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Directional and Stabilizing Selection for Developmental Time and Correlated Response in Reproductive Fitness in *Tribolium castaneum*

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Summary. Directional and stabilizing selection for developmental time (DT) were done for seven generations in replicated lines of *Tribolium castaneum.* There were no significant differences between sexes or among replicates in means or coefficients of variation. For directional selection, there were significant responses in both directions, measured as deviation from control, viz. –0.35 ± 0.15 day per generation for Fast (F) and 0.73 ± 0.15 day for Slow (S). The unselected control (C) and the stabilizing selection (I) lines were similar, with average response per generation not significantly different from zero. – Phenotypic variation, from the first generation, was larger in the S line than in the other three lines. The I line showed a significant decrease in phenotypic variation, due mainly to a decrease in genetic variance. The realized heritability was 0.219 ± 0.045 for F and 0.324 ± 0.036 for S, the difference being highly significant. – Correlated response in reproductive fitness (number of pupae produced) was significant only for S ($r_P = -0.88$ and $r_{G\ \text{realized}} = -0.79$). Regression of the correlated response on DT in this line was –19.28 ± 4.77 pupae per day (phenotypic) and –28.77 ± 10.06 pupae per day (genetic).

Key words: *Tribolium* – Directional selection – Stabilizing selection – Developmental time – Reproductive fitness

Introduction

The recognition of the importance of stabilizing selection in natural populations has led to a great deal of theoretical interest in this mode of selection and its evolutionary consequences (Maynard Smith 1979; Nicholas and Robertson 1980; Minvielle 1981).

As compared with the tremendous amount of research on the effects of directional selection, there have been few experimental studies of stabilizing selection. Most of these studies have used *Drosophila,* e.g. sternopleural bristles in a constant environment (Thoday 1959; Barnes 1968) and fluctuating environments (Gibson and Bradley 1974), scutellar bristles (Rendel 1960), duration of development (Prout 1962), wing veins (Scharloo 1964) and wing length (Tantawy and Tayel 1970). All reported a reduction in phenotypic and genetic variability. On the other hand, no change in genetic variability was detected by Falconer and Robertson (1956) for body weight in mice or by Falconer (1957) for abdominal bristle number in *Drosophila.* However, Bulmer (1976) reanalysed Falconer's (1957) experiment and found there had been a reduction in genetic variance.

Artificial directional selection for quantitative traits often leads to reduction in reproductive fitness. This reduction and the return to original levels upon subsequent relaxation of selection gives indirect evidence for the stabilizing role of natural selection, e.g. developmental time (Dawson 1965) and pupa weight (Enfield 1977) in *Tribolium.* In a long term experiment, Enfield (1977) found that natural selection opposed genetic progress for pupa weight after many generations of response, even though genetic variability was still present. Recently in an experiment designed to study the joint effect of natural and artifical selection, Minvielle and Gall (1980) imposed a negative relationship between genetic value for selected pupa weight and fertility in *T. castaneum.* They found that increasing the intensity of simulated natural selection slowed down the response to artificial selection.

The present study is concerned with the effect of artificial selection (both directional and stabilizing) on the developmental time of *T. castaneum.* The correlated changes in reproductive fitness also were studied.

Materials and Methods

Selection

Mass selection for developmental time (from oviposition to pupation, DT) was done using a laboratory population of the

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flour beetle, *T. castaneum* (Portugal), chosen from eight populations previously used by Soliman (1973) because it was intermediate in mean developmental time. Four replicates were started from a sample of 100 unsexed mass mated adults with eggs collected on each of four successive days. In generation 0, within each replication, four lines were started (fast, stabilizing, slow and control). In each generation, after all larvae had pupated, 15 males and 15 females were used as parents for the next generation for any selected line (early, intermediate and late pupae were selected for fast, stabilizing and slow lines respectively). The same number of males and females were randomly chosen within the control (unselected) lines. Selection for stabilizing developmental time was done by calculating the mean pupation time, and selecting individuals as close as possible to this mean. In most cases parents were selected from the yield of pupae within a single day if the mean pupation was very close to this day, but in a few cases parents from two days (proportional to the mean pupation time) were selected.

Experimental designs where (i) similar numbers of males and females were measured and each sex was selected with the same intensity; (ii) selection intensity was between 15–20%; and (iii) the measure of heritability was based on the regression of response on cumulated selection differential, should give maximum efficiency for estimating and comparing genetic parameters with least variance (Hill 1971). All of these conditions are met in the present design except for selection intensity for the slow line which averaged 37.42% over the seven generations of selection.

Experimental Procedure

Parents not less than seven days old were introduced into a plastic box (5×3.5×2.5 cm) containing 25 g whole wheat flour supplemented with 5% brewer's yeast. After three days the adults were transferred to fresh flour for 24 hours to lay eggs. Starting on the 14th day after oviposition, pupation was checked daily. The few larvae which had not pupated by the 30th day were discarded. At the same time every day, the flour was sifted, the pupae were removed, sexed and the remaining larvae were returned to the box.

Experimental Conditions

All cultures were maintained at 33±1 °C and 70±2% relative humidity. The same batch of flour was used and sifted in the same manner throughout, and standard procedures were followed for handling cultures.

Statistical Procedures

Mean developmental time was calculated from the frequency of daily pupation within each replicate, sex, generation and line.

Because of the dependence of variance on the mean developmental time, the coefficient of variation was used as the measure of variability. The squared coefficient of variation, if less than 30%, is an approximation of the variance if calculated using natural logarithm values (Lewontin 1966). All coefficients of variation were less than 15% in the present experiment, and consequently their squares were used in variance and regression analyses.

Replications and sex were pooled since there were no significant differences among means or coefficients of variation, when analysis of variance was done on the data over the seven generations of selection.

Results

Response to Directional Selection

Mean developmental time of the two lines over seven generations of selection is shown in Fig. 1. The divergence between the two lines was evident and significant from the first generation (fast = 18.75 and slow = 19.05 days).

The rates of change per generation (b ± SE) estimated using deviations from control (Fig. 2) were 0.73±0.15 day ($P<0.01$) for the slow line and –0.35±0.15 day ($P<0.05$) for the fast line.

Realized Heritability

The realized heritability was 0.219±0.045 ($P<0.001$) for F and 0.324±0.036 ($P<0.001$) for S. The difference between the two heritabilities was highly significant indicating asymmetrical responses to artificial selection.

Stabilizing Selection

Mean developmental time for stabilizing selection and unselected control lines are shown in Fig. 1. The two

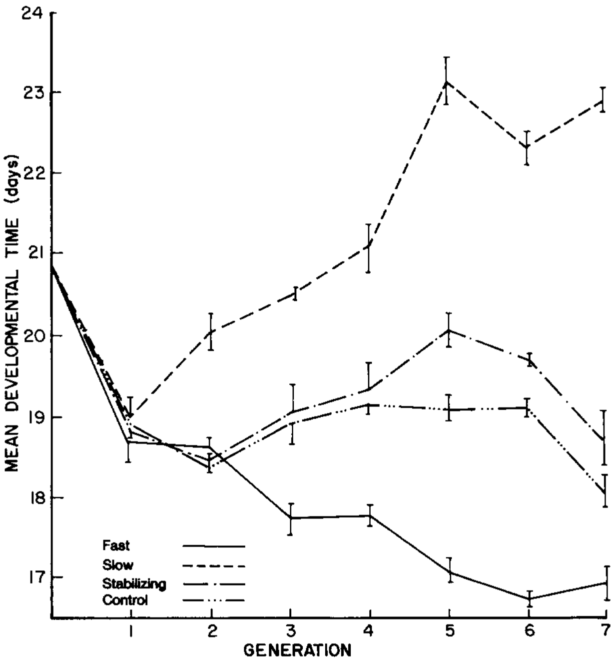

Fig. 1. Change in mean developmental time during selection (SE are based on 4 replicates)

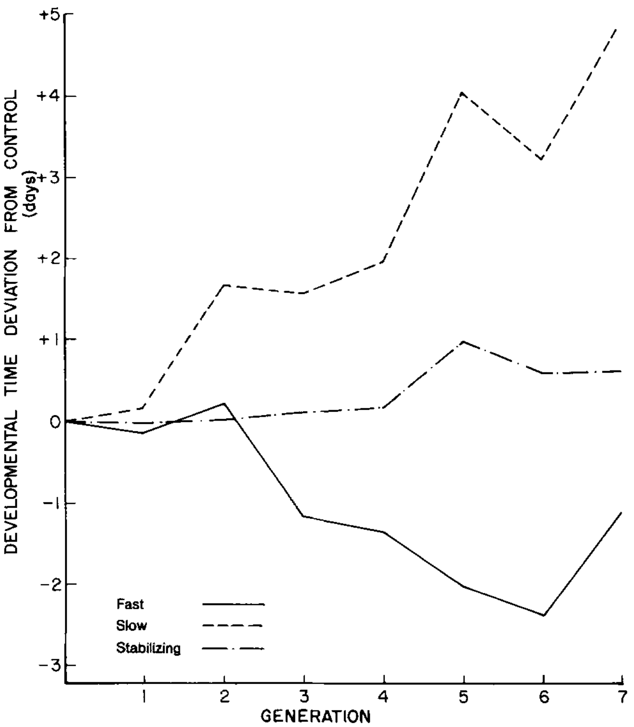

Fig. 2. Mean deviation from control during selection

lines did not show any significant change per generation. The average response per generation for the unselected line (b ± SE) was −0.03 ± 0.09 day and for the stabilizing selection line, estimated using deviations from control (Fig. 2) was 0.10 ± 0.06 day.

Changes in Variance

The coefficients of variation of the four lines (Fig. 3) differed significantly ($P < 0.001$), due to the larger variation for the slow line ($CV^2 = 72.4$, 77.2, 77.7 and 119.9 for I, F, C, and S) evident from the first generation. Stabilizing selection reduced phenotypic variability ($b = -0.40 \pm 0.14$, $P < 0.05$). The variance for the unselected and the selected fast and slow lines did not change significantly over generations ($b = -0.25 \pm 0.19$, -0.07 ± 0.09 and -0.07 ± 0.19 for the control, fast and slow lines).

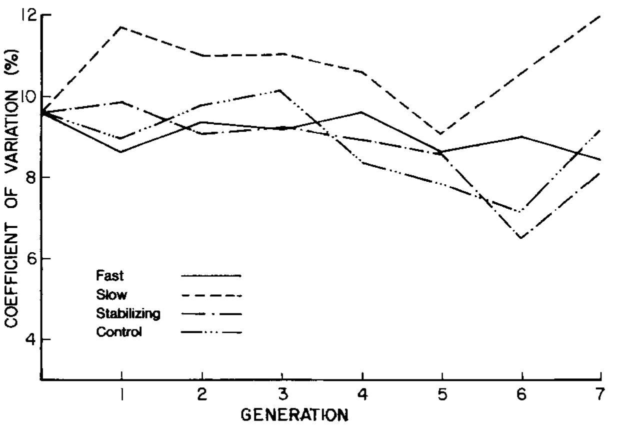

Fig. 3. Change in coefficient of variation during selection (SE are based on 4 replicates)

Correlated Responses in Reproductive Fitness

The numbers of pupae produced were used as a measure of reproductive fitness (Fig. 4). Productivity of all lines decreased from G_0 to G_1. The observed decrease in the number of pupae per generation produced by the slow line (measured as deviation from control) was significant ($b = -23.39 \pm 7.93$, $P < 0.05$). Stabilizing selection did not have any significant effect on productivity (Fig. 4).

A "realized genetic correlation" was estimated for each selected line using the deviations of both traits from the average control within each generation. The underlying assumptions for the validity of such correlations have been discussed by Englert and Bell (1970)

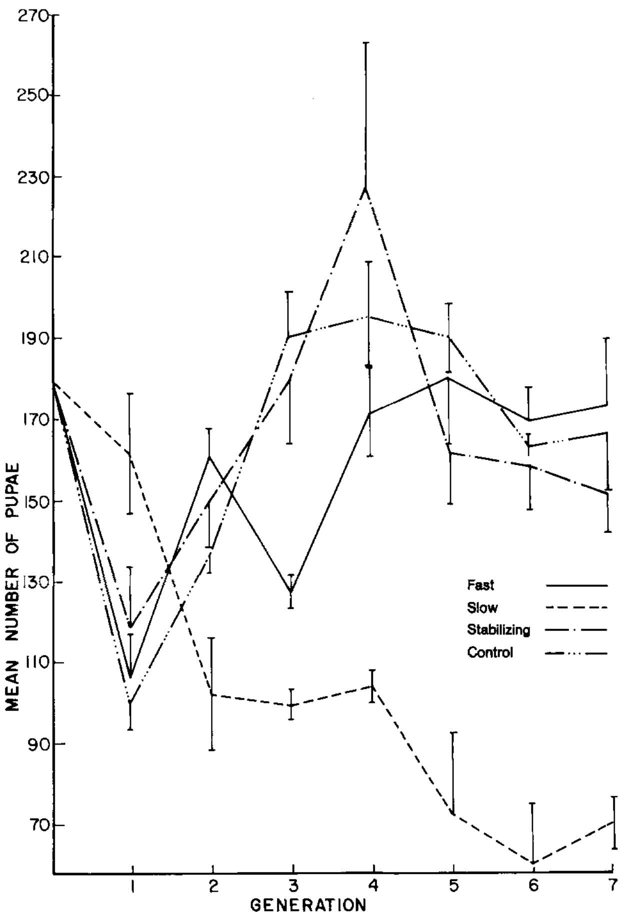

Fig. 4. Correlated change in mean productivity

who used this method in calculating the realized genetic correlation between developmental time and body weight in *T. castaneum.* The only significant phenotypic correlation (between mean pupation time and mean number of pupae) was for the slow line ($r_p = -0.88$ and $r_{\text{“g realized”}} = -0.79$). This genetic relationship was linear ($P = 0.035$) rather than quadratic ($P = 0.056$). The estimated phenotypic response (b ± SE) was −19.28 ± 4.77 pupae per day ($P < 0.01$) and genotypic response was −28.77 ± 10.06 pupae per day ($P < 0.05$).

Discussion

Englert and Bell (1970) reported changes in pupation time of −0.34 day per generation for fast and 0.70 day per generation for slow over six generations of selection. The present experiment shows very similar results, viz. −0.35 day per generation for fast and 0.73 day per generation for slow pupation time.

Figure 2 indicates that the fast line seems to resist the selection pressure during the first two generations. This was found also by Dawson (1965) for *T. confusum* and Englert and Bell (1970) for *T. castaneum* in the first generation. Recently, Dawson (1975) has demonstrated that natural selection opposes artificial selection for fast development through cannibalism of early pupae by larvae.

The apparent cessation of progress between generations 4 and 7 for the fast line (Fig. 2) does not necessarily mean that the line is fixed for loci contributing to the variation in developmental time. This stage of no response may be attained if the selection favours heterozygosity at some loci or if natural selection opposes artificial selection (Roberts 1966a; Minvielle and Gall 1980; Nicholas and Robertson 1980). However, the reason for failing to respond to the pressure of artificial selection may be different in the present fast and slow lines (Roberts 1966b). Enfield (1977) reported that when response to selection for pupa weight in *T. castaneum* ceased, effective selection differential was still attainable which he explained by the joint effect of natural and artificial selection. Selection differentials for slow and fast developmental times for generations 4–6 were almost as high as those for generations 0–3 (Table 1). Unfortunately no supplementary experiments were done, so that the exact cause(s) of the failure of directional selection to change the mean value of developmental times of the fast line after generation 5 cannot be specified.

Table 1. Selection differential (S) and selection intensity (i) for the three selected lines

Generation	Stabilizing		Slow		Fast	
	S	i (%)	S	i (%)	S	i (%)
0	0.43	26.43	2.72	19.07	1.49	29.04
1	0.08	20.44	2.27	31.79	2.09	18.54
2	−0.13	17.20	2.56	30.38	1.63	23.63
3	0.17	13.75	2.61	28.95	1.76	17.82
4	0.45	18.93	1.58	41.22	1.04	17.71
5	0.14	19.34	1.26	66.88	1.29	17.84
6	0.11	20.26	2.50	43.68	0.95	17.90
Mean	0.17	19.48	2.21	37.42	1.46	20.30

The present estimates of the realized heritability are of the same magnitude as those reported by Englert and Bell (1970), but their estimate for the fast line was higher than that for the slow line (0.38 and 0.26). Asymmetry in favour of slow developmental times was also observed by Dawson (1965) after seven generations of symmetrical response. Thus the direction of asymmetry seems to depend on the genetic composition of the base population, which was different in the three laboratories. The highly significant asymmetry observed in the present study could be explained by directional dominance for fast development or by sampling.

Relatively larger realized heritability for the slow than for the fast line could also result from larger selection differentials for this line (Table 1) due to change in the normality of the distribution by selection, as previously explained by Englert and Bell (1970). Directional selection would be expected to produce a skewed distribution (Fig. 5). Also reduction in number of pupae produced by the slow line (Figs. 4, 5), leads to increasing percentage of parents selected for each generation (Table 1). These factors together with the flat distribution (Fig. 5) could produce the larger selection differential in the slow line (Table 1).

Stabilizing selection resulted in a significant reduction in the phenotypic variation (Fig. 3). Thoday (1959), Prout (1962), Tantawy and Tayel (1970) and Gibson and Bradley (1974) working with *Drosophila,* and Kaufman et al. (1977) working with *T. castaneum,* obtained similar results in their studies of the effect of stabilizing selection on variability of various quantitative traits. Two main mechanisms were proposed to explain such reduction. One assumes reduction in non-genetic variance and the other reduction in genetic variance. The first mechanism results from increased stability of development (Waddington 1953). The reduction in genetic variance could be achieved by increased homozygosity (Robertson 1956; Maynard Smith 1979); by a building up of balanced repulsion linkage (Mather 1943), or by a decrease in the effect of segregating heterozygous loci (Robertson and Reeve 1952).

The effect of selection on variance has been studied extensively in experimental and simulated populations (e.g. Bulmer 1971, 1974, 1976). Using computer simulations, Bulmer (1976) found that under random mating, changes in gene frequencies and linkage disequilibrium are important components in changing the genetic variability in finite popu-

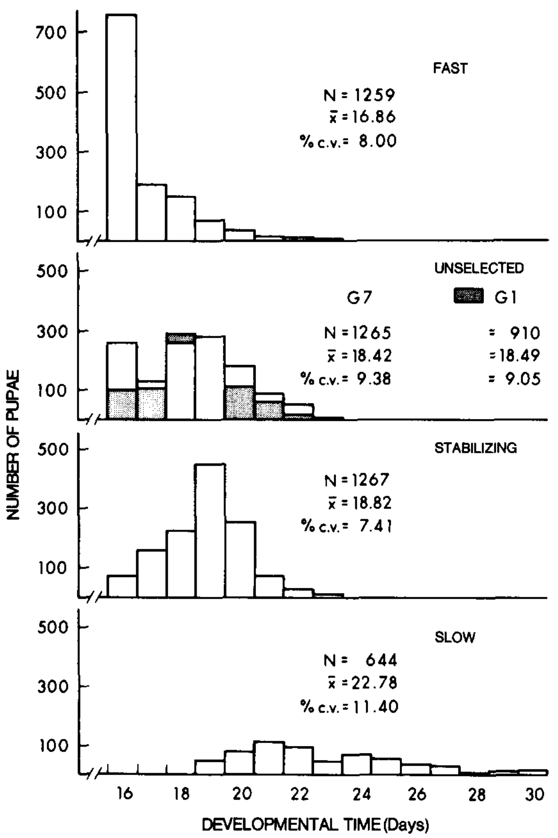

Fig. 5. Distribution of developmental time before selection and after seven generations of selection

lations. Changes in gene frequencies are more important under natural selection and linkage disequilibrium is more important under artificial selection.

The observed negative regression coefficient of variability of developmental time on generation number of stabilizing selection (–0.40 ± 0.14, $P < 0.05$) is not significantly different from that of the control line (–0.25 ± 0.19). Fast and slow lines (Fig. 3) also showed a negative tendency (–0.07 ± 0.09 and –0.07 ± 0.19). Bulmer (1976) explained the negative trend in a simulated control line by possible genetic drift and in simulated stabilizing and directional selection by linkage disequilibrium.

The present experiment extends the early findings of Soliman (1972) for the relationship between developmental time and productivity within and between twelve "wild" populations of *T. castaneum* (Table 2). In this earlier study, although the within population correlation coefficients between the two traits were not significant for most populations, most of these correlations were negative. On the other hand, the inter-population correlation was negative and highly significant ($r = -0.882$, $P < 0.01$). Similar results were also found for *Drosophila* (see Soliman 1972 for references). This negative correlation suggests that a balance between the two traits must exist within certain ranges for maximum population and species fitness. This balance is also evident from the results of the fast and stabilizing selection lines and from the fact that the only significant and negative correlation coefficients between the two traits among the "wild" populations were demonstrated for the two lines with extreme developmental time (Table 2). However, there is strong reason to believe that natural selection tends to favour faster developmental time. The study with the 12 "wild" populations confirms this point: although there is a wide variability among these populations (Soliman and Hardin 1972), only one population (Kyoto) had a mean adult emergence of 31.35 days and the rest ranged from 24.70 days (Madrid) to 27.20 days (Vicosa) (Table 2). However. Dawson (1975) argued that there is a limitation on the evolution of fast development in flour beetles imposed by cannibalism of early pupating larvae. The difficulty of interpreting stabilizing selection is also illustrated by the existence of negative correlations between quantitative traits and other components of fitness, e.g. body size in mice, where large animals have reduced survival and small ones reduced fertility (Falconer 1977). Even if heterozygotes were shown to be superior in a given environment this does not automatically imply that they will maintain that superiority in other environments (Soliman 1976).

Table 2. Average adult emergence time and number of progeny for twelve wild populations of *Tribolium castaneum* and their intra- and interpopulation correlation coefficients

Population[a]	Eclosion time (days)	Number of progeny	Intra-population correlation coefficient
Madrid	24.70	353.7	–0.44*
Edinburgh	24.80	386.8	–0.14
Vicosa	25.25	365.8	0.11
Capetown	25.65	332.4	–0.21
London	25.70	345.9	–0.01
Chicago	25.90	345.6	–0.11
Kingston	26.00	352.7	–0.06
Makakos	26.15	293.7	–0.30
Kano	26.60	289.6	–0.16
Lisbon	26.90	394.2	0.19
Vicosa	27.20	192.6	–0.20
Kyoto	31.35	169.5	–0.31*
Inter-population correlation coefficient[b]			–0.882**

[a] Populations are ranked according to their mean eclosion time. For more details see Soliman and Hardin (1972)

[b] From Soliman (1972), (Based on eight populations with four replicates)

* $P < 0.05$

** $P < 0.01$

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