STUDIES ON NATURAL POPULATIONS OF *DROSOPHILA*.
X. EFFECTS OF DISRUPTIVE AND STABILIZING
SELECTION ON WING LENGTH AND THE CORRELATED
RESPONSE IN *DROSOPHILA MELANOGASTER*

A. O. TANTAWY AND A. A. TAYEL¹

*Department of Genetics, Faculty of Agriculture, Alexandria
University, Alexandria, Egypt, U.A.R.*

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DIFFERENT forms of selection have proved useful tools in the study of quantitative variation. These may be classified as directional, stabilizing and disruptive. Stabilizing selection is believed to act against artificial directional selection, since its natural role is to maintain the mean of the population about a particular level, which is determined by adaptive requirements. Theoretical discussions of stabilizing selection have been given by WRIGHT (1935), ROBERTSON (1956), KOJIMA (1959), and CURNOW (1964). Disruptive selection has been discussed by MATHER (1955) and various experiments have been reported by THODAY and associates—e.g., THODAY and BOAM (1959); THODAY (1965).

The experiments dealt with in the present paper refer to the effects of disruptive and stabilizing selection for wing length in a natural population of *Drosophila melanogaster*. The investigations are therefore largely concerned with the genetic effects of different ways of selection on wing length as a character selected for and thorax length is a character measured in order to determine correlated response.

MATERIALS AND METHODS

Initial foundation population: The foundation population, from flies newly captured at the University of Alexandria Farm, is similar to that used by TANTAWY and MALLAH (1961). Wing and thorax lengths of live flies were measured and egg viability was estimated as suggested by ROBERTSON and REEVE (1952).

Experimental design: Means and heritability estimates of wing length, thorax length in the initial foundation population were estimated before starting the selection experiments. The procedure for the progeny tests was exactly similar to that used by TANTAWY and EL-HELW (1966).

Two different types of selection were used, i.e., disruptive selection (large males $\times$ small females) or the reciprocal cross (small males $\times$ large females) and stabilizing selection (medium males $\times$ medium females). Samples of flies from the initial population were taken at random to be fed and mated in ten different food bottles (20 pairs/vial) for three days. The mated flies were then placed in oviposition bottles and samples of eggs, from each bottle, were cultured in five food vials (70 eggs/vial). Six selected lines with their controls were carried out separately from the progeny of the first seven bottles. The first four bottles were used to establish the four disruptively selected lines; two lines in each type of mating. Another two lines were maintained by stabilizing selection and the seventh line was maintained by mass mating to act as unselected controls.

¹ Present address: Dept. of Genetics, Ain Shams University, Cairo, U.A.R.

The disruptively selected lines in which large males were mated with small females were designated as ALS and BLS. Similarly, the lines in which small males were mated with large females were designated as CSL and DSL. The stabilizing selected lines were designated as EMM and FMM.

Each selected line was treated by measuring 60 pairs of flies in three sublines (A', B' and C') 20 pairs in each subline, and the selected flies from each subline were mated together in a cyclical system of mating as shown by ROBERTSON and REEVE (1952) which minimizes the inbreeding inevitable in the selected lines. The flies in each line were selected on the basis of their deviations from the vial mean rather than their absolute size. In each line nine pairs of flies were used from a total number of 60 pairs, i.e., 15% of flies were selected to be the parents of the next generation. For details of the cyclical system used in the present experiments see TANTAWY, MALLAH and TEWFIK (1964).

In lines ALS and BLS the three largest males and the three smallest females, and in lines CSL and DSL the three smallest males and the three largest females, from each of the sublines were selected and mated within each type of mating according to the same kind of cyclic system. Lines EMM and FMM were maintained by calculating the means of wing length for all the sublines and the three males and females, with wing length closest to the population mean were selected and mated. This procedure was repeated for ten generations. In each selected line, one other mating was set up as a reserve to be used if the first mating did not breed, but hatching flies were used in the estimate of percentage emergence. The selected lines were always continued from the first mating.

Selection was relaxed, for five successive generations, in all the selected lines, after the 5th and 10th generations of selection. At each generation of relaxed selection in each selected line, 20 pairs of flies were measured for wing and thorax lengths and mass mated. Percentage emergence was estimated in the relaxed lines in the same way as in the selected lines.

After 10 generations of selection, lines BLS, DSL and FMM were terminated, while lines ALS, CSL and EMM were subjected to directional selection for five generations, using the same mating procedure, as mentioned before, except that the matings were between the largest or the smallest flies. A control population was carried out with mass mating at every generation of selection and given the same treatments as the selected lines.

Heritability estimates for wing and thorax lengths were calculated after the 5th and 10th generations of stabilizing and disruptive selection as well as after the five generations of directional selection. The technique used for the heritability estimates was essentially the same as that used in the base population, and the offspring-midparent regression method was used in the data of each progeny test.

In each generation and throughout the experimental work, records were kept for wing length, thorax length, number of eggs cultured and number of adults hatched to study the correlated response to selection. All the present experiments were carried out in a refrigerated incubator with a constant temperature of $25 \pm 0.5^\circ\text{C}$.

RESULTS

The base population: The means for each of the characters studied in the base population, their coefficients of variation and heritability estimates are presented in Table 1, which shows that body size, i.e., wing and thorax lengths in *Drosophila melanogaster*, possess high additive genetic variance and low phenotypic variation. The genetic correlation between wing and thorax length is very high in the positive direction. These results on the initial population agree well with those reported by TANTAWY and EL-HELW (1966; 1970) working on a similar population of *D. melanogaster*.

Response to selection for wing length and the correlated response on thorax length: The data obtained in the present experiments indicated, within a given

TABLE 1

*Means ($\bar{X}$) and coefficients of variation (C.V.%) for wing and thorax lengths
(units of measurements are of 1/100 mm)*

Character	Males		Females		Heritability estimates	Genetic correlation
	$\bar{X}$	C.V.	$\bar{X}$	C.V.		
Wing length	187.22	2.46	212.75	2.28	0.362 ± 0.032	0.774 ± 0.053
Thorax length	93.45	2.62	106.15	2.45	0.344 ± 0.024	

Heritability estimates and the genetic correlation between both dimensions in the initial foundation population are presented with their standard errors.

type of mating, that the response to selection in males is almost the same as in females. Therefore, the results for the two sexes within line in each type have been combined.

Figure 1 shows the response to selection for wing length in each of the selected lines as a primary character and on thorax length as a secondary one. The response to selection is presented as percentage deviations from controls. The results indicate clearly that stabilizing selection in both lines of EMM and FMM, as expected, has no effect on wing length; this character fluctuated around the control level at all generations of selection, while the disruptively selected lines behaved differently. Disruptive selection is effective in separating the initial population into high and low lines; this response depends on the type of mating and the response is in the male side. The results show that large males mated to small females (lines ALS and BLS) lead to little change, if any, in wing length, but small males mated to large females (lines CSL and DSL) cause a great reduction in wing length.

Figure 1b shows that, in the stabilizing selected lines, thorax length behaves like wing length. The disruptively selected lines show the effects of males on thorax length. The similarity in behavior of thorax length and wing length is expected due to the high positive genetic correlation between them (Table 1).

In all the characters, relaxed selection (data not included) caused the selected lines to go back to the control level.

Effects of directional selection: After the 10th generation of selection one line from each type of selection was subjected to directional selection for five generations. The aim of this test was to discover the genetic flexibility in the stabilizing and the disruptively selected lines.

Figure 2 shows the results for wing length as the primary character and thorax length as a secondary one. Directional selection is effective both in plus and minus directions especially in favor of selection to small size. In all the characters, the disruptively selected line when subjected to directional selection displays more response to selection than the stabilizing selection line.

Figure 3 presents the results as divergence between high and low lines; line I shows the results obtained when directional selection was practiced on the initial population. Results of line I were taken from the data published by TANTAWY

FIGURE 1.—Reponse to selection with different types of selection presented as percentage deviations from controls.

and EL-HELW (1966) who used a similar stock. The results show in both wing and thorax lengths, that directional selection, preceded by disruptive selection, shows more rapid divergence at least in the earlier generations than in the stabilizing or I lines. The data demonstrate that the genetic flexibility established by disruptive selection is greater than that in the original population from which the experiments began (line I) and greater than that in the stabilizing selection. Similar results were reported by THODAY (1965) on disruptively selected lines.

FIGURE 2.—Response to directional selection in the stabilizing (EMM) and in the disruptively (ALS and CSL) selected lines. The response is presented as percentage deviations from controls.

Coefficients of variation: Phenotypic variation for wing and thorax lengths are calculated as coefficients of variation in order to minimize the effects of change of mean on variance. It was found that males and females have nearly the same variation (Table 1) so that their coefficients have been averaged. The results, presented in Figure 4, indicate that the disruptively selected lines (CSL and DSL) display an increase in the coefficients of variation of both wing and thorax lengths. Lines ALS, BLS, EMM and FMM give almost the same variation as the control population. Examination of Figure 4 reveals that generally the variance changed in the expected directions, i.e., coefficients of variation decreased in the stabilizing selected lines and increased in the disruptively selected ones. The average of the disruptively selected lines differentiated from the rest at about the 4th generation and exhibited a steady increase throughout the experiment. These results are in agreement with those reported by THODAY (1959) who showed that the phenotypic variance in the disruptive selected lines is greater than either the original wild population or in the stabilizing selected lines. PROUT (1962) arrived at the same conclusions for the developmental time in *D. melanogaster* and stated that "the two modes of selection were the causes of the observed changes in variability."

FIGURE 3.—Divergence between high and low lines in the directional selected lines presented as deviations from controls. Line I presents the divergence when directional selection was practiced on the initial population.

When selection was relaxed (data are not included) the lines display almost the same variability as in the controls.

Figures 4c and d give the coefficients of variation for the five generations of directional selection. The data indicate, in general, that minus lines show more variation than plus lines. Moreover, the disruptively selected line CSL shows higher variation in the plus and minus directions than the other selected lines, which fluctuate around the control level.

Heritability and genetic correlation in the selected lines: The results of the heritability tests and the genetic correlation between wing and thorax lengths are presented in Table 2; heritability of thorax length is not shown since the estimates are almost the same as those found for wing length. Table 2 shows that the various estimates for wing and thorax lengths, at the 5th generation, do not show significant differences from the values in the base population. At the 10th generation, only line ALS shows a significantly higher estimate, compared with the controls. There is a general trend for the heritability of wing length in lines CSL and EMM to decrease. The same phenomenon was apparent in the values of the genetic correlation. PROUT (1962) reported that the stabilizing and dis-

FIGURE 4.—Coefficients of variation for wing and thorax lengths in the different selected lines. c and d show the C.V. % in the directional selected lines.

ruptively selected lines of *Drosophila melanogaster* gave lower heritability estimates for developmental time than the control population.

Heritability estimates in the directional selected lines were increased as compared with the controls; the disruptively selected lines ALS and CSL showed a higher increase than the EMM line. Comparing the heritability estimates in all the selected lines, all demonstrate an increase in the additive genetic variance as compared with the controls, while line I shows the least increase.

TABLE 2

Heritability estimates for wing length in the different selected lines at different generations of selection and the genetic correlation between wing length and thorax length with their respective standard errors

Lines and generations	Heritability estimates for wing length		Genetic correlation between wing and thorax lengths	
Generation 0	0.361 ± 0.041		0.774 ± 0.076	
Generation 5				
Controls	0.343 ± 0.054		0.793 ± 0.081	
ALS	0.359 ± 0.127		0.736 ± 0.059	
CSL	0.293 ± 0.040		0.703 ± 0.067	
EMM	0.258 ± 0.045		0.801 ± 0.071	
Generation 10				
Controls	0.346 ± 0.049		0.786 ± 0.080	
ALS	0.654 ± 0.063		1.000 ± 0.093	
CSL	0.240 ± 0.034		0.649 ± 0.083	
EMM	0.219 ± 0.091		0.632 ± 0.071	
Directional selection for five generations				
Controls	0.348 ± 0.049		0.804 ± 0.078	
Selected lines	Plus	Minus	Plus	Minus
ALS	0.568 ± 0.050	0.485 ± 0.049	0.798 ± 0.078	0.709 ± 0.071
CSL	0.520 ± 0.064	0.500 ± 0.051	0.854 ± 0.064	0.801 ± 0.066
EMM	0.402 ± 0.005	0.399 ± 0.048	0.723 ± 0.067	0.713 ± 0.074
I*	0.291 ± 0.038	0.299 ± 0.025	0.951 ± 0.068	0.936 ± 0.063

* Selected line by directional selection for six successive generations, after TANTAWY and EL-HELW (1966).

Percentage emergence: The percentage emergence was calculated as the number of flies that hatch from a given number of eggs. The results for all the selected lines, presented in Figure 5, indicate after the third generation, that CSL and DSL lines display the lowest percentage emergence which is much lower than the control level. One may conclude from the results of the average of ALS, BLS, CSL and DSL lines that the disruptive selection causes a greater decrease in viability than does stabilizing selection. These results agree with those reported by PROUT (1962).

Figure 5b shows the percentage emergence in the directional selected lines and these show that the minus selected lines have a lower percentage emergence than the plus ones. Lines ALS and CSL give lower values than does line EMM.

DISCUSSION

Results obtained from the present experiments indicate that the mean wing length as well as other correlated characters under stabilizing selection fluctuate, at every generation of selection, around the mean of the control population. These results agree with those reported by THODAY (1959), PROUT (1962) and others.

FIGURE 5a.—Percentage emergence in the different types of selected lines.
b.—Percentage emergence after five generations of directional selection.

The disruptively selected lines show various responses to selection. Large males mated to small females lead to an increase in body size; the reciprocal mating displays a reverse situation. Such a phenomenon may indicate the importance of male size, at least in the present experiments, in disruptive selection. A considerable element of chance is involved in the early selection. Alternatively, it suggests that sex-linked effects are important and that single-dose effects may allow selection to be more discriminating. The present results differ from those given by GIBSON and THODAY (1964) who reported insignificant divergence between the reciprocal crosses of the disruptively selected lines for sternopleural chaeta number in *Drosophila melanogaster*. However, the results of TANTAWY and EL-HELW (1966) show that the base population used in the present experiments responds more readily to selection for small than for large wing length. If we postulate that small wing length in this population is dependent upon rare recessive sex-linked genes to which such autosomal variance as there may be is essentially hypostatic, both the asymmetrical response to directional selection

and the difference between the reciprocal disruptive selection lines are explicable. The dominance would ensure that response to selection for long wings will be slight, and selection for short wings will be much more effective if produced on males than on females.

The record of phenotypic variation in the different selected lines indicates that stabilizing selection leads to less variability than does disruptive selection; the latter type of selection gives higher coefficients of variation than even the control population. These results indicate that disruptive selection would maintain a wide variety of genotypes in a population, and agree with those of THODAY and BOAM (1961). Reduction of variability in the stabilizing selected lines could be explained by two chief mechanisms. One is by reduction of nongenetic variance through increased stability of development (WADDINGTON 1953); the other by reduction of genetic variance, either through reduction of the frequencies of extreme alleles or through the build-up of balanced linkage relation among the genes concerned (MATHER 1943). The second mechanism is probably the main cause in the reduction of the phenotypic variation in the stabilizing selected lines of the present work due to the gradual decrease in the genetic variability (Table 2).

The estimated genetic variance for wing length in all the selected lines remained almost unchanged in the earlier generations of selection; in the later ones, line ALS almost doubled its heritability estimates while other selected lines displayed a decrease in the additive genetic variance. These results may indicate that selection in which large males were mated to small females may increase the genetic variability of the selected character and this may give a clue to the cause of the high plus response in lines ALS and BLS. Possibly this kind of disruptive selection would change the gene frequencies of the plus genes which affect body size and hence the genetic variance increases.

On the other hand, additive genetic variance remained almost constant in the CSL line, while line EMM demonstrates loss in the heritability estimates. The results obtained in the line EMM are in accordance with theory which predicts a decrease in the genetic variability (WRIGHT 1935; ROBERTSON 1956). GIBSON and THODAY (1963) reported higher heritability estimates in the stabilizing selection line than the controls and they attributed this behavior to maternal or cytoplasmic inheritance.

Changes in the viability of the selected lines follow expectation. All the selected lines show less viability than the controls. But in general, the disruptively selected lines (average of all lines) display the least percentage emergence as compared to the other selected lines. One may conclude, therefore that the fitness of phenotypic intermediates is greater than that of the extreme types, which indicates that natural selection favors individuals closer to the population mean. Such superiority in fitness is not entirely phenotypic but is based in great part on genetic differences in fitness.

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SUMMARY

It has been shown that the weighted means for the heritability estimates in the initial foundation population were found to be 36.17 and 34.42% for wing and thorax lengths, respectively. The genetic correlation between both dimensions was high in the positive direction.—Selected lines under stabilizing selection fluctuated around the population mean; disruptively selected lines displayed various responses to selection. When selection was changed, after the 10th generation to directional selection, the selected lines showed response both in the plus and especially in the minus direction. The disruptively selected lines demonstrated more response to directional selection than other types of selection. Correlated response to selection indicated that thorax length displayed almost the same behavior as wing length.—The phenotypic variability in the selected lines did not change under stabilizing selection or in the ALS and BLS lines, but lines CSL and DSL showed an increase.—Heritability estimates after the 5th generation did not show any significant differences from the base population, but after the 10th the disruptively selected line ALS gave a significantly higher value.

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