Individual selection on temperature sensitivity was applied to the relative length of the 4th vein of the mutant \( ci^{b-g} \) in four selection lines according to different selection schemes indicated in Figure 1. These selection systems include, besides the selection on temperature, disruptive selection. In all lines the disruptive component causes an increase of the phenotypic variance, but there are large differences in its composition. The selection changed temperature sensitivity in the expected direction in all lines. In one line (C-D-), however, the change in temperature sensitivity and the increase in variance were only small because the disruptive component and the canalizing component of the selection scheme restricted each other’s effect. The results are discussed in relation to earlier results obtained by disruptive selection at one temperature.

THE sensitivity of morphological characters to environmental factors is an important issue in the theory of evolution. The direction of the reaction and its extent are supposed to be controlled by natural selection. Only recently attempts have been made to imitate natural selection on sensitivity to environmental factors by artificial selection, and to analyse its action. (Waddington 1960; Kindred 1965; Druger 1967). These authors were successful in changing the temperature sensitivity of the expression of the mutants Bar and scute in Drosophila by family selection. Because family selection would probably not be important in nature, Waddington and Robertson (1966) used a different selection scheme, again on the expression of Bar. This system of selection is complex. It acts on temperature sensitivity. But it also includes disruptive selection. This is demonstrated in Figure 1. This diagram shows the application of Waddington’s selection scheme on relative vein length of the cubitus interruptus mutant \( (ci^{b-a}) \) used in our experiments. The relative length of the 4th vein increases at lower temperatures. Progeny of the same parents was reared at 22.5° and at 27.5°. Selection for decreased sensitivity (canalizing selection) is performed by selecting flies with a short vein from the 22.5° culture and flies with a long vein from the 27.5° culture. Selection for increased sensitivity (anticanalizing selection) was practised by selection of long-vein flies from 22.5° and of short-vein flies from 27.5°. When disruptive selection is applied at 25°C the extreme flies
with the shortest and the longest veins are selected as parents of the next generation.

Let us assume that there are no differences in temperature sensitivity between individuals. Then, by changing the temperature, the frequency distribution is shifted as a whole to higher or to lower values without a change of rank of the individuals. Under both anticanalizing and canalizing selection, then, the same individuals will be selected as under disruptive selection at 25°C. When individuals differ in sensitivity to temperature, canalizing and anticanalizing selection include both disruptive selection and selection on temperature reaction. But when canalizing selection is successful (as it was in Waddington’s experiments), there arises a sort of a paradox. Disruptive selection is the counterpart of stabilizing selection. It is supposed to increase variability, at least partly, by making development more sensitive to environmental factors. Canalizing selection, however, diminishes the sensitivity of development against at least one environmental factor.

An analysis of this problem must be based on a thorough understanding of the effects of disruptive selection on the same character at one temperature. In earlier experiments (Scharloo 1964a, b, 1970a, 1970b; Scharloo, Hoogmoed and ter Kuile 1967) we explored the effect of stabilizing selection and two types of disruptive selection on the expression of \( ci^{p-q} \) at 25°C. The results were explained in terms of a model for the development of the 4th vein in \( ci^{p-q} \).

It seemed worthwhile to explore the effects of canalizing and anticanalizing selection on \( ci^{p-q} \) in combination with both types of disruptive selection and to compare the results with our model.
SELECTION ON TEMPERATURE SENSITIVITY

MATERIALS AND METHODS

The mutant \( ci^{D-G} \) (cubitus interruptus-Dominant of Gloor) in \textit{Drosophila melanogaster} causes a terminal gap in the 4th wing vein \cite{Scharloo1963}. The relative length of the 4th vein was measured as the percentage ratio of the incomplete fourth vein to the length of the third vein \cite{Scharloo1964a}. The sum of the ratios of both wings of a fly was used as the quantitative character. This character has the same mean and variance in both sexes.

The base population for these experiments was formed by introduction of a fourth chromosome carrying \( ci^{D-G} \) into the background of a Pacific cage population \cite{Scharloo1964a}. Because \( ci^{D-G} \) is lethal when homozygous it was maintained over a normal fourth chromosome. Wild-type flies were segregating each generation. The flies were reared in \( \frac{1}{8} \) liter cream bottles with 33 ml of food medium (water 1000 ml, dried yeast 32 g, agar 19 g, sugar 54 g and propionic acid 5 ml). At the start of a selection line a large number of flies (20 pairs per bottle) of the base population were allowed to lay eggs in 4 culture bottles at 25°C. The same flies were transferred to a second series of 4 bottles. After egg laying the first series was kept at 22.5° and the second series at 27.5°.

In the starting generation the time for egg laying was 6–8 hr; in further generations the flies (then 4 pairs per culture) remained in the bottles for 3 days. This procedure was sufficient to prevent effects of population density on emergence and growth.

From each bottle \( 20 \Phi \) and \( 20 \delta \) were measured. From each sample of 20 flies, 4 flies were selected as parents of the next generation.

Each selection line consisted of 4 groups of 8 parents (A,B,C,D) and each group generated progeny in two cultures, one bottle kept at 22.5° and one bottle at 27.5°. The lines were maintained with a cyclical mating system; \( \Phi \) \( \delta \) progeny of group A mated with \( \delta \delta \) progeny of B, B \( \Phi \delta \times C \delta \delta \), C \( \Phi \delta \times D \delta \delta \) and D \( \Phi \delta \times A \delta \delta \). The cultures of the next generation were indicated A, B, C or D in accordance with the origin of the female parents.

Selection lines were started as indicated in Figure 1:

1. \textit{Selection against temperature sensitivity (canalizing selection, C):} From the cultures at 27.5° the flies with the longest fourth veins (H) were selected and from the corresponding 22.5° cultures the flies with the shortest fourth vein (L).

2. \textit{Selection for temperature sensitivity (anticanalizing selection, AC):} Here flies were selected with the shortest fourth vein (L) from the 27.5° cultures and with the longest fourth vein (H) from the 22.5° cultures.

In a first set of two lines, mating of the selected flies was at random (C-DR and AC-DR lines).

In a second set \( \Phi \Phi \) from 27.5° were mated with \( \delta \delta \) from 22.5° and \( \Phi \delta \) from 22.5° with \( \delta \delta \) from 27.5°. These matings were performed in separate vials. After 24 hr the \( \delta \delta \) were discarded and the \( \Phi \Phi \) transferred to one bottle. Because this procedure corresponds to disruptive selection with compulsory mating of opposite extremes (D- selection) the lines were designated C-D- and AC-D-.

In both AC lines from generation 8 (G8) until G11 flies were not measured before selecting the parents of the next generation. The extreme flies were selected by comparing the flies of a sample by eye. The rest of the flies was stored at \(-12^\circ C\). The means and variances during these generations were based on samples from these stored flies. In G8 the flies of both AC-lines were not measured.

Before the temperature experiments the \( cs^{D-G} \) mutant was balanced in all lines by introduction of 4th chromosomes carrying the lethal \( spe^{cat} \) (sparkling-Cataract) with the help of suitable marked stocks \cite{Scharloo1962}. In this procedure only a limited number of flies could be used. Three or four groups of 40–60 pairs of flies were allowed to lay eggs at 25° in \( \frac{1}{8} \) liter creamers. After twelve hours the flies were transferred to a new series of bottles. The old series was then transferred to one of the experimental temperatures. In the temperature experiment with the AC lines from most temperatures 160 flies were measured. Only in the AC-D- line the number was smaller, but, with the exception of the 17.5° and 15° series, always higher than 100. In the experiment with the C lines, 120 flies were measured from each temperature; here also numbers were somwat smaller at the lowest two temperatures.
RESULTS

Means: The result of the selection on temperature sensitivity is given as the difference between the means at the two temperatures (Figure 2). Regression coefficients of these differences on generation number are given in Table 1. In Figure 3 the values of the means at the two temperatures are represented and in Table 1 the regression coefficients of the means on generation number.

In both AC lines the sensitivity increases. In the AC-D line the mean at 27.5°
becomes lower and the mean at 22.5° becomes higher. In the AC-D\textsuperscript{R} line the mean increases at both temperatures.

The decrease of the difference between the means in the C-D\textsuperscript{−} line is only small but it is significant. In the C-D\textsuperscript{R} line the difference declines very rapidly until in G7 temperature does not have an effect on expression. Simultaneously, there was a rapid decrease of the mean values at both temperatures. After G7 the difference fluctuates violently and increases again.

**Phenotypic variance and its components:** Variances were computed within samples. The separate variances of the samples from the different cultures and from the two sexes were pooled in one estimate for the phenotypic variance ($V_p$) of the base population or of the selection lines. Therefore each estimate is based on 160 individuals.

In all four lines the phenotypic variance increases (Figure 4). In most lines this increase is large. The increase is small in C-D\textsuperscript{−} and occurs predominantly at one temperature (22.5°) in C-D\textsuperscript{R}.

In both AC lines $ci^{P-o}$ flies occurred which had in one wing a complete 4th vein. This indicates the possibility that occasionally $ci^{P-o}$ flies will have possessed complete 4th veins in both wings. Such flies could not be separated from the wild-type flies segregating in the same culture. This will have prevented selection of the most extreme $ci^{P-o}$ flies and a still larger increase of the phenotypic variance.

Because both wings of all the flies were measured, it is possible to compute within-fly variances ($V_{ WF}$) as the mean of the squared differences between the right and left wings (Figure 5). Also here C-D\textsuperscript{−} shows the smallest change. In AC-D\textsuperscript{R} and in AC-D\textsuperscript{−} there are fluctuations and perhaps a moderate increase. Remarkable is the increase in the last generations of C-D\textsuperscript{R}.

Progeny tests were performed in G7 and in G14. For this purpose, besides the
normal cultures of the selection line kept at 22.5° and 27.5°, a third one was reared at 25°. Heritabilities ($h^2$) were computed within cultures as regression coefficients of progeny means on midparent values (Table 2). The additive genetic variance ($V_A$) was calculated by multiplication of $h^2$ and the phenotypic variance ($V_P$) at 25° (only in G7 of C-D− the mean of the phenotypic variances at 22.5° and 27.5° was used because at 25° the number of flies was too small). A residual variance $V_R$ (the upper limit of the environmental variance) could be computed by subtraction of $V_A$ and $V_{WF}$ from $V_P$. The genetic variance increased

Figure 4.—The phenotypic variance in the course of the generations.
Figure 5.—The within-fly variance in the course of the generations.

Table 2

The phenotypic variances \((V_p)\) and its components of the base population and the selection lines reared at 25°C

<table>
<thead>
<tr>
<th></th>
<th>B</th>
<th>G7</th>
<th>G14+</th>
<th>G7</th>
<th>G14+</th>
<th>G7</th>
<th>G14+</th>
<th>G7</th>
<th>G14+</th>
</tr>
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<tbody>
<tr>
<td>(V_p)</td>
<td>207.3</td>
<td>609.3</td>
<td>584.5</td>
<td>206.5</td>
<td>607.2</td>
<td>333.2</td>
<td>1153.1</td>
<td>574.9</td>
<td>972.7</td>
</tr>
<tr>
<td>(h^2)</td>
<td>0.63</td>
<td>0.91</td>
<td>1.01</td>
<td>0.77</td>
<td>0.73</td>
<td>0.72</td>
<td>0.87</td>
<td>0.83</td>
<td>0.70</td>
</tr>
<tr>
<td>± 0.10</td>
<td>± 0.06</td>
<td>± 0.07</td>
<td>± 0.03</td>
<td>± 0.09</td>
<td>± 0.10</td>
<td>± 0.09</td>
<td>± 0.11</td>
<td>± 0.07</td>
<td></td>
</tr>
<tr>
<td>(V_A)</td>
<td>130.6</td>
<td>546.5</td>
<td>584.5</td>
<td>159.0</td>
<td>440.3</td>
<td>240.0</td>
<td>1003.2</td>
<td>477.2</td>
<td>680.9</td>
</tr>
<tr>
<td>(V_{WF})</td>
<td>26.2</td>
<td>23.7</td>
<td>19.2</td>
<td>18.9</td>
<td>35.5</td>
<td>37.1</td>
<td>29.5</td>
<td>34.2</td>
<td>40.9</td>
</tr>
<tr>
<td>(V_R)</td>
<td>50.5</td>
<td>31.1</td>
<td>—</td>
<td>28.6</td>
<td>132.4</td>
<td>56.2</td>
<td>120.4</td>
<td>63.5</td>
<td>250.9</td>
</tr>
<tr>
<td>(P)</td>
<td>75</td>
<td>48</td>
<td>57</td>
<td>41</td>
<td>61</td>
<td>58</td>
<td>45</td>
<td>28</td>
<td>45</td>
</tr>
</tbody>
</table>

Heritabilities \((h^2)\) were computed as the regression coefficient of progeny means \((\Phi \Phi, \delta \delta)\) on midparent values. Assortative mating of the parents was practised. Additive genetic variances \((V_A)\) were computed as the product of \(h^2\) and \(V_p\). The within-fly variance \((V_{WF})\) is the mean of the squared differences between the two wings of one fly. The residual variance \((V_R)\) is obtained by subtraction of \(V_A\) and \(V_{WF}\) from \(V_p\). \(P\) is the number of pairs in the progeny tests.
Figure 6.—Frequency distributions of relative 4th vein length in the selection lines. Full lines: distribution at 22.5°; broken lines: distribution at 27.5°C. Frequency distributions base-population (GO) based on 320 individuals, the other distributions on 160 individuals.
in all lines. The residual variance decreases in C-D\textsuperscript{R}. There is a large increase of the residual variance in both A-C lines and in the C-D\textsuperscript{D} lines. The frequency distributions are unimodal in the base population (Figure 6). In C-D\textsuperscript{D} there is only a broadening of the distribution with pronounced skewness at 22.5°. In C-D\textsuperscript{R} the distributions become very widely spread. In G6 (not included in Figure 6) the frequency distributions coincide more or less. In G7 the mode of the 22.5° distributions falls even below the mode of the 27.5° distribution. But there are still some 22.5° individuals with very high values. In following generations, when the differences of the means at the two temperatures increase again, there even appears a small mode at high values. In the C-D\textsuperscript{R} line flies occurred without \textit{ci}\textsuperscript{D-6}, which had nevertheless a small nonterminal interruption of the 4th vein. This effect is allelic to similar effects in some of the wild-type segregants in the D\textsuperscript{R} 25 line and the line selected for a short 4th vein in \textit{ci}\textsuperscript{D-6} (see SCHARLOO, HOOGMOED and TER KUILE 1967).

In both AC-lines, notwithstanding the increased difference in mean between the two temperatures, the distributions still overlap to a considerable extent. The distributions are far from normal, sometimes there are indications of bimodality (e.g. in G10 and G14 of AC-D\textsuperscript{D}).

Temperature experiments: In a first experiment, (Figure 7, Figure 9) the two AC-lines and the base population were tested simultaneously; in a second experiment the two C-lines and the base population (Figure 8, Figure 9) were tested.

Because \textit{ci}\textsuperscript{D-6} overlaps with wild type at lower temperatures, it was balanced in all stocks over another 4th-chromosome lethal \textit{spa}\textsuperscript{cat}.

Overlap with wild type is important only at low temperatures (20°, 17.5°, 15°). This causes the deflection of the graphs of the mean values at lower temperatures. Otherwise the relation between mean and temperature seems to be rather regular. But the relation of the phenotypic variance and the within-fly variance to temperature shows otherwise. Only the base population and the C-D-line have a constant phenotypic variance and within-fly variance (with the exception of the extreme temperature 15°). The linearity of the relation of relative vein length and temperature in the base population is borne out by the frequency distributions: at all temperatures the distributions are regularly unimodal.

In the AC-lines phenotypic variance and the within-fly variance have a maximum at intermediate temperatures (25°, 22.5°), in the C-D\textsuperscript{R} line maxima occur at lower temperatures (20°, 17.5°). The decrease of the phenotypic variance and the within-fly variance at lower temperatures (17.5°–15°) is partly a consequence of the overlap with wild type. The frequency distributions of AC-D\textsuperscript{D} and AC-D\textsuperscript{R} are bimodal at intermediate temperatures.

DISCUSSION

The scale of our quantitative character, the relative length of the fourth wing vein in \textit{ci}\textsuperscript{D-6} is linear over a large part of its range (SCHARLOO 1964a,b; SCHARLOO, HOOGMOED and TER KUILE 1967). This is revealed once more in the temperature experiments on the base population, in particular by the constancy of the phenotypic variance and the within-fly variance and by the regularity of the frequency
distributions. Only at lower values (below 80) changing the relative vein length becomes more difficult. Therefore, Rendel's (1967) conclusion that the definition of this character as a ratio of two vein-measurements would cause a non-linear scale and consequently a decrease of the variance when approaching wild type is not justified. In fact, the characteristics of the scale of the same character are very different in different mutants: in ci° changing the relative vein length becomes difficult when approaching wild type (Scharloo 1962); in ci+° they
In all selection lines temperature sensitivity (measured as difference between means at 27.5° and 22.5°, see Figure 2) changed. In both AC lines the temperature sensitivity increased. In the AC-D- line the mean became higher at 22.5° and lower at 27.5°. It is a real increase of temperature sensitivity. In the AC-D^R line the mean relative vein length increased at both temperatures, but more rapidly at the lower than at the higher temperature. Because both changes
occurred in the linear part of the scale this change too is a real change in temperature sensitivity.

In both AL lines there was a very large increase of phenotypic variance at both temperatures. The within-fly variance did not increase so much. The result of the progeny test at 25° (Table 2) shows that in the AC-DR line the
increase of the phenotypic variance was predominantly caused by an increase of the additive genetic variance although there was a two-fold increase of the environmental variance. In the AC-D\textsuperscript{+} line both the increase of the environmental and additive genetic variance was approximately five fold.

In the temperature experiment the difference in temperature sensitivity was maintained. The frequency distributions and the peculiar pattern of change of the phenotypic variance and the within-fly variance show that in contrast to the situation in the base population the scale was no longer linear. Both AC lines had bimodal frequency distributions when passing the temperature range from 22.5\degree to 27.5\degree. When the bimodal distributions occurred the within-fly variance is high. A similar situation was obtained in earlier experiments with D\textsuperscript{+} selection at 25\degree (D\textsuperscript{−25}, see Scharloo, Hoogmoed and ter Kuile 1967; Scharloo 1970b).

In both AC lines a change occurred in the development of the fourth vein similar to that in the D\textsuperscript{−25} line. The bimodal frequency distributions are caused by a threshold-like process in the development of the fourth vein. But in the AC-D\textsuperscript{+} line the distance between the modes was larger than in the AC-D\textsuperscript{R} line. This was reflected in the greater sensitivity to temperature of the AC-D\textsuperscript{+} line. This difference means in terms of our model a larger threshold region in the gradient of competence (Figure 10). A similar difference was found between inbreds derived from the D\textsuperscript{−25} line (Scharloo, Hoogmoed and ter Kuile 1967; Scharloo, unpublished).

The results in the AC-D\textsuperscript{R} and in the AC-D\textsuperscript{+} lines can be understood easily in terms of the changes caused by disruptive selection at 25\degree and the model used to explain the pattern of selection response (Scharloo 1970b). In D\textsuperscript{−25} the increase of the phenotypic variance was caused by a new threshold process in the formation of the 4th vein which increased temperature sensitivity. In the AC-D\textsuperscript{−} it

![Figure 10](image)

**Figure 10.**—Model for the development of the 4th vein in the base population and both AC lines. Formation of the 4th vein is supposed to be controlled by: (1) the concentration of a vein-forming substance in the wing varying according to a normal distribution, (2) a gradient of competence to react to the vein-forming substance with the formation of vein material. The competence decreases from wing base to wing tip. The gradient determines the pattern of vein formation and the variability of the relative vein length. In the selection lines, and in particular in the AC-D\textsuperscript{R} line, probably the distribution of the vein-forming substance will also be changed.
can be expected that the AC component and the D⁻ component enhance each other's effect. In D⁻R₂.₅⁰ the increase of the phenotypic variance was almost exclusively a consequence of an increase of the genetic variance, without change of the environmental variance. Therefore, in the AC-D⁻ selection it could be expected that the AC component would increase the sensitivity to temperature and cause the appearance of the threshold process in wing vein development, and that the D⁻ component would cause an independent increase of the genetic variance.

The results are in agreement with expectations. Sensitivity to temperature and the extent of the threshold zone are larger in the AC-D⁻ line, while genetic variance is more important in AC-D⁻. The threshold process causes a simultaneous increase of the genetic variance, the environmental variance, and the within-fly variance. It seems that this difference in scale between the base population and the AC-D⁻ line explains the increase of the variance components. In the AC-D⁻ line, besides the simultaneous increase of the 3 variance components, there is an independent increase of the genetic variance. This will be caused by changes in gene frequency or the generation of linked combinations of genes affecting the vein-forming substance.

When measured in terms of the difference between cultures at 22.5° and 27.5° (Figure 2) the C-D⁻ selection is very successful in the first 7 generations; but the rapid decrease of this difference coincides with a rapid decrease of the mean at both temperatures. The scale of the character is such that at lower values (lower than 80) it becomes more difficult to change vein length (Scharloo, Hoogmoed and ter Kuile 1967). However, the scaling properties cannot be the only cause. In G7 the means at both temperatures are almost equal. Nevertheless, although the mean value at 27.5° does not increase again, the expression difference between the two temperatures goes up. The frequency distributions at the two temperatures show that at least some of the flies with a short fourth vein can react to temperature. Although scaling properties contributed, there has occurred a real change in temperature sensitivity. Now the question arises what causes the decrease of the mean. Rendel (1967) suggests that under stabilizing selection the mean would move to that part of the scale where change of the character is more difficult. Moreover, the mean will only be constant when the effects of selecting high extremes at 27.5° and low extremes at 22.5° are in equilibrium. In the C-D⁻ scheme the low ♀ ♀ are grown at the lower temperature. They will be larger and therefore probably produce more eggs.

In G7 the mode of the frequency distribution at 22.5° is at lower values than the distribution at 27.5°. This points to the possibility of reversal of the temperature reaction by manipulation of the genetic background (Scharloo 1961, Druger 1967).

After G7 the temperature sensitivity increase again. This is probably caused by the decrease of the selection intensity on temperature sensitivity when the frequency distributions at the two temperatures overlap almost completely. Only when the frequency distributions are separate one can expect that the low flies at 22.5° and the high flies at 27.5° differ in temperature sensitivity. When the temperature sensitivity is abolished the low flies at 22.5° and the high flies at
27.5° may be extreme for other reasons, e.g. genetic factors, sensitivity to environmental factors other than temperature or sensitivity to factors acting within flies (developmental noise). Selection of these flies could easily increase temperature sensitivity again. That developmental noise is involved is suggested by its increase in the last generation of C-D selection when temperature sensitivity increases again.

The progeny test shows very high heritabilities, (in G14 the estimate of \( h^2 = 1.01 \)): the increase of the phenotypic variance is a consequence of an increase of the genetic variance. The parado that both the canalizing and disruptive components are successful in the C-D selection can be understood by comparing the results with D selection (see SCHARLOO, HOOGMOED and TER KUILE 1967). In that line the enormous increase of the phenotypic variance was caused by increase of the genetic variance. It can be concluded that under D selection there is still scope for canalizing selection to diminish the reaction to a specific environmental factor. This is what happened in the first stage of the C-D line: increase of genetic variance and decrease of environmental sensitivity.

In C-D there is a conflict between the selection against temperature sensitivity and the D selection, which is known from D-25 to promote temperature sensitivity by generating the threshold process in the development of the 4th vein. In the first half of the selection experiment both components are more or less in equilibrium. However, in the second half, both the genetic and the environmental variance must be a consequence of increased sensitivity for uncontrolled factors acting within cultures only. This accords with the linear scale which is revealed by the unimodal frequency distributions at all temperatures. A change of environmental variance without a change of temperature sensitivity was found earlier in lines subjected to stabilizing selection at 25° (SCHARLOO 1964a; SCHARLOO, HOOGMOED and TER KUILE 1967).

What could be the significance of these types of artificial selection in nature? D selection occurs when the environment has two subhabitats in which different expressions of the character are selected for and mating is still random. Selection of the D type will occur when selection optima are different in the two sexes. The AC type of selection will apply when in a heterogeneous habitat the genotype shows an adaptive phenotypic reaction to the environmental factors in which the subhabitats differ. The AC-D type will be found when individuals grown in the different subhabitats mate at random; the AC-D type will occur when the two sexes are exposed to different selective factors to which they show adaptive phenotypic reactions. From our experiments it can be concluded that these types of selection could be effective in obtaining better adaptation. However the variation around the optimal values will become large. When the difference between the means in the two subhabitats has reached the optimal value, variation around these means has to be checked by stabilizing selection within both habitats.

More difficult is the situation under canalizing selection. C-D selection would occur when individuals grow up under different conditions that divert development from attaining an optimal phenotype. When environmental deviation from
the optimal phenotype would diminish, the genetic variance would increase. Also, in this case, stabilizing selection will take over when the means in both habitats have attained their optimal values; that is, in the C-D<sup>R</sup> situation, when the frequency distributions coincide. The C-D<sup>-</sup> situation would be found when the two sexes are submitted to different environmental conditions to which they react with a deviation from one optimal phenotypic value for both sexes. From our experiments it can be concluded that this type of selection will not be very successful, because the canalizing and disruptive components conflict with each other.

All these types of artificial selection contribute to our understanding of the potentialities of the genetic and developmental systems. But it must be realized that the outcome of the complex selection schemes used in our experiments will be dependent upon the precise genetic situation in the base population. Moreover, these types of selection reveal the interplay of simple additive responses to selection and responses involving reactions to specific environmental conditions. Both types of reaction occur in the usual type of directional selection in one constant environment but remain then largely undetected.

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**LITERATURE CITED**


