Notes

Stabilizing selection in Drosophila melanogaster

J. W. CURTSINGER

THE operation of natural selection has been classified by Mather into three types: directional, in which an extreme phenotype is favored; disruptive, in which both extremes are favored; and stabilizing, in which an intermediate phenotype is favored. Mather has argued that the nature of the genetic variance found for a particular character reflects the type of selection operating on the character. A character with a history of stabilizing selection, for instance, is expected to show primarily additive effects, while characters under directional selection should show directional dominance. The theory is supported for a variety of characters, although it has been suggested that there is a lack of proven cases of stabilizing selection.

Proof of the operation of stabilizing selection is complicated by the possibility of "neutral characters." Falconer has proposed a mechanism whereby a character that has no functional relation to fitness may appear to undergo stabilizing selection. If the genetic variance is primarily additive, individuals with an intermediate phenotype may tend to be more heterozygous than individuals with extreme phenotypes. If heterozygosity confers a selective advantage, the intermediate individuals would be more fit than those with extreme phenotypes. Variation in the character would be more fit than those with extreme phenotypes. Variation in the character would thus appear to cause variation in fitness, although there may in fact be no causal relation. Sternopleural chaetae number in D. melanogaster has been viewed as a neutral character. Populations in which artificial directional selection has been relaxed show no tendency to return to the original population mean, even though genetic variance for the character may still exist. On the other hand, Barnes found that populations at two different temperatures reach different equilibria for chaetae number, and fitness declines with departure from the mean within each population. Since the populations were large and heterozygosity is not expected to differ between temperature lines, the results may be interpreted as evidence that variation in chaetae number causes variation in fitness. Because the results for chaetae number are contradictory, and there are no other appropriate data, the general significance of the neutral character model is unknown.

Evidence will be presented here showing that egg length in D. melanogaster is operated on by stabilizing selection, causing variation in fitness independent of heterozygosity. The component of fitness measured is hatchability.

Materials and Methods

Oregon-R flies were maintained in a large population cage at room temperature. Juveniles were collected within 12 hours of emergence and isolated in pairs on cornmeal medium. On the fifth day after emergence, pairs were transferred to empty shell vials inverted on black food for collecting eggs (charcoal and 2 percent agar added to the cornmeal medium). The charcoal aids in sighting the eggs, and the agar prevents the females from burying the eggs. Parsons has shown that egg length and hatchability vary with maternal age, hence the necessity of collecting eggs on the same age date for all females. Eggs were isolated and maximum length (not including the filaments) measured with an ocular micrometer, to the nearest micrometer unit. One micrometer unit equals 0.006 mm. Eggs were kept moist with damp cheesecloth for three days, after which they were scored for hatching with a dissecting microscope. Most eggs hatched in one day, and none that hatched took longer than three days. All statistical tests are as described by Sokal and Rohlf.

Results and Discussion

From 41 pair matings, 846 eggs were measured and scored for hatching. Egg lengths ranged from 76-101 micrometer units, and were normally distributed (chi-square goodness-of-fit, $P = 0.1$). Sixty-three eggs failed to hatch (7.5 percent). Summary statistics on egg lengths and variation are shown in Table 1.

The operation of stabilizing selection on egg length is suggested by several facts. The mean lengths of hatched and unhatched eggs do not differ, but the latter show a much larger variance. Further, the proportion of eggs hatching in each size class shows an

<table>
<thead>
<tr>
<th>Table 1. Egg lengths in micrometer units</th>
</tr>
</thead>
<tbody>
<tr>
<td>No.</td>
</tr>
<tr>
<td>-----</td>
</tr>
<tr>
<td>All eggs</td>
</tr>
<tr>
<td>Hatched</td>
</tr>
<tr>
<td>Unhatched</td>
</tr>
</tbody>
</table>

The author is associated with the Department of Biological Sciences, Stanford University, Stanford, Ca. 94305. Much of the work was done at the University of Chicago, at the suggestion of Dr. L. Van Valen. Drs. M. W. Feldman and C. Sassaman gave useful advice on the data analysis.
intermediate optimum, as shown in Figure 1. A regression of arcsine percentage hatch on absolute deviation from the population mean size gives a negative slope; the slope is significantly different from zero, and the regression accounts for a significant proportion of the variation \((F = 15.5, P < 0.02; r = 0.92, P < 0.05)\). The percentage of eggs of egg length. The data suggest an intermediate optimum egg
tion of the variation \((F = 15.5, P < 0.02; r = 0.92, P < 0.05)\). The percentage of eggs hatching as a function of egg length. The data suggest an intermediate optimum egg

distance of stabilizing selection and the regression accounts for a significant propor-
tion from the population mean size gives a negative

tation between the unselected distribution (all eggs) and the distribution after selection (hatched eggs).

While stabilizing selection is implicated by the above argument, further analysis is necessary to determine if the apparent advantage of intermediate sized eggs is due to association with heterozygosity. The neutral character model may be tested by observing the relation-
ship between parent, egg length, and hatchability. The results of a three-way test of independence using the \(G\) statistic are shown in Table II. Both parent and egg length influence hatching, but there is no significant second-order interaction. This implies that the degree of association between egg length and hatchability is independent of parental genotype. Since hatchability is also independent of the heterozygosity of the egg\(^2\), the neutral character model cannot explain the apparent stabilizing selection. Variation in egg length must be causally related to fitness, although it does not explain all of the variation in fitness; there is a parental component on hatching independent of length.

These results shed some doubt on the applicability of the neutral character model. Also, since the genetic variance for egg length is primarily additive\(^3,4,8,10\), the results support Mather's proposed connection between the nature of the genetic variance and the mode of selection.

**Summary**

Stabilizing selection operates on egg length in *Drosophila melanogaster*. The percentage of eggs hatching decreases with departure from the population mean size; this effect cannot be explained by the model of neutral variation in a quantitative character. The finding of stabilizing selection agrees with expectations for a character inherited primarily through additive effects.

**Literature Cited**