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The Relationship between Fitness and Response to Selection in *Drosophila melanogaster*[*]

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Summary. The relationship between the selection response exhibited by a morphological trait and the correlated response observed on fitness values has been investigated to improve our understanding of micro-and macro-evolutionary processes. The research was designed to test the validity of the "homeostatic" and "metric deviation" models (Robertson 1956). The results show that:

1) correlated changes in fertility values are larger when selection for minus-variant wing length is applied to males than when it is performed on females,

2) within each of the selected lines, M, F and MF, the reproductive fitness of the populations obtained from $vg/vg \times +/vg$ crosses differs from that of the populations derived from $+/vg \times vg/vg$ crosses,

3) reproductive fitness values of populations derived from $vg/vg \times +/vg$ crosses are fairly constant in selected lines obtained by means of different selective procedures, while mean wing length changes; the corresponding populations from $+/vg \times vg/vg$ crosses show, on the contrary, a proportionality between fitness and selected trait values.

The lack of consistency of these results with the currently accepted hypotheses on the relationship between selection response and correlated changes in fitness leads to the conclusion that the two models considered do not satisfactorily interpret our results; these are better explained by a developmental relationship between fitness and selected trait.

Introduction

The commonly observed decline in reproductive fitness correlated with selection for metric traits could be the result of phenotypic and/or genetic effects. Theoretical phenotypic and genetic models were discussed by Robertson (1956) and Latter (1960) as the "metric deviation model" and "homeostatic model", respectively, and by Lewontin (1964a, b) as the "optimum model" and "heterotic model". According to the metric deviation model, the decline in fitness results only from the extreme phenotypes being intrinsically less fit and not from their underlying genetic constitution. The "homeostatic model", derived from Lerner's (1954) concept of genetic homeostasis, states that the extreme phenotypes are less fit because they are more homozygous than intermediate ones: fitness declines as a correlated selection response due to increased homozygosity at loci affecting the metric trait. Experimental evidence of the relation between changes in fitness and morphological traits in the course of selection has been given by Scossiroli (1959), Latter and Robertson (1962), Sheldon (1963) and Verghese and Nordskog (1968): they suggest, however, that predicting the outcome of a selective process is still unsatisfactory. Previous work performed by Cavicchi (1970) on our selected lines in *Drosophila* suggested that factors other than the genetic or phenotypic structure of a *D. melanogaster* population may be responsible for the determination of the reproductive fitness values, e. g. the sex on which selection is actually performed. Because of the importance of the rôle of reproductive fitness in understanding evolutionary processes, we have collected further information on these topics.

Materials and methods

Artificial selection for minus-variant wing length was performed on male or female flies from a Canton strain (*Drosophila melanogaster*). Measurements were made on flies maintained heterozygous at the vestigial locus (*vg*, 2nd chromosome) throughout the experiment by crossing them with homozygous vestigial flies, segregating within the selection line. 36 flies were selected out of 200 measured in each of the following lines:

Line *M* = minus-variant heterozygous males crossed with vestigial females.
Line *F* = minus-variant heterozygous females crossed with vestigial males.

After these selected lines had reached a plateau of response for the selected trait, *MF* and *FM* selection lines were started from the *M* and *F* lines respectively, by changing the sex of the selected parent:

Line *MF* = minus-variant heterozygous females crossed with vestigial males,
Line *FM* = minus-variant heterozygous males crossed with vestigial females.

After 12 selection generations two populations were derived from the *MF* and *FM* lines, again changing the sex of the selected parent: the two selection lines were *M'* and *F'*, from *MF* and *FM* respectively.

Fertility was estimated as the percentage of flies hatched out of the total number of eggs observed at each selection generation in *M* and *F* lines. Reproductive

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fitness was estimated as the number of adult flies originating from a single inseminated female in a period of six days (3rd to 9th after eclosion); in each selected line two types of crosses were involved,

a) Cross 1 = *vg*/*vg* female × +/*vg* male and
b) Cross 2 = +/*vg* female × *vg*/*vg* male

using vestigial and heterozygous flies segregating within the same population.

Results

The fertility values collected at each selection generation are given in Fig. 1 as percentage of flies on the total number of eggs observed. Both the selection response for wing length and the fertility correlated response were markedly different in the M selection (where selection was applied to heterozygous males) compared with the F lines (heterozygous females selected).

The relationship between mean wing length and fertility values was estimated by means of the correlation and regression coefficients reported in table 1. The high values of the correlation coefficients obtained suggest a good correlation between the two variables on the hypothesis of a linear relationship; the regression coefficient in selection *F* is significantly smaller than in selection *M*, which indicates that, for an equal amount of response in wing length, there is a greater decrease in fertility when selection is performed on males than on females.

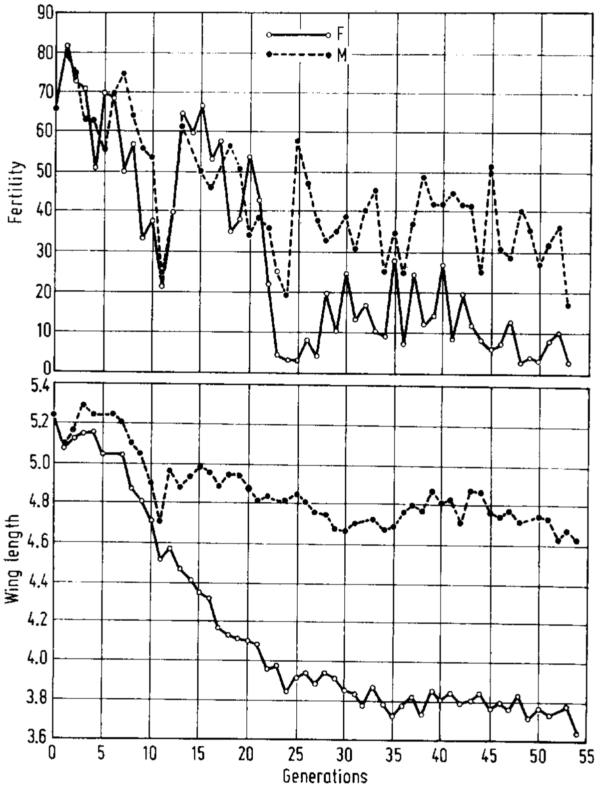

Fig. 1. Fertility and wing length values at each selection generation in lines *M* (selection applied on males) and *F* (females selected)

Table 1. *Correlation coefficients "r" and regression coefficients "b" between fertility and mean wing length at different selection generations. "t" values refer to the comparison between b's from M and F selection lines*

		r	b	"t"
Repl. 1	M	0.671*	82.66*	3.24*
	F	0.847*	47.21*	
Repl. 2	M	0.774*	63.61*	2.57*
	F	0.843*	41.17*	

* = $P < 0.01$

A comparison of the reproductive fitness (average number of flies produced by a single mating per day over the period between the third and the ninth day after eclosion) was made on four populations having different selection backgrounds. The values given in table 2 suggest that crosses of type 1 (vestigial female × heterozygous male) in different selection lines have similar reproductive fitness values, while crosses of type 2 (heterozygous females by vestigial males) differ according to the population considered; moreover, crosses 1 and 2 within each selection line show a significant difference in fitness in lines *M*, *F* and *MF*, which does not correspond to differences in wing length, as it is suggested by the observation of the mean wing length values in the last column of the same table 2.

Table 2. *Reproductive fitness values in the selected lines studied together with the corresponding mean wing length. 't' values refer to the comparison between 1 and 2 crosses within each selection line*

Selection line	Cross	Fitness	"t"	Mean wing length
M	1	18.9±1.79	9.41*	4.75±0.011
	2	49.4±2.68		4.74±0.011
F	1	18.3±1.83	3.97*	3.76±0.020
	2	30.4±2.43		3.78±0.019
MF	1	19.8±2.28	2.97*	4.48±0.011
	2	30.6±2.87		4.47±0.010
M′	1	18.6±1.87		4.69±0.015
FM	1	23.9±1.94	0.45	3.37±0.008
	2	22.9±1.57		3.39±0.009
F′	2	29.1±2.02		3.77±0.019

* = $P < 0.01$

A comparison of mean wing length and fitness values also suggests that there is a rough proportionality between the two characters in crosses of type 2 in the different selection lines considered, but the same does not hold true for the results obtained from crosses of type 1. These observations are even more significant when considering the results obtained from the *F′* and *M′* selected lines, which were derived from *FM* and *MF*, respectively: in fact, when selection for wing length is continued, there is an increase of the mean wing length and an increase in fitness value for F', while for M' no significant change is observed.

Discussion

Reproductive fitness is an important parameter for a correct evaluation of micro- and macro-evolution, because phenotypic changes have different evolutionary values according to their reproductive fitness. It is a common observation in selection experiments that a change in fitness values occurs parallel to the response in the selected metric character. A major difficulty in understanding this relationship has been its non-linear manifestation; in particular, it seems difficult to reconcile the correlated additive effects of selection on fitness and their reversibility. A more general problem is the contrast between the continuous effect of selection on evolutionary processes and the need for a high level of fitness to pay for the cost of selection. It is our opinion that the homeostatic model and the metric deviation model are not sufficiently comprehensive to account for all the available observations and that a different model is needed based on a more flexible relationship between the morphology of an organism and its evolutionary value.

Our results suggest that different values of reproductive fitness show a certain amount of independence from the genetic structure of the organisms involved, and provide evidence that individuals with similar genetic structure may have very different fitness values. On the other hand, the same experimental work points out that different phenotypic and genetic values do not result in different reproductive fitness values.

Our hypothesis is that fitness is largely controlled by the developmental processes underlying the manifestation of a given phenotype. Two points are especially relevant in our results:

1) fertility under artificial selection for minus-variant wing length decreases at different rates in M and F selection lines, and

2) the reproductive fitness values in different selection lines are similar when crosses of type 1 (between vestigial females and heterozygous males) are considered, while there is a rough proportionality between the mean value of the selected trait and the reproductive fitness in crosses of type 2 when these traits are measured in progenies from plateaued selected populations obtained by crossing heterozygous females with vestigial males.

These results are clearly inconsistent with both the homeostatic and the metric deviation models; in fact, the differences in the rate of fitness decrease, obtained as correlated responses of the same selection procedures applied to the different sexes, suggest that the same quantity of morphological change has different meanings when obtained by selecting males rather than females. Therefore, it is assumed that from the same population more than a simple correlated response is to be expected; this is supported by the reproductive fitness values observed in crosses between different phenotypes in the same population. The influence of different selections is manifested only in the populations obtained from the crosses of type 2 ($+/vg \times vg/vg$). Reciprocal crosses (vestigial females by heterozygous males) seem to be unaffected by selection suggesting that the correlated response on fitness, observed in crosses of type 2, is neither attributable to additive (genetic or non-genetic) factors nor to any type of interaction between additive and environmental factors, because crosses 1 and 2 should be identical in their additive structure when considered within the same selection line.

Palenzona, Vanelli and Rocchetta (1971, in press) suggest that the differences in selection response on wing length, observed by selecting males or females, seem to be due to different rearrangements of the developmental patterns responsible for the changes in the manifestation of the selected trait consequent to the selection applied; these authors also suggest that the developmental pattern of the selected trait could be specifically modified in its entirety only when selection is performed on heterozygous females.

Using this hypothesis in the analysis of wing length response, we would expect that fitness values would decrease in cross 2 (heterozygous females crossed with vestigial males) according to the following order: M, MF, F, FM. The fitness value in the F' selection (derived from FM line by changing the selected parent) would be expected to revert to the value observed in the F population.

The observed results agree with these expectations, suggesting that the model proposed by Palenzona, Vanelli, and Rocchetta (1971) to explain the results of selection on wing length may be extended to explain the correlated response on reproductive fitness.

The hypothesis of a relationship between reproductive fitness and rearrangements of the developmental pattern of the selected trait is of interest because it offers the possibility of linking, on the same theoretical background, ontogenesis and evolution, while explaining all the observed results which are not satisfactorily explained by currently accepted models.

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