

## DISRUPTIVE SELECTION ON I-MAZE ACTIVITY IN *DROSOPHILA MELANOGASTER*

JERRY A. COYNE<sup>1</sup> AND BRUCE GRANT

*Department of Biology, The College of William and Mary  
Williamsburg, Virginia 23185*

Manuscript received January 5, 1972

SYMPATRIC speciation as one theoretical consequence of disruptive selection has not gained wide acceptance due, in part, to the paucity of laboratory evidence confirming the efficacy of this process. Only one study to date (THODAY and GIBSON 1962) has shown reproductive isolation as a result of disruptive selection on a meristic trait (sternopleural chaeta number in *Drosophila melanogaster*); attempts to corroborate the work have produced some divergence in this character but have shown no evidence of reproductive isolation between selected optima (SCHARLOO, DEN BOER and HOOGMOED 1967; CHABORA 1968; BARKER and CUMMINS 1968). THODAY and GIBSON (1970), reviewing this series of experiments, concluded that their results were due to a fortunate choice of experimental fly stock.

Behavioral traits are likely candidates for artificial disruptive selection since some have been demonstrated to be correlated with mating behavior and hence possibly with reproductive isolation. GRANT and METTLER (1969) have performed disruptive selection on a trait of this type: induced vertical I-maze activity ("escape" reaction) in *D. melanogaster*. A marked response to directional selection for high and low maze activity was accompanied by increased mating discrimination between the diverging lines, but with disruptive selection no evidence for either bimodality or nonrandom mating was indicated. The present experiments were undertaken to examine more rigorously the conditions which might be necessary to attain sympatric divergence with disruptive selection on vertical I-maze performance in *D. melanogaster*; several aspects of the experimental design of GRANT and METTLER were modified in order to increase the probability of detecting incipient divergence.

### MATERIALS AND METHODS

Much of the design of the experiment and the base population used were those of GRANT and METTLER. For each maze trial, fifty flies were run through a vertical I-maze constructed from 21 one-ounce polyethylene funneled dropping bottles numbered from 0 (starting chamber) to 20. As an excitatory stimulus the entire maze was manually raised to a height of 8 cm and then dropped vertically to the floor. This tapping was performed twice every twenty seconds for the duration of the trial (five minutes). The score of each fly was the numbered chamber in which it was located at the end of a run. (See GRANT and METTLER [1969] for further details of the procedure.)

Two replicate lines were maintained for the ten generations of selection. In each line the ten

TABLE 1  
*Performance of selected extremes*

Generation	High mean	Low mean	t or t'	Wilcoxin's s.r.
<i>Population 1 Males</i>				
0	4.98 ± .43	4.98 ± .43		
1	5.82 ± .51	3.60 ± .37	3.54***	....
2	2.70 ± .25	0.38 ± .10	8.53***	....
3	2.57 ± .34	3.68 ± .33	2.32*	....
4	4.46 ± .37	2.61 ± .28	3.99***	....
5	3.22 ± .31	2.54 ± .32	1.54	....
6	4.63 ± .44	3.58 ± .40	1.78	....
7	4.03 ± .34	2.10 ± .26	4.48***	....
8	5.06 ± .52	4.98 ± .49	0.11	....
9	7.54 ± .63	3.76 ± .46	4.82***	....
10	9.81 ± .53	5.77 ± .36	6.35***	P<.02 (10 gen)
<i>Population 1 Females</i>				
0	6.87 ± .55	6.87 ± .55		
1	6.35 ± .62	5.37 ± .48	1.26	....
2	5.38 ± .42	2.41 ± .33	5.56***	....
3	4.90 ± .40	4.63 ± .44	0.45	....
4	6.88 ± .39	3.32 ± .28	7.36***	....
5	5.07 ± .31	1.96 ± .22	8.24***	....
6	7.90 ± .61	4.67 ± .41	4.42***	....
7	5.96 ± .44	3.55 ± .28	4.62***	....
8	6.60 ± .50	5.84 ± .51	1.06	....
9	9.08 ± .78	6.27 ± .49	3.86***	....
10	10.42 ± .56	7.87 ± .44	3.58***	P<.01 (10 gen)
<i>Population 2 Males</i>				
0	5.24 ± .44	5.24 ± .44		
1	4.08 ± .37	3.92 ± .43	0.28	....
2	3.66 ± .34	4.38 ± .32	1.54	....
3	5.02 ± .45	4.06 ± .40	1.60	....
4	4.35 ± .38	2.94 ± .30	2.36**	....
5	3.96 ± .32	3.48 ± .27	1.15	....
6	6.12 ± .47	4.16 ± .35	3.33**	....
7	4.60 ± .43	3.02 ± .31	2.99**	....
8	7.69 ± .62	3.65 ± .35	5.67***	....
9	7.20 ± .78	6.33 ± .58	0.92	....
10	11.63 ± .62	5.62 ± .42	8.07***	P<.02 (10 gen)
<i>Population 2 Females</i>				
0	7.79 ± .69	7.79 ± .69		
1	6.70 ± .56	4.00 ± .45	3.74***	....
2	4.18 ± .30	3.82 ± .31	0.83	....
3	6.36 ± .40	5.15 ± .35	2.26*	....
4	6.37 ± .39	4.43 ± .32	3.89***	....
5	5.50 ± .41	4.09 ± .37	2.54*	....
6	7.92 ± .46	4.96 ± .41	4.87***	....
7	5.45 ± .43	4.53 ± .35	1.67	....

8	7.94 ± .51	5.72 ± .59	2.84**	....
9	9.65 ± .73	6.88 ± .62	2.90**	....
10	11.87 ± .48	7.02 ± .49	6.59***	P < .01 (10 gen)

\* P < .05  
 \*\* P < .01  
 \*\*\* P < .001

highest—or lowest—scoring flies of each sex from the appropriate subpopulation were selected as parents of the next generation (20% selection intensity). (Thus migration between selected optima, present in the experiments of GRANT and METTLER, was precluded.) These forty high and low selected flies were placed in a single vial and allowed to mate at random for twenty-four hours. In contrast to GRANT and METTLER's experiment, females from each scoring group were separated after mating and placed in culture vials (flies were identified by subtle wing-clipping). The progeny from these cultures were scored as to maze performance in a manner identical to the parents.

Tests for sexual isolation were conducted at generations 7 and 10 and were similar to those of GRANT and METTLER. Random and phenotypic controls were run to determine whether wing-clipping per se or high and low maze performance in non-selected control lines affected mating behavior. For the disruptive lines the 16 males and 16 virgin females from the highest-scoring 30% of high-line flies and the same number from the lowest-scoring 30% from the low subpopulation were employed in each of several replicate mating tests.

#### RESULTS AND DISCUSSION

Table 1 shows the mean maze performance for both disruptively selected populations over the course of the experiment. Both the *t* (or *t'*) and WILCOXON's signed rank test indicate the development of significant divergence between high and low lines of each population during the period of selection. The results of the sexual isolation tests were pooled and are presented in Table 2 along with the results of a heterogeneity chi-square test of significance and SCHAFER's (1968) measure of discrimination in mating. In disruptive population 1, significant departure from random mating was observed ( $P = 0.00007$  for pooled data). In generation 7 the mating was highly assortative ( $P = 0.00009$ ); in generation 10, mating, though in the assortative direction, was not significantly different from random mating ( $P = 0.10$ ). No evidence for non-random mating was evinced in tests on population 2 flies.

TABLE 2

*Sexual isolation tests shown as numbers of matings observed*

DISRUPTIVE POPULATION 1				DISRUPTIVE POPULATION 2			
MALES	High	Low		MALES	High	Low	
FEMALES				FEMALES			
High	35	10		High	23	18	
Low	15	29		Low	17	20	
<i>n</i> = 89				<i>n</i> = 78			
<i>S</i> = + 43.24%				<i>S</i> = + 10.11%			
Adj. Het. $\chi^2 = 15.52$ ( $P = .00007$ )				Adj. Het. $\chi^2 = 0.45$ (n.s.)			

*S* = SCHAFER's index of mating discrimination.

Although the GRANT and METTLER experiment described large increases in the phenotypic variance under disruptive selection, there was little evidence or resolution of bimodality with their scheme. The contrast between the earlier experiments and those reported here is most probably attributable to the difference in the experimental design: the separation of high and low females after mating and the complete lack of migration between the two selected extremes save for heterogamic matings. Although competitive viability differences between larvae resulting from the various possible matings were not tested and flies from both extremes were not run through the maze concurrently, it does seem reasonable that the lack of migration between extremes contributed to the maintenance of divergence. In the experiments of SCHARLOO *et al* (1967), significant divergence occurred only in that population which experienced the smallest amount of migration between optima.

The indication of assortative mating in population 1 is, to our knowledge, the first demonstration of the production of reproductive isolation under disruptive selection in one species of *Drosophila* since the results of THODAY and GIBSON (1962). Since the phenotypic controls apparently mated at random, the assortative mating in this population must have been concomitant with selection.

As it is admittedly difficult to envision a natural situation corresponding to the design of this experiment, few generalizations can be made from the work about the possibility of sympatric speciation in nature. The separation of females after random mating may correspond to a type of habitat selection, but the disallowing of migration between extremes—which led to selective differences between flies “phenotypically” identical in maze activity—somewhat vitiates this analogy. What may be applicable to a natural situation, however, is the demonstration in these experiments that reproductive isolation may develop under initial conditions of random mating.

#### LITERATURE CITED

- BARKER, J. S. F. and L. J. CUMMINS, 1969 Disruptive selection for sternopleural bristle number in *Drosophila melanogaster*. *Genetics* **61**: 697–712.
- CHABORA, A. J., 1968 Disruptive selection for sternopleural chaeta number in various strains of *Drosophila melanogaster*. *Am. Naturalist* **102**: 525–532.
- GRANT, B. and L. E. METTLER, 1969 Disruptive and stabilizing selection on the “escape” behavior of *Drosophila melanogaster*. *Genetics* **62**: 625–637.
- SCHAFFER, H. E., 1968 A measure of discrimination in mating. *Evolution* **2**: 125–129.
- SCHARLOO, W., M. DEN BOER and N. S. HOOGMOED, 1967 Disruptive selection on sternopleural chaeta number in *Drosophila melanogaster*. *Genet. Res.* **9**: 115–118.
- THODAY, J. M. and J. B. GIBSON, 1962 Isolation by disruptive selection. *Nature* **193**: 1164–1166. —, 1970 The probability of isolation by disruptive selection. *Am. Naturalist* **104**: 219–230.