THE EFFECTS OF DISRUPTIVE AND STABILIZING SELECTION ON BODY SIZE IN DROSOPHILA MELANOGASTER. II. ANALYSIS OF RESPONSES IN THE THORAX SELECTION LINES

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ABSTRACT

An analysis was made of changes in mean and variance in some thorax selection lines. The decrease of mean thorax length in the stabilizing selection lines (S) was a consequence of a directional selection component, caused by the skewness of the frequency distributions. The slight or temporary increase of the phenotypic variance and the large increase of the mean value in the disruptive selection lines with random mating (D^R) could be attributed to differences in reproduction between small and large flies (egg production and mating success). Phenotypic variability was high in two disruptive selection lines with compulsory mating of opposite extremes (D^-). The mechanism of the change in variability was different in these replicate lines. In D^-1 the change was obtained by an increase of the environmental and the non-additive genetic components of the variance. In D^-2 almost exclusively an increase of additive genetic variance occurred.

EXPERIMENTS on the effects of disruptive and stabilizing selection on thorax length (Bos and Scharloo 1973) showed some striking features: (1) Disruptive selection with compulsory mating of opposite extremes (D^-) caused a considerable increase in phenotypic variability. (2) Disruptive selection with random mating of extreme phenotypes (D^R) caused a large increase of the mean value but only a temporary increase in phenotypic variance. This could be a consequence of a difference in reproduction between small and large flies. (3) Stabilizing selection (S) caused a decline of body size but no decrease of the phenotypic variance. This decline could be a consequence of inbreeding depression caused by loss of genetic variability or of a directional component in this type of selection.

Interpretation of changes in phenotypic variance can only be obtained by an analysis of its composition. Therefore progeny tests were done at several stages of the selection lines. Further, D^- lines were compared to the base population and to a control line for their responsiveness to divergent directional selection. Inbred lines from the D^- lines and the base population and crosses of these inbred lines
were compared to obtain direct estimates of environmental variances. In order to
detect the causes of the increase of thorax length in $D^R$, egg production and
mating success of the large and the small flies in two $D^R$ lines and their control
were compared. The possibility that inbreeding depression caused the decrease of
the mean in the $S$ lines was tested by crossing the two $S$ lines.

MATERIALS AND METHODS

The selection lines used in this analysis are described in Bos and Scharloo (1973). Culture
methods, nomenclature, population densities, measuring procedure and mating systems are the
same unless stated otherwise. Flies were reared at $25^\circ \pm 0.5^\circ$ and 60-80% humidity.

Variance: As in the earlier paper (Bos and Scharloo 1973) variances were computed as
squared coefficients of variation (C.V.2) with the purpose to remove the effect of differences in
mean between sexes and between selection lines. In this paper phenotypic variance ($V_p$), genetic
variance ($V_g$), additive genetic variance ($V_{a}$), nonadditive genetic variance ($V_{na}$), residual
variance ($V_r$) and environmental variance ($V_e$), are always expressed as squared coefficients
of variation.

Progeny tests: Tests have been performed with flies hatching from cultures of the selection
lines. Of the series of lines started in July 1967 ($C-1, C-2, D--1, D--2, S-1, S-2, D^R-1, D^R-2$) tests
were done on generations $G_{0}, G_{6}, G_{12}, G_{19}$ ($D--1$ in $G_{30}$), $G_{30}$ and $G_{45}$. Mating occurred
between flies from the same culture. In $G_{6}$ and $G_{30}$ mating was random; in all other test positive
assortative mating was used. Heritabilities were computed as regressions of offspring means
on midparent-values. At least four daughters and four sons were measured from each pair. Of
the lines started in September 1968 ($C-3, D^R-3, D^R-4$) tests were done on $G_{0}, G_{10}$ and $G_{34}$.

Divergent directional selection: The effect of divergent directional selection was measured on
the base population (simultaneously with $G_{11}-G_{21}$ of $C-2, D--1$ and $D--2$) and on $G_{32}$ of the
$S$ and the $D$ lines. In each line $20 \Phi \Phi$ and $20 \delta \delta$ from each of the three sublines were meas-
ured. From each sample of 20 flies 4 flies of each sex were selected as parents of the next
generation.

Inbred lines: Four series of inbred lines (full-sib mating) were made: $IB_{67}$ from the base
population at the start of the selection experiments in 1967 and $IB_{69}, ID--1$ and $ID--2$ from the
base population and the $D--1$ and $D--2$ selection lines, respectively, at $G_{27}$ in 1969. Thorax
length of the inbred lines and of a number of crosses between these inbred lines was investigated
in three different tests. In these tests the flies were reared under conditions of low population
density. In the first test (February, 1969) from each of 8 cultures per line (4 cultures per cross),
and in the second test (November, 1969) from each of 2 cultures per line or cross, $20 \Phi \Phi$ and
$20 \delta \delta$ were measured. In the third test (November, 1970) from each of 3 cultures per line or
cross, 15 $\Phi \Phi$ and 15 $\delta \delta$ were measured.

Crosses of $S$ lines: Reciprocal crosses between two stabilizing selection ($S$) lines were made
in $G_{9}$ and $G_{21}$. For each reciprocal cross four cultures were used, each with four pairs of parents.
From each offspring, $20 \Phi \Phi$ and $20 \delta \delta$ were measured.

Mating choice experiments: In two $D^R$ thorax selection lines and their control ($D^R-3, D^R-4$
$C-3$; see Bos and Scharloo 1973) mating success of large and small flies was tested in a mating
choice experiment. As in the usual mating system of the $D^R$ lines, two large $\Phi \Phi$ and two large
$\delta \delta$ were brought together with two small $\Phi \Phi$ and two small $\delta \delta$ in one culture vial. The
copulation combinations which were observed within a period of three hours were scored. Flies
were marked with a small spot of feltpen ink on the wing tips. Marks were fitted in turn on
large or on small flies in consecutive experiments. Tests were performed at ages varying between
four and twelve days after emergence. All flies from one line were of the same age when
tested. Flies were measured and marked 24 hours before the tests.

Large and small flies differed by at least 0.07 mm in thorax length. Egg production of the
individual females was scored in the 24-hour period after copulation in the mating choice exper-
iments.
RESULTS

Progeny tests: Heritabilities were obtained by progeny tests at various stages of the selection. They are presented in Table 1 and Table 2. Additive genetic components of the variation ($V_A$) were computed by multiplication of the squared coefficients of phenotypic variation in the relevant generation with the heritabilities. Residual components ($V_R$) were obtained by subtracting the additive genetic component from the phenotypic variance. The residual component is the upper limit of the environmental variance and includes dominance and interaction components when they are present. The variance components (C.V.) are given in Figure 1. The phenotypic variance $V_P$ did not change much in $S-1$, $S-2$, $D^r-1$ and $D^r-2$ in comparison to the base population and the controls. The addi-

<table>
<thead>
<tr>
<th>Generations</th>
<th>$h^2$</th>
<th>$s$</th>
<th>$n$</th>
<th>$h^2$</th>
<th>$s$</th>
<th>$n$</th>
<th>$h^2$</th>
<th>$s$</th>
<th>$n$</th>
<th>$h^2$</th>
<th>$s$</th>
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<th>$s$</th>
<th>$n$</th>
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<tr>
<td>6</td>
<td>0.67</td>
<td>±0.14</td>
<td>20</td>
<td>0.63</td>
<td>±0.17</td>
<td>17</td>
<td>0.59</td>
<td>±0.08</td>
<td>60</td>
<td>0.31</td>
<td>±0.25</td>
<td>27</td>
<td>0.35</td>
<td>±0.10</td>
<td>71</td>
</tr>
<tr>
<td>12</td>
<td>0.53</td>
<td>±0.12</td>
<td>55</td>
<td>0.41</td>
<td>±0.12</td>
<td>46</td>
<td>0.34</td>
<td>±0.12</td>
<td>57</td>
<td>0.28</td>
<td>±0.11</td>
<td>66</td>
<td>0.38</td>
<td>±0.09</td>
<td>43</td>
</tr>
<tr>
<td>19</td>
<td>0.26</td>
<td>±0.14</td>
<td>39</td>
<td>0.32</td>
<td>±0.13</td>
<td>36</td>
<td>0.25</td>
<td>±0.09</td>
<td>62</td>
<td>0.19</td>
<td>±0.13</td>
<td>38</td>
<td>0.03</td>
<td>±0.09</td>
<td>66</td>
</tr>
<tr>
<td>30</td>
<td>0.14</td>
<td>±0.14</td>
<td>29</td>
<td>0.43</td>
<td>±0.12</td>
<td>37</td>
<td>0.32</td>
<td>±0.14</td>
<td>63</td>
<td>0.14</td>
<td>±0.12</td>
<td>35</td>
<td>0.06</td>
<td>±0.09</td>
<td>67</td>
</tr>
<tr>
<td>45</td>
<td>0.09</td>
<td>±0.09</td>
<td>33</td>
<td>0.47</td>
<td>±0.13</td>
<td>34</td>
<td>0.44</td>
<td>±0.09</td>
<td>53</td>
<td>0.09</td>
<td>±0.12</td>
<td>32</td>
<td>0.08</td>
<td>±0.09</td>
<td>36</td>
</tr>
</tbody>
</table>

TABLE 1

Heritabilities ($h^2$) for thorax length and the number of pairs used in the tests ($n$), in the Groningen 1967 base population (B), in controls (C) and thorax selection lines (S, D$^r$ and D$^-r$)

$h^2$ in G 0 (base population) was $0.53 \pm 0.11$ ($n = 51$).

<table>
<thead>
<tr>
<th>Generations</th>
<th>C-1</th>
<th>C-2</th>
<th>S-1</th>
<th>S-2</th>
<th>S-3</th>
<th>S-4</th>
<th>D$^r-1$</th>
<th>D$^r-2$</th>
<th>D$^-r-1$</th>
<th>D$^-r-2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>0.26</td>
<td>0.14</td>
<td>0.28</td>
<td>0.14</td>
<td>0.09</td>
<td>0.13</td>
<td>0.13</td>
<td>0.14</td>
<td>0.15</td>
<td>0.10</td>
</tr>
<tr>
<td>12</td>
<td>0.32</td>
<td>0.12</td>
<td>0.32</td>
<td>0.13</td>
<td>0.06</td>
<td>0.20</td>
<td>0.13</td>
<td>0.20</td>
<td>0.14</td>
<td>0.10</td>
</tr>
<tr>
<td>19</td>
<td>0.32</td>
<td>0.14</td>
<td>0.32</td>
<td>0.14</td>
<td>0.12</td>
<td>0.20</td>
<td>0.12</td>
<td>0.12</td>
<td>0.15</td>
<td>0.10</td>
</tr>
<tr>
<td>30</td>
<td>0.32</td>
<td>0.14</td>
<td>0.32</td>
<td>0.14</td>
<td>0.12</td>
<td>0.20</td>
<td>0.12</td>
<td>0.12</td>
<td>0.15</td>
<td>0.10</td>
</tr>
<tr>
<td>45</td>
<td>0.32</td>
<td>0.14</td>
<td>0.32</td>
<td>0.14</td>
<td>0.12</td>
<td>0.20</td>
<td>0.12</td>
<td>0.12</td>
<td>0.15</td>
<td>0.10</td>
</tr>
</tbody>
</table>

* In G 20.

TABLE 2

Heritabilities ($h^2$) for thorax length and the number of pairs used in the tests ($n$) in C-3, D$^r-3$ and D$^r-4$

$h^2$ in the base population was $0.64 \pm 0.08$ ($n = 120$).

<table>
<thead>
<tr>
<th>Generations</th>
<th>C-3</th>
<th>D$^r-3$</th>
<th>D$^r-4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.24</td>
<td>0.32</td>
<td>0.32</td>
</tr>
<tr>
<td>34</td>
<td>0.33</td>
<td>0.41</td>
<td>0.41</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Generations</th>
<th>C-3</th>
<th>D$^r-3$</th>
<th>D$^r-4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.24</td>
<td>0.32</td>
<td>0.32</td>
</tr>
<tr>
<td>34</td>
<td>0.33</td>
<td>0.41</td>
<td>0.41</td>
</tr>
</tbody>
</table>
Divergent genetic component $V_A$ decreased in C-2 and to a lesser extent in S-1. While $V_A$ declined in C-3, it remained on the same level or increased in $D^{R-3}$ and $D^{R-4}$. In both $D^{-1}$ and $D^{-2}$ there was a large increase of $V_P$. But in $D^{-1}$ the increase was almost completely a consequence of increase of the residual variance $V_R$, while in $D^{-2}$ the contribution of $V_A$ was predominant.

Divergent directional selection: The different composition of the phenotypic variance of $D^{-1}$ and $D^{-2}$ was reflected in the effect of divergent directional selection (Figures 2 and 3): the response of $D^{-2}$ was very much larger than responses in $D^{-1}$, B and C-2. After 7 generations of selection, divergence between the large and the small lines was 23.6 in $D^{-2}$ against 13.6 in $D^{-1}$. The phenotypic variance went down in all lines selected from the $D$-stocks and increased in the lines selected for small thorax from the base population and the control line.

While the response in $D^{-2}$ was symmetric, there was asymmetry in selection response in the lines started from $D^{-1}$, B and C-2: selection for small thorax progressed faster than selection for a long thorax. The asymmetry remained when realized heritabilities were computed after 1, 3, 5 and 7 generations of directional selection (Table 3). So, it could not be attributed to causes operating through the selection differential. The realized heritabilities were in reasonable agreement with the heritabilities obtained in the progeny tests. But at the end of the selection realized heritabilities did not differ so much as at the start.

Scoring of flies with abnormal (>4) numbers of scutellar bristles (Table 4) in
Figure 2.—Divergent directional selection from $D^{-1}$, $D^{-2}$ and $C^{-2}$ (sexes averaged) in G 32. Means and squared coefficients of variation (C.V.²) of thorax length. S and L: selection for respectively small and large size.

Table 3

Realized heritabilities in the divergent directional selection experiments from the base population (B), C-2, D-1 and D-2 after 1, 3, 5 and 7 generations of selection

Heritabilities from the progeny tests in generations from which the selection was started are given for comparison in the last column.

<table>
<thead>
<tr>
<th>Lines</th>
<th>$U_p^1$</th>
<th>$D_{Down}$</th>
<th>$U_p^3$</th>
<th>$D_{Down}$</th>
<th>$U_p^5$</th>
<th>$D_{Down}$</th>
<th>$U_p^7$</th>
<th>$D_{Down}$</th>
<th>$h^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>+0.70</td>
<td>+0.02</td>
<td>+0.23</td>
<td>+0.06</td>
<td>+0.13</td>
<td>+0.32</td>
<td>+0.63</td>
<td>+0.17</td>
<td></td>
</tr>
<tr>
<td>C-2</td>
<td>+0.14</td>
<td>+0.06</td>
<td>+0.05</td>
<td>+0.01</td>
<td>+0.04</td>
<td>+0.19</td>
<td>+0.19</td>
<td>+0.13</td>
<td></td>
</tr>
<tr>
<td>D-1</td>
<td>+0.25</td>
<td>+0.14</td>
<td>+0.35</td>
<td>+0.21</td>
<td>+0.19</td>
<td>+0.25</td>
<td>+0.17</td>
<td>+0.14</td>
<td></td>
</tr>
<tr>
<td>D-2</td>
<td>+0.50</td>
<td>+0.50</td>
<td>+0.50</td>
<td>+0.41</td>
<td>+0.35</td>
<td>+0.34</td>
<td>+0.92</td>
<td>+0.11</td>
<td></td>
</tr>
</tbody>
</table>

* In G 1: ratio of response to selection differential.
In G 3, 5 and 7: regression coefficients of response on cumulative selection differential.
these lines confirmed the positive correlation between thorax length and bristle number which was found within cultures (Bos and Scharloo 1973).

Inbred lines and their crosses: The pooled values of thorax length, phenotypic variance (C.V.$^2$) and emergence in the four series of inbred lines are given in Table 5 separately for inbreds (I) and crosses (C) between the inbred lines descending from one series. The C.V.$^2$ values of the individual lines and their crosses in the third test are presented in Figure 4. In all tests and all series the mean thorax was larger, the phenotypic variance smaller and the emergence percentages larger in the crosses than in the inbred lines. These are the normal

**TABLE 4**

Percentage of females with abnormal number of scutellar bristles in the directional selection lines of C-2, D-1 and D-2

Large = lines selected for large thorax length. Small = lines selected for small thorax length

<table>
<thead>
<tr>
<th>Generations</th>
<th>Large C-2</th>
<th>Small</th>
<th>Large D-1</th>
<th>Small</th>
<th>Large D-2</th>
<th>Small</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>2.0</td>
<td>2.0</td>
<td>15.0</td>
<td>5.0</td>
<td>50.0</td>
<td>6.7</td>
</tr>
<tr>
<td>2</td>
<td>3.3</td>
<td>0.0</td>
<td>10.0</td>
<td>6.7</td>
<td>43.3</td>
<td>5.0</td>
</tr>
<tr>
<td>3</td>
<td>5.0</td>
<td>0.0</td>
<td>8.3</td>
<td>5.0</td>
<td>31.7</td>
<td>1.7</td>
</tr>
<tr>
<td>4</td>
<td>1.7</td>
<td>0.0</td>
<td>11.7</td>
<td>1.7</td>
<td>45.8</td>
<td>0.0</td>
</tr>
<tr>
<td>5</td>
<td>0.0</td>
<td>1.7</td>
<td>11.7</td>
<td>0.0</td>
<td>57.9</td>
<td>3.3</td>
</tr>
<tr>
<td>6</td>
<td>1.7</td>
<td>0.0</td>
<td>3.3</td>
<td>0.0</td>
<td>35.0</td>
<td>1.6</td>
</tr>
<tr>
<td>7</td>
<td>5.0</td>
<td>0.0</td>
<td>13.3</td>
<td>0.0</td>
<td>28.0</td>
<td>1.7</td>
</tr>
</tbody>
</table>
DISRUPTIVE AND STABILIZING SELECTION

TABLE 5

Mean (0.01 mm) and variance (C.V.²) of thorax length in the four groups of inbred lines (I) and their crosses (C)

The figures of the different lines and crosses descending from one population or selection line are pooled in one estimate.

<table>
<thead>
<tr>
<th>Series</th>
<th>Data of tests</th>
<th>Number of Inbred lines or crosses</th>
<th>Number of flies</th>
<th>Thorax length mean (C.V.²)</th>
<th>Percent emergence</th>
<th>Generations of inbreeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>IB 67</td>
<td>2/69</td>
<td>I 3</td>
<td>851</td>
<td>97.7</td>
<td>8.44</td>
<td>53.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C 3</td>
<td>480</td>
<td>101.6</td>
<td>4.50</td>
<td>62.9</td>
</tr>
<tr>
<td></td>
<td>11/70</td>
<td>I 9</td>
<td>810</td>
<td>97.2</td>
<td>6.91</td>
<td>58.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C 9</td>
<td>806</td>
<td>101.0</td>
<td>3.99</td>
<td>62.9</td>
</tr>
<tr>
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<td>I 9</td>
<td>585</td>
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<td>13.26</td>
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</tr>
<tr>
<td></td>
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<td>I 8</td>
<td>463</td>
<td>95.4</td>
<td>12.48</td>
<td>28.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C 8</td>
<td>662</td>
<td>100.9</td>
<td>3.62</td>
<td>47.7</td>
</tr>
<tr>
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<td>7.73</td>
<td>39.6</td>
</tr>
<tr>
<td></td>
<td>11/70</td>
<td>I 11</td>
<td>862</td>
<td>98.8</td>
<td>13.39</td>
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<tr>
<td></td>
<td></td>
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<td>941</td>
<td>100.9</td>
<td>9.89</td>
<td>59.9</td>
</tr>
<tr>
<td>ID-2</td>
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<td>880</td>
<td>100.4</td>
<td>8.35</td>
<td>52.7</td>
</tr>
<tr>
<td></td>
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<td>785</td>
<td>98.9</td>
<td>9.23</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>C 11</td>
<td>853</td>
<td>103.6</td>
<td>3.78</td>
<td>43.2</td>
</tr>
</tbody>
</table>

features of hybrid vigor for body size in the crosses of inbred lines (F. W. Robertson 1955). It is clear that the variability of the homozygous inbred lines cannot be used as an estimate of the environmental variance in the heterozygous base population or in the D⁻ selection lines. Only the heterozygous F₁'s generated by crossing the inbred lines will have a level of heterozygosity comparable to the populations from which the inbreds were started. Therefore, the pooled phenotypic variance for the crosses within each series of inbreds was used as an estimate of the environmental variance for the population or selection line from which the series of inbreds was started.

The average phenotypic variances of the crosses in the IB 67, IB 69 and the

FIGURE 4.—Squared coefficients of variation (C.V.²) of the individual inbred lines (I) and their crosses (C). Pooled estimates within each series are indicated by broken lines.
Table 6
Mean (0.01 mm) and phenotypic variability (squared coefficients of within-culture variation) in crosses between two stabilizing (S) selection lines—thorax length (sexes averaged)

<table>
<thead>
<tr>
<th>Type of cross and generation</th>
<th>Type of cross and generation</th>
<th>Mean</th>
<th>Variability (G.V.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>P1-P2</td>
<td>F1-M.P.</td>
</tr>
</tbody>
</table>

**S-1 × S-2—G 9**
101.2–101.7 = -0.5 102.2–101.4 = +0.8 5.73 7.45 6.59 6.47

**S-2 × S-1—G 9**
101.7–101.2 = +0.5 102.5–101.4 = +1.1 7.45 5.73 6.59 4.47

**S-1 × S-2—G 21**
95.7–97.6 = -1.9 97.0–96.7 = +0.3 8.71 10.47 9.59 7.17

**S-2 × S-1—G 21**
97.6–95.7 = +1.9 96.5–96.7 = -0.2 10.47 8.71 9.59 9.56

P₁ and P₂: parental values of S-1 and S-2, respectively.
F₁-M.P.: difference between progeny value and midparent value.

**ID-2 series were all about 3 to 4, which is on the same level as the residual variance obtained in the progeny tests on the base population. But the phenotypic variance of the crosses in the D-1 series was 2 to 3 times larger.**

**Crosses of S lines:** Mean value and phenotypic variance in the F₁’s of crosses between the S lines in G 9 and G 21 did not differ consistently from these values in the parental lines (Table 6). Therefore the decrease of the mean and the increased residual variances in the S-1 line could not be attributed to increasing homozygosity caused by the stabilizing selection.

**Directional component in the stabilizing selection:** In the base population the frequency distributions of the thorax length fitted normal distributions. But after some generations of selection very small individuals appeared in the S lines:

![Figure 5.](image)

_Figure 5._—The cumulated difference between the mean value of the selected individuals and the modal (Σ( \bar{x}_S - \bar{x}_M )) in the stabilizing selection (S) lines.
distribution became skew with a tail to small values (see also Robertson 1955). In these stabilizing lines selection was practiced for individuals nearest to the mean value of their sample. But after the appearance of the skewness the mean did not coincide anymore with the mode of the distribution. Then a difference appeared between the modal value and the mean of the selected individuals resulting in a negative selection differential with respect to the mode of the distribution. This cumulated selection differential is given in Figure 5. The selection differential became negative between G 5 and G 10, which was also the period when mean values of the S lines started to decline.

*Mating choice experiments* $D^r$ lines: In all $D^r$ lines mean thorax length increased. In $D^r$.3 and $D^r$.4 the possibility that mating success and egg production of large flies were responsible was investigated. The combinations at copulation are shown in Table 7. Generally, large $\delta \delta$ were more successful than small $\delta \delta$ — in particular, in the first stages of the selection of $D^r$.4. Further, there was a tendency for positive assortative mating in both selection lines and controls. Egg production seemed to be somewhat higher in large flies than small flies (Table 8).

**DISCUSSION**

In our $S$ lines and $D^r$ lines the most conspicuous response was the change of the mean value (Bos and Scharloo 1973). The decrease of the mean in the $S$ lines is a consequence of a directional component caused by skewness of the frequency distributions. The negative selection differential with respect to the mode of the distribution seems to be sufficient to explain the decrease of the mean value. Changes in variance were small in the $S$ lines: there is at most a small decrease of the genetic variability which is then compensated by an increase of the residual variance.

Several authors obtained a decrease of the phenotypic variance by stabilizing selection: in sternopleural chaetae number (Thoday 1959) and in developmental time (Prout 1962) by a decrease of the genetic variance, in $ci^{D-r}$ expression by a decrease of both the genetic and the environmental variance (Scharloo 1964; Scharloo, Hoogmoed and ter Kuile 1967). But no appreciable change of variance was caused in wing length (Tantawy and Tayel 1970), in 'escape' behavior (Grant and Mettler 1969) and in abdominal chaetae number (Falconer 1957). So, our results are not exceptional. The failure to obtain a decrease of the variance—and, in particular, the environmental variance—could be a consequence of the directional component in the selection system. Although this is a consequence of the peculiar properties of the character—the skewness of the frequency distribution—it cannot be concluded that the additive genetic variance necessary for a decrease of the environmental variance by stabilizing selection was not present. In particular no conclusion can be made on the possibility that a continuous pressure of natural stabilizing selection maintains the maximum of stabilization of body size, attainable by the additive variance which is present in the population.

Disruptive selection with random mating ($D^r$) was found to increase the phenotypic variance by increase of the genetic component (Thoday and Gibson 1962;
### TABLE 7

*Number of the four possible types of mating, recording in the mating choice experiments*  
(*L* = *Large*, *S* = *Small*) in generations 5, 10, 30 and 32

P-values are presented for the hypothesis of (1) a 1 to 1 ratio of large to small matings;  
(2) a 1 to 1 ratio of matings of likes to matings of unlikes. (*χ²*-tests)

| Ψ × φ  | G5  | 10  | 30  | 32  | Σ   | G5  | 10  | 30  | 32  | Σ   | G5  | 10  | 30  | 32  | Σ   | G5  | 10  | 30  | 32  | Σ   |
|--------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| L × L  | 6   | 8   | 8   | 13  | 35  | 10  | 12  | 10  | 13  | 45  | 6   | 3   | 9   | 16  | 34  |
| S × L  | 4   | 10  | 6   | 10  | 30  | 10  | 12  | 6   | 12  | 40  | 5   | 2   | 4   | 7   | 18  |
| L × S  | 2   | 9   | 3   | 10  | 24  | 1   | 4   | 3   | 10  | 18  | 2   | 4   | 3   | 7   | 16  |
| S × S  | 5   | 6   | 11  | 9   | 31  | 1   | 8   | 4   | 13  | 26  | 3   | 5   | 8   | 10  | 26  |
| Total matings obs. | 17 | 33  | 28  | 42  | 120 | 22  | 36  | 23  | 48  | 129 | 16  | 14  | 24  | 40  | 94  |
| Number of pairs | 20  | 40  | 60  | 64  | 184 | 28  | 44  | 64  | 64  | 200 | 24  | 16  | 48  | 64  | 152 |
| P-values | 1) | 0.48 | 0.62 | 1.00 | 0.55 | <0.01 | 0.05 | 0.06 | 0.78 | 0.14 | 0.29 | 0.69 | 0.36 |
| 2) | 0.23 | 0.40 | 0.06 | 0.75 | 1.00 | 0.49 | 0.32 | 0.59 | 0.64 | 0.61 | 0.04 | 0.06 |
Mean egg production / 9 / 24 hr. Within brackets the number of eggs which yielded adults.

<table>
<thead>
<tr>
<th>Generation</th>
<th>♀♂</th>
<th>DR-3 Production</th>
<th>n</th>
<th>DR-4 Production</th>
<th>n</th>
<th>C-3 Production</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-5 and 10</td>
<td>Large</td>
<td>16.3 (7.4)</td>
<td>38</td>
<td>21.2 (10.9)</td>
<td>44</td>
<td>21.8 (12.2)</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Small</td>
<td>12.6 (7.5)</td>
<td>38</td>
<td>12.0 (8.9)</td>
<td>44</td>
<td>12.5 (6.3)</td>
<td>42</td>
</tr>
<tr>
<td>32</td>
<td>Large</td>
<td>12.7 (8.0)</td>
<td>16</td>
<td>12.0 (8.9)</td>
<td>16</td>
<td>12.5 (6.3)</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Small</td>
<td>11.3 (6.3)</td>
<td>16</td>
<td>11.0 (8.9)</td>
<td>16</td>
<td>11.5 (6.3)</td>
<td>16</td>
</tr>
</tbody>
</table>

n = number of females tested.

SCHARLOO, HOOGMOED and TER KUILE 1967; BARKER and CUMMINS 1969). In our $D^{a-3}$ and $D^{a-4}$ lines there is a gain in variance at the end of the selection, but the contribution of genetic differences is small. In our $D^{a-1}$ and $D^{a-2}$ lines, however, there is only a temporary increase of the phenotypic variance. This increase in variance is at least partly a consequence of an increased genetic component, because after the disappearance of the small flies there is a large permanent increase of the mean value simultaneously with a decrease of variance.

That increase of the genetic variance is only temporary in $D^{a-1}$ and $D^{a-2}$ is a consequence of the positive correlation between reproductive success (egg production and mating success) and body size. Although the genetic variance in body size seems to be present, it cannot be used because of this interrelation with other characters. Such interrelations will occur more frequently as the character selected for is more bound to general physiology and growth.

The most striking effects of selection were observed in the $D^{-}$ lines. As is shown in Table 9, the large increase of phenotypic variance had about the same magnitude in both lines; however, the progeny tests show that the mechanism by which this increased variance is obtained is completely different. In $D^{-2}$ it is the additive genetic variance which increased while the residual variance remained on the same level as in the base population and the controls. This is confirmed by the large reaction of $D^{-2}$ to directional selection for thorax length. Moreover the phenotypic variance of crosses of inbred lines, which represents the environmental variance, is on the same level for the $D^{-2}$ line and the base population.

The components of variance (C.V.%) in the Groningen 1967 base population (B) and in two disruptive (D-) selection lines

<table>
<thead>
<tr>
<th></th>
<th>$B_{GO}$</th>
<th>$D^{-1}:G20+30$</th>
<th>$D^{-2}:G19+30$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phenotypic</td>
<td>$V_P$</td>
<td>6.50 100</td>
<td>23.45 100</td>
</tr>
<tr>
<td>Additive genetic</td>
<td>$V_A$</td>
<td>3.45 53</td>
<td>5.63 24</td>
</tr>
<tr>
<td>Nonadditive genetic</td>
<td>$V_{NA}$</td>
<td>-0.94 -14</td>
<td>7.93 34</td>
</tr>
<tr>
<td>Environmental</td>
<td>$V_E$</td>
<td>3.99 61</td>
<td>9.89 42</td>
</tr>
</tbody>
</table>

The phenotypic variances and heritabilities in the selection lines are the averaged values from two generations near the starting point for inbreeding. $V_E$ from crosses of inbred lines (11/70 tests); $V_A = h^2 \times V_P$; $V_{NA} = V_P - (V_R + V_A)$. 
In contrast, in $D^-1$ the additive genetic variance did scarcely change, but there is a huge increase of the residual variance. That this is in large part an increase of the environmental variance is shown by the phenotypic variance of the crosses of the inbred lines, which is 2–3 times larger as the same value of the base population and the $D^-2$ line. The difference between the environmental variance obtained from the crosses of the inbred lines and the residual variance from the progeny tests suggests that dominance and interaction between loci is also responsible for part of the increase of the phenotypic variance of $D^-1$. The composition of variance in the Groningen base population is in good agreement with the composition of variance in a Crianlarich stock of Robertson (1957).

The results of the two $D^-$ lines could not be more contrasting: in one line the only increase was of additive genetic variance; in the other the only increase was of residual variance. One would expect that both types of reaction could occur simultaneously in one selection line—an increase of phenotypic variance as a consequence of an independent, simultaneous increase of both the genetic and environmental variance.

The response in the $D^-1$ line is similar to the response of the $D^-$ line of Prout (1962) in which selection was practiced on developmental time. Prout, however, did not distinguish between increase of environmental variance and variance due to genetic interaction. Increase of genetic variance by $D^-$ selection could have occurred by change of gene frequencies to intermediate values (Robertson 1956) or by generation of linked complexes of genes acting in the same direction (Mather 1955). A factor with large effect—either one gene or a complex of linked genes—as the cause of the increased genetic variance in our $D^-2$ line is suggested by the pattern of response to directional selection: large advance at the start which declines rapidly. Moreover, the genetic differences between extreme flies in $D^-2$ are located on the third chromosome (Bos and Scharloo 1974). A small increase of genetic variance was found in Thoday's $D^-$ line selected for sternopleural chaetae (Thoday 1959). In Scharloo's $ci^{b-a}$ line (Scharloo, Hoogmoed and ter Kuile 1967) there was also increase of the genetic variance component—besides other components—which was a consequence of a general change of canalization of the character selected for (Scharloo 1970).

What are the causes of the striking difference in response between our two $D^-$ lines started simultaneously from the same base population, with the same selection regime, under the same environmental conditions? It is obvious that in this kind of selection experiments, where the number of animals measured is small and the number selected as parents of the next generation still smaller, there is plenty of scope for sampling effects (see A. Robertson 1970). The difference between the two $D^-$ lines must be a consequence of random genetic drift. Different sets of genes were probably present in the flies from the base population which were used at the start of the two lines.

This result shows clearly that generalizations about the effect of certain types of selection ought not to be based on the result obtained in one selection line. On the other hand they show that the same outward result—increase of phenotypic variance—can be obtained from a single population by the same mode of selec-
tion by completely different mechanisms. The different outcomes show some of
the potential reactions of the base population on this type of disruptive selection.
In \( D^{-2} \), genes (or complexes of genes) with effects on size were brought together
in the extreme individuals which were selected in every generation. In the \( D^{-1} \) line, genes which render growth more sensitive to environmental differences
were accumulated in all flies. Experiments on body size (this paper) and develop-
ment time (Prout 1962) showed comparatively small—although clear—changes
in variances and no polymorphism, while the experiments on sternopleural chaetae (e.g., Thoday and Gibson 1962) and \( c^{D-6} \) expression (Scharloo, Hoog-
moed and ter Kuile 1967) showed rather spectacular results. So, it is obvious
that the properties of a character will affect the result of stabilizing and disrup-
tive selection. Characters with predominantly additive genetic variance which
differentiate in a short period of development will generally show a larger and
less complicated reaction than characters which are more associated to the gen-
eral physiology of the organism. But simple generalizations are not possible; only
a list of possible outcomes can be made, from which perhaps probabilities can be
indicated on the basis of the structure of the genetic variance of the character in-
volved.

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