GENETIC HOMEOSTASIS AND DEVELOPMENTAL RATE IN *TRIBOLIUM*[1]

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GENETIC analysis of a variety of traits in populations of several species has revealed a similar pattern for many traits which are important components of fitness. In general such characters have intermediate optima, and prolonged artificial selection for extreme expression leads to a reduction in fitness. LERNER (1954, 1958) has postulated that one possible mechanism for natural selection in favor of phenotypic intermediates is superiority of heterozygotes with respect to fitness.

Thus, although the value of a metric character may be determined by additively acting alleles, the pleiotropic effects of these genes on fitness are overdominant in nature. It has been shown that this situation will lead to maintenance of genetic variability in a population (ROBERTSON 1956).

The recent studies of LERNER and Ho (1961), which demonstrated that the outcome of interspecific competition trials with flour beetles is influenced by genetic as well as environmental factors, has made it of increased interest to attempt to determine the importance of various components of competitive ability. Developmental rate, which is an important component of fitness in Drosophila, according to HIRAIZUMI (1961), was chosen to be used in the present investigation.

An extensive review of pertinent literature on the genetics of developmental rate was made by DAWSON (1964a). Selection for rate of development has been used several times as a tool for studying other problems: HUNTER (1959) examined correlated responses in DDT resistance in *Drosophila melanogaster*; CLARKE, SMITH and SONDHI (1961) used it for a study of asymmetrical response to selection in *D. subobscura*; MARIEN (1958) investigated the variable outcome of replicate selection experiments with *D. pseudoobscura*; PROUT (1962) studied the effects of stabilizing and disruptive selection in *D. melanogaster*. HOLLINGSWORTH and SMITH (1955) combined selection with inbreeding to study the correlation between slow development and infertility.

Other relevant studies include those of BONNIER (1961a, b, and BONNIER, JONSSON and RAMEL 1959) in which it was demonstrated that in *D. melanogaster* heterozygous individuals exhibit a faster rate of development and a better competing ability than homozygotes. SMITH and SMITH (1954) and HOLLINGSWORTH

and SMITH (1955) found that in *D. subobscura* heterozygous flies also developed faster than homozygotes.

In the present studies, which were initiated in late 1960, selection for developmental rate was used as a tool to produce strains differing in their rates of development for use in competition experiments. This report summarizes the results of the selection program; the results of the various competition trials will be described elsewhere.

MATERIALS AND METHODS

Mass selection for developmental rate was started from synthetic strains of the flour beetles *Tribolium castaneum* (hereafter referred to as CS) and *T. confusum* (CF). These strains have been maintained in this laboratory as closed populations since their inception in 1958 (for details regarding the construction and husbandry of these strains see LERNER and Ho 1961). CS was selected for both fast and slow development, and CF for fast development only. In each generation, about 40 males and 40 females were chosen from among the fastest (or slowest) developing individuals to serve as parents for the next generation. Selection pressure was maintained at a reasonably low level (80 parents chosen from a variable number of offspring ranging from 387 to 1,270) in order to minimize the effects of inbreeding.

In the experiments to be described, rate of development was usually measured as follows: a known number of parents was introduced into a shell vial (9.5 × 2.3 cm) containing about 12g fine-ground whole wheat flour enriched with 5% brewer's yeast. After a two or three day period, the beetles were transferred to fresh flour at a specified time of day, and the original vial was discarded. The adults were then transferred daily at the same time until the desired number of vials was obtained. Each vial thus contained one day's eggs produced by the set of parents introduced. The cultures were left undisturbed until pupation began. Then, again at the same time every day, the flour was sifted, the pupae were removed, sexed and recorded and the remaining larvae were returned to the vial.

The measured trait was thus the number of days required to develop from egg to pupa. The use of the pupal stage was favored over that of the adult stage, because of the ease and rapidity of sexing pupae, the shortness of the pupal stage relative to the total elapsed time from egg to adult, and the fact that this procedure insured that all saved females were virgin. A further advantage in using the pupal stage rather than the adult stage is that adult beetles secrete ethylquinone gases which might have an inhibiting effect on development of individuals still in larval stages. It is known that the quinones can cause a number of types of terata (ROTH and HOWLAND 1941) and it seems reasonable to expect that they may also influence developmental time. This fact has not been taken into account in some investigations where developmental time was measured in mass cultures as the number of days from egg to adult.

An effort was made to keep environmental conditions as constant as possible, in view of the dependence of developmental rate on temperature and humidity (HOWE 1956, 1960) and on the type of flour (MILLER 1944), as well as because of the very great fluctuations between generations observed in selection experiments involving this character in Drosophila (see SANG 1962). To this end, all cultures were maintained in a converted Jamesway Poultry Incubator kept at 29°C and 70% relative humidity. Owing to a change in personnel, the humidity in the incubator was accidently altered to 60% in July, 1962. Discussion of the effects of this change will be deferred to later sections. Flour was obtained from commercial suppliers and sifted in the same manner throughout the course of the experiments, although it was not possible to obtain flour from the same source at all times.

The laboratory is not maintained at constant temperature and humidity but is serviced by a heating and air conditioning system which keeps the room temperature reasonably constant. Standard procedures were adopted during the course of the research for removing cultures from the incubator in order to assay for developmental rate.

Full experimental details, including some minor variations in selection procedure are given by DAWSON (1964a). Suffice it here to say that, with one exception, none of the variations were of any significance in these studies. In the CS strain selected for slow development, the procedure described above for selecting parental beetles was only followed for five generations. Productivity declined so rapidly in this line that the selection method had to be modified so that 40 pairs of adults near or above the average for the generation were used.

The following system of notation has been established for designating various strains used in these investigations. The synthetic strains used as foundation populations for selection are denoted CS-stock and CF-stock. Selected lines are designated as CS-fast, CS-slow and CF-fast; or as CS-n fast, etc., where n is the number of generations of selection to which the strain had been subjected. Lines in which selection was suspended are marked with an S prefix; thus SCS-11 fast is a suspended selection line from the 11th generation of selection for fast development. Similarly reverse selection lines are marked with an R prefix. Inbred lines are listed with numbers used in the laboratory (e.g., CS 3).

RESULTS

The foundation populations: Developmental times for the CS and CF synthetic strains were measured at various times during the course of the study. Combined averages from these several assays are as follows (in days from egg to pupa):

	n	$\bar{x}$	s^2	$\bar{x}(\male)$	$\bar{x}(\female)$
CS	10,929	23.29	5.70	23.20	23.39
CF	7,689	24.26	2.53	24.43	24.07

Thus the CF synthetic stock requires almost one day more to pass from egg to pupa than the CS stock. There also appear to be differences between the sexes in both species; CF females develop considerably faster than males, whereas CS males are somewhat faster than CS females. The differences are highly significant in both species on the basis of MANN-WHITNEY rank tests.

The data given above further indicate that the CS-stock is considerably more variable in its developmental rate than the CF-stock. Extensive experiments carried out to partition phenotypic variance for developmental rate in the CS and CF synthetic populations have not yet been completely analyzed and will be reported separately.

Since each selection generation was initiated with the progeny of approximately 40 pairs of parents rather than with a specified number of eggs, there were fluctuations in the number of pupae obtained from a vial. To find ways of eliminating this variable, a study of the effect of density on developmental rate was carried out with the synthetic stocks. The results of this investigation are given by DAWSON (1964a). Within the range of densities used in the selection program, regression of developmental time on density was found to be linear. Hence a correction factor could be applied to vial means to eliminate differences in density.

Developmental time is not normally distributed, and it is therefore necessary to exercise some precaution in the application of various statistical tests. For comparisons where parametric methods could not be utilized, the MANN-WHIT-NEY rank test was substituted. Since the numbers of observations were generally quite large, a normal approximation given by SIEGEL (1956) was used.

Response to selection: The results of selection for fast and slow development in CS and for fast development in CF are given in Figure 1. It is readily seen that selection has been effective in producing strains differing in their developmental rates. By the second generation of selection all three lines had diverged significantly from the synthetic stocks on the basis of MANN-WHITNEY rank tests.

Since the primary purpose of the selection program was to produce strains with different rates of development, and not to study quantitative aspects of selection, no controls or replicate selection lines were maintained except for CF-fast (two replicates). The absence of replications and control lines turned out to be a significant oversight, and may reduce to some extent the reliability of the observed results. The synthetic stocks, used as foundation populations for selection, were assayed for developmental rate a number of times throughout the course of the selection program, usually in connection with other experiments (Figure 1). No consistent changes in rate of development were observed. Although this type of control is not ideal, it will suffice for the present purposes.

Coupled with the increase in developmental time in the CS-slow line was a tremendous increase in variance. On the other hand, variance decreased somewhat in the fast selected line of this species. Means, variances and coefficients of variation (in percent) for the final generations of selection in these two lines and for the CS-stock are given below. The CS-stock data chosen were some for which the density per vial was about the same as that of the fast line.

	$\bar{x}$	s^2	CV
CS-20 fast	20.40	3.93	9.70
CS-stock	23.92	6.65	10.79
CS-13 slow	49.11	166.19	26.25

Since changes in variance with selection occur in the same direction as changes in means, it is possible that they are merely scale effects. Although genetic variance has undoubtedly increased in the CS-slow line (see Table 1), it is tempting to suggest that the great increase in variance in this strain indicates a loss of buffering resulting from a reduction in heterozygosity due to selection of genes which, when homozygous, lead to slow development. However, FALCONER (1960) correctly points out that such a deduction may be misleading when scale effects are present.

Scale effects arise as the result of improper choice of the scale of measurement and may be eliminated by transformation of the data to a more suitable scale. The most useful transformation is the logarithmic one. If the variances of two distributions on a logarithmic scale are equal, then the coefficients of variation on the arithmetic scale should be equal. The above data indicate that most of the observed decrease in variance in CS-fast was probably a scale effect on this criterion. However, the coefficient of variation of CS-slow is still much higher than that of the synthetic stock, thus lending some support to the hypothesis of decreased buffering in this strain.

It was noted previously that in July, 1962 the humidity in the incubator was accidentally changed from 70% to 60%. At the time the generations of selection
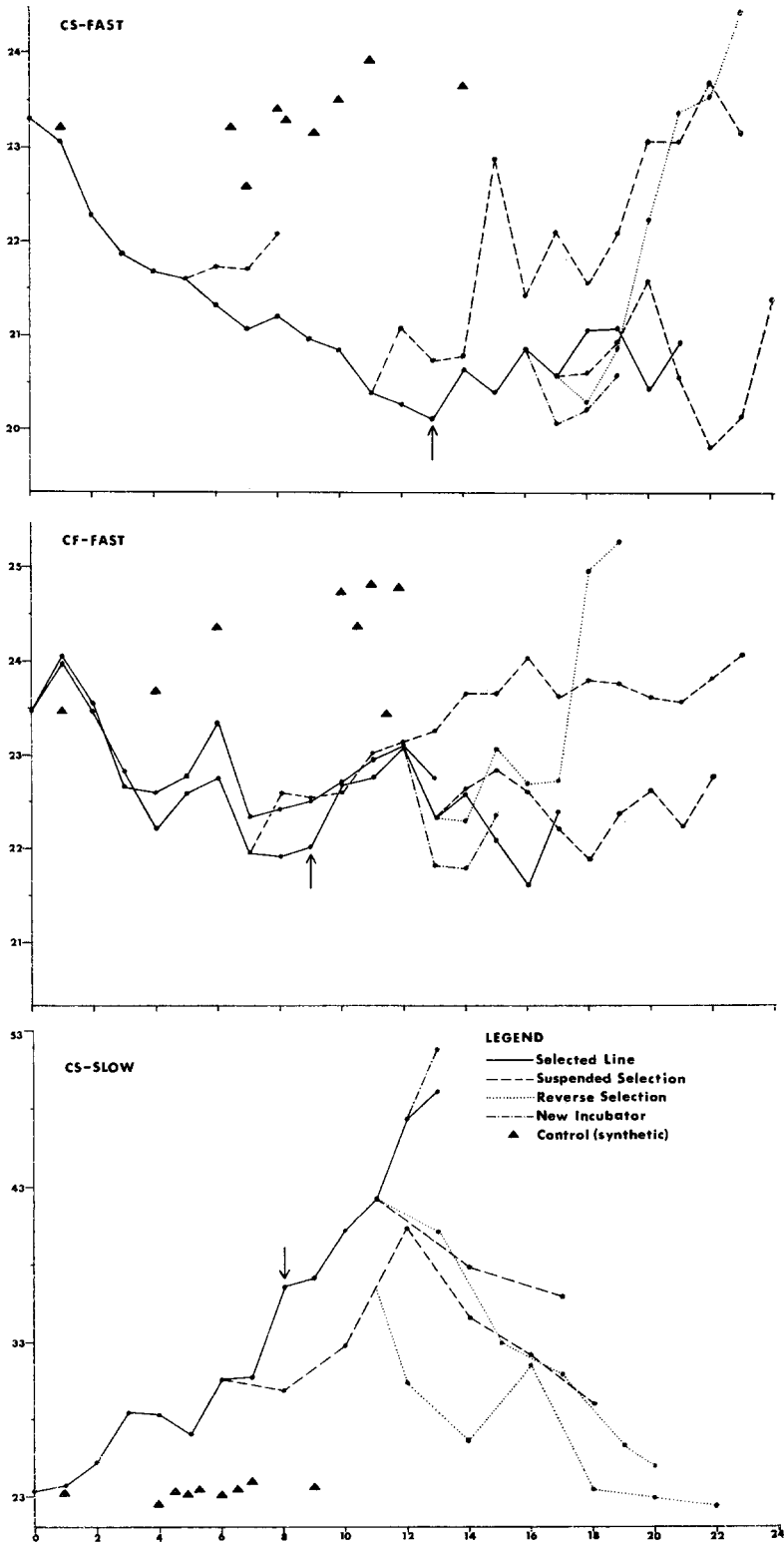
FIG. 1.—Response to selection for developmental time (days from egg to pupa) in CS and CF. Arrows indicate time when humidity was changed (see text). Note differences in ordinate scale.

in progress were CS-13 fast, CS-8 slow and CF-9 fast. At about the same time the humidity change occurred, negative responses to selection were observed in the CS and CF fast selection lines. Before the change was discovered (December, 1962) the negative responses were thought to be the result of natural selection acting against artificial selection. After the change was discovered, sublines of the selected lines were taken and placed in another incubator at 70% humidity (Figure 1). In spite of the initial response to the more favorable humidity (HOWE 1956, 1960), both fast selection lines continued to exhibit negative responses to selection. Thus it seems safe to conclude that natural selection was indeed opposing artificial selection.

On the other hand, when a subline from CS-slow was placed in the new incubator, it developed more slowly than the one in the lowered humidity. Further studies indicated that although the normal reaction of this species to decreased humidity is an increase in developmental time, the later generations of the CS-slow strain did not behave in the predicted manner (DAWSON 1965). We shall return to this point in the next section.

Heritability estimates were obtained from the selection experiments using FALCONER's (1954) realized heritability method. To compute this statistic, selection response is plotted as a function of cumulative selection differential and a least squares regression line is fitted to the set of points obtained. The slope of the regression line is then a measure of effective heritability. In view of the problems associated with change in humidity, heritability estimates were computed only through Generations 13 and 9 for the CS and CF fast lines respectively.

The estimates obtained are listed in Table 1, from which it is seen that the response to two-way selection in CS was symmetrical for the first seven generations and then became asymmetrical. The estimate for 13 generations of selection in CS-slow is probably inflated as a result of the humidity change. These points will be discussed in more detail later. The realized heritabilities obtained from selection are comparable to estimates obtained from several other methods.

It is interesting to note that these estimates are of the same order of magnitude as the ones reported by CLARKE et al. (1961) from selection for developmental rate in Drosophila subobscura. Using a somewhat different selection procedure, they found realized heritabilities of 0.06 and 0.19 for fast and slow development respectively. HUNTER (1959) selecting for length of larval period in D. melano-

TABLE 1

Realized heritability estimates for developmental rate
in T. castaneum *(CS) and* T. confusum *(CF)*

Species	Direction of selection	No. of generations	Realized h^2
CS	Fast	7	0.142 ± 0.013
		13	0.109 ± 0.007
CS	Slow	7	0.139 ± 0.025
		13	0.321 ± 0.042
CF	Fast (A)	9	0.175 ± 0.027
	(B)	9	0.120 ± 0.036

gaster, obtained heritabilities of 0.42 to 0.70 for slow and 0.17 to 0.24 for fast lines. PROUT (1962) found heritability of developmental rate in *D. melanogaster* to be about 0.25.

Suspension of selection and reverse selection: Several times during the course of the selection program, sublines were established by suspending selection. In addition, reverse selection was started in sublines from CS-17 fast, CS-11 slow and CF-13 fast. Only one of the replicate CF lines was used for these studies. The suspended and reverse selection lines were kept in the same incubator in which competition experiments involving contemporary beginning populations were maintained. Thus all suspended selection lines from CS-5 fast, CS-11 fast, CS-6 slow and CF-7 fast were placed in the incubator in which the humidity was later changed.

Procedures used for suspending selection generally followed those used for the selected lines. Forty pairs of adults were placed in a vial, the females were allowed to lay eggs for one day, and the developmental rate of their offspring was measured. Forty pairs were then chosen at random from among the progeny to be used as parents for the next generation. Reverse selection from the fast lines was carried out by taking the 40 slowest males and females in each generation; for the CS-slow line the 40 fastest pairs were chosen. In these lines two vials, each containing one of two successive days' egg production, were usually collected. All of the suspended and reverse lines from CS-fast and CF-fast were assayed every generation. For the slow line, however, time limitations made it inconvenient to measure developmental rate every generation. Thus all lines taken from CS-slow were assayed every two generations except SCS-11 slow which was measured every third generation.

The results of suspending and reversing selection are included in Figure 1. For the fast lines of both species, these two procedures led to the return of developmental rate to or at least toward the original level of the foundation populations. The change in the SCS-5 fast line was rapid and quite uniform for the three generations it was carried. A sporozoan infection among third-generation progeny necessitated the discarding of this line.

Developmental rate in the SCS-11 fast line also returned to the original level. Unfortunately, the experiments had to be terminated after only seven generations of suspended selection in the SCS-17 fast line. Reverse selection from CS-17 fast was, as expected, more effective than suspension of selection.

Suspended selection lines from CF-fast behaved similarly to the SCS-fast lines. Developmental rate returned to the original level of the synthetic stock more rapidly in SCF-7 fast, but the selection response had been considerably less than that of the CS-fast line.

On the other hand, suspending selection from CS-slow was not as effective in returning developmental rate to the original level. When selection was suspended from CS-6 slow, developmental rate continued to move *away* from that of the synthetic stock for the first few generations. This may have resulted, in part, from the humidity change in the incubator which occurred after one generation of suspended selection (during which developmental time decreased). Although

CS-12 slow developed even more slowly when placed in another incubator maintained at 70% humidity, it is not certain that this abnormal response to the humidity change was characteristic of the CS-slow strain after six generations of selection.

In addition, reverse selection was much less effective in the RCS-slow line than in the RCS-fast strain. It is not readily observable in Figure 1, but selection differentials were much greater in the RCS-slow line, and although accurate heritability estimates for the effectiveness of reverse selection from CS-slow cannot be computed, it is certain that the CS-fast line responded more readily to reverse selection.

The slow return of developmental rate toward the level of the synthetic stock in the SCS-slow lines indicates that considerable progress toward homozygosity of genes for slow development was being made. It will be shown later that this is the expected result under a genetic model derived from the results of this study.

Crosses between selected lines: In an effort to obtain some information on dominance of genes for developmental rate and the presence or absence of maternal effects, reciprocal crosses involving the selected lines and the synthetic stocks were carried out. Initially, the 8th and 13th generations of the CS slow and fast lines respectively were used. A more extensive study was performed

TABLE 2

Developmental times (days from egg to pupa) of selected lines, synthetic stocks and reciprocal hybrids among them in three experiments. The strains used are indicated in each subsection

Mating	Female parent	Male parent	Total pupae observed	Develop-mental time*	Productivity (pupae/female/day)
A. CS-13 fast and CS-8 slow					
1.	Fast	Fast	959	19.27	8.00
2.	Fast	Slow	951	22.34	7.92
3.	Slow	Fast	538	24.23	4.48
4.	Slow	Slow	430	36.31	3.58
B. CS-21 fast, CS-14 slow and CS-stock					
1.	Fast	Fast	355	19.64	. . .
2.	Fast	Stock	385	20.21	. . .
3.	Stock	Fast	420	20.32	. . .
4.	Fast	Slow	360	21.16	. . .
5.	Slow	Fast	410	22.12	. . .
6.	Stock	Stock	394	22.66	. . .
7.	Stock	Slow	373	24.09	. . .
8.	Slow	Stock	404	25.14	. . .
9.	Slow	Slow	332	35.99	. . .
C. CF-17 fast and CF-stock					
1.	Fast	Fast	306	21.70	. . .
2.	Fast	Stock	297	22.31	. . .
3.	Stock	Fast	302	22.63	. . .
4.	Stock	Stock	269	23.53	. . .

* Corrected for regression of developmental time on density.

with beetles from the 14th, 21st and 17th generations of CS-slow, CS-fast and CF-fast respectively.

The data from the initial study are given in part A of Table 2. Developmental rates of the two reciprocal crosses are much closer to the fast parental strain. These observations can be accounted for on the basis of simple dominance of genes for fast development at some loci affecting developmental rate. Under this hypothesis one would expect much more fixation from selection for slow development than for fast development. In fact, it appears that some fixation may have occurred in the CS-slow line (see previous section).

The reciprocal crosses also indicate the presence of a maternal effect on developmental rate. This topic will be the subject of a separate report (see also DAWSON 1964b). Additionally, the previously mentioned drop in productivity in the CS-slow line apparently is the result of female infertility or reduced fecundity; at least it is not in large part associated with the males.

Parts B and C of Table 2 present the results of the experiment involving the terminal generations of the selection program. Once again, both reciprocal crosses between the fast and slow lines show developmental rates closer to the fast parent. In addition, hybrids involving the synthetic stocks and any of the selected lines are closer to the faster of the parents. Maternal effects were also observed in these experiments.

Further selection experiments: One further series of selection experiments, initiated from F_2 populations derived from reciprocal crosses between pairs of inbred lines may be briefly mentioned. Two pairs of CF inbred lines and one pair for CS were utilized. Data on the progress of selection for three generations were previously reported by DAWSON and LERNER (1962) in another connection. Realized heritability estimates from selection in the six hybrid populations are listed in Table 3. The estimates are quite similar to those obtained in previously described selection experiments.

DISCUSSION

The behavior of developmental rate in these studies follows closely that expected of a trait which is an important component of fitness in LERNER's (1954) model of genetic homeostasis. According to this model, fitness, which comprises

TABLE 3

Realized heritability estimates for developmental rate from three generations of selection from F_2 populations of hybrids between three sets of inbred lines

Selected line	$h^2 \pm$ SE
CF 9 × 11	0.131 ± 0.024
11 × 9	0.091 ± 0.045
CF 1 × 11	0.095 ± 0.076
11 × 1	0.044 ± 0.057
CS 3 × 5	0.204 ± 0.040
5 × 3	0.146 ± 0.029

the combined action of all traits affecting the reproductive value of a population, is based on overdominance. Metric traits which are important fitness components may have intermediate optima that result from superiority of heterozygotes with respect to fitness.

ROBERTSON (1956) has examined two models for reproductive superiority of intermediate phenotypes. In one model, where intermediate phenotypes are better merely because they are intermediate, fixation of genes controlling the trait is inevitable. However, when superiority of intermediates is based on heterozygosity, genetic variability will be maintained in the population.

Thus the intermediate optima for metric traits in LERNER's model arise from pleiotropic effects of genes for the metric trait which confer higher fitness on heterozygous individuals. Under this scheme the metric character may well possess an additive component of variance, but artificial selection for extremes leads to a reduction in fitness.

If this be the case, natural selection should oppose artificial selection for extremes to such an extent that response to selection may cease even though additive genetic variance is still present. Suspension of selection should lead to a return of the mean value of the metric trait toward its original level or to a new adaptive peak if the proper gene complexes are available, provided that fixation has not occurred.

The results from the present studies are for the most part in accord with this model. Selection for fast development in both species has been opposed by natural selection to such an extent that in later generations negative responses to selection were observed. Suspension of selection in these lines resulted in the return of developmental rate to or at least toward the original level of the foundation populations. Effective heritability is low; from 10 to 20% of the variation in rate of development is attributable to additive genetic sources.

Selection for slow development in CS presumably led to considerable progress toward homozygosity, and as a result the response to suspension of selection was weaker than in the fast selection lines. The change in humidity conditions in the incubator complicated the observation of progress under suspended selection. Artificial selection for slow development continued to be effective, indicating that additive genetic variance for developmental time was still present, and reverse selection was effective, though much less so than in the fast lines, in returning rate of development to its original level. Productivity also decreased considerably as a correlated response to selection. The tremendous increase in variance of developmental time further suggests a loss of heterozygosity and breakdown of buffering capacity.

This asymmetrical homeostasis is not particularly surprising in a trait so closely related to fitness. Models for the relationship between fitness and components of fitness lead to expected asymmetry of effect on fitness from two-way selection for the component character (ROBERTSON 1955; LERNER 1954, 1958).

The observed asymmetry of response to two-way selection in CS is easily explained by the model on the basis of directional dominance (FALCONER 1960; CLARKE et al., 1961). The model predicts that genes for developmental rate are

maintained at intermediate frequencies, possibly as a result of overdominance with respect to fitness. If there is simple dominance in the direction of fast development at some loci which affect developmental rate, selection progress will be greater in the slow direction. This is also the direction in which the mean should normally change under inbreeding. Directional dominance of this type would not be expected to result in asymmetry for the first few generations of selection, but only as gene frequencies become differentiated in the selected lines. Finally, this model predicts that the developmental rates of hybrids between the selected lines should be closer to the fast parent than the slow one.

All of these requirements are met by the selected lines. The response in early generations of selection was quite symmetrical; realized heritability estimates computed for seven generations of selection were 0.142 and 0.139 for CS-fast and CS-slow respectively. Asymmetry was observed in later generations, leading to a greater response to selection for slow development, although the exact amount of difference between fast and slow lines was obscured by the humidity change. Hybrids between the selected lines were found to be much closer to the fast parent.

Preliminary results of variance component analysis (DAWSON, unpublished) offer further support for the proposed model. Heritability estimates, averaged from several different methods of determination, are between 0.10 and 0.15 for both species. Maternal effects account for another 8 to 10% of the variation. In addition, on the basis of two experiments, there is evidence for a substantial dominance component of variance.

Finally, developmental rates were measured in 11 CF and 6 CS inbred lines which had been maintained by brother × sister mating for 32 to 35 generations (DAWSON 1964a). In all lines, development was slower than that of the synthetic strains from which inbreeding had been initiated, as predicted by the postulated model.

Asymmetrical response to selection for developmental rate was also observed by CLARKE et al. (1961) in Drosophila subobscura. As was the case with Tribolium, they found selection for slow development to be more effective. Crosses between selected lines were intermediate between the parents. This result invalidated an explanation based on directional dominance. Their explanation involved a "developmental barrier" and epistatic interactions between genes at different loci. It is not necessary in the present study to postulate the existence of such physiological limits, since the observations may be accounted for on the basis of the homeostatic model.

As previously mentioned, the proposed model leads to the prediction that fitness should decrease with artificial selection for either fast or slow development. A test for the model, utilizing competitive ability as a measure of fitness, will be described elsewhere.

SUMMARY

Artificial selection for fast and slow development in *Tribolium castaneum* and for fast development in *T. confusum* was successful in producing strains which differed from the foundation stocks with respect to this character. A genetic model, based on LERNER's notions of genetic homeostasis, was constructed to account for the selection responses and the results of other studies with the selected lines. It appears that developmental rate is maintained at an intermediate level in the foundation populations, possibly as a result of superiority of heterozygotes with respect to fitness.

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