Phenotypic Variability and Divergence in Disruptive Selection

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Summary. Two types of disruptive selection (HL and LH) were performed on three lines (M, F and K) which had reached different plateaus, following a previous directional selection applied independently on the two sexes. Increase in phenotypic variability and the appearance of a bimodal frequency distribution of wing length measurements were considered as responses to disruptive selection.

These responses are shown not to be linearly related; moreover both responses seem not to be related to the genetic and phenotypic variability present in the population when disruptive selection was started.

These results and the persistent differences between LH and HL selections are interpreted as to suggest that the effects of disruptive selection are mainly dependent on changes in the developmental patterns of the genes involved and of their connections.

The suggestion is advanced that the results presented are inconsistent with the assumption that the effects of disruptive selection be explained by genetic or developmental switch mechanisms or by chromosomal polymorphism.

Introduction

Fairly general agreement has been reached on the validation of Mather's (1955) statement that disruptive selection results in increased phenotypic variability, while the mean value of the selected character remains unchanged. Until now, however, no clear cut interpretation has been available for the genetic basis of such phenotypic variation. Earlier experiments by Falconer and Robertson (1956) and by Thoday (1958, 1959) showed the presence of a large additive portion of variance. Thoday and Boam (1959) and Thoday (1960) analyzed populations under disruptive selection, and concluded that the increased variability was dependent on genetic polymorphism resulting from, and maintained by, the disruptive selection performed. On the other hand, Robertson (1970) was unable to prove that the increased phenotypic variability following disruptive selection could be related to a similar increase in the additive genetic component of the variance. Again, Scharloo (1970a, b) argues that two types of increased variability, developmental and genetic, may be found, which result from developmental and genetic switch mechanisms respectively; different results on the developmental and genetic systems may be reached according to the procedures by which disruptive selection has been carried out.

Given these difficulties in understanding the genetic basis of the increased phenotypic variability, it follows that the relationships between disruptive selection and divergence within a population become a disputable topic. It would seem that the understanding of the genetic basis for the outcome of disruptive selection should be approached from various points-of-view, to obtain the largest possible amount of experimental information.

Starting from the suggestion by Palenzona and Graziani (1972), that directional selection is able to change the relationships between phenotypic and genetic variabilities, the present paper reports the results obtained by applying disruptive selection to populations where these changes had occurred.

Material and Methods

Three populations of *Drosophila melanogaster* were subjected to a disruptive selection by assortative negative mating over sixteen generations. These lines were derived from a single initial population obtained by crossing flies from a Canton and a *vg* strain; subsequently, females and males were independently selected for short wing and then backcrossed to vestigial flies from the *vg* strain. The subsequent generations of selection were produced as follows:

M line = directional selection on heterozygous $(+/vg)$ ♂♂ mated to vestigial ♀♀ from the same line;

F line = directional selection on heterozygous $(+/vg)$ ♀♀ mated to vestigial ♂♂ from the same line.

After 78 generations of selection the two populations had reached different plateaus of response; F line showed a mean wing length lower than that of M line while manifesting a larger amount of phenotypic variability (further details in Palenzona and Alicchio, 1973a, where the same lines were indicated as HF and HM, respectively).

From the plateaued F line another (K line) was obtained by selecting for short wing heterozygous males instead of females. K selection resulted in a decrease of the character's mean value and phenotypic variability.

The effects of disruptive selection were then studied, starting from these three populations characterized by different degrees of phenotypic and genetic homogeneity. From each population two lines of disruptive selection were obtained:

HL = ♀♀ showing a high value of wing length mated to ♂♂ with a low value;

LH = ♀♀ showing a low value of wing length mated to ♂♂ with a high value.

At each generation the wing length of 100 females and 100 males was measured on the fourth longitudinal vein (the same as for the previous directional selection) by means of a micrometer (1 micrometric unit = 0.39 mm.). The whole experiment was replicated twice at a constant 25 °C. temperature, under the same experimental conditions.

Results

The differing responses of the M, F, and K lines to directional selection are schematically represented in figure 1.
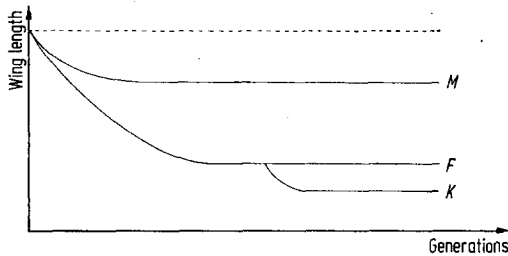

Fig. 1. Schematic representation of the response to directional selection in M, F and K lines

Results obtained from disruptive selection (figures 2, 3 and 4) are given only for the measurements taken on females, since no relevant differences were found between the measurements taken on the different sexes as far as the responses to disruptive selection were concerned.
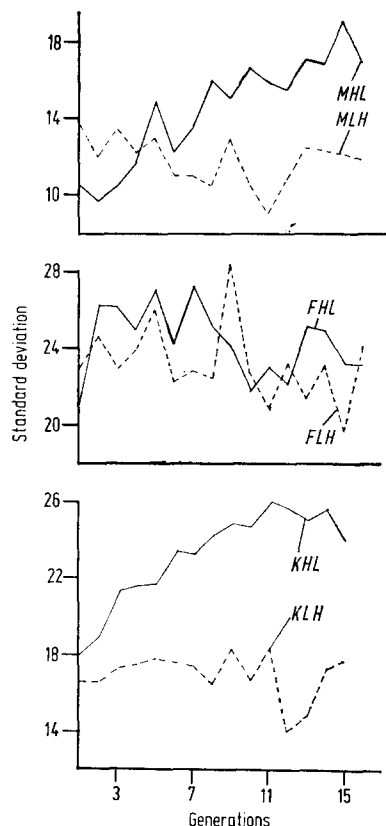

Fig. 2. Standard deviation values at each generation of disruptive selections (HL and LH) in M, F and K lines

Standard deviation values of wing length measurements at each generation of selection are shown in figure 2 for the three lines (M, F, K) and the two selections (HL and LH) considered. Phenotypic variance shows a large increase in lines M and K following disruptive selection HL, while only a small increase is detectable in LH selections. FHL and FLH lines do not manifest an increase in variability during disruptive selection; in these lines standard deviation values are already large from the start, and larger than in the M and K lines. Consequently, variability is quite similar in the HL and LH selections within F line, while the two selections HL and LH become differentiated for wing length variability in the M and K lines.
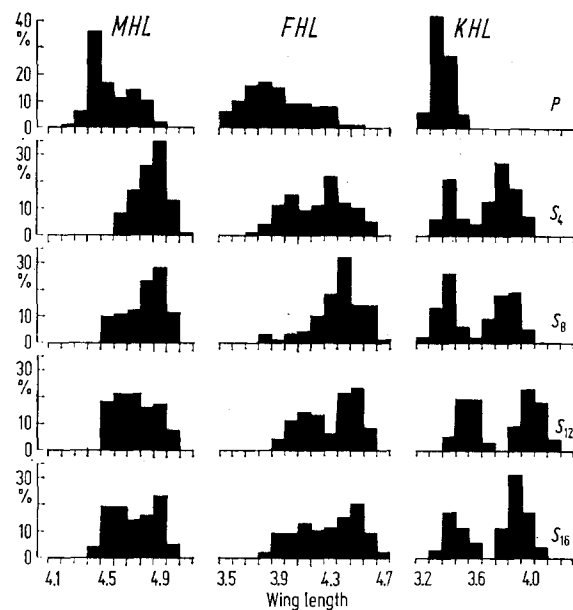

Fig. 3. Frequency distribution of wing length measurements HL selection. M, F and K lines

It might be expected that the increase of phenotypic variability due to disruptive selection would result in polymorphism for wing length. The frequency distribution of the wing measurements taken on the parental populations and at the 4th, 8th, 12th, 16th generation of selection are shown in figures 3 and 4 (which report the results obtained in HL and LH selections, respectively); they suggest that in both selections some kind of bimodality does indeed appear, and is more evident in the selection HL and the K line. This bimodality seems to be manifest in the three lines in proportion to the intensity of response to the previously completed directional selection. In particular, bimodality is less evident in F than in K, and in M than in F, lines. It is also apparent that in K line the bimodality of the frequency distribution becomes detectable at an earlier generation than in the F and M lines.
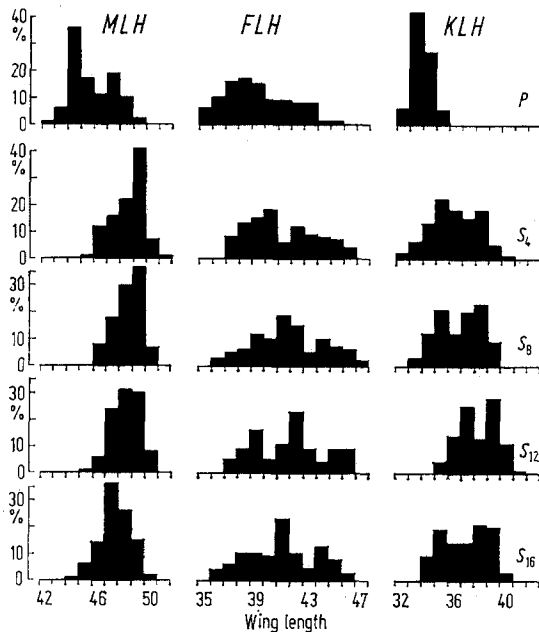
Fig. 4. Frequency distribution of wing length measurements. LH selection. M, F and K lines

Examining the results of the LH selection, a similar trend may be noticed for the appearance of bimodality in the frequency distribution, except that the intensity of the phenomenon is considerably less pronounced than in the HL selection.

Mean values seem to increase in all the populations considered and these changes seem to be independent of the increase in phenotypic variability; the intensity of bimodality exhibited seems also to be unrelated to the changes in phenotypic variability and to the mean values of the character.

Discussion

It has been suggested that, even if it is not a necessary condition for it (Mather, 1955), stable polymorphism is usually followed by reproductive isolation (Thoday and Gibson, 1962). The rise in divergence resulting from disruptive selection has been attributed to switch mechanisms, developmental and/or genetic, (Scharloo, 1970a, b) or to linkage disequilibrium and related chromosomal polymorphism (Thoday, 1960). These hypotheses are based on the preliminary assumptions that there is a certain degree of correspondence between phenotypic and genetic variability and that disruptive selection is able to reach and use genotypic differences through phenotypic variation.

If these preliminary assumptions hold true, the presence of an "amplifier", be it a switch mechanism controlling the phenotypic divergence or a chromosomal polymorphism, may be the simplest interpretation of the phenomenon.

From these hypotheses it follows that disruptive selection results in an increase of genetic and/or developmental variability, followed by an increase of phenotypic variability and the appearance of a bimodal or multimodal frequency distribution of the selected trait. This is identified as the starting point of a divergence process within a population, whose intensity depends on the amount of variability already present in the population (Thoday, 1967; Thoday and Gibson, 1970, 1971; Scharloo, 1971).

The results obtained from the experiments reported in the present paper seem to suggest that the response to disruptive selection is neither dependent on genetic nor on phenotypic variability present in the population; moreover it seems that the relationship between increase of phenotypic variability and bimodality of frequency distribution may not be as simple as suggested by the previously mentioned authors.

Directional selection is supposed to result in increased homozygosity due to the fixation of alleles, and the degree of this fixation is directly proportional to the response to selection. As a consequence it might be expected that the genetic variability available for a further response to disruptive selection would decrease from M to F to K lines. In fact, phenotypic variability reaches its maximum value following directional selection in the F line; M line shows a phenotypic variability lower than F and the lowest value is observable in K. Disruptive selection, on the contrary, results in a large increase of phenotypic variability in lines K and M when selection HL is carried out. It seems evident that this effect of disruptive selection is neither related to the genetic variability left by directional selection nor to the phenotypic variability present in the population when disruptive selection was started. This suggests that:

a) disruptive and directional selection utilize different types of genetic variability; or

b) disruptive selection utilizes genetic heterogeneity in a different way with respect to directional selection; or

c) disruptive selection does not use genetic variability.

Considering now the appearance of bimodality in the frequency distribution of wing length in the populations examined, it may be observed that its manifestation is inversely proportional to the genetic variability supposedly left after directional selection has reached the plateau. Moreover the clearness of bimodality does not seem to be in direct relationship with the increase of phenotypic variability following disruptive selection. These results seem to be in complete disagreement with the switch mechanism concept as an amplifier and also with the hypothesis of a chromosomal polymorphism underlying the phenotypic polymorphism.

In fact these hypotheses are strictly dependent on a direct relationship between increased phenotypic variability and phenotypic polymorphism.

An explanation for the action of disruptive selection might possibly be found in the differences between the M, F and K lines prior to the start of disruptive selection itself. Palenzona and Alicchio (1973 a, b) suggested that, in these lines, directional selection on the different sexes accumulates genes having distinct development patterns; the different limits of response in the three lines were reached largely because of the different developmental arrangements of the genes involved.

From this suggestion the hypothesis can be derived that disruptive selection is active on the developmental patterns of the genes involved and on their connections; in particular disruptive selection may be thought to affect the canalization of development, without the need of a pre-existing switch mechanism.

This explanation is quite consistent with the results obtained: in particular the observed difference between HL and LH selections seems to be given a convincing explanation.

In fact directional selection has been supposed to build up differences in developmental patterns among M, F and K lines related to the sex phenotypes: if the subsequent disruptive selection acts on these changed patterns it seems reasonable that different responses are to be expected according to the different sex phenotypes acted upon. It must be added that while the phenotypic variability in F line appears to be similar in the HL and LH selections, genetic analysis (Alicchio and Palenzona, 1973) has revealed a differentiation between the two, possibly due to the disruptive selection applied; this is probably the best supporting evidence that no structural differences such as switch mechanisms or chromosomal polymorphisms are really needed for a disruptive selection to be effective.

Literature

Alicchio, R., Palenzona, D. L.: Genetic heterogeneity and disruptive selection. Boll. Zool. **40**, 223—229 (1973).

Falconer, D. S., Robertson, A.: Selection for environmental variability of body size in mice. Z. indukt. Abstamm.- u. -Vererb.lehre **87**, 385—391 (1956).

Mather, K.: Polymorphism as an outcome of disruptive selection. Evolution **9**, 52—61 (1955).

Palenzona, D. L., Alicchio, R.: Differential response to selection on the two sexes in Drosophila melanogaster. Genetics **74**, 533—542 (1973a).

Palenzona, D. L., Alicchio, R.: Genetic variability and selection progress. Polymorphism as an outcome of directional selection. I. Sexual dimorphism for wing length. Atti Accad. Sci. Bo. Memorie Ser. III **2**, 27—38 (1973b).

Palenzona, D. L., Graziani, M.: Control of phenotypic variability in selected populations of Drosophila melanogaster. Theor. Appl. Genet. **42**, 316—318 (1972).

Robertson, A.: A note on disruptive selection experiments in Drosophila. Am. Natur. **106**, 561—569 (1970).

Scharloo, W.: Stabilizing and disruptive selection on a mutant character in Drosophila. II. Polymorphism caused by a genetical switch mechanism. Genetics **65**, 681—691 (1970a).

Scharloo, W.: Stabilizing and disruptive selection on a mutant character in Drosophila. III. Polymorphism caused by a developmental switch mechanism. Genetics **65**, 693—705 (1970b).

Scharloo, W.: Reproductive isolation by disruptive selection: did it occur? Am. Natur. **105**, 83—86 (1971).

Thoday, J. M.: Effects of disruptive selection: the experimental production of a polymorphic population. Nature, Lond., **181**, 1124—1125 (1958).

Thoday, J. M.: Effects of disruptive selection. I. Genetic flexibility. Heredity **13**, 187—203 (1959).

Thoday, J. M.: Effects of disruptive selection. III. Coupling and repulsion. Heredity **14**, 35—49 (1960).

Thoday, J. M.: The general importance of disruptive selection. Genet. Res. **9**, 119—120 (1967).

Thoday, J. M., Boam, T. B.: Effects of disruptive selection. II. Polymorphism and divergence without isolation. Heredity **13**, 205—218 (1959).

Thoday, J. M., Gibson, J. B.: Isolation by disruptive selection. Nature, Lond., **193**, 1164—1166 (1962).

Thoday, J. M., Gibson, J. B.: The probability of isolation by disruptive selection. Am. Natur. **104**, 219—230 (1970).

Thoday, J. M., Gibson, J. B.: Reply to Scharloo. Am. Natur. **105**, 86—88 (1971).

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