selected female breeder were transformed to the arc-sine scale. Since the number of eggs set from each hen varied, binomial weights were used (Cochran, 1943). The hatchability regressions were weighted by the number of fertile eggs, while the fitness index regressions were weighted by the number of hatching eggs. Seven years of data on the fitness traits in the Leghorn lines and 6 years in the Fayoumi lines were available at the time this study was under way. Because of the nature of the experiment, data on fertility and hatchability were available only on the selected breeders. To simplify the analyses for the fitness components, measurement of egg production was also restricted to the selected breeders. Since the breeders were selected strictly on the basis of body weight or egg weight, their use to measure trends in fitness components over generations should not give biased results.

To evaluate the results statistically, a factorial analysis of variance was performed on the data for each trait in the Leghorn and Fayoumi lines. The analysis was performed according to the 'Model 1' analysis of Snedecor (1956), which assumes that lines and generations are fixed effects. The various sums of squares were then separated into orthogonal contrasts.

The body weight lines are symbolized with W and the egg weight lines with Z . For lines selected upwards the symbols have a hat (^) and for those selected downwards an inverted hat (v).

Most of the results are shown relative to the controls: i.e. in percentage of the controls. The word 'relative' will not always be used, but this should not lead to confusion.

3. RESULTS

(i) Direct selection response

The success of two-way selection for body weight and egg weight, respectively, is demonstrated in Figs. 1 and 2. The mean body weights and egg weights of the selected lines are expressed as percentages of the corresponding means of the A line for the Leghorns and of the J line for the Fayoumis. The solid lines in these graphs represent direct responses to selection; the dotted lines show correlated responses. Thus, in Fig. 1, the B line reached a body weight of approximately

155 % of the *A* line by generation six from direct selection. For line *D*, body weight increased to approximately 115 % of the *A* line as a correlated response to selection for high egg weight. The direct and correlated responses in body weight and egg weight in the Fayoumi lines closely parallel the corresponding Leghorn lines. These results are discussed more fully by Festing & Nordskog (1967).

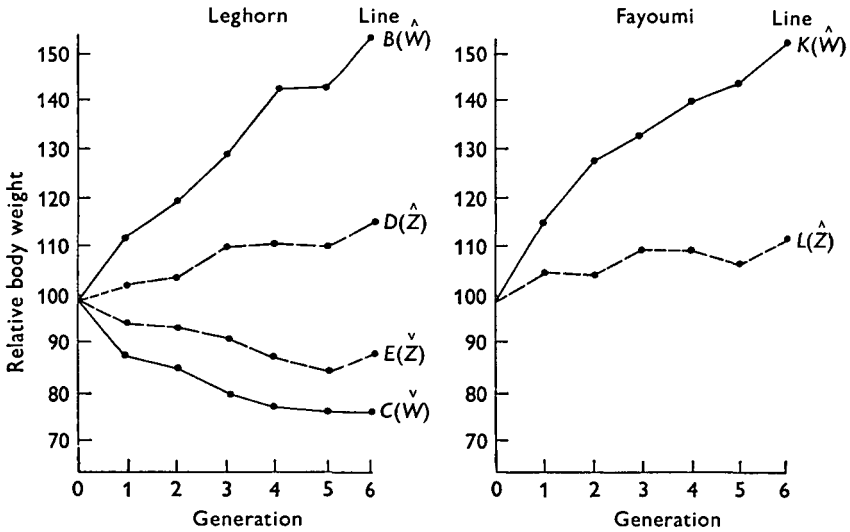


Fig. 1. Relative response in body weight to selection up (\wedge) and down (\vee) for body weight (W) and egg weight (Z). Solid lines are direct responses and dotted lines are correlated responses.

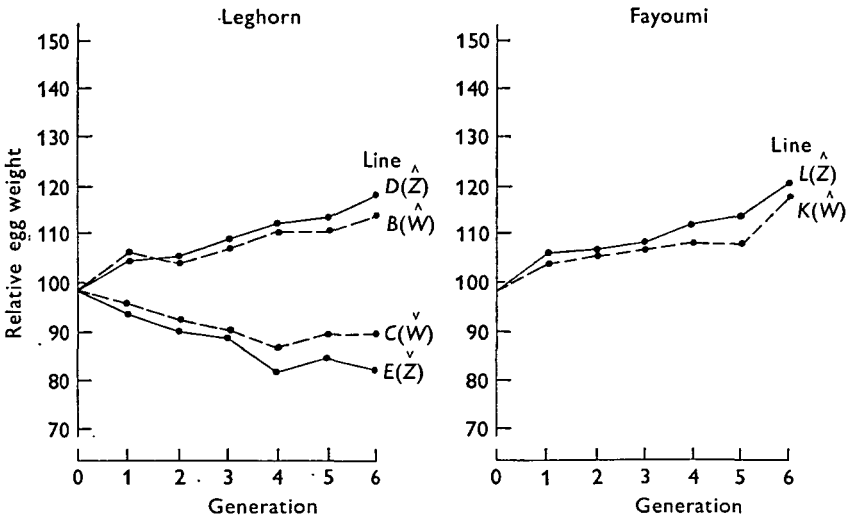


Fig. 2. Relative response in egg weight to selection up (\wedge) and down (\vee) for body weight (W) and egg weight (Z). Solid lines are direct responses and dotted lines are correlated responses.

The change in fitness components and total fitness over generations are presented in Figs. 3–6. That the selected lines deviate from the control in generation zero is because the fitness data were available only on the selected breeders. Statistical significance for the line and generation mean squares and certain orthogonal comparisons between lines in the analysis of variance of the line-generation means are given in Table 2. The ‘lines \times linear’ orthogonal contrasts show that the various lines may not have the same linear trends over generations.

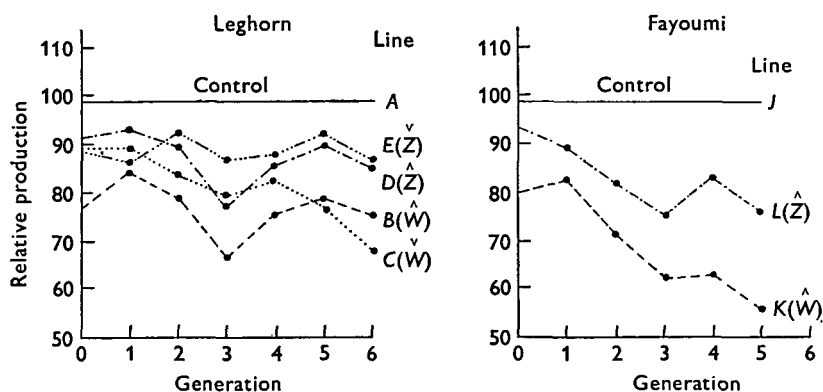


Fig. 3. Correlated response in egg production to selection up (^) and down (v) for body weight (W) and egg weight (Z).

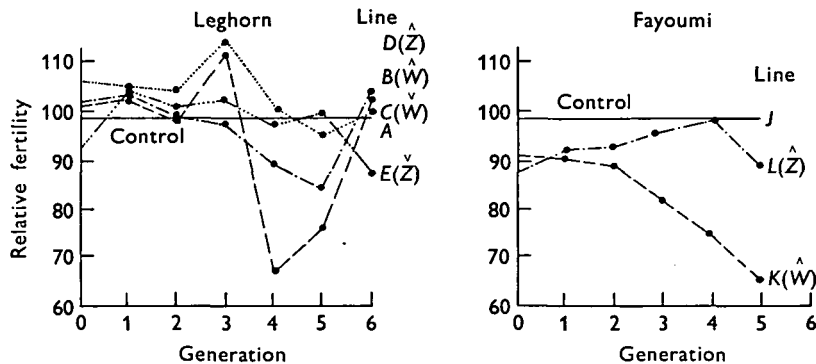


Fig. 4. Correlated response in fertility to selection up (^) and down (v) for body weight (W) and egg weight (Z).

(ii) Egg production

The selected lines were significantly lower in egg production than their controls (Fig. 3). Egg production was significantly lower in the body weight lines than in egg weight lines for both breeds, indicating that selection for body weight was more detrimental to egg production than selection for egg weight. The linear regression coefficients in the body weight lines were significantly greater than in the egg weight lines (Table 2). Also, the regression in line B(W) was steeper than in line C(W). No difference could be demonstrated for the egg weight lines.

(iii) *Fertility*

Fertility relative to the control lines declined only moderately in the Leghorn lines, with a somewhat steeper decline in the body weight than in the egg weight lines (Fig. 4). The extreme decline in line *B* came from generally lower fertility in all matings rather than in a single mating pen. In the Fayoumi breed, line *K*

Table 2. *Analysis of variance of fitness components P, F, H and S and the fitness index I*

	<i>d/f</i>	Statistical significance of mean squares for components and index				
		<i>P</i>	<i>F</i>	<i>H</i>	<i>S</i>	<i>I</i>
Leghorn						
Lines	4
Control <i>A</i> minus selection lines	. 1	+**	+	+**	+	+**
Body wt. minus egg wt. lines	. 1	-**	+	+	0	-
Up minus down lines	. 1	-	-	-**	+	-**
Generations	6	.	**	.	.	*
Linear	. 1	**	*	.	**	.
Quadratic	. 1	**	.	**	.	.
Lines × generations	24
Lines × linear	4
Control <i>A</i> vs. selection lines	. 1	**	.	.	.	*
Body wt. vs. egg wt. lines	. 1	*
Up vs. down lines	. 1	.	.	**	.	.
Remainder	. 20
Fayoumi						
Lines	2
Control <i>J</i> minus selection lines	. 1	+**	+**	+**	+	+**
Body wt. minus egg wt. line	. 1	-**	-**	-	0	-**
Generations	5	.	*	**	*	**
Linear	. 1	*	**	**	.	**
Quadratic	. 1	.	**	.	*	**
Lines × generation	10
Lines × linear	2
Control <i>J</i> vs. selection lines	. 1	**	*	*	.	**
Body wt. vs. egg wt. line	. 1	*	**	.	.	.
Remainder	. 8

** $P < 0.01$, * $P < 0.05$.

Note: For those comparisons of minus effects with a single degree of freedom the sign of the difference is shown. For example, under Leghorns, the 'Control *A* minus selection lines' difference was positive for each fitness component.

declined sharply while line *L* increased slightly in fertility the first four generations.

The factorial analysis of variance for percentage fertility (Table 2) gave no significant difference between the Leghorn lines, while in the Fayoumi lines fertility was significantly lower in line *K* than in line *L*. The linear regression coefficient of line *K* was significantly different from that of line *L*, demonstrating that fertility decreased more sharply in the *K* line.

(iv) Hatchability

Hatchability was more severely depressed by up selection than by down selection for both body weight and egg weight (Fig. 5). The curves for the up lines declined steadily, while those for the down lines fluctuated rather widely. The rate of decline in hatchability was statistically significant for all up lines except the Fayoumi *K*. The latter partly recovered in the fifth generation; otherwise, the *K* line hatched more poorly than the *L* line. In the case of the Leghorns, the line $B(\hat{W})$ hatched slightly better than line $D(\hat{Z})$.

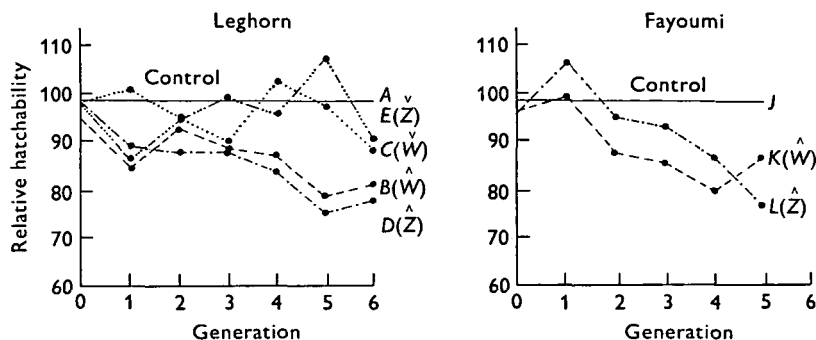


Fig. 5. Correlated response in hatchability to selection up (^) and down (v) for body weight (*W*) and egg weight (*Z*).

From the orthogonal comparisons (Table 2) the difference in hatchability between the up and down Leghorn lines was highly significant. Also, the difference between the regression coefficients of the high and low Leghorn lines was statistically significant. No significant decline could be demonstrated in the down lines. The linear regression of the selected Fayoumi lines was significantly different from that of the *J* line control.

(v) Offspring survival

Since offspring survival could be measured only during the period from housing to 9 months of age, no great differences in this trait could be detected between the various lines (Table 2). Although none of the linear regression coefficients were statistically significant, it appears that in the Leghorn lines offspring survival tended to increase slightly while a slight decline seemed to occur in the Fayoumi lines.

(vi) Fitness index

The changes in fitness index over successive generations of selection are shown in Fig. 6. The body-weight up lines of both breeds showed by far the lowest mean fitness. Fitness in the egg-weight up lines was similar in both breeds, being approximately 75% of the corresponding controls. The Fayoumi lines decreased in fitness more rapidly than the comparable Leghorn lines. The extreme decline in the *K* line prevented effective body weight selection in generation 6, for only enough birds were available to maintain the population.

The factorial analysis (Table 2) shows that the selected lines were significantly lower than the controls; the up and down Leghorn lines were significantly different, and the rate of decline in the fitness index in the selection lines was significantly

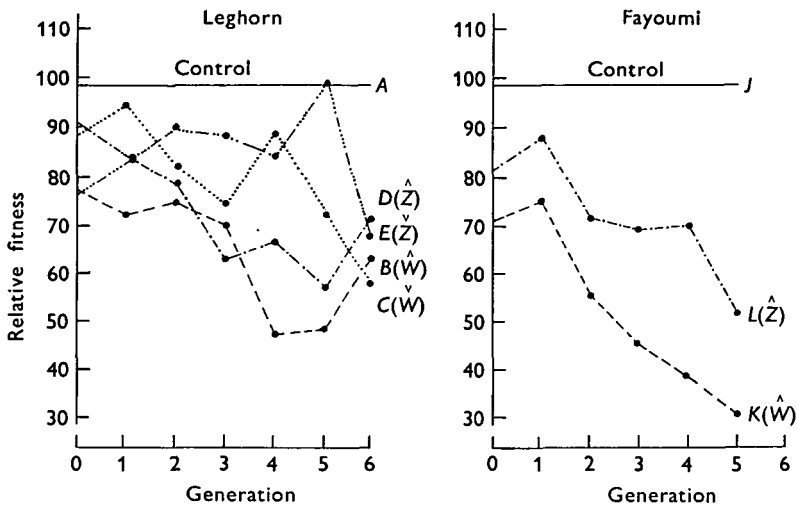


Fig. 6. Correlated response in fitness index to selection up (^) and down (v) for body weight (W) and egg weight (Z).

Table 3. Means and regressions on generation number of relative fitness (I) and components of relative fitness: egg production (P), fertility (F), hatchability (H) and survival (S)

Line		P	F	H	S	I
Leg. B(W)	mean†	78.0	95.8	88.4	99.8	66.0
	regr.	-0.75	-2.78	-2.13*	0.05	-4.19
Leg. C(W)	mean	82.6	105.2	97.5	95.8	81.4
	regr.	-3.05**	-1.40	-1.10	0.31	-4.59**
Leg. D(Z)	mean	88.5	98.0	87.2	98.0	74.4
	regr.	-1.11	-1.07	-3.25*	0.31	-4.43**
Leg. E(Z)	mean	89.6	99.1	97.4	98.4	85.4
	regr.	-0.21	-1.02	0.60	0.21	-0.13
Fay. K(W)	mean	70.6	83.4	90.8	98.7	54.2
	regr.	-5.28**	-5.35**	-3.02	-0.26	-9.25**
Fay. L(Z)	mean	84.5	93.5	93.9	98.7	73.5
	regr.	-3.15*	0.72	-4.55**	-0.24	-5.76**

† Mean is relative control = 100, and I = P.F.H.S.

* P < 0.05, ** P < 0.01.

different from the control lines. Selection for small eggs seemed to have little effect on fitness. Actually, fitness increased in the E line up to the fifth generation of selection.

The linear regression coefficients of the fitness components and total fitness are given in Table 3. On the whole, the average decline per generation in the Leghorn

B, *C* and *D* lines was about 4–4½% per generation, while line *E*, selected for small eggs, showed essentially no decline in total fitness. The Fayoumi lines declined more steeply than the Leghorn lines. This was not anticipated, because the Fayoumi breed has not been subjected to intensive selection on a commercial level for performance as an egg-laying strain as compared with the Leghorn breed.

Table 4. *Percentage of variance in fitness index contributed by the four components of fitness: egg production (P), fertility (F), hatchability (H), and survival (S)*

Line	<i>P</i>	<i>F</i>	<i>H</i>	<i>S</i>
Leg. <i>A</i>	24	38	20	13
<i>B</i>	40	27	35	8
<i>C</i>	46	8	22	16
<i>D</i>	26	21	26	16
<i>E</i>	37	27	14	16
All	39	24	23	14
Fay. <i>J</i>	27	24	28	8
<i>K</i>	45	28	25	6
<i>L</i>	34	38	30	9
All	35	30	27	8

The average proportion of variation in the fitness index attributable to each of its four components is given in Table 4. Egg production contributed nearly half of the variation in the body weight lines. These were the lines which declined most in egg production. Fertility and hatchability accounted for roughly 20–30% of the total variation of fitness. The low values for fertility in the *C* line and hatchability in the *E* line were not surprising, since these lines remained high in fertility and hatchability, respectively. Offspring survival did not account for more than 16% of the fitness index variation in any line.

(vii) *Relation of fitness to body weight and egg weight*

The changes in relative fitness are plotted against selection response in body weight in Fig. 7 and against egg weight in Fig. 8. The arrows in the graph refer to the direction of selection and not to the regression coefficients.

The average intra-generation regression coefficients of fitness index on body weight and egg weight are given in Table 5.

Downward selection in the Leghorn lines gave positive regressions but upward selection gave negative regressions of fitness index on body weight. The Leghorn body weight lines had considerably larger coefficients than the Leghorn egg weight lines. The regression for the Leghorn line *D* (\hat{Z}) differed only a little from the *A* line control, while Leghorn line *E* (\hat{Z}) differed considerably. This is explained by the relatively small correlated changes in *W* in line *D* (\hat{Z}) compared with the large direct change in *W* in the line *B* (\hat{W}). The correlated changes in the line *E* (\hat{Z}) followed the direct changes in line *C* (\hat{W}) much more closely (Fig. 1).

The Fayoumi line *K* (\hat{W}) had the lowest regression coefficient of fitness on body

weight. This was not expected, because the mean fitness of the *K* line is extremely low. Compared with the regressions for the Fayoumi control line *J* and line *L* (\hat{Z}), this suggests that factors other than extreme body weight must account for the drastic decline in fitness in the *K* line.

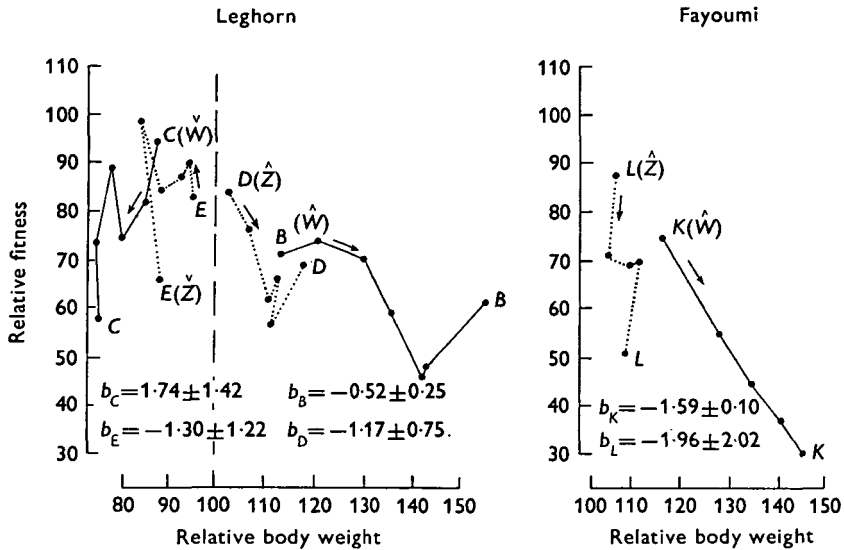


Fig. 7. Changes in fitness index with selection responses in body weight. Solid lines are for body weight lines (*W*) and dotted lines for egg weight lines (*Z*).

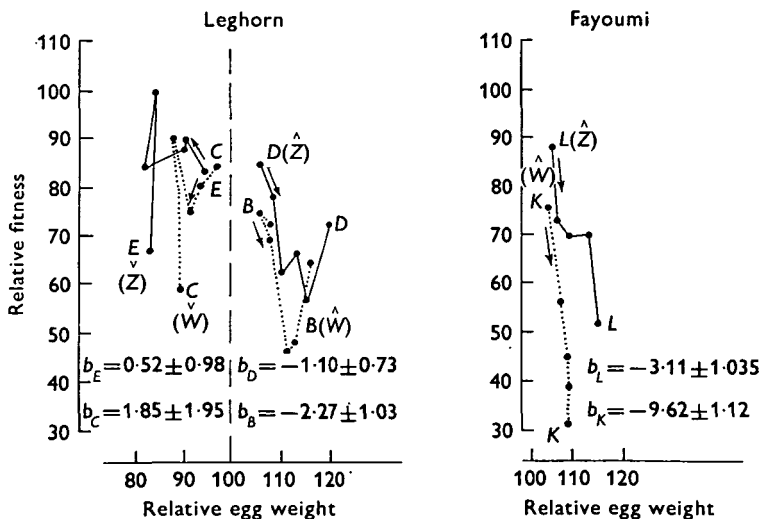


Fig. 8. Changes in fitness index with selection responses in egg weight. Solid lines are for egg weight lines (*Z*) and dotted lines for body weight lines (*W*).

A factorial analysis of the regression coefficients (data not presented here) proved that the difference between the linear regression coefficients of the up and down Leghorn lines was highly significant.

The regression of fitness index on egg weight for the Leghorn lines was similar to the results for body weight as the independent variable (Table 5). Regressions on egg weight were larger in the lines selected directly for egg weight than in those selected for body weight. The coefficients for the down lines were positive and for the up lines negative. The difference between the regression coefficients for the up and down lines was statistically significant (Table 3).

Table 5. Average intra-generation regression coefficients of fitness index on body weight (W) and on egg weight (Z)

Breed	Line	Fitness regressed on	
		W	Z
Leghorn	A (control)	- 0.70	- 0.12
	$B(\hat{W})$	- 4.77	- 0.39
	$C(\check{W})$	+ 11.53	+ 0.78
	$D(\hat{Z})$	- 0.75	- 0.54
	$E(\check{Z})$	+ 5.03	+ 0.95
	Av. s.e.	± 2.56	± 0.44
Fayoumi	J (control)	- 1.98	- 0.16
	$K(\hat{W})$	- 1.01	- 0.02
	$L(\hat{Z})$	- 1.64	- 0.71
	Av. s.e.	± 1.55	± 0.16

The regression of fitness index on egg weight from the Fayoumi data was in agreement with the Leghorn data; the regression coefficient in the Fayoumi line $L(\hat{Z})$ was significantly larger than in the Fayoumi line $K(\hat{W})$. This was expected, since the L line was selected for egg weight while the K line was selected for body weight.

The influence of body weight and egg weight on fitness was evaluated by a multiple regression equation containing linear, quadratic and product terms as follows:

$$I = \beta_1 W + \beta_2 W^2 + \beta_3 Z + \beta_4 Z^2 + \beta_5 WZ + k, \quad (1)$$

where the β 's are partial regression coefficients and k is a constant.

This model assumes that maximum fitness is associated with intermediate values of a metric trait and that fitness is a function of both linear and quadratic deviations. The product term fixes the direction of the regression plane. In effect, we have an equation for a response surface with fitness jointly dependent on body weight and egg weight. Data consisting of the line by generation means from the four Leghorn lines relative to the control were fitted to equation (1).

The solution to equation (1) and the resulting response surface are shown in Fig. 9. The ellipses represent fitness contours on the response surface. At the peak, the fitness is 100 relative to the control and falls off in all directions shown by the contour lines. The direction of the elliptic contours indicates that fitness declines more sharply for extremes in egg weight than for extremes in body weight. Also, the graph indicates that the basic population from which the selected lines were

derived was near the optimum in body weight, while egg weight was about 10% above the optimum. Presumably, the commercial stocks from which the control (and selected lines) were derived had previously been selected for large egg size to satisfy market demand. This would explain why the 95% contour line is below the point of origin in Fig. 9.

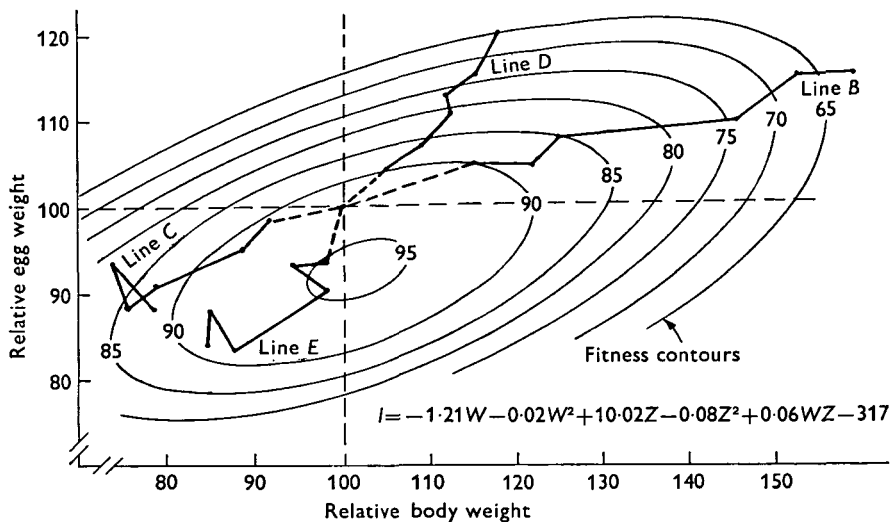


Fig. 9. The fitness response surface as a function of changes in body weight and egg weight. Lines *B* and *C* are selected for body weight up and down, respectively. Lines *D* and *E* are selected for egg weight up and down, respectively.

4. DISCUSSION

The observed decline in reproductive fitness with selection for metric traits could result from both phenotypic and/or genetic effects. Theoretical phenotypic and genetic models are discussed by Robertson (1956) and Latter (1960) as 'metric deviation models' and 'homeostatic models', respectively, and by Lewontin (1964*a, b*) as optimum models and heterotic models, respectively. In this paper we use Robertson's concepts. The metric deviation model assumes that the decline in fitness results solely from the extreme phenotypes being intrinsically less fit and not because of their underlying genetic constitution. Natural selection in this case is for a fixed phenotypic value and gene fixation is inevitable (Fisher, 1930) unless the inheritance of the metric trait deviates in specific ways from simple additivity (Kojima, 1959; Curnow, 1964; Lewontin, 1964*b*). The homeostatic model is derived from Lerner's (1954) concept of genetic homeostasis, which assumes that fitness exhibits overdominance, while other metric traits are controlled by many loci with small additive effects. In this case, the extreme phenotypes are less fit because they are more homozygous than intermediates; fitness declines as a selection response due to an increase in homozygosity at loci affecting the metric trait. Maintenance of genetic variance is a property of this model. Under both

models, the change in mean fitness of a population selected for a metric trait is proportional to the square of the selection advance in accordance with Wright's (1935) quadratic deviation model. Consequently, the ratio $(-\ln \bar{w})/g^2$, where \bar{w} is the mean fitness of the selected line relative to the control after a shift in the mean of the selected trait by g genetic standard deviations, should remain constant over generations (Latter & Robertson, 1962). The ratio for the various lines for generations 3 and 6 are given in Table 6.

These results fail to demonstrate such a simple relationship between fitness decline and selection response, except possibly in the case of the Fayoumi *K* line, where the fitness index declined regularly over generations.

Table 6. Comparison of the ratio $(-\ln \bar{w})/g^2$ by lines and generations (see text for explanation)

Leghorn	Value of $(-\ln \bar{w})/g^2$	
	Generation 3	Generation 6
<i>B</i> high body weight	0.047	0.021
<i>C</i> low body weight	0.033	0.053
<i>D</i> high egg weight	0.130	0.029
<i>E</i> low egg weight	0.021	0.030
Fayoumi		
<i>K</i> high body weight	0.039	0.035
<i>L</i> high egg weight	0.068	0.049

As expected under either model, the sign of the intra-generation regression coefficients of fitness on the selection criterion in the selected lines is always opposite to the direction of selection. The magnitude of the linear regressions should be proportional to the selection response as a consequence of the quadratic deviation effect. This relationship seemed to hold for all lines except the Fayoumi *K* line. The intra-generation regressions of fitness on the correlated traits, e.g. on egg weight in the body weight lines and vice versa, were also proportional to the correlated responses and opposite in sign to their direction. Although these data may be biased since only the selected breeders could be studied, they still should give a valid indication of the direction of regression as well as a useful estimate of the slope of the regression line of fitness on each of the selected traits. This is supported by data from a separate study of the relationship of hatchability to egg weight based on more representative samples of the same five Leghorn lines.

The inter-generation regression of fitness on generation number estimates the loss in fitness over generations from selection on a metric trait. Consider the linear regression $Y_i = a + bg_i$, where Y_i is the fitness response in generation i and g_i is the generation number. Because we measure fitness only on the selected breeders in each generation, Y contains a downward bias k . That is, the mean fitness of the selected breeders underestimates the mean fitness of the unselected generation mean by a quantity k . If the amount of selection practised each generation is constant, then k is constant and b is not biased from selection. Also, if the selection

intensity from generation to generation shows no trend, then b would also be unbiased.

The inter-generation regression is 'genetic' in the sense that it represents a genetic change in fitness for a unit of genetic change in the metric trait measured over generations. In contrast, the intra-generation regression is 'phenotypic' since it estimates the phenotypic change in fitness for a unit of phenotypic change in the metric trait.

(i) *Asymmetry of fitness response*

Under the assumptions of strict overdominance for fitness and additivity for metric traits, the relatively symmetric selection response in egg weight in the Leghorn lines should have been accompanied by symmetric correlated changes in fitness. If egg weight in the base population was above optimum for maximum fitness, some asymmetry could be expected. This seems a reasonable explanation, since the Leghorn base population had commercial origin in which selection would have been directed to maintain at least a standard egg weight.

Asymmetric correlated response in fitness could also be explained in terms of directional dominance (Falconer, 1960). In this case, the smaller decline in fitness in the down Leghorn lines compared with the up Leghorn lines could have resulted from differences in the intensity of selection for heterozygous genotypes. The relative selection response in the down lines was less than that of the up lines in the last three generations. This would be expected if selection in the down lines favoured heterozygotes more than in the up lines.

Bohren, Hill & Robertson (1966) demonstrated that pleiotropic loci producing negative covariance contributed most to asymmetrical correlated responses in a study on a simple genetic model. Of less importance were contributions from unequal numbers of loci influencing two traits. They deduced that symmetrical correlated responses were more the exception than the rule.

(ii) *Inbreeding and fitness decline*

Some of the loss in fitness should be attributable to inbreeding effects, since random gene fixation is expected to occur from restricted population size. Under slow inbreeding from small population size, Tebb (1958) calculated a decline of 0.47 pullets to breeding age for each ten per cent increase in inbreeding in an egg production flock selected over 10 years. Similarly, Duzgunes (1950) found that reproductive fitness in chickens (measured as number of chicks per hen surviving to breeding age) declined by 50% when inbreeding reached 25% in 3 years.

In our study, however, differences in fitness among the selected lines should not be accounted for by differences in inbreeding, since the population size was essentially the same for all selected lines. Yet, inbreeding would tend to make the lines different, which would account for some of the variation in fitness between the lines. The average difference between the inbreeding coefficients of the selected lines (based on effective population size) and their control was approximately 0.65% per generation for the Leghorns and approximately 0.72% for the

Fayoumis. Actually, the amount of inbreeding would be somewhat less because sib matings were avoided. If the regression of percentage egg production on percentage inbreeding is 0.43 (Stephenson, Wyatt & Nordskog, 1953), egg production percentage in all the selected Leghorn lines can be corrected for the difference in inbreeding compared with the control line from the factor

$$0.43 \times 0.65 = 0.28,$$

while the correction factor for the selected Fayoumi lines would be 0.31. Similarly, a correction for hatchability equal to 0.24% in the Leghorns and 0.27% in the Fayoumis can be estimated from the regression coefficient of -0.37 for hatchability on percent inbreeding (Blow & Glazener, 1953).

Since these correction estimates are rather small, it seems that inbreeding from restricted population size is responsible for only a small portion of the observed differences in fitness between the selected lines and the control lines. Moreover, the rate of inbreeding per generation is probably important in determining the amount of inbreeding depression in fitness. Latter & Robertson (1962) showed that, at theoretically the same level of inbreeding, *D. melanogaster* lines from continued full-sib matings had much lower fitness than lines from populations maintained by ten pairs of parents each generation. Although the rate of inbreeding in our selected lines should be considerably greater than in the control lines, it would still not seem to be high enough to account for all of the observed differences in fitness between the selected lines and the controls.

It has been pointed out to us by a referee that in a selection programme in which extreme pressure is applied to a highly heritable trait such as body weight, the true inbreeding coefficient may be much larger than calculated by a simple formula based on effective population size (N_e). As a check on the validity of calculating inbreeding from N_e , we estimated inbreeding by the pedigree sampling method of Wright & McPhee (1925). In each line, 240 two-column pedigrees were obtained. Inbreeding per generation was estimated to be $1.90 \pm 0.20\%$ as an average of the selected Leghorn lines. For the Leghorn control the estimate was $1.50 \pm 0.25\%$. Thus, the difference of the selected lines from the control was 0.40% per generation. This is in fair agreement with, but less than, the 0.65% estimated from N_e . For the Fayoumis, inbreeding in the selected lines was $1.70 \pm 0.27\%$ and in the control, $1.39 \pm 0.30\%$, for a difference of 0.41% per generation. This compares with 0.72% as estimated from N_e . These results demonstrate that selection was not sufficiently extreme to inflate the inbreeding very much, if any, over that expected from finite population size. In fact, the amount of selection pressure per generation averaged only about one standard deviation per generation which we regard as rather moderate selection pressure.

(iii) Linkage and fitness decline

Besides directional and random increases in homozygosity, linkage and pleiotropy will also influence changes in fitness with directional selection. Mather & Harrison (1949) for instance, attributed the decline in fertility in their high

abdominal bristle lines of *D. melanogaster* mainly to linkage, and Latter & Robertson (1962) also held linkage responsible for the reduction in fitness in two of their high and low abdominal bristle lines of the same species, but concluded that pleiotropy was also important. In our data, it seems that the observed correlated changes in fitness index in the Leghorn egg weight lines could be explained by linkage. Since the Leghorn base population came from a four-way cross of four different strains, this population may have been further away from linkage equilibrium than the Fayoumi base population. An excess of repulsion phase linkages between egg weight and fitness alleles could then account for the decline in fitness in the high egg weight line *D* and the increase in fitness in the low egg weight line *E* during the first generations. The fluctuations in fitness in these two lines during the later generations could have resulted from an approach to linkage equilibrium. The steady decline in fitness with continued selection response in the Fayoumi lines could also be accounted for by linkage. The data for the *K* line suggest tight linkage between body weight and fitness loci in this population. Since no evidence of any break between this relationship could be obtained so far in the *K* line, however, the sharp reduction in fitness could be explained just as well by pleiotropy.

SUMMARY

The correlated changes in reproductive fitness with selection for single traits for six generations in five Leghorn lines and five generations in three Fayoumi lines were analysed. The Leghorn lines, originating from crosses between four commercial strains, were: line *A*, selected for high egg production; lines *B* and *C*, selected for high and low nine-month body weight; and lines *D* and *E*, selected for high and low nine month egg weight. The Fayoumi lines, *J*, *K* and *L*, corresponding to the *A*, *B* and *D* Leghorn lines, respectively, were selected from a random mating population maintained over several years without selection. The breeding populations for the *A* and *J* lines each consisted of 16 sires mated to 9–16 dams each, while all the other lines were produced from eight sires, each mated to 9–16 dams. The *A* and *J* lines showed no consistent improvement in egg production or reproductive fitness and were used as control lines in this study. Body weight in the *B* and *K* lines increased by 55.8 and 45.2 %, respectively, while egg weight in the *D* and *L* lines increased by 17.7 and 15.1 %, respectively. The *C* line declined in body weight by 21.5 %, while the *E* line declined in egg weight by 16.3 %.

A reproductive fitness index was measured as the product of rate of egg production, fertility, hatchability, and percent survival of offspring from housing to nine months of age. The mean values of the fitness index as percentages of the control lines were Leghorn lines *B* 66, *C* 81, *D* 74, *E* 85 and Fayoumi lines *K* 54 and *L* 74.

Reproductive fitness and all fitness components except offspring survival declined more in the high lines than in the low lines. The body weight lines were lower in fitness than the egg weight lines, mainly because of lower rate of egg production. The patterns of correlated changes in the fitness index were more regular in the Fayoumi than in the Leghorn lines. The linear regressions of fitness index on direct

selection response in the *K* and *L* Fayoumi lines were statistically significant. Offspring survival contributed only 14% to the variation in the fitness index in the Leghorn lines and only 8% in the Fayoumi lines. The relative contributions to the variation in fitness index were 35% for rate of egg production, 24% for fertility and 23% for hatchability in the Leghorn lines. The corresponding figures were 35, 30 and 27% for the Fayoumi lines, respectively.

The average linear regression coefficients of fitness index on body weight, calculated on an individual hen basis (selected breeders only) within lines and generations, were -4.77 for the *B* line, 11.53 for the *C* line, and -1.01 for the *K* line. The corresponding coefficients of fitness index on egg weight in the egg weight lines were -0.543 for the *D* line, 0.947 for the *E* line, and -0.712 for the *L* line. With the exception of the *K* line, the regressions on body weight were larger in the body weight lines than in the egg weight lines, and, similarly, the regressions on egg weight were larger in the egg weight lines than in the body weight lines. The differences between the regression coefficients of the high and low lines were statistically significant.

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