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Selection for larval growth in *Tribolium* under two levels of nutrition*

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1. INTRODUCTION

Genotype–environment interaction has been studied from different points of view by many geneticists and breeders. McBride (1959) presented an extensive summary of relevant papers and their opposing arguments. According to Hammond (1947), a favourable environment enhances the effectiveness of selection, while Lush (1945) recommended that the environmental conditions for a breeding herd should be similar to those prevailing for the general population or breed under improvement. Furthermore, one can establish a hypothetical model whereby an unfavourable environment accompanied by increased physiological stress would accelerate genetic improvement (e.g. James, 1961). Such speculation can be useful in stimulating experimentation to identify the model which more nearly fits biological reality.

The approach of Falconer (1960*a*) to this problem has greatly influenced the direction of experimentation. He developed the concept of considering a particular trait in two different environments as two traits with genes conditioning high performance in one environment not necessarily producing the same effect in another environment. Thereby the consequences of a genotype–environment interaction existing for two environments can be predicted from (1) the genetic correlation between the two traits as defined, (2) their heritabilities, and (3) their phenotypic variances. A partial experimental check of the model was reported by Falconer & Latyszewski (1952) when they selected for increased body weight in mice on high and low planes of nutrition. A practical application to swine breeding was made by Fowler & Ensminger (1960). Alan Robertson (1959) showed that, at least in theory, the above could be extended to encompass many environments. Later, Yamada (1962) presented a revision of Robertson's theory by extending the idea to statistical models for a variety of experiments.

Extensive experiments relating to the above problem have been made with laboratory insects. In a series of studies on the ecological genetics of *Drosophila*,

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Robertson (e.g. 1959, 1963) revealed the interdependency of genetic and environment factors in determining the nature of quantitative variation, in particular the effects of nutrition on body size. Parsons (1959) reported genotype–environment interactions with respect to survival of *Drosophila* at different temperatures. Druger (1962) studied the responses from positive and negative selections for wing length of *Drosophila pseudoobscura* cultured at different temperatures. He found that the magnitude of the correlated response for wing length under the temperature other than that of selection was influenced by both direction of selection and culturing temperature. In studies of growth of *Tribolium* cultured in different humidities, McNary & Bell (1962) and Bray, Bell & King (1962) found genotype–environment interactions significantly influencing the responses to selection. During a comparison of positive and negative selection for growth of *Tribolium* under two levels of nutrition, Hardin & Bell (1967) observed significant genotype–environment interactions and described their effects on direct and correlated responses.

The present study with *Tribolium* expands the latter study to include populations selected each generation on (1) average performance under the two levels of nutrition, and (2) performance on each of the two levels in alternating generations. Unexpected results are examined in terms of quantitative genetic theory including the possibility that components of growth may be altered differentially by direction and environment of selection.

2. MATERIALS AND METHODS

The experimental phase of this study, initiated late in 1961, was divided into two replications of nine experimental populations as described in Table 1. Sixteen generations of selection were made with generations cycling at intervals of 5 weeks. All populations within a replication were reproduced simultaneously, but the replications were scheduled 1 week apart to facilitate the data collection. The two replications were initiated from different but recent subcultures of the Purdue '+' Foundation stock of *Tribolium castaneum*.

Two levels of nutrition as originally developed by Hardin, Rogler & Bell (1967) were chosen as contrasting (GOOD *v.* POOR) test environments for this study. In addition to common ingredients, the ration for the GOOD environment contained

Table 1. *Descriptions of experimental populations*

Population code*	Direction and environment of selection
GL	Large in GOOD each generation
PL	Large in POOR each generation
$\overline{\text{GPL}}$	Large in both GOOD and POOR each generation
GPL	Large in GOOD and POOR in alternating generations
GS	Small in GOOD each generation
PS	Small in POOR each generation
$\overline{\text{GPS}}$	Small in both GOOD and POOR each generation
GPS	Small in GOOD and POOR in alternating generations
C	Unselected control

* Replication is given as a subscript (GL_1 or GL_2) when identification is desired.

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10% dried brewer's yeast and 5% corn (maize) oil while the ration for the POOR environment contained neither. The reproduction of all populations occurred in STANDARD *Tribolium* medium consisting of 95% whole-wheat flour enriched with 5% dried brewers' yeast. All populations were reared at a uniform 33 °C and 70% relative humidity.

The quantitative trait chosen to manifest growth, 13-day larval weight, was the same trait Hardin & Bell (1967) had observed in their study of selection response under the GOOD and POOR environments.

For convenience of handling, all mates were paired at the pupal stage. All populations were reproduced with forty single pair matings per generation with the exception of twenty matings for each of the two control populations. Mated pairs were initially placed in $\frac{3}{4}$ oz creamers containing 2 g of STANDARD medium and left for 10 days to provide time for adult emergence, mating and approach to peak fecundity. Thereafter, a precise cycle of egg collections was followed. A 48 h egg collection from each mating in all populations was taken in 4 g of STANDARD for perpetuating the populations. Then each mated pair was transferred for progeny testing to a creamer containing 2 g of GOOD for a 24 h egg collection to be followed by a 24 h collection in 2 g of POOR. A third 24 h egg collection was taken from each mated pair in either GOOD or POOR so as to provide two collections for the environment of selection as specified in Table 1. Beginning with generation 8, two 24 h egg collections in both GOOD and POOR were made per mating for all populations.

Thirteen days after each of the above 24 h egg collections all offspring within a creamer were screened from the medium. Five larvae were chosen at random from each creamer and weighed as a group on a micro-analytical balance. All weights were recorded to the nearest 10 μg (10^{-2} mg). Selection within each population was based on average family merit as determined by the ten full-sib larvae sampled from the two egg collections specified for selection. The weights of other full-sibs which had been reared in the opposite environment were taken when needed to provide a measure of correlated response. All progeny cultured each generation in either GOOD or POOR were discarded after weights were recorded.

The eight best families, as specified by direction and environment of selection, were chosen within each selected population and their full-sibs from the 48 h egg collection in STANDARD were sexed at the pupal stage. Five males and five females randomly taken from each of the eight selected families were mated at random (excluding full-sib matings) to provide forty single pair matings for the next generation. Each control population was reproduced from one male and one female taken at random from each of the twenty matings made each generation. Since all parents were cultured each generation in STANDARD, any possible 'Dauermodifikationen' effect on the offspring through maternal nutrition was eliminated.

Statistical analyses for assessment of genotype–environment interaction were not made across environments and generations since heterogeneity of variances was observed between environments and directions of selection. Transformations of the data to various scales were made but failed to yield homogeneous variances

For instance, all large lines showed a negative correlation of means and variances in both environments while all small lines showed a positive correlation. Such complications being the case, 13-day larval weights obtained in the two environments were treated as different traits. The genetic correlation between those two traits was studied since this statistic is not affected by scaling effects. On the other hand, it should be noted (Yamada, 1962) that the genotype–environment interaction component is equal to the average of the genetic variances in the two environments minus the genetic covariance.

3. EXPERIMENTAL RESULTS AND DISCUSSION

Initial parameters. Phenotypic and genetic parameters estimated for 13-day larval weight of the foundation strain used here, when cultured in similar environments, were recently reported by Hardin & Bell (1967). They had studied this population only a few months previous to the present investigation. Initial parameters for the present study were obtained from pooled analyses of generations 0 and 1 of all populations and are compared by replication in Table 2 with those previously reported. Mean 13-day larval weight in the GOOD environment was about twice that observed in POOR in both studies. While homogeneous phenotypic variances across environments were observed previously, both replications of the present study revealed these variances to be heterogeneous. Furthermore, our estimates for genetic parameters were higher than those found in the earlier study.

Table 2. *Phenotypic and genetic parameters for 13-day larval weight of the Purdue '+' Foundation Strain of* Tribolium *reared in GOOD and POOR environments*

Parameters for 13-day larval weight	Hardin & Bell (1967)	Present experiment	
		Replication 1	Replication 2
Mean (10^{-2} mg) in GOOD	236·2	227·2	220·3
Mean (10^{-2} mg) in POOR	113·0	115·7	116·9
Phenotypic variance in GOOD	1091	1433	1830
Phenotypic variance in POOR	1185	818	740
Heritability in GOOD	0·21 ± 0·06	0·30 ± 0·06	0·44 ± 0·06
Heritability in POOR	0·19 ± 0·05	0·35 ± 0·06	0·51 ± 0·06
Genetic correlation between weight in GOOD and in POOR	+0·60 ± 0·21	+0·82 ± 0·04	+0·78 ± 0·04

These discrepancies resulted, in our opinion, from differences among procedures used for estimating the parameters rather than from other possible causes. For example, phenotypic variances of the earlier study were calculated directly from individual observations while comparable variances in the present study were estimated from variation among means of five full sibs. Since each mean was confounded with the common environmental effect shared by the larvae cultured in a single creamer, the larger phenotypic variances found in Table 2 for both replications of GOOD could simply represent this bias. The smaller variances estimated for both replications in POOR may have resulted from biased sampling

procedures. This hypothesis is supported by the asymmetrical selection differentials observed only in POOR (Table 7). Apparently, the smaller larvae in POOR had either passed unobserved through the sieves or died before emergence (in order to

Table 3. *Direct and correlated responses for the first eight generations by replication and selection method*

(Direct responses are in italics.)

		Gain (10^{-2} mg) per generation by environments		
Rep.	Population	GOOD	POOR	AVERAGE ($\overline{GP}$)
I	GL	*6·7 ± 1·2*	8·2 ± 2·2	7·5 ± 1·5
	PL	4·2 ± 1·3	*13·5 ± 2·5*	8·9 ± 1·7
	$\overline{GP}$L	4·6 ± 1·3	10·6 ± 1·8	*7·6 ± 1·3*
	GPL	4·9 ± 0·8	11·3 ± 2·7	8·1 ± 1·7
	GS	*−12·3 ± 0·7*	−8·1 ± 1·8	−10·2 ± 0·9
	PS	−12·8 ± 0·9	*−11·4 ± 1·6*	−12·1 ± 1·0
	$\overline{GP}$S	−11·6 ± 1·1	−6·3 ± 1·7	*−7·2 ± 1·3*
	GPS	−13·4 ± 0·8	−7·6 ± 1·6	−10·5 ± 1·0
II	GL	*11·6 ± 1·2*	9·1 ± 2·3	10·4 ± 0·7
	PL	10·6 ± 1·1	*13·0 ± 1·3*	11·8 ± 0·5
	$\overline{GP}$L	9·3 ± 1·8	9·1 ± 1·7	*9·2 ± 1·7*
	GPL	9·5 ± 1·5	8·5 ± 0·8	9·0 ± 0·8
	GS	*−14·6 ± 1·0*	−9·4 ± 2·1	−12·0 ± 1·7
	PS	−14·6 ± 1·2	*−11·4 ± 1·4*	−13·0 ± 0·9
	GPS	−10·5 ± 2·6	−7·1 ± 1·6	*−8·8 ± 1·8*
	GPS	−11·4 ± 1·5	−7·3 ± 1·9	−9·4 ± 1·1

Table 4. *Direct and correlated responses for the last eight generations by replication and selection method*

(Direct responses are in italics.)

		Gain (10^{-2} mg) per generation by environments		
Rep.	Population	GOOD	POOR	AVERAGES ($\overline{GP}$)
I	GL	*6·3 ± 1·1*	4·4 ± 1·7	5·3 ± 1·2
	PL	2·8 ± 1·3	*3·6 ± 1·3*	3·2 ± 0·6
	$\overline{GP}$L	4·2 ± 1·3	5·3 ± 1·5	*4·8 ± 0·7*
	GPL	3·0 ± 0·9	1·6 ± 3·0	2·3 ± 1·5
	GS	*−5·7 ± 1·1*	−2·5 ± 2·4	−4·1 ± 1·4
	PS	−6·1 ± 1·9	*−2·6 ± 2·6*	−5·2 ± 3·1
	$\overline{GP}$S	−9·7 ± 1·5	−3·1 ± 2·2	*−4·0 ± 2·5*
	GPS	−5·5 ± 1·2	−3·2 ± 2·3	−4·4 ± 1·5
II	GL	*5·2 ± 2·0*	1·5 ± 2·6	1·7 ± 1·9
	PL	5·2 ± 1·9	*8·5 ± 1·4*	6·9 ± 0·6
	$\overline{GP}$L	4·6 ± 1·9	5·4 ± 1·4	*5·3 ± 0·7*
	GPL	8·3 ± 1·5	8·3 ± 1·9	8·3 ± 0·9
	GS	*−9·0 ± 1·9*	−1·4 ± 0·7	−5·2 ± 0·9
	PS	−1·0 ± 1·5	*−1·6 ± 0·8*	−1·3 ± 1·0
	$\overline{GP}$S	−3·8 ± 1·7	−3·0 ± 0·8	*−3·4 ± 1·1*
	GPS	−4·5 ± 1·4	−2·2 ± 0·4	−3·4 ± 0·8

survive and undergo metamorphasis a 13-day larva must reach some minimum size.)

Genetic parameters in the present study, in view of its design, were estimated from full-sib covariances and thus would be inflated by both dominance and maternal effects, while those listed for the earlier study were estimated from half-sib covariances. In fact, this earlier report presented evidence which indicated that the full-sib covariances were inflated by dominance rather than maternal effects.

Table 5. *Direct and correlated responses over all sixteen generations by replication and selection method*

(Direct responses are in italics.)

Rep.	Population	Gain (10^{-2} mg) per generation by environment: GOOD	POOR	AVERAGE ($\overline{GP}$)
I	GL	*5·6 ± 0·4*	5·5 ± 0·5	5·6 ± 0·5
	PL	3·9 ± 0·5	*9·3 ± 0·9*	6·6 ± 0·6
	$\overline{GPL}$	5·2 ± 0·5	8·7 ± 0·7	*7·0 ± 0·4*
	GPL	4·9 ± 0·4	8·5 ± 1·2	6·7 ± 0·7
	GS	*−8·7 ± 0·6*	−5·5 ± 0·9	−7·1 ± 0·6
	PS	−8·8 ± 0·7	*−7·9 ± 1·0*	−8·4 ± 0·8
	$\overline{GPS}$	−9·5 ± 0·5	−6·3 ± 0·8	*−7·9 ± 0·5*
	GPS	−9·7 ± 0·7	−6·2 ± 0·8	−7·9 ± 0·7
II	GL	*7·3 ± 0·7*	6·5 ± 1·0	6·9 ± 0·6
	PL	6·9 ± 0·7	*10·4 ± 0·6*	8·6 ± 0·5
	$\overline{GPL}$	5·4 ± 0·8	5·7 ± 0·7	*5·5 ± 0·6*
	GPL	6·7 ± 0·6	7·6 ± 0·6	7·2 ± 0·4
	GS	*−12·5 ± 0·8*	−4·9 ± 0·8	−8·7 ± 0·7
	PS	−8·6 ± 1·0	*−6·4 ± 0·8*	−7·5 ± 0·9
	$\overline{GPS}$	−7·4 ± 0·9	−5·5 ± 0·6	*−6·4 ± 0·7*
	GPS	−9·3 ± 0·7	−5·5 ± 0·6	−7·4 ± 0·5

Trends in population means. Selection responses for the various populations reared in both GOOD and POOR environments are presented by replication for the first eight generations (Table 3), the last eight generations (Table 4) and over all sixteen generations (Table 5). Responses are expressed as the linear regression of gain on generation of selection when gain is measured as the deviation between the mean of a selected population and that of its unselected control. With minor exceptions, the two replications showed similar responses and are combined for presenting the general picture of selection methods under different environments (Figs. 1–3).

It can be noted from a comparison of Tables 3 and 4 that selection responses observed in the early generations, with a single exception, are greater than those observed in the later generations. This phenomenon, characteristic of long-term selection experiments, will not be discussed in detail since other aspects of these results are of greater interest. While some of the over-all responses may have departed significantly from linearity, the authors feel that a more precise

mathematical description would not have enhanced materially the biological interpretation.

It is evident from the results presented above that direct selection responses are generally larger than indirect or correlated responses in either Good or Poor

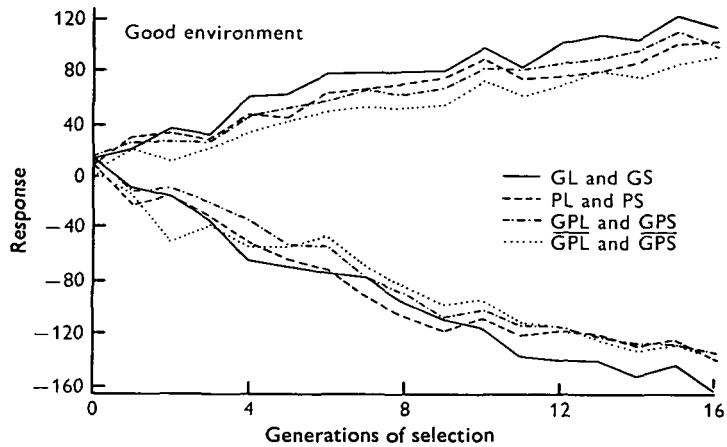

Fig. 1. Relative responses in the Good environment over sixteen generations for various methods of selection summed over both replications. Ordinates are expressed as deviations (10^{-2} mg) from unselected controls.

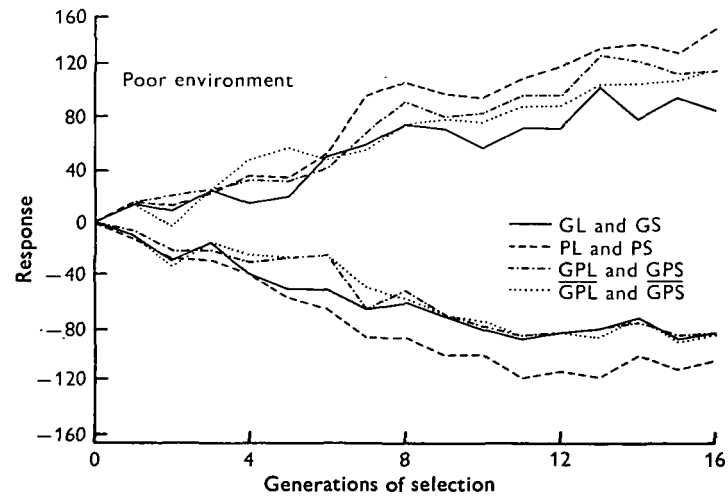

Fig. 2. Relative responses in the Poor environment over sixteen generations for various methods of selection summed over both replications. Ordinates are expressed as deviations (10^{-2} mg) from unselected controls.

environment. For example, GL and GS are both extremes when all populations are tested in Good (Fig. 1) while PL and PS are the extremes when all are tested in Poor (Fig. 2). Yet, populations selected for average performance in both environments ($\overline{GP}L$, GPL, $\overline{GP}S$ and GPS) were not superior for the criterion of

direct selection (average performance). Thus Fig. 3 shows that three of the lines selected for performance in a single environment (PL, PS and GS) excelled in respect to average performance over both environments. During the first eight generations of selection (Table 3), direct selection for average performance was clearly inferior in both replications. This surprising result deserves further consideration.

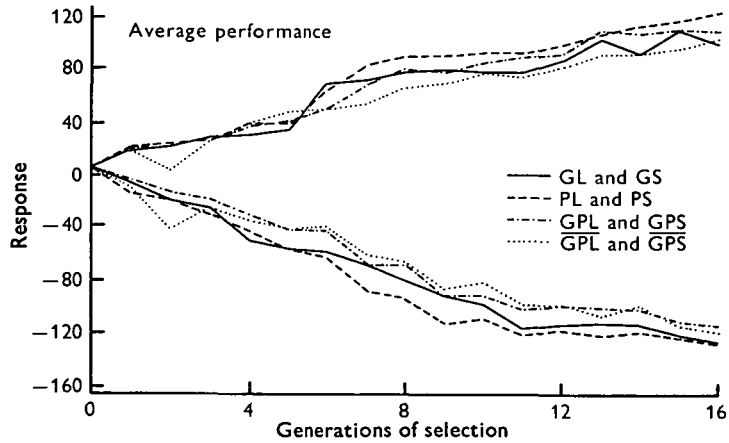

Fig. 3. Relative responses in AVERAGE PERFORMANCE (both environments) over sixteen generations for various methods of selection summed over both replications. Ordinates are expressed as deviations (10^{-2} mg) from unselected controls.

Selection for average performance. The effectiveness of selection based on average performance in two environments (X and Y) relative to that of selection based on performance in a single environment (X) when the goal is improved performance in both X and Y can be expressed, if one assumes truncation selection and equal selection intensities (standardized selection differentials), as follows:

$$\frac{\Delta G_{\overline{xy}}}{\Delta_{\overline{x}} G_{\overline{xy}}} = \frac{h_{\overline{xy}}}{h_{\overline{x}} r\{G_{\overline{x}} \cdot \overline{xy}\}}, \tag{1}$$

where $\Delta G_{\overline{xy}}$ is the genetic gain from direct selection for 'average performance', $\Delta_{\overline{x}} G_{\overline{xy}}$ is the genetic gain for 'average performance' as a correlated response from direct selection for performance in the single environment (X), and $h_{\overline{xy}}$ and $h_{\overline{x}}$ are the square roots of family heritabilities of 'average performance' and performance in X, respectively, and $r\{G_{\overline{x}} \cdot \overline{xy}\}$ is the genetic correlation between 'average performance' and performance in X. These genetic variables are defined on an individual basis as

$$h_{\overline{x}}^2 = \frac{2nh_x^2}{1+(2n-1)h_x^2}, \tag{2}$$

$$h_{\overline{xy}}^2 = \frac{n(1+k^2+2kr\{G_{xy}\})h_x^2}{1+w^2+[n(1+k^2+2kr\{G_{xy}\})-(1+k)]h_x^2} \tag{3}$$

and

$$r\{G_{\overline{x}} \cdot \overline{xy}\} = \frac{1+kr\{G_{xy}\}}{\sqrt{(1+k^2+2kr\{G_{xy}\})}}, \tag{4}$$

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where h_x^2 is heritability of individual phenotype in environment X, k and w are ratios of genetic variances $V(G_x)/V(G_y)$ and phenotypic variances $V(P_x)/V(P_y)$ in the two environments, respectively, and $r\{G_{xy}\}$ refers to genetic correlation between performance in X and performance in Y. Also, n refers to the number of sibs per 24 h egg collection.

In the case of equal genetic and phenotypic variances in the two environments, the ratio of genetic gains becomes

$$\frac{\Delta G_{\overline{xy}}}{\Delta_x G_{\overline{xy}}} = \sqrt{\frac{1+(2n-1)\,h_x^2}{1+[(1+r\{G_{xy}\})n-1]\,h_x^2}}, \tag{5}$$

and it can be seen that the ratio will be greater than unity (signifying the superiority of direct selection) in all cases except when $r\{G_{xy}\}$ approach unity and in this extreme case the ratio of gains approach unity.

If the assumption of equal variances in different environments is not satisfied and w is much larger than k, the ratio tends to be less than unity. Consequently, it is possible for direct selection for average performance to be inferior to indirect selection.

When the initial parameters from Table 2 were substituted into the above formulae, the predicted ratios of genetic gains in average performance exceeded unity in every case. Yet the observed results did not confirm these predictions. However, it should be noted that such predictions of genetic gains are valid only if the genetic and phenotypic parameters remain constant throughout all generations. Evidence of change in some parameters over generations of selection was found. Therefore, extrapolation from initial parameters may be of doubtful reliability.

Factors other than the above variables, such as unequal selection intensities and genetic sampling, could have contributed to the reduced efficiency observed for selection based on average performance. For example, the skewed phenotypic distributions found by Hardin & Bell (1967) for larval weight in these two environments could have caused unequal selection intensities. Such distributions would reduce the intensity of selection in the direction of skewness and thereby penalize selection in that direction (large in Good and small in Poor). Undoubtedly, this situation contributed to the asymmetrical responses to be discussed later, but it could not be a major factor in the present discussion since indirect selection methods (GL, PL, GS and PS) excelled in both directions for 'average performance' (Table 3).

Within the limits of the present study, none of the factors discussed appeared to contribute significantly to the inefficiency observed for selection based on average performance.

Parellelism of direct and indirect responses. The degree of parallelism of responses, direct and indirect, in the two environments for a particular population selected on the basis of performance in a single environment represents one manifestation of a genotype–environment interaction. In order to examine this relationship, linear regressions lines fitted to the direct and indirect responses of each population are

shown graphically in Fig. 4. One sees that direct responses in both replications of large selection in GOOD have remarkably parallel indirect responses in POOR, e.g. $GL_1(G)$ *v.* $GL_1(P)$. On the other hand, both replicates of large selection in POOR show obvious non-parallelism of direct and indirect responses, e.g. $PL_1(P)$ *v.* $PL_1(G)$.

A second significant point revealed in Fig. 4 relates to selection for small 13-day larval weight. In contrast to the results observed for large selections, populations selected for small size in POOR (PS) showed parallelism of direct and indirect responses while both replicates of selection for small in GOOD (GS) did not. As an extreme, the GS_2 regression lines actually intersect and indicate a reversal in the ranking of the means under the two environments. This reversal was observed initially at generation 12 and remained throughout subsequent generations. Details of this population will be described later.

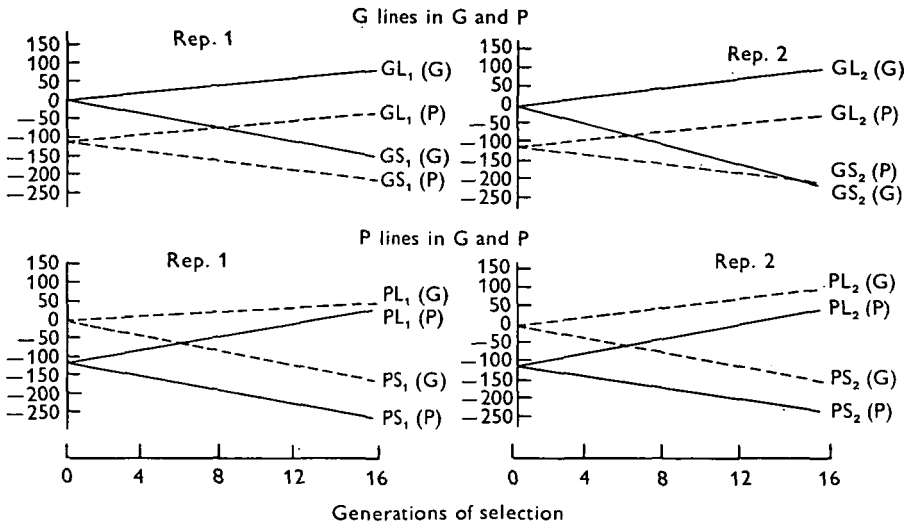

Fig. 4. Trends in selection responses by replications expressed as linear regression. Ordinates have origin to represent the average 13-day larval weight of all populations in the GOOD environment prior to selection with deviations expressed as 10^{-2} mg. Solid and broken lines represent direct and correlated responses respectively. Testing environments are identified by (G) or (P).

The non-parallelism of responses under the two environments suggests that a significant genotype–environment interaction was present. Selection has aided in identifying this phenomenon but did not necessarily cause or create it. Disclosure of genotype–environment interaction by selection was also suggested by Bray *et al.* (1962) in their study of control populations in *Tribolium* under two humidity conditions. Parsons (1959) reported that the magnitude of genotype–temperature interactions in emergence rate of *Drosophila* was larger when the genotypes were inbred lines than when single crosses of these inbred lines were studied. Thus the magnitude of genotype–environment interactions becomes a function of genetic diversity. Such interactions might be a minor source of variation within any

particular population, but they could become important in a comparison among several populations which had been selected on different criteria or under different environments.

Asymmetrical selection responses. Asymmetrical responses in two-way selection experiments are now considered the general rule rather than the exception. However, one of the interesting aspects of the present study is the dependency of asymmetry on the environment of selection (Tables 3–5; Figs. 1 and 2). When selection was based on performance in the GOOD environment, more rapid responses were observed downward than upward. The results in POOR were reversed in that upward selection was favoured. The general nature of this asymmetry can be observed in Table 6, where the average response of all populations selected in the same direction are presented. Hardin & Bell (1967) reported similar results in their study of two-way selection. This matter will be re-examined in a later section in the light of realized genetic parameters.

Table 6. *Average responses over sixteen generations when all populations are summarized by direction of selection and environment*

	Average gain per generation (10^{-2} mg)			
	GOOD		POOR	
Direction of selection	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Large	4·9	6·6	8·0	7·5
Small	−9·2	−9·4	−6·5	−5·6

Selection differentials. Sib selection was practiced uniformly in this study and full-sib groups for all populations were observed in both GOOD and POOR environments. Thus it was possible to calculate both direct and indirect selection differentials for each of the populations selected on performance in a single environment (GL, GS, PL and PS). Interest in the association between them arises from the fact that the magnitude and direction of the indirect selection differential is a function of the genetic correlation between larval weights in the two environments. They are summarized in Table 7 by early, late and over-all generations of selection for each population selected on performance in a single environment. In all cases the direct selection differentials are larger than indirect ones. Only in those populations selected for small size (GS and PS) were the selection differentials consistently smaller in late generations than in early. This situation resulted from two factors: (1) the observed phenotypic variation declined in all 'small' populations, and (2) reproductive difficulties in the late generations of selection caused a reduction in the effective selection intensities.

The ratios of direct to indirect selection differentials as given in the last column of Table 7 are of interest. Since the comparable differentials are based on means of full-sib families cultured in the two environments, it can be shown that as the number of individuals within each full-sib family becomes large this ratio for any particular population approaches the genetic regression (ratio of the genetic

Table 7. *Average direct and indirect selection differentials in early and late generations for populations selected for a single environment*

(Direct selection differentials in italics.)

Population	Selection differentials per generation (10^{-2} mg)						Ratio of indirect to direct
	Early generations		Late generations		All generations		
	GOOD	POOR	GOOD	POOR	GOOD	POOR	
GL_1	*25·6*	11·1	*26·8*	10·1	*26·2*	10·6	0·40
GL_2	*25·2*	13·9	*20·5*	7·6	*22·9*	10·8	0·47
PL_1	12·1	*26·1*	10·3	*23·9*	11·2	*25·0*	0·45
PL_2	14·8	*26·6*	10·1	*29·5*	12·5	*28·1*	0·44
GS_1	*−30·1*	−11·9	*−24·1*	−8·1	*−27·1*	−10·0	0·37
GS_2	*−30·5*	−11·8	*−15·4*	−7·4	*−23·0*	−9·5	0·41
PS_1	−15·0	*−18·0*	−9·7	*−10·6*	−12·4	*−14·3*	0·87
PS_2	−10·1	*−19·5*	−5·1	*−7·7*	−7·6	*−13·6*	0·56

covariance to the genetic variance of the selected trait), a statistic of value for predicting correlated responses. Since the number of full sibs per environment in this study was not large, these ratios will underestimate the true genetic regression. However, their relative values are of interest. Those for populations selected large are similar in both replications of the experiment. Comparisons among the small lines show striking differences. The GS ratios are smaller than those observed for the large lines, while the PS ratios are obviously larger. A comparison of ratios in the early versus late generations reveals the correlation between family means to be increasing in all small lines and decreasing in all large lines. The significance of this observation is not apparent unless it relates to the approach of a lower limit in size.

Table 8. *Realized heritabilities of family mean 13-day larval weight by population during early, late and all generations of selection*

Population and replication	Early generations	Late generations	All generations
GL_1	0·269 ± 0·047	0·236 ± 0·038	0·231 ± 0·015
GL_2	0·460 ± 0·059	0·256 ± 0·101	0·368 ± 0·033
PL_1	0·523 ± 0·082	0·147 ± 0·055	0·320 ± 0·035
PL_2	0·498 ± 0·037	0·288 ± 0·048	0·362 ± 0·018
$\overline{GP}L_1$	0·361 ± 0·051	0·256 ± 0·087	0·372 ± 0·018
$\overline{GP}L_2$	0·301 ± 0·058	0·210 ± 0·041	0·203 ± 0·023
GS_1	0·396 ± 0·024	0·238 ± 0·046	0·321 ± 0·016
GS_2	0·451 ± 0·035	0·608 ± 0·078	0·527 ± 0·022
PS_1	0·624 ± 0·089	0·298 ± 0·260	0·592 ± 0·048
PS_2	0·582 ± 0·073	0·202 ± 0·101	0·486 ± 0·035
$\overline{GP}S_1$	0·333 ± 0·056	0·237 ± 0·151	0·399 ± 0·031
$\overline{GP}S_2$	0·347 ± 0·075	0·250 ± 0·078	0·338 ± 0·030

Realized heritabilities. A realized family heritability was calculated for each population where suitable techniques for the estimation of selection differentials were available. These estimates by early, late and over-all generations are given in Table 8 for each population and replication and are illustrated in Fig. 5. All populations except GS_2 showed a decline in heritability when the last eight generations are compared with the early generations of selection. If one assumes no common environment effects contributing to the observed variance between family means, the realized family heritabilities of Table 8 when converted to heritabilities of individual differences more nearly agree with the estimates from Hardin & Bell than with the estimates from this experiment (Table 2) based on full-sib covariances. This confirms the earlier conclusion that 13-day larval weight is influenced significantly by dominance or maternal effects.

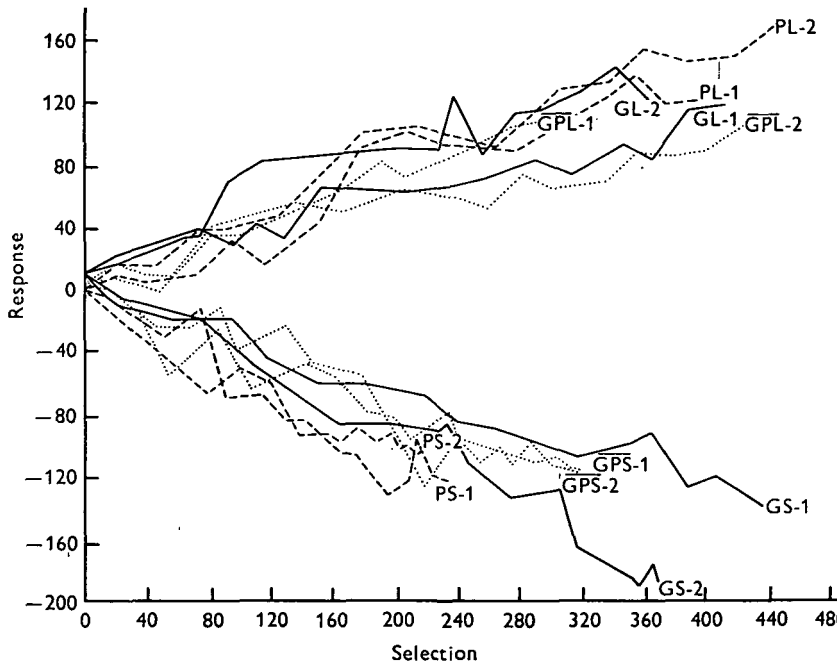

Fig. 5. Direct responses for various populations as deviations from control plotted against cummulative selection differentials. Ordinate and abscissa are scaled to 10^{-2} mg.

The relative magnitude of realized heritabilities for different directions of selection is of special interest in studies of this nature. The average realized heritabilities of family differences for populations selected large are compared in Table 9 with those of the small populations. The lower heritability for large in contrast to that observed in the small direction is in agreement with the findings of Hardin & Bell (1967).

Trends in other parameters. Genetic and phenotypic variances of 13-day larval weight in the environment of selection plus the genetic covariance of body weight

in the two environments were estimated for each of the first eight generations of selection for all populations except $\overline{GPL}$ and $\overline{GPS}$. In the remaining eight generations these parameters were estimated for all populations in both environments. The technique used in the estimation of heritability and genetic correlation was based on the covariance of full sibs reared in the same or different environments as appropriate.

Table 9. *Average realized heritabilities of family mean 13-day larval weight for all populations summarized by direction of selection during early, late and all generations of selection*

Direction of selection	Early generations	Late generations	All generations
Large	0·404	0·236	0·309
Small	0·456	0·306	0·444

Considerable fluctuation in the heritability estimate from generation to generation was observed in all populations. The general decline between early and late generations seen in Table 8 for realized heritabilities was not detected when the estimates were based on full-sib covariances. While a downward trend in the magnitude of heritability was observed in some populations, others revealed upward trends. Such trends appear random in nature rather than associated with a particular selection method or environment. Fluctuations among estimates of genetic correlation were even more erratic. Whether these large fluctuations observed for estimates of genetic correlation and heritability were due to genetic sampling or some unknown experimental bias could not be determined.

The phenotypic variability observed each generation in both environments revealed an initial positive correlation between means and variances. Such an association would suggest the desirability of an appropriate scale transformation. However, selection response in various populations was accompanied by a change in the pattern of variability. Both direction and environment of selection contributed to this change. In order to illustrate the changes in variability related to selection, both standard deviations and coefficients of variability were pooled every four generations for those populations selected on performance in a single environment. These trends are presented in Fig. 6.

Both replications revealed a larger phenotypic variance initially in the GOOD environment than in POOR for all populations (see Table 2). It can be seen in Fig. 6 that the larger variance in GOOD continued throughout the experiment for most small lines but did not hold for the populations selected for large. While not consistent, the tendency among the latter was for a greater variance in the POOR environment. The sharp terminal decline in variance for the GS population in replication 2 was unique and will be discussed later. In general, the trend within the large lines was for the phenotypic variance to increase as mean larval weight increased over generations. The variance within the small lines responded differently. Here one sees the variances in GOOD increasing during the initial generations

even while mean larval weight was decreasing. However, the magnitude of the phenotypic variances took a downward trend in the latter generations of all small lines cultured in both environments.

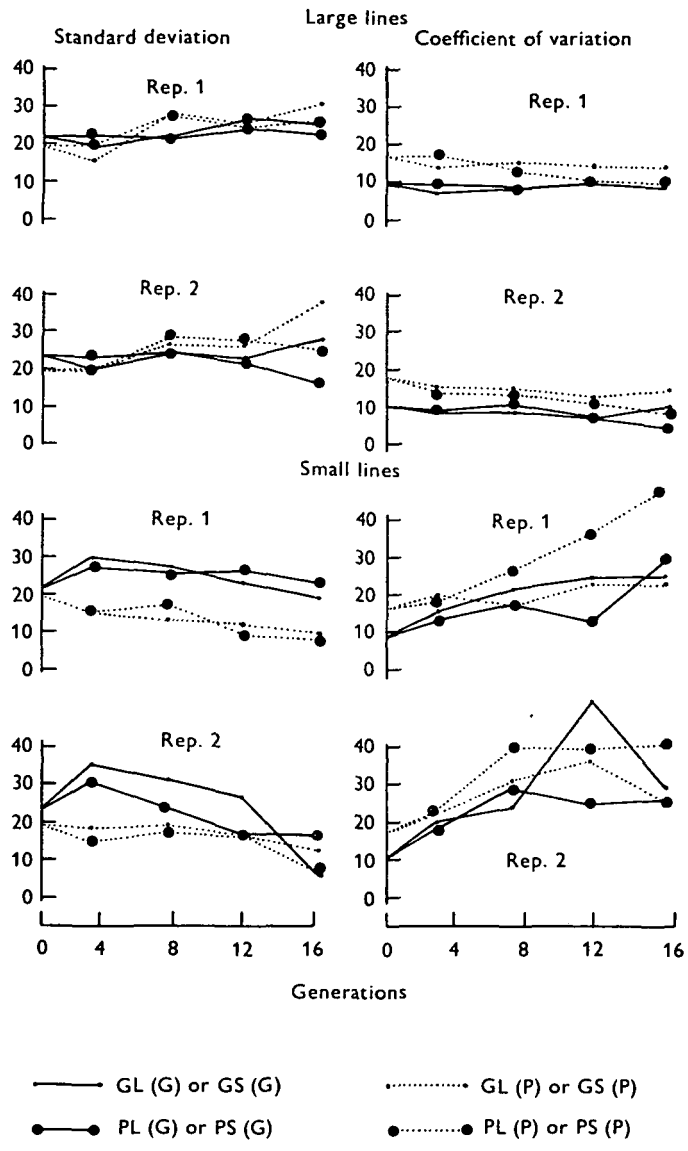

Fig. 6. Trends in phenotypic standard deviations (10^{-2} mg) and coefficients of variation (%) during selection. Lines selected for large are shown by replication in upper graphs with those selected small in the lower graphs.

Trends observed among coefficients of variability as shown in Fig. 6 fail to reveal an over-all consistent pattern as one could anticipate from the above discussion. Of special interest is the influence of direction and environment of selection on relative changes in the coefficients of variation. During the early generations of

selection the primary cause of differences among coefficients of variability was the culturing environment with the relative variation within each population being consistently greater in POOR than in GOOD. Yet the coefficients of variation in the late generations declined for both replications of PL cultured in either GOOD or POOR while the two replications of GL showed no decline in either environment.

While the coefficients of variation for all 'large' populations declined or showed no change, all 'small' populations revealed an increase in this measure of variation, but the increase was more exaggerated when the populations were cultured in the environment of selection, e.g. PS(P) and GS(G).

Behaviour of GS_2 population during selection. Among the various populations, GS_2 behaved uniquely in that the number of families which were larger under POOR than under GOOD increased from one in each of generations 5 and 7 to three in generation 8 and gradually increased until all families of GS_2 showed this response by generation 13. None of the other populations, including GS_1, showed this reversal of response in the two environments. This unique response for GS_2 is evidenced in Fig. 4 by the intersection of its regression lines. Also, Table 5 shows GS_2 to have the largest direct and smallest indirect response of any population in either replication. These facts, plus the exceptionally large realized heritability (0·61) observed for GS_2 during the late generations, suggested the possible presence of unique genetic variation. Even so, a biometrical description of response and variation for GS_2 as made in this study is considered appropriate.

A subsequent investigation (Costantino, Bell & Rogler, 1966) has revealed that the corn oil in GOOD specifically retards larval growth in the GS_2 population. Appropriate genetic studies found this population to be homozygous for a recessive gene, *cos*, which caused the corn-oil sensitivity. The mutant allele may have been present at a low frequency in the base population or it could have been a 'favourable' mutation occurring in GS_2 after the experiment was initiated. The latter appears the more plausible since the other replication of small selection in GOOD, GS_1, did not develop this response.

Correlated responses. If larval weight in an environment other than that of selection is considered a correlated trait, it is possible to predict the response of such traits provided certain parameters are known (Falconer, 1960*a*). The basic formula for predicting change in a correlated trait due to selection for a different trait can be stated as follows:

$$\Delta_x G_y = \Delta_x G_x r\{G_{xy}\}\left[\frac{V(G_y)}{V(G_x)}\right]^{\frac{1}{2}} = \Delta_x G_x \frac{\mathrm{cov}(G_{xy})}{V(G_x)}, \tag{6}$$

where $\Delta_x G_y$ is the change in trait Y by selecting for trait X, $\Delta_x G_x$ is the change in trait X by direct selection, $r\{G_{xy}\}$ is the genetic correlation between the two traits, and $\mathrm{cov}(G_{xy})$ is the genetic covariance between the two traits. The formula which uses the genetic regression has wider application in that it may be applied in the absence of one of the genetic variances. For example, in this study the genetic variances in the environment other than that of selection, $V(G_y)$, could not be estimated for the first eight generations, yet the other variables could be estimated.

Two sets of genetic parameters, (1) those of the initial generations and (2) the genetic regressions pooled over all generations were used for predicting the responses for 13-day larval weight in the environment other than that of selection. These predicted correlated responses are compared in Table 10 with those observed for each population. It is apparent, with minor exceptions, that the second column of predicted responses agrees better with those observed than does the first. The pooling of genetic regressions over all generations within each population allowed or changes in the genetic parameters to be reflected in the predicted response.

Table 10. *Observed correlated responses* (10^{-2} *mg per generation*) *for 13-day larval weight of various populations compared with those predicted from two types of parameters*

Population	Predicted correlated responses ($\Delta_x G_y$)* by source of paramenters: Initial generations	Predicted correlated responses ($\Delta_x G_y$)* by source of paramenters: All generations	Observed correlated response	Pooled genetic regressions
GL_1	3·8 ± 0·3*	4·2 ± 0·3*	5·5 ± 0·5	0·74
GL_2	3·9 ± 0·4	6·7 ± 0·7	6·5 ± 1·0	0·91
PL_1	9·4 ± 0·9	7·3 ± 0·7	3·9 ± 0·5	0·78
PL_2	11·8 ± 0·6	8·1 ± 0·4	6·9 ± 0·7	0·78
GS_1	−5·8 ± 0·4	−4·9 ± 0·3	−5·5 ± 0·9	0·56
GS_2	−6·6 ± 0·4	−6·0 ± 0·4	−4·9 ± 0·8	0·48
PS_1	−8·0 ± 1·0	−7·8 ± 1·0	−8·8 ± 0·7	0·98
PS_2	−7·3 ± 1·0	−7·4 ± 1·0	−8·6 ± 1·0	1·15

* $\Delta_x G_y \pm$ S.E. $= (\Delta_x G_x \pm \text{S.E.})\text{cov}(G_{xy})/\sqrt{(V(G_x))}$, where x is the trait of selection and y is the correlated trait (see text for further details).

This average genetic regression for each population is listed in the last column of Table 10. While statistical tests of significance are not readily available for this variable, the relative magnitude of these regressions appears to be associated with direction and environment of selection. For example, both PS populations had regressions about twice the magnitude of those observed for the GS populations. The values for the populations selected large were intermediate. It is interesting to note that corresponding genetic regressions in the initial generations (0–1) of populations selected on performance in Good (GL and GS) were 0·67 and 0·54 for the two replications. The initial genetic regressions for the two replications of selection in Poor (PL and PS) were 1·06 and 1·13. The twofold difference between initial values for the two environments was caused by consistently larger genetic variances in Good. While the pooled genetic regressions in Table 10 for the lines selected small (GS and PS) agree with the initial regressions, the pooled values for the large lines (GL and PL) do not agree. During the course of the experiment the genetic regression apparently increased in both replications of GL and decreased in the PL populations.

The average genetic correlation of larval weights in the two environments over the sixteen generations of selection can be estimated by taking the square root of the product of the pooled genetic regressions for any two lines selected in the

same direction but in different environments. The resulting estimates are 0·76, 0·74, 0·84 and 0·74 for the combinations of GL_1–PL_1, GS_1–PS_1, GL_2–PL_2 and GS_2–PS_2, respectively. They are obviously of the same order and are similar to the initial estimates of the genetic correlation observed in Table 2. Yet agreement results from the combination of dissimilar genetic regressions.

4. GENERAL DISCUSSION

Generally speaking, selection in animals for large or small body size at a fixed age has been accompanied by changes in the physiology of the selected trait as well as in related characteristics. These changes are often associated with degree of maturation or development on a chronological scale. It is not surprising therefore to find genetic parameters substantially changed during selection. Quantitative genetic theory recognizes that changes in parameters can result from certain genetic changes, e.g. gene frequency, genetic drift, etc., but it assumes the measured variable or the selected trait has remained the same over the specified period of study. Yet many traits, especially those relating to growth at a fixed age, will themselves become changed by selection. Genetically speaking this introduces into the theoretical model not only the possibility of additional effective gene loci but previously active loci may no longer contribute to variation of the new 'trait' and certainly the genotypic values at any particular locus may change.

Selection for body size under different environmental conditions is subject to the above argument since the trait under optimal and sub-optimal environments may have different physiological manifestations (Robertson, 1959, 1960, 1963; Taylor, 1965). An examination of growth in *Tribolium* under different levels of nutrition (Y. Yamada & A. E. Bell, unpublished data) revealed that maximum larval, pupal and adult weights were not altered by the POOR environment. However, larval weight at a fixed age and age to pupation were adversely influenced. This leads to the inference that selection for body size in different environments could alter growth in different ways depending on when selection was practiced.

The selected trait in the present study, 13-day larval weight, can be considered a 'compound' trait in which ultimate body size and developmental rate are major components. While selection for 13-day larval weight under either GOOD or POOR environment acts on the same trait chronologically, unequal emphases on the major components are likely consequences. For example, large selection in GOOD (GL) would emphasize ultimate body size more than developmental time while the reverse would be true for POOR (PL). Likewise, selection for small 13-day larval weight in each of the two environments would affect the components differently. Such was actually observed by Robertson (1963) in extensive studies of growth in *Drosophila* under different nutritional regimes. The differential response of component characters is well illustrated in Falconer's (1960*b*) study of selection for 6-week weight of mice reared on full and restricted diets. One line responded with a dimensional change, while the other altered its fat deposition.

The expected correlated response of a compound trait (e.g. 13-day larval weight

in POOR for a population selected in GOOD) becomes a bit complicated from a theoretical viewpoint. Under the environmental conditions of the present study, selection for 13-day larval weight in GOOD (GL) puts primary emphasis on ultimate body size while selection for the same compound trait in POOR emphasizes both developmental time and ultimate body size. Intuitively, such a situation should result in a greater correlated response for the populations selected large in POOR than for those selected large in GOOD, but these expectations were not realized in our study. Also, the genetic correlation between 13-day larval weights under the two environments should be higher in the PL populations than in GL, but the estimates from our study were not conclusive.

The above approach adds little to our understanding of the observed inefficiency of selection for 'average performance' when compared to selection based on performance in a single environment. However, it may relate to the observed dependency of direction and magnitude of asymmetrical selection responses on the environment of selection.

Even when the observed realized parameters, e.g. realized heritabilities and effective selection differentials, seem to explain or account for asymmetrical responses, it should be realized that these are historical descriptions rather than predictive parameters. The underlying causes for differential realized parameters should be researched. The causative factors identified by Falconer (1960*a*) could account for many cases of asymmetry. However, they hardly appear adequate for the situation where the direction of the asymmetry is environmentally rather than genetically dependent, unless one incorporates the concept of a compound trait with the number of effective loci, genotypic values at specific loci and even the direction and degree of dominance being environmentally influenced.

The nature of the environmentally dependent asymmetry observed in this particular experiment may be related to a physiological limit for manifesting extreme phenotypes. The range of this limit would be a function of the previous evolution of a population. One can reasonably assume that 13-day larval in our foundation population (maintained for many generations on STANDARD medium) was near some optimum and was equally distant from its upper and lower physiological or developmental limit. When this population was cultured in the more luxuriant GOOD environment, the population mean increased towards the upper limit and a greater response within the assumed limits was possible for 'small' selection than for 'large'. Likewise, when the mean was depressed with the POOR environment a greater response resulted in large direction. Thus, anything which shifts a population mean towards either limit could cause an asymmetrical response in short term two-way selection experiments.

SUMMARY

Selection for large and small 13-day larval weight in *Tribolium castaneum* was studied for sixteen generations in a replicated experiment to evaluate the effectiveness of various selection methods and the importance of genotype by environment interactions under two levels of nutrition.

Direct selection responses generally were larger than correlated ones under both GOOD and POOR nutritional environments. However, contrary to theoretical expectations, those populations selected on average performance in both environments were not superior for this attribute.

Asymmetrical responses were observed to be dependent on the environment of selection. When selection was based on performance in the optimal environment, the asymmetry was observed toward small size. This situation in the sub-optimal environment was completely reversed. This phenomenon was discussed in terms of physiological limits rather than gene frequency and directional dominance.

It was proposed that selection of compound traits such as body weight at a fixed age may affect the component characters quite differently. As the latter are differentiated by direction and environment of selection, the compound trait may reflect parametric changes and enhanced genotype by environment interactions. Such changes hamper the precision of current selection theory for predicting response even in the short run.

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