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Two-way selection for body weight in *Tribolium* on two levels of nutrition*

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1. INTRODUCTION

A fundamental concept of quantitative genetics is that the phenotype of an individual is a function of its genotype and environment. This is important in the application of quantitative genetics to the improvement of economic animal and plant species where one of the major problems is the choice of the environment or environments in which phenotypes should be selected. This point takes on added significance in an industry such as poultry where the number of breeders in North America and Europe has decreased in the past decade. Obviously, the progeny from the remaining breeding operations are being distributed into a wider range of environments than before. Although experimental verification of the best environment for a breeding operation is essentially lacking, two outstanding animal breeding textbooks (Lerner, 1950; Lush, 1948) recommend that breeders should maintain environmental conditions that are the same as the average environmental conditions existing in the flocks of their customers. However, in 1960 Lerner added that this may not always be the best practice.

Many of the recent investigations into the choice of environment were stimulated by Hammond (1947) who stated: 'The character required is best selected under environmental conditions which favor its fullest expression and that once developed, it can also be used in other environments provided that other characters specially required by that new environment, are also present in the animal.'

Falconer (1952) has indicated that for the choice of environments in a selection program, there are two possibilities, (1) rear parents under the environmental conditions which are the same as those under which the progeny will be reared or (2) rear the parents under other conditions such that more progress may be made than if the parents were kept under the same conditions as those of the progeny. While not desirable from a viewpoint of maximum genetic progress, there is a third

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alternative: the parents may be reared under some environment which results in less progress than would be obtained if the parents were raised under the same conditions as the progeny.

Much of the early work concerning the relationship between environment and genotype has been summarized by McBride (1958). He indicated that two approaches, static and dynamic, have been used for the study of this relationship. The static approach involves placing relatives in different environments, while the dynamic approach involves a selection experiment over several generations in two or more environments.

Although many experiments have been performed using the static approach, studies utilizing the dynamic approach are few in number, (McBride, 1958). Falconer & Latyszewski (1952) selected for increased body weight in mice at 6 weeks of age under two levels of nutrition, and in 1960 Falconer selected mice for small and large body size on high and low planes of nutrition. Fowler & Ensminger (1960) selected for increased growth in pigs on full and restricted feed. McNary & Bell (1963) reported that direct responses to selection for increased pupal weight in Tribolium reared under two levels of humidity agreed with that predicted by genetic theory, but found an unexpected asymmetrical correlated response. The above studies were initiated with little or no information regarding the genetic parameters essential to test the validity of genetic theory for predicting direct and correlated responses to selection. With this in mind, the study reported here on two-way selection for 13-day larval weight in Tribolium cultured on two levels of nutrition was divided into two phases. The first was a measurement of the static state of the base population in two experimental environments in order to provide reliable estimates of the parameters needed for predicting direct and correlated responses. The second phase was a replicated selection experiment to ascertain whether responses validated those predicted by quantitative genetic theory.

2. MATERIALS AND METHODS

(i) *Experimental organism*

The genetic material for this study was the Purdue '+' Foundation Population of the flour beetle, *Tribolium castaneum*, that had been formed in 1954 by combining eight (8) non-inbred laboratory stocks, and had been propagated thereafter by mass matings. When the present study was started in early 1961, it was assumed that this base population was in genetic equilibrium.

(ii) *Culturing techniques*

The environments chosen were two levels of nutrition (Table 1), hereafter called POOR and GOOD, which gave repeatable differences in 13-day larval weight. Detailed information regarding these rations was presented by Hardin *et al.*, 1966. Environmental temperature was maintained at 33°C. and relative humidity at 70%.

A 24-hour egg collection in the appropriate ration was made each generation from those selected to reproduce each population. The resulting offspring were weighed as 13-day larvae (computed from the time the parents were placed on the ration for egg collection) and each larva was placed in individual $\frac{3}{4}$ oz. coffee creamers (20 ml. glass bottle with cardboard pull-cap) containing 1 g. of standard medium (whole wheat flour plus 5% dried brewer's yeast) for pupation and sex identification.

Table 1. *Composition and chemical analysis of the two levels of nutrition (Rations)*

		Rations (%)	
	Ingredient	POOR	GOOD
Composition	Vitamin premix*	3·3	10
	Soybean meal	11·3	17
	Corn meal	85·3	58
	Dried brewer's yeast	—	10
	Corn oil	—	5
Chemical Analysis	Moisture	9·9	10·4
	Protein	13·2	18·3
	Fat	4·2	8·5
	Ash	2·2	2·8

* The vitamin premix consisted of pyridoxine, 0·5 g.; thiamine, 1 g.; folic acid, 0·1 g.; biotin, 0·01 g.; inositol, 10 g.; riboflavin, 0·5 g.; niacin, 2 g.; calcium pantothenate, 1 g.; vitamin B_{12}, 0·7 g.; choline, 20 g.; ascorbic acid, 0·8 g.; para amino benzoic acid, 1·5 g.; corn meal, 961·89 g.

(iii) *Base population*

A separate experiment was designed to obtain reliable estimates of the static parameters for larval weight in the base population when cultured in GOOD and POOR environments. The procedures are outlined in Table 2. It was arbitrarily decided to use seven replications with each sub-divided into one group of parents reared on GOOD and a second group reared on POOR. Since each group of parents was a separate sample from the base population, their offspring provided fourteen sub-populations for statistical analyses.

Observations made for each mating included weight of sire and dam reared on GOOD or POOR media plus weight and sex of five offspring reared on each of two rations. Utilizing this information, heritability of 13-day body weight in each of the two environments, the genetic correlation between growth in GOOD and growth in POOR, and the phenotypic variance in each environment were estimated.

Heritability was estimated within each replication sub-group by both intra-class correlation and intra-sire regression of offspring on dam. The methods of calculating the genetic correlation were that of covariance outlined by Hazel *et al.* (1943) and the analysis of variance outlined by Robertson (1959), Dickerson (1962) and Yamada (1962). The analysis of variance yields expected values identical with those of covariance.

The model for the analysis of variance was:

$$Y_{ijkl} = u + S_i + D_{ij} + E_k + ES_{ik} + ED_{ijk} + P_{ijkl},$$

where Y_{ijkl} was the measurement of the lth progeny of the jth dam and ith sire and reared in the kth environment. Environments were considered to be fixed and the effects of dams, sires, and progeny were considered to be random. Dams which did not have five progeny in each environment were excluded from the analysis.

Table 2. *Experimental procedures for estimating base parameters*

Day	Experimental procedure
0	One hundred (100) unsexed Tribolium placed in each of two nutritional environments (GOOD and POOR) for 24-hour egg collection.
1	Adult beetles removed and medium with 24-hour egg collection returned to incubator.
13	Two hundred (200) 13-day larvae individually weighed from each environment, placed into individual creamers and returned to incubator for pupation.
17–24	Pupae sexed.
30	One male mated to three females, each replication consisting of thirty to thirty-five males. Females identified by clipping antenna; either right, left or both.
35	Mated females placed into individual creamers containing one of two nutritional media for 24-hour egg collection.
36	Each female removed from creamer and placed in another creamer containing other medium for a 24-hour egg collection.
48	Five 13-day larvae from day 35 egg collection of each dam were individually weighed.
49	Five 13-day larvae from day 36 egg collection of each dam were individually weighed.
50–60	Pupae sexed.

Analysis of variance utilized for the estimation of the genetic correlation was also used for the static estimation of genotype X environment interaction (McBride, 1958).

(iv) *Selection experiment*

The selection experiment consisted of two-way selection, i.e., High (large 13-day larval weight) and Low (small 13-day larval weight), in each of the two environments, GOOD and POOR. Also a non-selected control population (Random), was maintained for each environment. In addition to observing the direct response to selection, progeny of the selected parents were also reared on the other environment to allow a measurement of indirect or correlated response. It was arbitrarily decided to have four replications and to select for eight generations. The number of

Table 3. *Experimental design showing strain code and various treatment combinations per generation in each of four replications*

Direction of selection	Environment of selection	Number observed	Strain and response code: Direct response	Strain and response code: Correlated response
High	GOOD	150	HG	HG-P
	POOR	150	HP	HP-G
Low	GOOD	150	LG	LG-P
	POOR	150	LP	LP-G
Random	GOOD	100	RG	RG-P
	POOR	100	RP	RP-G

observations and the designation for treatment combinations are shown in Table 3. The schedule for the selection experiment was as shown in Table 4. Thirty females and twelve males were selected to reproduce the next generation. If one assumes that 13-day larval weight is normally distributed and equality in sex ratio, the expected selection intensity would be $0{\cdot}97\sigma$ for females and $1{\cdot}52\sigma$ for males or $1{\cdot}24\sigma$ combined.

Table 4. *Experimental procedures during the 5-week generation cycle for each population and replication*

Day	Experimental procedure
0	Prospective parents placed in environment of selection for 24-hour egg collection.
1	Prospective parents removed from environment of selection.
1	Prospective parents placed in other environment (for correlated response) for 24-hour egg collection.
2	Prospective parents removed from other environment and discarded.
13	Offspring (13-day larvae) reared on environment of selection individually weighed and placed in individual containers.
14	Offspring (13-day larvae) reared in other environments weighed in three groups of fifty and discarded after weighing.
17–28	Pupae sexed which had been weighed on day 13 as larvae.
29	Selections made.
30	Matings made (mass mating of 30♀♀ and 12♂♂)
35	Selected parents placed on environment of selection to start a new cycle.

3. RESULTS

(i) *Base population*

The genetic and phenotypic parameters estimated in the base population are presented in Table 5. All sires had progeny on both rations and are listed under

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both rations. Only dams with progeny on both rations were included in the estimations of 'dam by environment' interactions and in the genetic correlation between 13-day larval weight on GOOD and the same trait on POOR. However, for estimating the other parameters, dams were included in the analysis regardless of whether they had progeny on both rations; thus, the same number of dams are not listed for both. Obviously the progeny cultured on each ration were different even though they, with few exceptions, had full and half sibs on the other ration.

Table 5. *Base population parameters for 13-day larval weight of Tribolium reared on two levels of nutrition (Rations)*

Variable	Rations	
	GOOD	POOR
Number		
Sires	420	420
Dams	1179	1205
Progeny	5880	6015
Heritability		
h^2 sire	$0{\cdot}21 \pm 0{\cdot}06$	$0{\cdot}19 \pm 0{\cdot}05$
h^2 dam	$0{\cdot}79 \pm 0{\cdot}07$	$0{\cdot}69 \pm 0{\cdot}07$
h^2 intra-sire	$0{\cdot}20 \pm 0{\cdot}03$	$0{\cdot}27 \pm 0{\cdot}05$
Genetic correlation	$0{\cdot}60 \pm 0{\cdot}21$	
Mean weight (mg.)		
Males	$2{\cdot}29 \pm 0{\cdot}01$	$1{\cdot}09 \pm 0{\cdot}01$
Females	$2{\cdot}40 \pm 0{\cdot}01$	$1{\cdot}14 \pm 0{\cdot}01$
Phenotypic variance (mg^2)		
Males	0·102	0·108
Females	0·106	0·128

Effects	% of total variance (excluding environments)
Sires	5·76
Dams	13·45
Sires × Environments	5·92
Dams × Environments	6·79
Offspring/Dams/Env.	68·08

The sums of squares and degrees of freedom from each of the fourteen subpopulations were pooled to provide the estimates listed. Heritabilities of 13-day larval weight were similar on the two rations, but the estimates based on the dam component were three times those based on the sire component. Apparently, the inflation of the dam component was due to dominance rather than maternal effects since heritabilities estimated from intra-sire regression of progeny on dam were of the same order as those based on sire component. The heritability estimates from the sire component and intra-sire regression were averaged for predicting response in the selection phase.

The genetic correlation between larval weight on GOOD and POOR was positive ($0{\cdot}60 \pm 0{\cdot}21$) but of a magnitude to suggest that some genes act differently in the

two environments. The relative magnitudes of the interaction components for sires and dams listed in the lower part of Table 5 tend to confirm this hypothesis. The average contribution of each to the total variation approximates that for sires but was less than half that of the dam component.

The other parameters of interest in the base population are the means and phenotypic variances. Although 13-day larval weight on the GOOD ration was about double that observed on POOR and females were slightly larger than males, no differences in phenotypic variance were observed between rations or sexes in the base population.

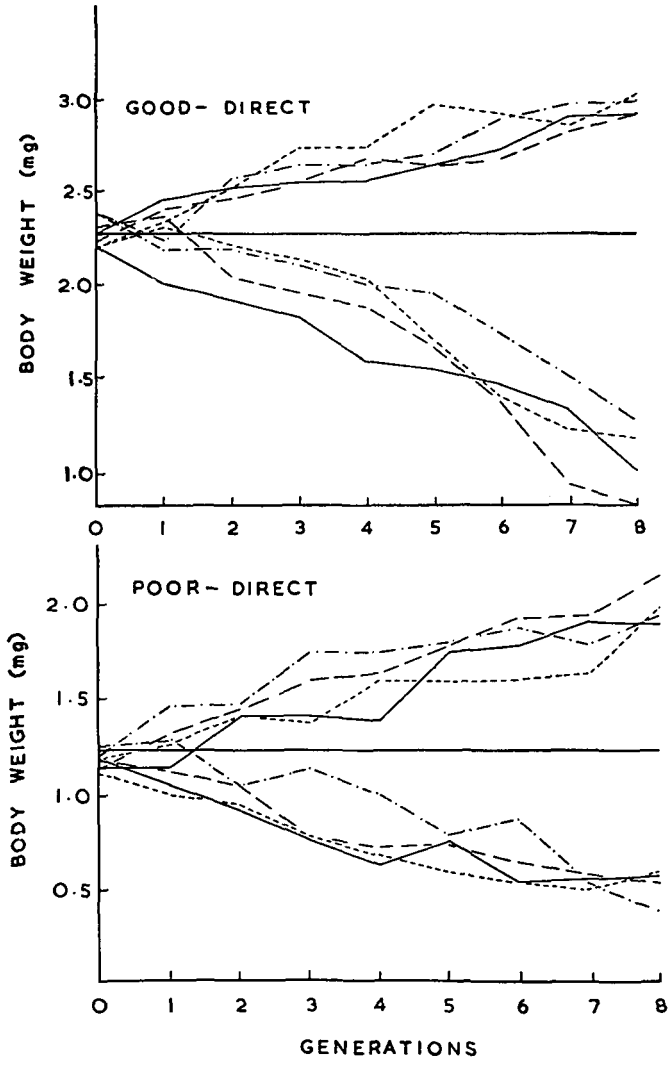

Fig. 1. Observed responses in four replications of mass selection for large and small 13-day larval weight on two levels of nutrition. (Each replication plotted as deviations from its control, horizontal line.)

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(ii) *Selection experiment*

The four replications, presented graphically in Fig. 1 as deviations from their respective controls, emphasize that the direct selection (DR) for large and small larval weight was effective. Although responses were reasonably symmetrical in POOR, an asymmetrical response was observed for all four replications in GOOD. Analysis of variance of the population means by generation showed that 'Environments' (GOOD and POOR) and 'Directions' (High, Low, and Random) contributed the major portion of variation, however, other effects were significant and of more interest. A significant mean square for 'Generations' was caused largely by the asymmetrical response observed in Fig. 1. Since this asymmetry was observed only in GOOD, a significant environment by generation interaction resulted. An increasing divergence between 'High' and 'Low' lines caused a significant 'D × G' interaction.

Table 6. *Observed and predicted direct responses to High-Low selection for 13-day larval weight of Tribolium reared on GOOD and POOR environment*

		Average change (10^{-2} mg.) per generation					
		Observed by replication					
Environment	Direction of selection	1	2	3	4	Overall mean	Predicted
Good	High	+ 7·2(0·9)*	+ 9·3(0·8)	+ 8·2(1·1)	+ 8·7(1·5)	+ 8·4	+11·6
	Random	− 1·6(1·0)	+ 1·6(0·6)	− 1·5(1·0)	+ 0·5(0·3)	− 0·2	0
	Low	−16·0(1·6)	−20·6(2·8)	−16·0(2·2)	−19·7(1·4)	−18·1	−11·6
Poor	High	+ 8·7(1·5)	+11·3(2·2)	+ 8·8(1·7)	+ 6·3(2·1)	+ 8·8	+10·0
	Random	− 2·4(1·2)	− 1·2(1·1)	+ 2·2(1·8)	− 3·6(1·6)	− 1·2	0
	Low	−10·8(0·6)	−10·3(0·7)	−10·9(1·4)	−10·9(1·0)	−10·7	−10·0

* ( ) Standard error for the regression coefficient.

If we assume the response to selection to be linear, the regression of population means on generations gives a measure of the average gain per generation (Table 6). An analysis of variance of the regression coefficients (Absolute values) indicated that the response for GOOD was significantly greater than POOR and that Low was significantly greater than High.

Utilizing the information in Table 6, the observed responses may be compared with those predicted from the initial base parameters. HG responded less than expected in all four replicates while LG responded more than expected in all four replicates. The agreement between observed and expected responses was much better in POOR though HP responded a little less, and LP a little more, than expected. Some of the eight randomly selected populations drifted slightly down while others showed slight increases in average larval weight, indicating that no environmental trend occurred during the course of this study.

To determine why the observed response deviated from the predicted, we need to consider the response to selection (R) and the selection differential (S) since the response to selection may be stated as $R = h^2S$. The realized selection differentials

(Fig. 2) were obviously different (confirmed by an analysis of variance). A mechanical malfunction of the incubator at Generation 0 caused the selection

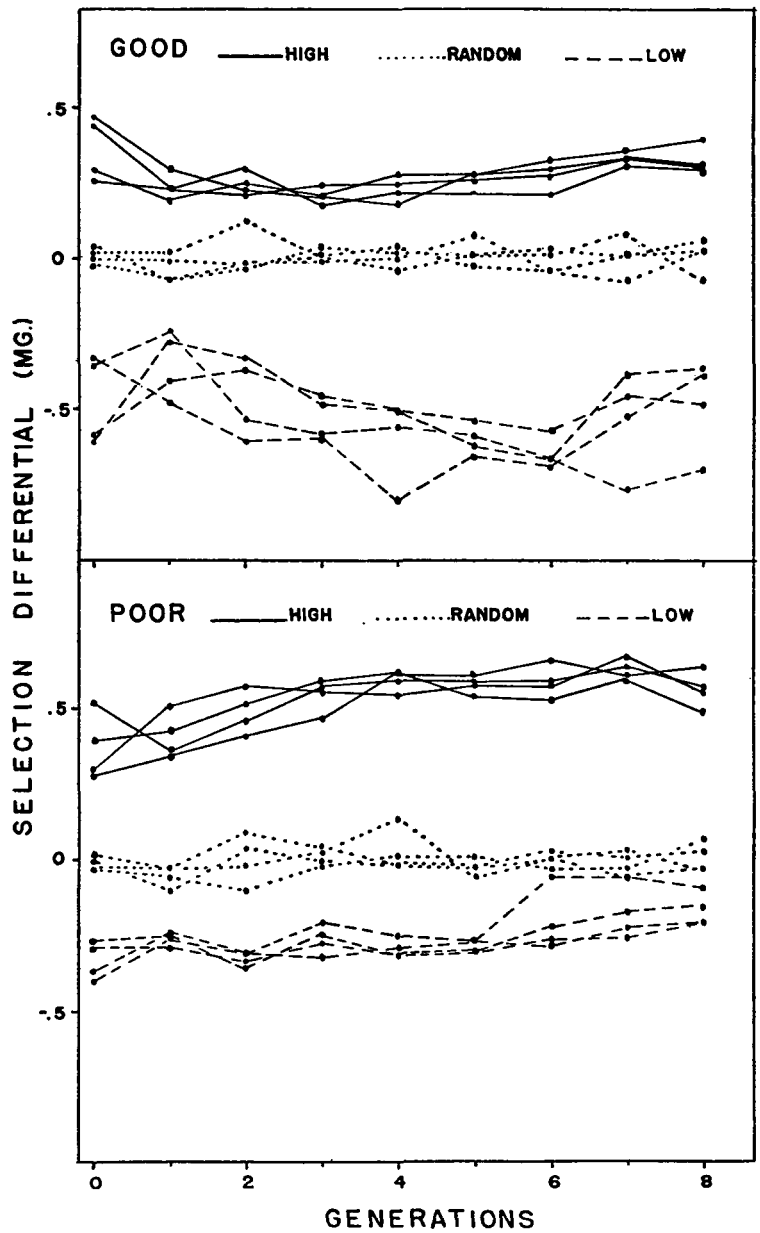

Fig. 2. Selection differentials observed in four replications of high, low and random selected populations by generation and environment of selection.

differential for HG to exceed that for HP for Replicates 3 and 4. Replications 1 and 2 at this generation and all replicates in subsequent generations had larger selection differentials for HP.

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Linear regression coefficients of the realized selection differentials on generation means indicated that the selection differentials for LG and HP were increasing, that of LP decreasing and HG increasing for Replicates 1 and 2 and decreasing for Replicates 3 and 4. Although the linear regression coefficient indicated an increase in the selection differential of LG, observation of Fig. 2 indicates the increase of a curvilinear nature with a large initial increase followed by a gradual decrease. This differed from the selection differential for HP which had increased but then levelled off at a value much higher than the original estimate.

The selection differential for LP was decreasing because of a correlated response; longer developmental time was observed in all replicates of LP and the smaller larvae in late generations were not reaching the adult stage in time to be mated in

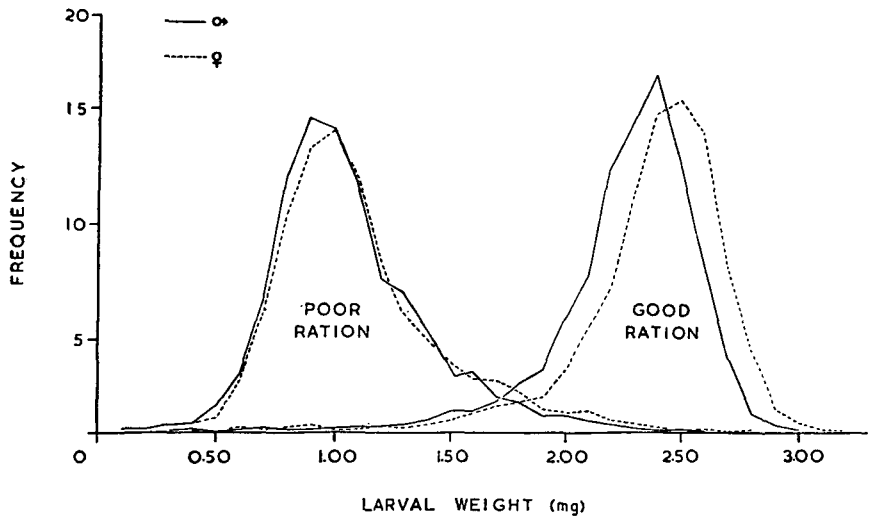

Fig. 3. Distributions of 13-day larval weights for males and females of the base population reared on two levels of nutrition.

the predetermined cycle. The actual selection differential became numerically less with increasing generations, although in terms of standard units the decrease was not as large—it will be shown later that the phenotypic variance was decreasing for the LP.

Although the selection differentials were changing slightly, the values for the various treatment combinations were amazingly consistent over several generations and differences were present from the initial generation. Comparison of the realized selection differentials (Fig. 2) with the predicted values (0·400 for GOOD and 0·413 for POOR) shows that the observed was consistently greater than predicted for HP and LG, and consistently less than predicted for HG and LP.

While a preliminary study of 13-day larval weight on standard ration had indicated that the trait was normally distributed, it was decided to look more carefully at the distribution of weights by sex in the base population on GOOD and POOR rations. These distributions (Fig. 3) show that 13-day larval weight differed

greatly on the two rations and more significantly they reveal the major reason for unequal selection differentials. The distributions were asymmetrical (significantly different from normal) and the distribution in one environment was almost the mirror image of the distribution in the other environment. The asymmetry in the GOOD could be due to slow hatching, but such should be equally true for the population on POOR. Since a transformation to normalize both distributions was not readily apparent, the base parameters were estimated from the untransformed data.

In view of the asymmetrical distributions of larval weights for the two environments as demonstrated by the base population, the subsequent selection as practiced should have yielded unequal selection differentials. In fact, the prescribed intensities would have given selection differentials for the large direction of 0·31 and

Table 7. *Analysis of phenotypic variation for 13-day larval weight within various treatment groups. (Phenotypic variance within generation and treatment combination transformed to logarithms for analysis of variance)*

Source	d.f.	Mean squares
Replications (R)	3	0·087*
Environments (E)	1	4·619**
R × E	3	0·004
Directions (D)	2	0·672**
R × D	6	0·008
E × D	2	0·008
R × E × D	6	0·036
Generations (G)	8	0·119**
R × G	24	0·022
E × G	8	0·134**
R × E × G	24	0·024
D × G	16	0·153**
R × G × D	48	0·032
G × E × D	16	0·121
R × E × G × D	48	0·024

* Significant at the 0·05 level of probability.
** Significant at the 0·01 level of probability.

0·46 mg. for GOOD and POOR respectively. In the small direction, comparable selection differentials would have been 0·42 and 0·35 mg. When these values are compared with those observed during the selection phase (Fig. 2) it becomes apparent that the asymmetry of selection differentials was enhanced with increasing generations of selection.

Phenotypic variances for individual 13-day larval weights were calculated for each population by generation. These values were transformed to logarithms as suggested by Bartlett & Kendall (1946) and analysed for identifiable sources of variation (Table 7). To clarify the nature of significant trends for phenotypic variances, they are plotted by directions and environments in Fig. 4. Randomly selected populations (RG and RP) were included in the statistical analyses, but are not shown in

Fig. 4 since phenotypic variance within these lines remained essentially unchanged over the course of the study. In fact, regressions of phenotypic variances on generations revealed a statistically significant change in only one of the eight randomly selected lines.

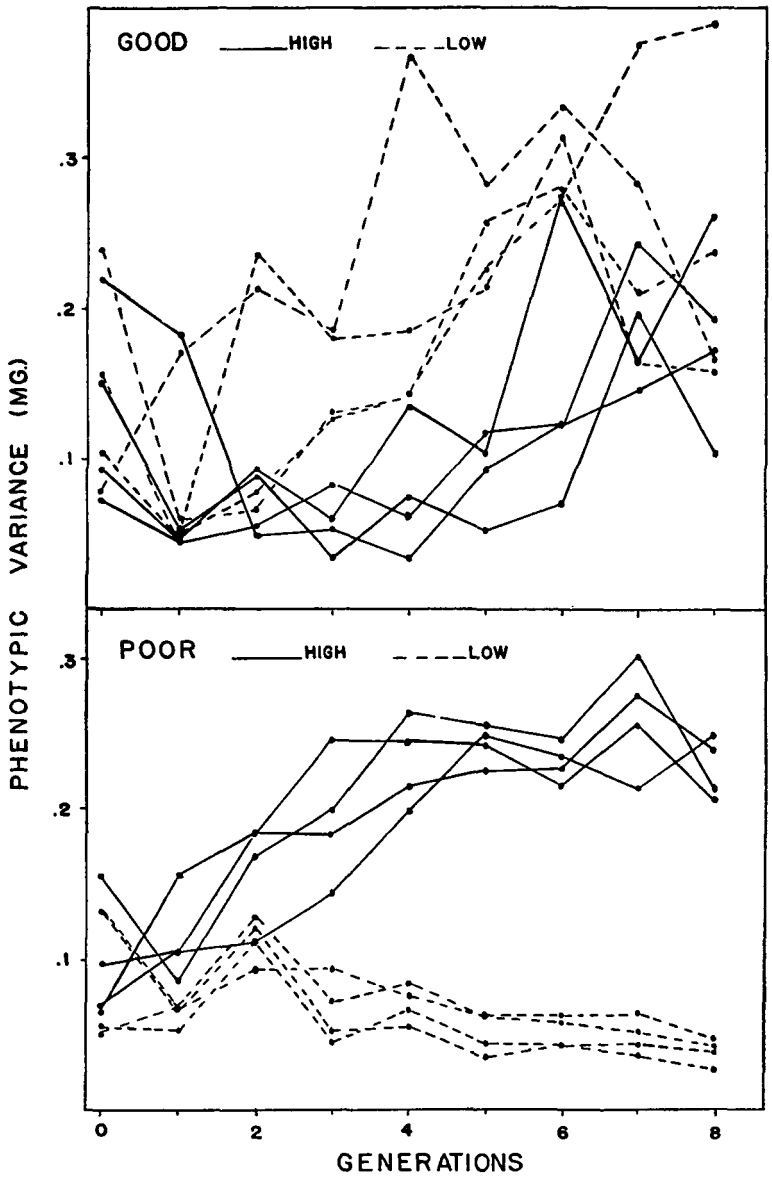

Fig. 4. Phenotypic variances for 13-day larval weight observed in four replications of high-low selection by generation and environment of selection.

It is apparent from Fig. 4 and confirmed statistically by Table 7 that phenotypic variation of the measured variable had been influenced by several factors. The 'Direction' effect in POOR was consistent for all replications and followed the

pattern usually observed in body size selection studies where the means and variances are positively correlated. Yet this simple relationship did not exist in GOOD where the observed variances in all four Low lines were larger than any of the High lines. Overall, the variances for GOOD were significantly larger than those for POOR. The significant effects of 'Generations' and their interactions (D × G and E × G) resulted from the trends evidenced in Fig. 4 where phenotype variances within both High and Low lines increased over generations in GOOD while only the High lines increased in POOR.

Falconer (1960) states that the equation $R = Sh^2$ may be rewritten as $h^2 = R/S$ and thus used to estimate heritability from the results of a selection experiment. Such estimates, called realized heritabilities, are descriptive of the effectiveness of selection and are listed by replication, environment and direction combinations in

Table 8. *Realized heritabilities and standard errors observed for four replications of High-Low selection for 13-day larval weight on two environments*

	Realized h^2 by environments and directions			
	Good		Poor	
Replication	High	Low	High	Low
1	0·25 ± 0·05	0·24 ± 0·03	0·14 ± 0·04	0·37 ± 0·03
2	0·30 ± 0·03	0·43 ± 0·06	0·17 ± 0·03	0·44 ± 0·03
3	0·33 ± 0·04	0·30 ± 0·03	0·15 ± 0·03	0·38 ± 0·05
4	0·37 ± 0·07	0·42 ± 0·03	0·11 ± 0·04	0·40 ± 0·04
Average	0·31	0·35	0·14	0·40

Table 8. If these values are compared with heritabilities found in the base population (Table 5) the agreement is not good. Obviously, heritability estimates based on the dam component grossly overestimated the effective heritability. Yet the sire estimate which eliminates biases due to both dominance and maternal effects underestimates the effective heritability in three out of four environments by direction classes. All replications of HG, LG, and LP had realized heritabilities (Table 8) greater than the initial parameter based on the sire component. On the other hand, all replications of HP selection yielded realized heritabilities significantly smaller than the base estimate.

If these significant trends for phenotypic variances and effective heritabilities occurred only in occasional replications they could be relegated to chance. However, the consistent patterns of response for all four replications in this experiment clearly show that both phenotypic variances and heritabilities can be functions of direction and/or environment of selection.

If 13-day larval weight in the environment of selection represents direct response, then 13-day larval weight in the other environment measures a correlated or indirect response. These correlated responses as deviations from their respective

controls are shown for all four replications in Fig. 5. Analysis of variance of population means by generations for correlated responses indicated that in addition to 'Generations' again being significant one finds the same significant interactions as found among direct responses. Yet these interactions for both direct and correlated responses were not the result of specific genetic changes in the same popula-

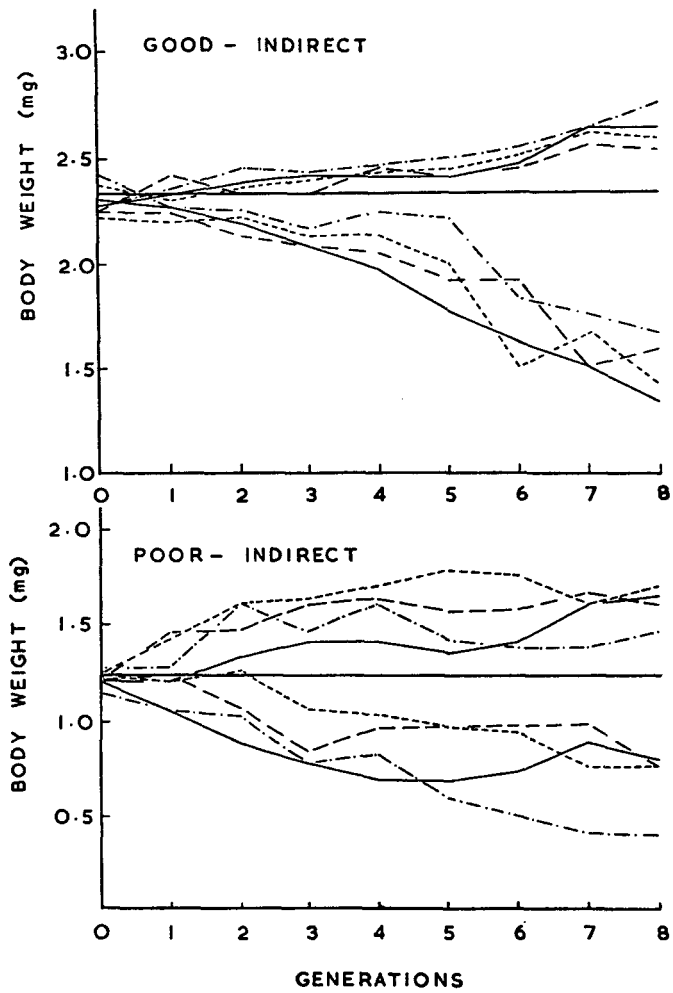

Fig. 5. Correlated responses in four replicates for 13-day larval weight in the opposite environment to that used in selection. Population means by generation are plotted as deviations from replication control mean, horizontal line.

tions. For example, the populations with symmetrical correlated responses (LG and HG on POOR) showed asymmetrical direct responses (Fig. 1). It appears that these interactions are conditioned more by the environments than by genetic changes.

For short term selection experiments such as reported here, the regression of population means on generations of selection is probably the best single criterion of

genetic gain. Barring any obvious deviation from linearity, it provides an objective statistic to contrast with predicted genetic gain based on genetic theory. Such observed and predicted correlated responses are presented in Table 9. The replications within any one of the four treatment groups were reasonably uniform; however, asymmetrical correlated responses were observed in both testing environments. It should be noted that the group with the largest correlated response (LP) was not the group in Table 6 with the largest direct response (LG).

Table 9. *Observed and predicted correlated responses to High-Low selection for 13-day larval weight of Tribolium reared on environment other than that of selection*

		Average change (10^{-2} mg.) per generation					
Testing environment	Population used	Observed by replication				Overall mean	Predicted
		1	2	3	4		
Good	High Poor	+ 4·2(0·6)*	+ 4·2(0·9)	+ 3·4(0·6)	+ 2·7(0·6)	+ 3·6	+ 6·2
Good	Random Poor	− 0·5(1·1)	+ 0·6(0·8)	− 2·5(0·6)	− 2·5(0·9)	− 1·2	0
Good	Low Poor	−15·4(1·5)	−10·1(2·2)	−12·5(2·6)	−17·0(2·8)	−13·7	− 6·2
Poor	High Good	+ 2·0(1·1)	+ 1·4(1·9)	− 1·3(1·8)	+ 1·6(2·0)	+ 0·9	+ 6·0
Poor	Random Good	− 3·7(1·5)	+ 0·7(1·0)	− 3·3(1·2)	− 1·0(1·0)	− 1·8	0
Poor	Low Good	− 7·8(0·8)	−10·4(0·8)	− 7·2(1·3)	− 8·8(1·4)	− 8·6	− 6·0

* ( ) Standard error for the regression coefficient.

The average gain of all four LP populations, when tested in the GOOD environment, was twice that predicted and all four LG populations showed greater gains in the POOR environment than predicted. Yet all populations selected high (HP and HG) revealed less correlated responses than were predicted from base parameters.

The genetic correlation between the trait of selection and the trait being measured in the correlated response is an essential parameter for predicting the direction and magnitude of the correlated response. Falconer (1960) has shown that the effective genetic correlation can be estimated from the ratio of direct and correlated responses.

$$r_A = \frac{CR_E}{R_E}\frac{i_E}{i_N}\frac{h_E}{h_N}$$

where r_A = genetic correlation, CR = correlated response to selection, R = direct response to selection, i = intensity of selection (standardized selection differential), h = square root of the heritability, E = one environment, N = second environment.

The effective genetic correlations were calculated from the appropriate direct and correlated responses for each replication in the experiment (Table 10). While genetic correlations calculated in this manner hardly lend themselves to statistical analyses since little is known regarding their distribution, two points deserve mention. Firstly, the effective genetic correlation for each replication, as well as the overall average correlation, closely agree with the genetic correlation (+0·61) found in the base population by analysis of variances and covariances among relatives. Secondly, an asymmetrical genetic correlation for direction of selection seems

evident since six out of eight estimates for Low selection were greater than the overall average while a corresponding number of estimates from the High lines were less than the overall average.

Responses for each population in each environment together with average responses for the two environments, as suggested by James (1961), are listed in Table 11. If we first examine performance on a single environment, the results in Table 11 show, without exception, that parents should be selected in the environment in which progeny will be reared. In other words, regardless of direction of selection or environment, greatest response in a particular environment was found in those populations selected in that environment.

Table 10. *Effective genetic correlations estimated from direct and correlated response by environment, direction of selection and replication*

	Environment and direction				
	Good		Poor		
Replication	High	Low	High	Low	Average
1	0·50	0·84	0·66	0·66	0·66
2	0·29	0·58	0·18	1·14	0·55
3	0·70	0·74	0·48	0·51	0·61
4	0·51	1·00	0·43	0·68	0·66
Average	0·50	0·79	0·44	0·75	0·62

For three out of the four selected groups (HG, HP, and LG) the direct responses to selection were greater than their correlated responses. However, the correlated responses for three out of four LP populations were greater than their direct responses. The exact nature of this unusual response from indirect selection is not evident from these results. Accrediting it to a scaling effect or proportionality hardly seems justified.

From the performance, average for both rations, as summarized in Table 11, it is not clear which is the best single environment for selection. For response for large (High direction) on both rations, an advantage was observed in three replications (1, 2, and 3) for selection based on performance in POOR, while replication 4 showed a small advantage for the opposite. The results in the Low direction showed an advantage in favor of selection in GOOD. An additional point evident from Table 11 is that the unexpected asymmetry of both direct and correlated responses as seen in Figs. 1 and 5 acted to yield significant asymmetry for growth in both environments regardless of environments of selection.

4. DISCUSSION

Most studies concerned with predicting the response of quantitative traits to selection give no indication as to the normality of the distribution of phenotypes in the populations under study. The lack of information on this important point may

result from: (1) normally distributed populations as determined by a statistical test but not reported or (2) not enough information available for making the test and the need for it ignored. It is believed that the latter is the usual situation. Quite often

Table 11. *Direct, correlated and average responses in 13-day larval weight from eight generations of High-Low selection on performance in one environment.* (*Direct responses are in italics*)

		Average response (10^{-2}mg.) by environments		
		Testing environments		
Population	Replication	GOOD	POOR	Average response
High Good	1	+ *7·2*	+ 2·0	+ 4·6
	2	+ *9·3*	+ 1·4	+ 5·4
	3	+ *8·2*	+ 1·3	+ 3·5
	4	+ *8·7*	+ 1·6	+ 5·2
	Average	+ *8·4*	+ 0·9	+ 4·7
High Poor	1	+ 4·2	+ *8·7*	+ 6·5
	2	+ 4·2	+ *11·3*	+ 7·8
	3	+ 3·4	+ *8·8*	+ 6·1
	4	+ 2·7	+ *6·3*	+ 4·5
	Average	+ 3·6	+ *8·8*	+ 6·2
Low Good	1	− *16·0*	− 7·8	− 11·9
	2	− *20·6*	− 10·4	− 15·0
	3	− *16·0*	− 7·2	− 11·6
	4	− *19·7*	− 8·8	− 14·3
	Average	− *18·1*	− 8·6	− 13·2
Low Poor	1	− 15·4	− *10·8*	− 13·1
	2	− 10·1	− *10·3*	− 10·2
	3	− 12·5	*10·9*	− 11·7
	4	− 17·0	*10·9*	− 14·0
	Average	− 13·8	− *10·7*	− 12·3
Random Good	1	− 1·6	− 3·7	− 2·7
	2	+ 1·6	+ 0·7	− 1·2
	3	− 1·5	− 3·3	− 2·4
	4	+ 0·5	− 1·0	− 0·3
	Average	− 0·2	− 1·8	− 1·1
Random Poor	1	− 0·5	− 2·4	− 1·5
	2	+ 0·6	− 1·2	− 0·3
	3	− 2·5	− 2·2	− 0·2
	4	− 2·5	− 3·6	− 3·1
	Average	− 1·2	− 1·2	− 1·3

when there are extremes in environments, the variation in one environment will differ from the variation in another environment. Becker *et al.* (1959), using the domestic fowl, found that the phenotypic variances were greater on a 'Poor' level of

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nutrition than on a 'Good'. McLaren & Michie (1956) proposed from their studies on growth in mice that the phenotypic variances will increase as the environment deviates from normal.

While 13-day Tribolium larval weight in the GOOD environment of this experiment averaged about twice that observed on POOR, phenotypic variances were initially the same. In exploring possible causes for asymmetrical responses, the distributions of phenotypes in the base population were found to differ significantly from normal. Plotting of the distributions for GOOD and POOR environments revealed both to be skewed, but in opposite directions. They were, in fact, mirror images of each other (Fig. 3). Such results were unexpected. Although the skewed distributions for GOOD could result from some larvae being unusually slow in growth this would not be true for POOR. A possible explanation for the skewed distributions on POOR is that most individuals in POOR were restricted in growth, but that some were able to grow almost normally on the sub-optimal diet, on an optimal diet such differences might be expected to disappear. The reduced distribution for very small larvae in POOR undoubtedly resulted from different factors. A physiological minimum in terms of growth and metamorphosis probably limited the lower tail of the POOR distribution. The slight skewness in the distribution of phenotypes such as were found might not be detected in the small populations usually maintained in selection studies. This may explain why predicted responses based on the normal curve are frequently unreliable.

The asymmetrical responses observed in this study might be a matter of scale and thus could be corrected or made symmetrical with the proper transformation. However, a different transformation would be needed for each environment and possibly each direction of selection. Interpretation of such transformed variables would be difficult.

Falconer (1953) indicated that most scaling effects, if present, can be largely eliminated by measuring the response per unit of selection differential. This, of course, is the realized heritability. The realized heritabilities for the GOOD environment were almost the same for both directions of selection which suggests that responses would have been symmetrical had the selection differentials been equal. While the proportion selected was the same in both directions the skewed distribution gave a larger selection differential for Low selection. Since the selection differentials were larger for Low selection than for High, the asymmetry of response was obviously not a matter of scale. The realized heritabilities on POOR were not the same for both directions of selection. All replications of High selection had significantly smaller values than those observed in the Low lines. Thus we observed that both heritability and selection differentials were asymmetrical in the POOR environment. However, the directions of their asymmetry were opposite and the resulting selection response, by chance, was reasonably symmetrical.

In his investigation of asymmetrical response to selection, Falconer (1953) considered three factors: scaling effect, unequal gene frequencies, and directional dominance. Assuming different combinations of unequal gene frequencies and directional dominance, he calculated theoretical response curves. Since some of

the curves were similar, it would be impossible to differentiate as to whether the results were due to only unequal gene frequencies or directional dominance. However, Clarke *et al.* (1961) pointed out that although directional dominance may explain asymmetrical response, under many conditions it would not be possible to base the results on directional dominance. In their experiment they made various crosses at the end of the experiment and if there had been directional dominance then the crosses should have been nearer the superior line. Such was not the case and they proposed that rather than directional dominance, epistasis would be necessary to explain the asymmetrical response. While crosses of selected populations were not made in the experiment reported here, previous work (Englert & Bell, 1963) showed heterosis for high larval weight. In the presence of non-additive genetic effects, an attempt to distinguish between the effects of unequal gene frequencies, directional dominance and epistasis hardly seems justified.

In addition to asymmetrical selection differentials and heritabilities this study revealed asymmetrical genetic correlations. Yet the overall effective genetic correlation between growth in the two environments agreed remarkably well with estimates in the base population. Therefore, the asymmetrical genetic correlations depend upon the direction of selection. Asymmetrical genetic correlations have been obtained in other studies in which the effective genetic correlation between two traits depended upon which trait was being selected. For example, Bell & McNary (1963) reported realized genetic correlations of $+0{\cdot}64$ and $+0{\cdot}67$ between Tribolium pupal weights in 'Wet' and 'Dry' environments for two replications of selection in 'Wet'. Corresponding realized genetic correlations for the two replications of selection in 'Dry' were $+0{\cdot}93$ and $+1{\cdot}12$. Also Abplanalp *et al.* (1963) found in turkeys that the genetic correlation for response in 8-week weight due to 24-week selection was 1·0; whereas the genetic correlation for 24-week weight due to 8-week selection was only 0·4. However, these authors did not fully consider the part-whole relationship existing between the two traits. For example, selection on 24-week basis includes 8-week weight *in toto*, but selection on 8-week weight includes a fraction of the 24-week trait. Bohren *et al.* (1966) concluded from a theoretical study of asymmetrical correlated responses that changes in the genetic covariance between traits from selection would be more likely than changes in genetic variances. While our findings do not relate directly, the significant changes observed for phenotypic variances and effective heritabilities (Tables 8 and 9) seem to be as important in accounting for the unpredictable results as were possible changes in the genetic correlation (Table 12).

Other experiments, including those of Korkman (1961) and Falconer & Latyszewski (1952), have shown that for any particular environment, selection for that environment should be made in the environment itself. This was vividly illustrated here, where out of a possible sixteen treatment combinations there was only one case where the correlated response was greater than the direct response. Therefore, the results of this experiment suggest that for maximum genetic progress selection should be made in the environment in which the progeny will be maintained.

Since the progeny from most breeding operations are eventually placed in many environments, the results from this study were extended to consider the average response in GOOD and POOR environments. In general, High selection in POOR gave some 25% more gain, as measured by the average of response in GOOD and POOR, than did selection in GOOD. This is in agreement with Falconer's (1960) concept that the greatest mean response in a variety of environments comes from selecting for performance in the environment least favorable for maximum expression of the trait in question. On the other hand, selection for small body weight in either environment appeared to be equally effective in obtaining minimum size in both environments.

In general, this study confirms that, in the presence of a significant genotype by environment interaction (genetic correlation between performance in two environments being less than perfect), indirect selection is less effective in improving a trait than direct selection. In a practical situation a breeder would be faced with the choice of either selecting special strains adapted to each major ecological niche or selecting on an index of combined over-all performance. A choice between these alternatives would rest on economic consideration as well as genetic information.

SUMMARY

Parameters necessary for predicting direct and correlated responses for large and small 13-day larval weight in *T. castaneum* on two levels of nutrition were estimated in the base population. Larval weight in the GOOD environment was approximately twice that observed in POOR. Heritabilities (estimated from the ratio of sire component to total phenotype variance) of larval weight on the two rations were similar, $0{\cdot}21 \pm 0{\cdot}06$ and $0{\cdot}19 \pm 0{\cdot}05$ for GOOD and POOR, respectively. Heritabilities based on dam-offspring covariances were similar to these, but those obtained from full-sib covariances were much larger ($0{\cdot}97 \pm 0{\cdot}07$ for GOOD and $0{\cdot}69 \pm 0{\cdot}07$ for POOR). This suggested that considerable dominance rather than maternal effects were present. The genetic correlation between growth on GOOD and growth on POOR was estimated as $+0{\cdot}60 \pm 0{\cdot}21$.

The selection experiment was replicated four times with each replication extending over eight generations. Good agreement between predicted and observed values for direct selection was observed for large selection in both environments and small selection in POOR. However, response to small selection in GOOD was significantly greater than predicted in all four replications and was associated with increased selection differentials. Realized heritabilities were approximately the same for both directions in GOOD yet asymmetrical responses occurred for all replications due to unequal selection differentials. On the other hand, realized heritabilities were asymmetrical in POOR. Those observed for small selection were more than twice the size of those calculated for large lines. However, the responses in POOR were symmetrical since the selection differentials varied inversely with the realized heritabilities.

Because of the asymmetry observed for heritabilities and selection differentials,

correlated responses were poorly predicted. The average effective genetic correlation between growth in GOOD and growth in the POOR environment agreed remarkably well with the base estimate, yet asymmetry of the genetic correlation was a consistent phenomenon with values for the large lines being less than the base parameter while small lines were uniformly larger.

Asymmetries of the various genetic parameters were not anticipated from base estimates. They were not caused by sampling or chance fluctuations since all four replications were remarkably consistent. Asymmetry for any one genetic parameter (e.g. heritability) was associated with a particular environment or direction of selection while other genetic parameters reacted asymmetrically in populations exposed to a different set of environmental treatments.

For maximum performance in a single environment, these results show that selection should be practiced in that environment. With regard to mean performance in GOOD and POOR environments, selection for large size in POOR gave some 25% more gain than selection in GOOD. Selection for small size in either environment was equally effective in obtaining minimum size in both environments.

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