

Quantitative Inheritance and Divergence in *Drosophila* Populations¹

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Summary. Divergent sub-populations were obtained following relaxation of artificial selection for short wing in a population of *Drosophila melanogaster*. Different results were obtained by relaxing the selection pressure in lines resulting from different selection procedures. The divergence was actually observed between lines derived by reciprocal crosses between vestigial and wild-type heterozygotes belonging to the same selection line. There was a difference in phenotypic variability in the two sub-lines from the start, which might be responsible for the differential response to natural selection. No difference in reproductive fitness has been detected between the divergent lines. The results can not be easily understood in the framework of an additive polygenic model; it is suggested that some complex interaction may be involved, acting on the developmental processes. It seems, however, safe to suggest that the divergence observed is determined by factors which are present in the FM line.

Introduction

The establishment of a phenotypic divergence within a population is assumed to be due to environmental and genetic causes: it requires the presence of a convenient amount of genetic variability to be utilized by selection and of genetic isolation to produce different sub-populations. A number of authors following Mather's view (1955) that disruptive selection may result in polymorphic populations, questioned the necessity for isolation: Thoday and Boam (1959) and Millicent and Thoday (1960, 1961) presented evidence that divergent populations can be obtained without interruption of gene-flow. On the other hand, Wallace (1968, p. 397) and Mayr (1970, p. 472) argued that all available evidence indicates that disruptive selection is not likely to occur under natural conditions.

However the question of the relative roles of extrinsic versus intrinsic factors in determining the appearance of a phenotypic divergence in a population is far from settled. The aim of the present paper is to gather further evidence on the possibility that divergence might arise from a continuous process involving mainly changes in population structure.

Material and Methods

Directional selection for short wing was performed on either sex of a *Drosophila melanogaster* population: lines *M* and *F* have been described elsewhere (Palenzona and Graziani 1972); Line FM was obtained from the line at the 54th selection generation, and maintained by mating the heterozygous males showing the shortest wing length to randomly chosen vestigial females from the same selection line. Selection pressure was relaxed after 54 generations of selection in *M* and *F* and 12 generations of selection in FM. The two subpopulations obtained by

crossing heterozygous with vestigial flies within the same population without selection are indicated by the following symbols:

1. S. R. M. = heterozygous male crossed with vestigial female ($\varphi\ vg/vg \times \delta\ +/vg$)

2. S. R. F. = heterozygous female crossed with vestigial male ($\varphi\ +/vg \times \delta\ vg/vg$)

and in particular,

from selected line M: 1 = S. R. M. (M)
2 = S. R. F. (M)

from selected line F: 1 = S. R. M. (F)
2 = S. R. F. (F)

from selected line FM: 1 = S. R. M. (FM)
2 = S. R. F. (FM)

The crossing design by which the S. R. (selection relaxed) lines have been obtained from the selected lines are shown in Tables 1, 2 and 3.

All the populations considered above were raised in duplicate, each replicate consisting of the progenies from 18 single matings. Care was taken to avoid the differential effect of crowding and temperature was kept constant at 25 °C. The results reported below refer to the 54th generation of selection in the *F* and *M* lines as "generation 0". 1 unit of wing length measures 0.39 mm.

Results

The results obtained in the two independent replications of each experiment, as well as those obtained for flies of different sexes within each line did not show significant differences: therefore only the measurements taken from female flies are reported as averages of the two replicates. In Figure 1 it may be seen that a significant additional response is obtained by selecting the males in the *F* population, where selection in females has already reached a plateau (FM line). Relaxation of selection pressure in lines *M*, *F*, and FM produced the results shown in Figures 2, 3 and 4 respectively. A clear cut divergence between the relaxed lines derived from the

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Table 1. Crosses used to obtain the initial generations S. R. M.(M) S. R. F.(M) from line M

Line	Generation	Genotypes in line M, 53rd generation			
		♀♀ + vg	♂♂ vg vg	♀♀ vg vg	♂♂ + vg
M	54th	—	—	random × selected	—
S. R. M.(M)	1st	—	—	random × random	—
S. R. F.(M)	1st	random × random	—	—	—

Table 2. Crosses used to obtain initial generations S. R. M.(F) and S. R. F.(F) and selected line FM from line F

Line	Generation	Genotypes in line F, 53rd generation			
		♀♀ + vg	♂♂ vg vg	♀♀ vg vg	♂♂ + vg
F	54th	selected × random	—	—	—
S. R. M.(F)	1st	—	—	random × random	—
S. R. F.(F)	1st	random × random	—	—	—
FM	1st	—	—	random × selected	—

Table 3. Crosses used to obtain initial generations S. R. M.(FM) and S. R. F.(FM) from line FM

Line	Generation	Genotypes in FM line, 11th generation			
		♀♀ + vg	♂♂ vg vg	♀♀ vg vg	♂♂ + vg
FM	12th	—	—	random × selected	—
S. R. M.(FM)	1st	—	—	random × random	—
S. R. F.(FM)	1st	random × random	—	—	—

same selected population, i. e. between S. R. M.(FM) and S. R. F.(FM), is seen in Figure 4, in other words, between progenies from the crosses ♀ *vg|vg* × ♂ *+|vg* and ♀ *+|vg* × ♂ *vg|vg*, respectively. The vestigial and heterozygous flies were initially drawn from the same FM selection line. No divergence has been observed between the similarly relaxed lines from the F selection line (Figure 3), while the small diver-

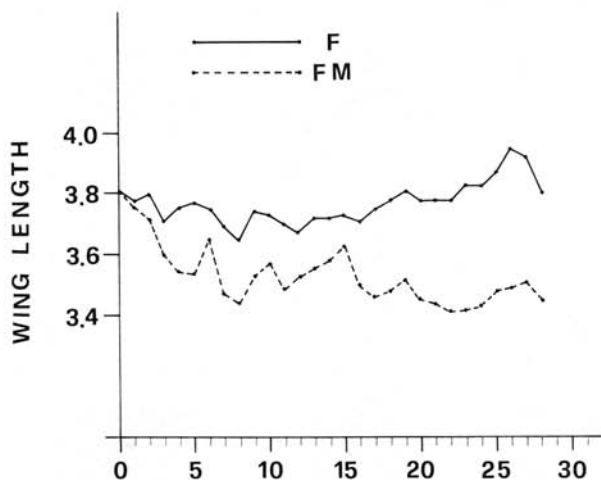


Fig. 1. Mean wing length in the F (selected females) and FM (males selected after selection in females) selection lines

gence seen after relaxation of the selection pressure in the lines derived from M (Figure 2) does not seem to be as clear-cut as that observed in the subpopulations from the FM selected line (cf. Figure 4).

The effect of relaxing the selection pressure in lines F and FM when crossing heterozygous females with vestigial males within the same population is shown in Figure 5. It can be seen that after a few generations the mean wing length in S. R. F. (FM) becomes very similar to that of line S. R. F.(F), thus reversing the effect of the FM selection. A similar comparison performed in Figure 6, for the relaxed lines which were maintained by crossing heterozygous males to vestigial females from the same population, shows that the line derived from the FM selection line is not able to return with respect to the direction of selection.

Discussion

The divergence observed between sub-populations derived from the FM selected line is quite unexpected on the basis of the classical hypothesis of quantitative inheritance. In fact, the two lines, S. R. M. (FM) and S. R. F.(FM) were both obtained by crossing a heterozygous fly with a vestigial one belonging to the same FM population: vestigial female with heterozygous (*+|vg*) male and heterozygous (*+|vg*) female with vestigial male, respectively. The two crosses are reciprocal with respect to the vestigial locus and the associated chromosome II°, but otherwise share

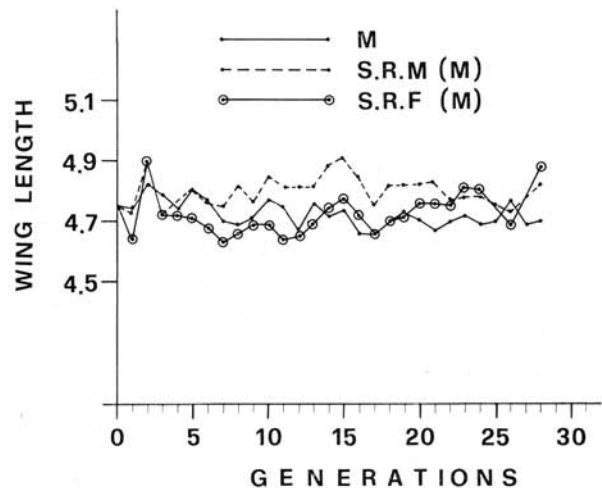


Fig. 2. Mean wing length after relaxation of selection pressure in line M

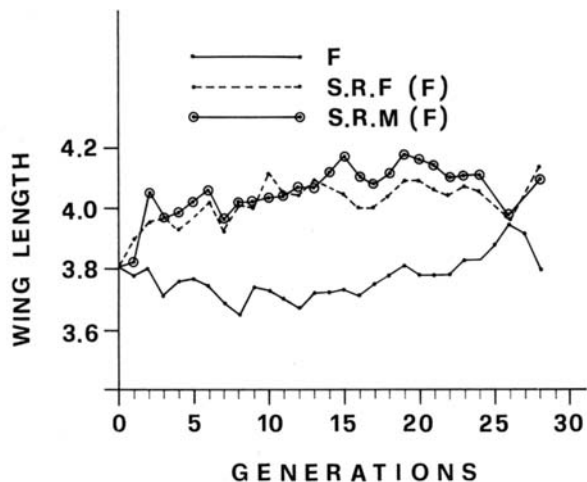


Fig. 3. Mean wing length after relaxation of selection pressure in line F

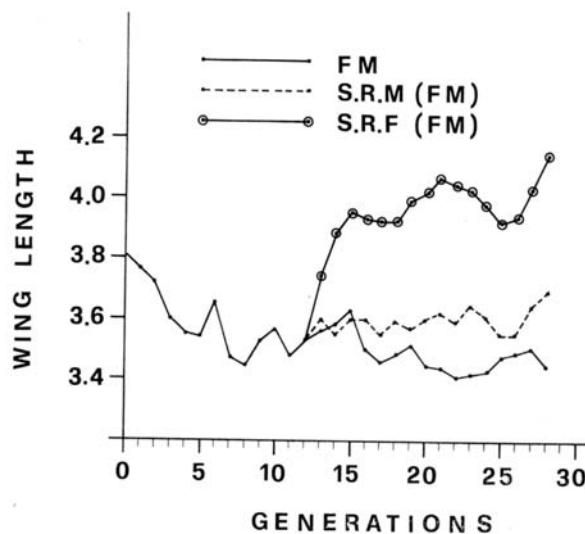


Fig. 4. Mean wing length after relaxation of selection pressure in line FM

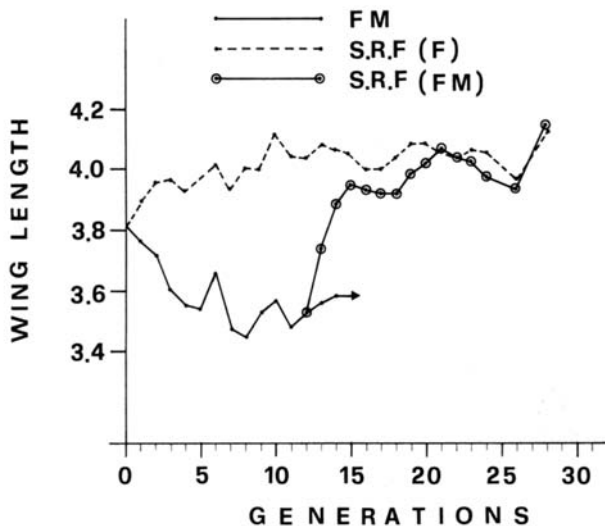


Fig. 5. Comparison between mean wing lengths in lines S. R. F.(F) and S. R. F.(FM)

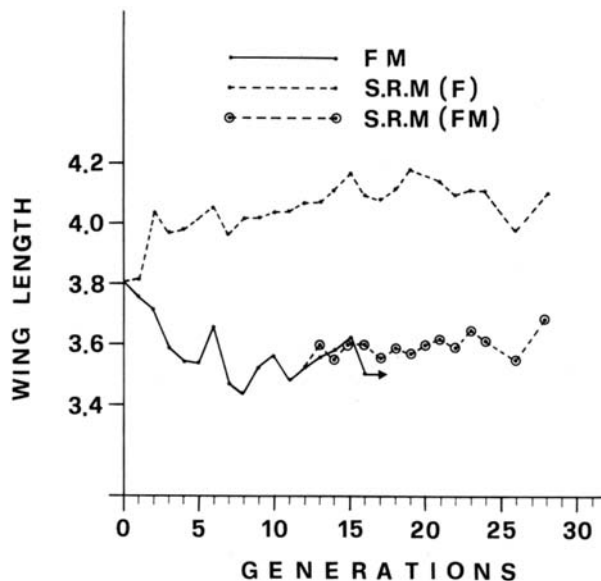


Fig. 6. Comparison between mean wing length in lines S. R. M.(F) and S. R. M.(FM)

a common cytoplasm and a common genotype. It would be very difficult to explain the divergent behavior observed in terms of differences between the two sub-populations involving nuclear or extranuclear factors.

On the other hand, isolation can be ruled out in this case because the divergence observed:

- a. appears immediately in the progenies of the first generation after selection pressure has been relaxed;
- b. may be detected any time the experiment is repeated with the same procedures;
- c. seems to result from blocking the action of natural selection in line S. R. M.(FM), in which no reversal of the effect of artificial selection occurs.

It may be concluded that the divergence observed depends neither on hereditary factors (nuclear or extranuclear) nor on environmental ones; conse-

quently, it must be assumed that the different wing length values in the two sub-populations S. R. M. (FM) and S. R. F. (FM) depend on different phenotypic expressions of the same hereditary factors in the two sexes.

Palenzona, Rocchetta and Jacuzzi (1972) report differences between the reproductive fitness values for the reciprocal crosses ♀ +/vg × ♂ vg/vg and ♀ vg/vg × ♂ +/vg within lines M and F. Corresponding differences in fitness have not been found in line FM, suggesting that the divergence observed between the two sub-populations derived from line FM is not attributable to differences in reproductive fitness. Palenzona and Graziani (1972) have shown that the

variability present in line F could be made to assume values similar to those observed in line FM, by obtaining progenies from the cross ♀ *vg/vg* × ♂ *+/vg* using flies from the F line; moreover, in these progenies the original variability value of the F line reappears by switching the mating scheme back to that used in the F line, that is, ♀ *+/vg* × ♂ *vg/vg*.

This phenomenon is maintained throughout the FM selection line which is derived from the F line, so that S. R. F. (FM) has, from the start, a higher variability than S. R. M. (FM). This could indeed be an explanation for the divergence in wing length observed between the two populations, but it remains difficult to understand the observed differences in variability. In fact, it must be remembered that the flies used to make up the reciprocal crosses are taken from within the same line and therefore no genetic difference is expected between them.

All the results gathered up to now indicate that the divergence observed between S. R. M. (FM) and S. R. F. (FM) is controlled by factors which are present in the FM line; moreover, it seems that the activity of these factors is realized through complex interactions, since no simple genetic explanation is available, to our knowledge, to account for the results obtained. Given the genetic similarity of the

divergent lines, we suggest that the differential activity of the factors involved may be inherent to changed developmental processes.

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