Theoretical and Applied Genetics 46, 233-238
© by Springer-Verlag 1975

Interaction between Artificial and Natural Selection*

Domenico Lorenzo Palenzona, Rita Alicchio and Gabriella Rocchetta

Institute of Genetics, University of Bologna (Italy)

Summary. In order to understand how divergence may appear within a gene pool without limitations on gene flow, experiments were performed to investigate whether the genetic structure of a population may be effective in controlling the response to natural selection. Starting from plateaued populations of *Drosophila melanogaster* selected for wing length on the two sexes separately, the response to natural selection was studied after artificial selection had been discontinued. The results show that populations derived from artificial selection applied to the different sexes respond to subsequent natural selection in dissimilar ways, so as to suggest that the relationships between fitness and wing length have been changed. A second experiment comparing the response to natural and to artificial reversed selection suggests that different genes or gene complexes may be involved in wing length determination: these different genes show a dissimilar response in the different sexes and to natural and artificial selection. This variety of responses suggests that the interactions of different genes or gene complexes with artificial and natural selection could possibly lead to differentiation within the population.

Introduction

The possibility that populations may diverge while living in the same territory has been advanced recently on the basis of reasonable models (Maynard-Smith, 1966; Bush, 1969; Pimentel, Smith and Soans, 1967; Ehrlich and Raven, 1969); a considerable amount of experimental evidence seems to indicate that a gradual divergence between populations may take place even if there are no barriers to gene flow (Thoday, 1958; Thoday and Boam, 1959; Millicent and Thoday 1961; Thoday and Gibson, 1971; Streams and Pimentel, 1961; Dobzhansky and Spassky, 1967; Endler, 1973). If gene flow can not be thought of as the cohesive force which holds large populations together, it may be that selection should be considered as both the primary cohesive and disruptive agent (Ehrlich and Raven, 1969). This requires that different responses to selection should be found within the same population.

Experiments in artificial selection performed separately on males and females of *Drosophila melanogaster* led Palenzona and Alicchio (1973) to the conclusion that the differing response observed is the effect of complex interactions between the genetic factors involved in the determination of wing phenotype. These results suggest that the response to selection is controlled by interaction mechanisms which result in different gene combinations in the genotype, and that these mechanisms are activated by differences between the two sexes, that is, by the genetic structure of the population itself.

The purpose of the present paper is to investigate whether the difference built up by artificial selection can affect the response to subsequent natural selection in such a way as to identify a possible condition for a divergence phenomenon.

Artificial selection

The populations used were obtained by selection for short or long wing, performed in different lines on male or female *Drosophila melanogaster* flies. In order to avoid unconscious selection, the unselected parent had vestigial wings and was maintained in each selection line by mating to a selected parent which was heterozygous at the vg locus (vestigial, 2nd chromosome). A more detailed account of the methods used and of the results obtained can be found elsewhere (Palenzona and Alicchio, 1973).

The selection lines considered in the present paper were the following:

Line T =heterozygous (+/vg) males selected for long wing
Line Z =heterozygous (+/vg) females selected for long wing
Line M =heterozygous (+/vg) males selected for short wing
Line F =heterozygous (+/vg) females selected for short wing
Line K =derived from the plateaued F lines (after fifty-four generations of selection) by selecting heterozygous (+/vg) males for short wing.

The selection response of these lines is schematically outlined in figure 1: a difference is evident between the limits reached by selection performed in the same direction on different sexes (compare T vs. Z and M vs. F); again a difference in the selection limits of F and K is

---

* Research partially supported by C.N.R., grant N° 71.00740/29 115.379.0

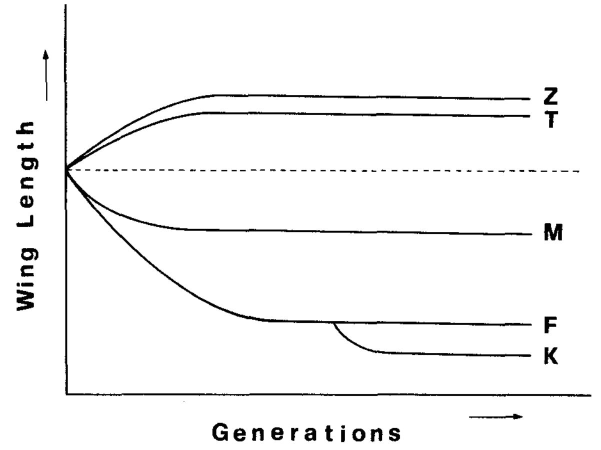

Fig. 1. Schematic representation of the observed responses to artificial selection for wing length

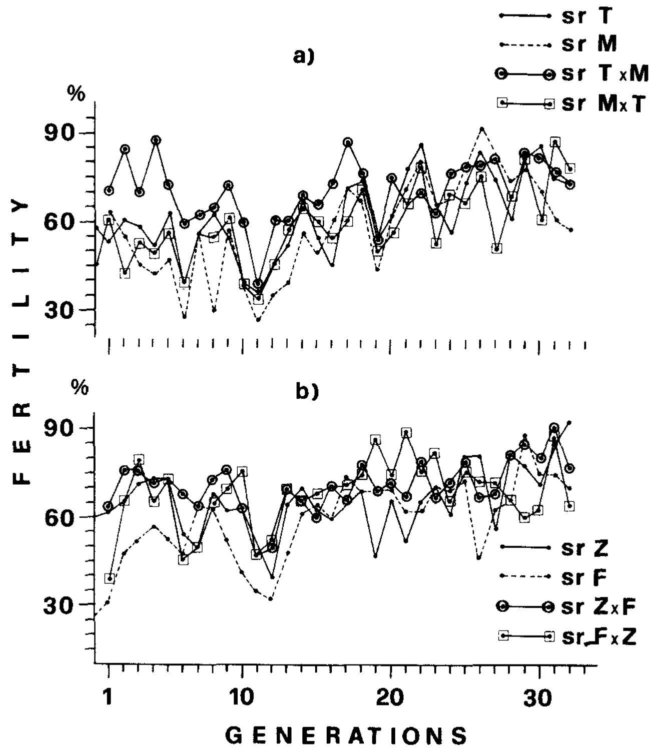

Fig.2. Fertility values observed after relaxation of artificial selection pressure: a) = populations from male-selected (M and T) lines; b) = populations from female-selected (F and Z) lines

observed which suggests that the mechanisms by which selection on males and females elicit the population response are independent. It has been suggested (Palenzona and Alicchio, 1973) that these differences can largely be attributed to complex interactions modifying the relationships between the genotype and the phenotype. It may be assumed that if genetic variability is still present in the plateaued populations considered, the different limits reached should be described as different points of equilibrium (genetic homeostasis) between artificial and natural selection: these different equilibria depend on the action of different gene complexes which are apparently kept together by the selective forces acting in each population at the plateau. The possibility that these gene complexes may in turn control the dynamics of the populations considered when artificial selection is discontinued has been the aim of the investigation described in the present paper. The results refer to two independent experiments, the relaxation of artificial selection and the comparison between reversion and relaxation of selection, which will be described separately.

Relaxing the artificial selection

a) Methods

Flies from the selected lines T, Z, M, and F were used to establish populations reared in mass culture without artificial selection applied. The following populations were obtained:

sr T; sr Z; sr M; sr F;

with males and females taken from the same line, and, moreover,

sr MxT; sr TxM; sr ZxF; sr FxZ;

which represent reciprocal crosses between flies from lines selected in opposite directions (short and long wing) on the same sex; the capital letters indicate the selection line from which the flies were taken; sr means "selection relaxed".

At every generation measurements were taken of the wing length of 100 flies from each of four independent replicates; a constant number of eggs was put in each culture and the number of emerged flies was recorded.

b) Results and comments

The average number of flies obtained from 100 eggs is given in figure 2 as 'fertility' at each generation; these values show that changes in this fitness component follow a similar trend in the eight populations considered. The increase in fertility values was rather slow and only become detectable twelve generations after artificial selection had been relaxed. No heterosis was observed for this trait in the population established by crossing flies from different selection lines.

Mean wing length values (figure 3) showed a decrease in the first few generations after artificial selection was discontinued, followed by a slow increase; this trend is common to all the lines considered, except for sr F line where a steady increase was observed. Populations obtained by crossing flies from the selected lines showed

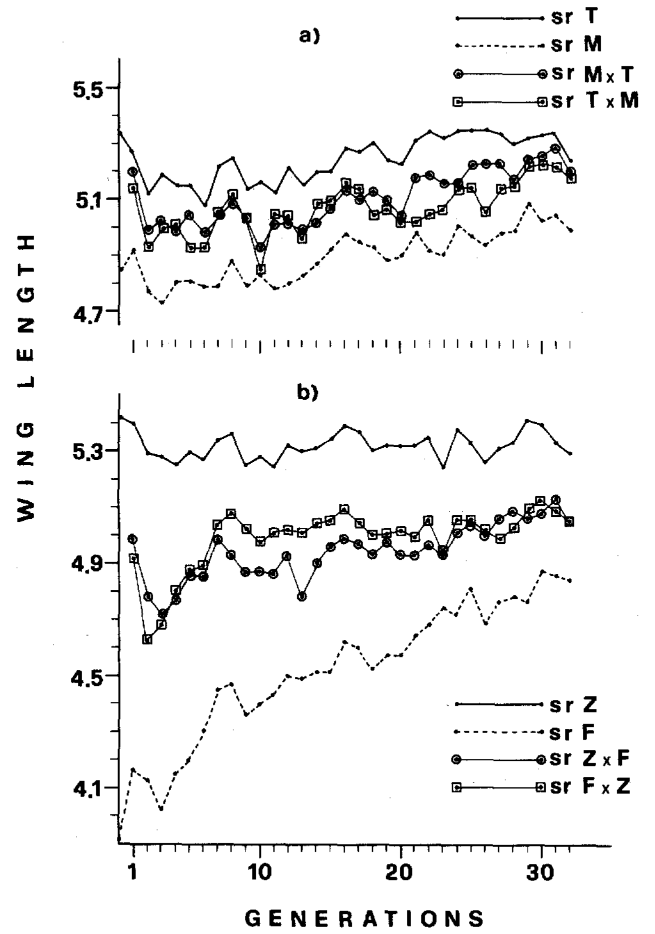

Fig. 3. Mean wing length values observed after relaxation of artificial selection pressure: a) populations from male-selected (M and T) lines; b) = populations from female-selected (Z and F) lines

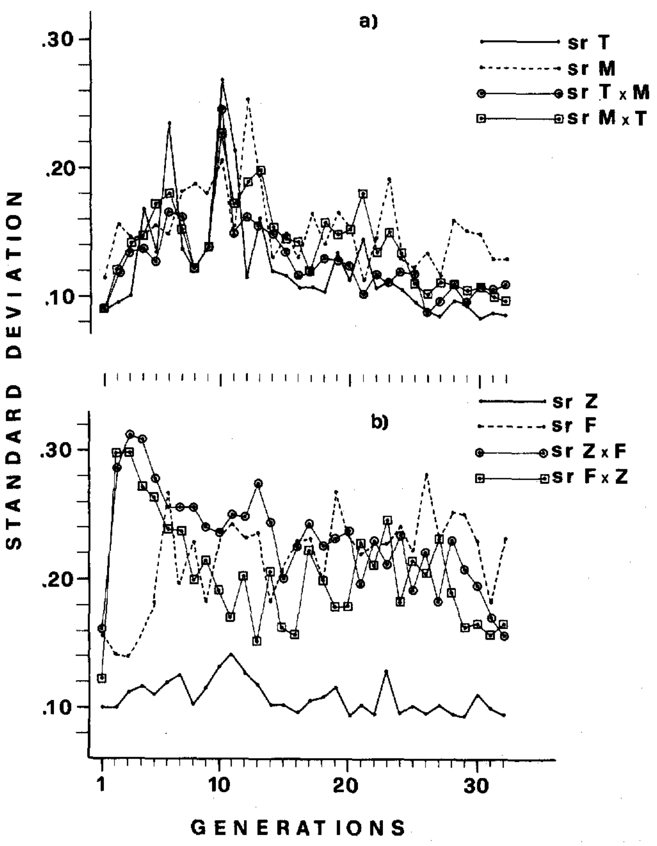

Fig. 4. Standard deviation of wing length values after relaxation of artificial selection pressure: a) = populations from male-selected (M and T) lines; b) = populations from female-selected (F and Z) lines

mean wing length values intermediate between those of the parental lines at every generation, suggesting that there is no heterosis for this trait.

Considering the standard deviation values shown in figure 4, there are strong differences in the trend of the populations derived from lines M and T compared with those derived from F and Z; the former show a delayed increase of variability followed by a steady decrease, while the latter show a sudden increase after which a very slow decrease is unable to reduce variability to the normal values in the thirty-two generations considered. The differences between the two groups of populations strongly suggest that there are different mechanisms controlling the dynamics of the gene pool components. In fact, since the experiments were started from plateaued populations under artificial selection pressure, there should be two sets of expectations, after selection was discontinued:

1) genetic variability has been completely fixed under artificial selection: natural selection has no effect on wing length while fitness may be restored by changes in the genetic background;

2) there is genetic variability left in the populations under artificial selection, and the plateau is a consequence of genetic homeostasis (Lerner, 1954): wing length changes are due to an increase of frequency of the fittest alleles, which in this case must have phenotypic values less favourable for response to artificial selection. Changes of mean wing length must follow the increase of variability, and, after a sudden increase, variability should be reduced by elimination of the less fit alleles.

The results shown in figures 2, 3 and 4 suggest that genetic variability is present in the plateaued lines. However, the observed results are at odds with the expectations at point 2) and the discrepancies between the observed and expected results differ according to whether the populations are derived from lines where the artificial selection had been performed on males or from those obtained by selection on females. In particular we observe that:

1) the increases in variability for populations derived from one selection line and for those derived by crossing flies from lines selected in opposite directions, are similar: this may be explained assuming that the response to artificial selection performed does not consistently reduce the genetic heterogeneity within the selected lines;

2) the increase of variability appears at different times in different lines during relaxation of selection, suggesting that the recombination effect is dissimilar in the two groups of populations considered (artificial selection performed on males or on females).

3) changes in mean wing length do not parallel those of variability in time, suggesting that the two parameters are estimates of the dynamic behaviour of different complexes.

4) mean wing length in populations derived from crosses between lines selected in opposite directions shows intermediate values between the relaxed parental lines at every generation. These results are obtained either through a large reduction of variability (as observed in populations derived from lines selected on males) or through a small reduction in the standard deviation values (figure 4) in the populations derived from lines where females were selected.

One has therefore to assume that the relationship between fitness and wing length (and the resulting natural selection) is different in the two groups of populations; this implies that the genes or gene complexes involved are dissimilar. Otherwise, since a large amount of variability is manifested within each population, we would expect that mean wing values should converge towards a similar optimal common value.

The results shown in figure 2, 3, and 4 suggest, therefore, that changes resulting from artificial selection may affect the subsequent natural selection; this could imply that the same artificial selection applied on different sexes is able to change the relationship between fitness and a phenotypic trait in different ways within a population.

Natural vs. reversed artificial selection

Methods

One hypothesis which would explain the existence of different relationships between fitness and the genes affecting the same trait is that the same phenotype may be determined by factors having different fitness values. Since it would be a frustrating task to measure differences of fitness between genes, we tried to detect genes having dissimilar fitness values by comparing the responses of the same population to natural selection (which depends directly on fitness) and to artificial selection (which, on the contrary, is only indirectly related to fitness). In order to simplify the experimental procedures we exploited the apparent ability (observed in the results shown above) of selection on different sexes to discriminate between genes (or gene complexes) differing in their relationships with fitness.

Two lines, (F and K, figure 1), obtained by artificial selection for short wing applied on heterozygous females at the vg locus (F line) and on heterozygous (+/vg) males (K line) were considered; the latter was started using flies from the F selection. For each plateaued line two populations were derived: one maintained without any conscious selection for wing length (rel. F and rel. K, respectively from F and K); and a second selected for long wing, that is, subjected to an artificial reverse selection (rev. F and rev. K). All the lines were reared by single mating under controlled temperature and crowded conditions. Measurements of wing length were taken at every generation on 100 phenotypically normal flies from each of two genetic replicates. Since no consistent dissimilarity was observed between the replicates' wing lengths the average of the two is shown in figure 5.

Results and comments

It is clear that natural (rel. F) and artificial reversed (rev. F) selection result in very different wing length values when started from the F line (cf. rel. F and rev. F), while no difference is detectable between rel. K and rev. K. The four populations showed a consistent response indicating that genetic variability is still present in both the plateaued lines F and K. The lines rel. F and rel. K became stabilized around similar wing length values in spite of the fact that they started from different values of the plateaued F and K populations. This suggests that the limit of response to natural selection has not been affected by F and K artificial selections. In contrast, artificial selection has been affected by dissimilarities between the two sexes; in fact K line shows a further response to artificial selection when started from the plateaued F line. The differences between F and K were effective in determining different responses to the reversed artificial selection even if in both populations the reversed selection was applied to females. It seems that the genetic differences between F and K are due to at least two types of factors, one involved in the response to natural selection and the second affected by the reversed artificial selection. This is supported by the fact that the ratio between the responses to natural and artificial reversed selection is altered in populations started from F compared with those started from K. It seems reasonable to suppose that genes determining

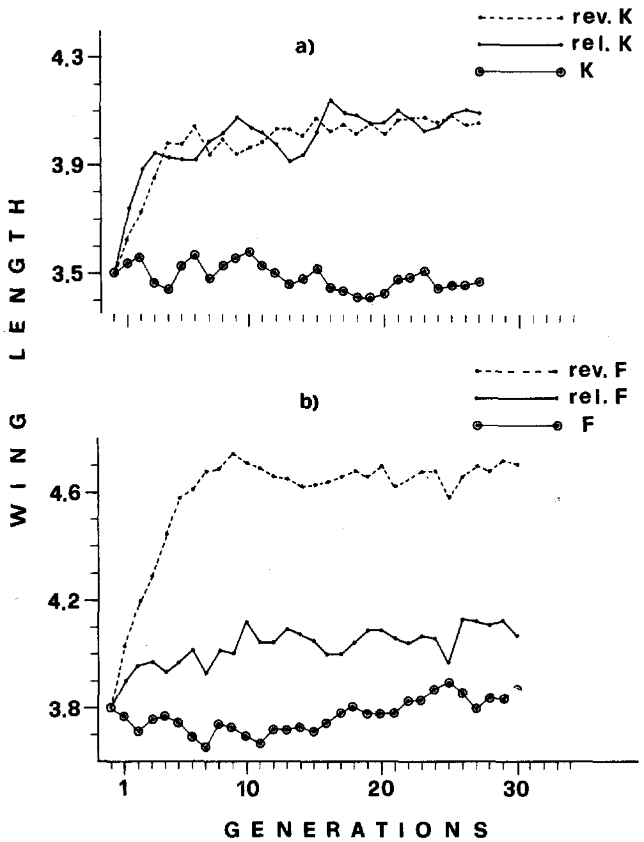

Fig.5. Mean wing length observed in responses to natural and artificial reversed selection: a) = populations from male-selected K line; b) = populations from female-selected F line

wing length may have dissimilar fitness values and that selection on different sexes is able to detect these dissimilarities. The existence of differences between factors responsible for the determination of the same quantitative character has already been suggested by Mather and Harrison (1949) and Spickett and Thoday (1966): they found genetic factors localized at different points on a chromosome or in different chromosomes showing a different quantitative effect on the same phenotypic trait and a combined effect denoting the existence of interaction between them. The experimental evidence reported in the present paper suggests that the dissimilarity between genetic factors affecting the same phenotypic character may also involve fitness, thus representing the condition for different responses to natural selection.

Conclusions

The growing body of experimental evidence quoted in the introduction to the present paper suggests that divergence can arise within the gene pool even in the presence of gene flow. The possibility has been considered here that different genes affecting the same phenotypic trait and having different phenotypic and fitness values exist within a population; if these genes have a cumulative effect in determining the phenotypic trait, it might be thought that the cohesive force which keeps them combined is given by the fitness value of their combination. Therefore, since many types of integration are possible for the different genes determining the same character, it is possible to see how different phenotypic values with the same fitness could originate within the same gene pool. The results obtained seem to support this view and, moreover, suggest that the same selection pressure applied on different sexes may result in gene combinations which show a different pattern of response under natural selection. This could indicate that the interaction between selection and the sexes constitutes an effective mechanism in producing different gene combinations within the same population.

Since this interaction may be of general occurrence, it seems that the problem of population differentiation can be studied in terms of the genetic structure of the population itself as resulting from the interaction between artificial and natural selection.

Acknowledgments.

The authors thank Miss Brunaleschi, Miss Laffi and Mr. Baricordi for their capable technical assistance.

Literature

Bush, G.L.: Sympatric host race formation and speciation on frugivorous flies of the genus *Rhagoletis*. Evolution 23, 237-251 (1969)
Dobzhansky, Th.; Spassky, B.: Effects of selection and migration on geotactic and phototactic behaviour of *Drosophila* I. Proc. R. Society B 168, 27-47 (1967)
Ehrlich, P.R.; Raven, P.H.: Differentiation of populations. Science 165, 1228-1232 (1969).
Endler, J.A.: Gene flow and population differentiation. Science 179, 243-250 (1973)
Lerner, I.M.: Genetic homeostasis. Edinburgh: Oliver and Boyd 1954
Mather, K.; Harrison, D.J.: The manifold effects of selection. Heredity 3, 1-162 (1949)
Maynard-Smith, J.: Sympatric speciation. Am. Nat. 100, 637-650 (1966)
Millicent, E.; Thoday, J.M.: Effects of disruptive selection. Heredity 16, 199-217 (1961)
Palenzona, D.L.; Alicchio, R.: Differential response to selection on the two sexes in *Drosophila melanogaster*. Genetics 74, 533-542 (1973)
Pimentel, D.; Smith, G.J.C.; Soans, J.: A population model for sympatric speciation. Am. Nat. 101, 493-504 (1967)
Spickett, S.G.; Thoday, J.M.: Regular responses to selection. III. Interaction between located polygenes. Genet. Res. Camb. 7, 96-121 (1966)

Streams, F.A.; Pimentel, D.: Effects of immigration on the evolution of populations. Am. Nat. 95, 201-210 (1961)

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

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.: Reply to Scharloo. Am. Nat. 105, 86-88 (1971)

Received February 27, 1975
Communicated by H. Stubbe

Professor Domenico Palenzona
Istituto di Genetica
Università degli Studi
Via F. Selmi, 3
I-40126 Bologna (Italy)