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Interocellar Bristles in *Drosophila melanogaster*

Part 3: Response to Disruptive Selection

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Summary. A population of *Drosophila melanogaster* has been exposed to disruptive selection for interocellar bristle number for fifteen generations. Two different mating systems have been employed: quasi-random and mating-choice.

The expected results of an increase in phenotypic variance and divergence of extreme mating groups were not found when the mating-choice system was used, while a clear divergence (2.04% of overlap) was found at the end of the experiment in one line where the quasi-random system (QR1) had been used.

A possible explanation for our results, which is also suggested by those of several other authors, could be that of hybrid vigor. Thus, the reason for the absence of effect in MCh may be that the progeny of "hybrid" matings are likely to be less inbred and therefore have higher viability, mating ability and egg production.

Key words: Interocellar bristles – *Drosophila melanogaster* – Disruptive selection – Mating system

Introduction

Classically, the effect of selection on a continuous character, whether natural or artificial, may be classified in three ways: directional, stabilizing and disruptive (Mather 1953). Disruptive selection ("centrifugal": Simpson 1944; "diversifying": Dobzhansky and Spassky 1967) is selection for more than one value, that is, selection which favours different phenotypes in an interbreeding population.

The expected effect of disruptive selection on a metrical trait is an increase in favoured phenotypes and, eventually, the development of bimodality. Under some conditions it is also possible to obtain polymorphism and/or isolation (Mather 1955).

General agreement has been reached that disruptive selection is able to increase the phenotypic variance of a metrical trait while the mean value remains without significant changes. This increase of variance may lead to divergence in two subpopulations (Thoday 1972; Alicchio et al. 1973).

The divergence produced by disruptive selection usually appears rapidly, although many authors find that it has stabilized within a few generations. Barker and Cummins (1969) have shown that the divergence between extreme phenotypes increases throughout the first seven generations but remains unchanged thereafter. Robertson's results (1970) are similar.

The results obtained by Thoday and Boam (1959) and Millicent and Thoday (1961), with 50% and 25% gene flow respectively, differ from the above results and leave no doubt that disruptive selection is capable of bringing about the divergence of high and low components in a population in spite of the existence of gene flow between both.

In the face of the diversity of the published results, we have carried out the present study in order to provide new information about the effects of disruptive selection.

Materials and Methods

We have used a *Drosophila melanogaster* population collected in Prat de Llobregat (Barcelona) in May 1973 (Marcos 1977 a) and maintained in our laboratory since then. The trait selected was the number of interocellar bristles, one which presents a good response to directional selection (Marcos 1977 b, 1978; Marcos and Creus 1981).

Disruptive selection was carried out using two different mating systems: quasi-random and mating-choice.

Quasi-random Lines

We followed the method used by Gibson and Thoday (1963, 1964) with many modifications. From the base population a sample of 100 males and 100 females was removed and the 20 higher individuals (H) and the 20 lower (L) in each sex were selected. Each selected group (high or low) was separated into two subgroups. This allowed us to build four sublines: LL (10 low females and 10 low males), LH (10 low females and 10 high males), HL (10 high females and 10 low males), and HH (10 high females and 10 high males). From the offspring of each subline, 50 random flies were measured (25 of each sex) and the 20 lowest and highest of the 100 males and females were used as parents of the four sublines in the next generation. This process was repeated for each generation. Two replicates were set up from this mating system, denotated QR1 and QR2.

Mating-choice Lines

The method followed has been the one employed by Thoday and Gibson (1962) with some variations. From the base population a sample of 50 females and 50 males was removed and the 10 higher individuals and the 10 lower of each sex were selected. The 40 selected flies were placed together in the same vial to mate for 24 h. The males were then discarded and the females separated again into high and low sublines according to chaeta number. From the offspring of each subline a random sample of 50 individuals (25 of each sex) was scored and the 10 highest and 10 lowest of each sex selected to produce the next generation, as described above. This process was repeated throughout the experiment. Two replicates were set up, designated MCh1 and MCh2.

At first, the selection intensity was 20%; this changed to 10% at the 10th generation in QR2 and MChl and at the 12th generation in QR1 and MCh2.

All experiments were made at 25 ± 1 °C.

Table 1. Metrical parameters of interocellar bristles in the base population

	Mean	Variance	Coefficient of variation
Males	6.089 ± 0.062	0.778 ± 0.077	14.486 ± 0.720
Females	6.475 ± 0.054	0.592 ± 0.059	11.886 ± 0.594
Total	6.281 ± 0.042	0.721 ± 0.050	13.521 ± 0.476

Results

Prior to selection we estimated the metrical parameters of the base population (Table 1).

The proportion of eggs hatching was 83.3%, which is similar to that calculated by Mènsua (1969) and Creus (1978) in populations collected from the same place.

The selection was carried out for fifteen generations. The whole analysis included the study of the variation of means, variance and variability coefficients, modifications in the phenotypic distribution, overlap of extreme groups, and divergence between them.

Quasi-random Lines

In Table 2 we can see that in both QR1 and QR2 the mean does not change during the experiment. However, in QR1 the variance in the last five generations is 116% greater than in the first five. This increase is not observed in QR2.

Figure 1 shows the divergence between the means of extreme mating groups (H×H and L×L). The divergence is clear in QR1, which explains the increase of variance quoted above. On the contrary, QR2 does not show significant divergence at any time.

The selection intensity change manipulated by us did not seem to have any effect.

The overlap between the distributions of extreme sublines is also a good mesurement of the response. Figure 2 shows this overlap. Again the response of QR1 is clear; starting from the 9th generation, there is a progressive decrease until the 15th generation (2.04% of overlap).

Mating-choice Lines

Table 3 shows the mean and the variance from MCh1 and MCh2. There are no changes in the mean of MCh1,

Table 2. Means and variances of interocellar bristle number in QR1 and QR2

	QR1		QR2	
Generation	Mean	Variance	Mean	Variance
G 2	6.290 ± 0.068	0.940 ± 0.094	6.095 ± 0.076	1.157 ± 0.116
G 3	6.270 ± 0.059	0.710 ± 0.071	5.995 ± 0.067	0.899 ± 0.089
G 4	6.205 ± 0.071	1.018 ± 0.101	6.080 ± 0.069	0.958 ± 0.095
G 5	6.240 ± 0.062	0.776 ± 0.077	6.429 ± 0.065	0.855 ± 0.085
G 6	6.250 ± 0.066	0.891 ± 0.089	6.350 ± 0.054	0.590 ± 0.059
G 7	5.830 ± 0.069	0.956 ± 0.096	5.805 ± 0.069	0.961 ± 0.096
G 8	6.220 ± 0.080	1.288 ± 0.128	6.060 ± 0.076	0.900 ± 0.090
G 9	6.340 ± 0.063	0.818 ± 0.081	6.070 ± 0.069	0.969 ± 0.096
G 10	6.205 ± 0.079	1.249 ± 0.124	6.105 ± 0.056	0.637 ± 0.063
G 11	6.212 ± 0.077	1.423 ± 0.192	6.137 ± 0.042	0.857 ± 0.055
G 12	6.242 ± 0.059	1.422 ± 0.100	6.155 ± 0.044	0.787 ± 0.055
G 13	6.202 ± 0.076	2.303 ± 0.163	6.120 ± 0.049	0.960 ± 0.068
G 14	5.957 ± 0.069	1.915 ± 0.137	6.122 ± 0.045	0.824 ± 0.058
G 15	6.185 ± 0.107	2.312 ± 0.231	6.195 ± 0.064	0.831 ± 0.083

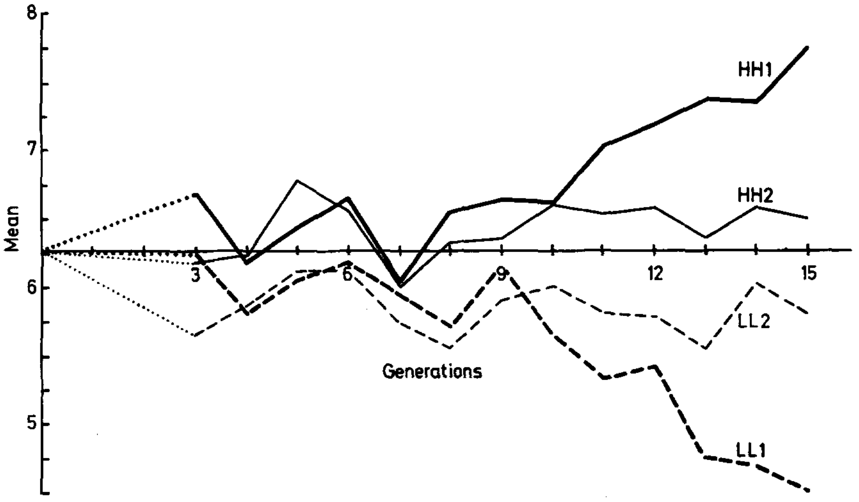

Fig. 1. Divergence under disruptive selection with quasi-random mating

though in MCh2 the mean increases significantly. In MCh1 the variance in the last five generations is 75% larger than that in the first five generations.

Figure 3 shows the divergence between the progeny of H and L females. There is no divergence in either line. From this figure we can observe the mean increase of MCh2. The overlap between extreme phenotypes (see Fig. 2) remains unchanged during the experiment.

The manipulation of intensity of selection does not affect the response.

Viability changes

Dobzhansky (1956) pointed out that in all selection experiments, correlated responses are also found in characters other than those under selection. Thus, in selection experiments with *Drosophila* the viability is often affected.

Table 4 shows the egg-adult viability values for the four selected lines at generation 15. The viability has decreased in all lines in relation to the value found in the base population. This decrease may be the result of inbreeding due to the use of only a few individuals as parents in each generation.

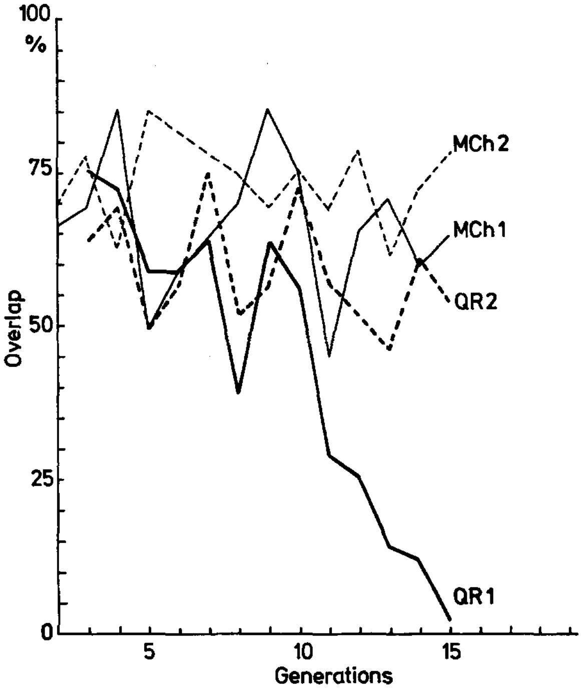

Fig. 2. Overlap between the extreme sublines in quasi-random and mating-choice lines

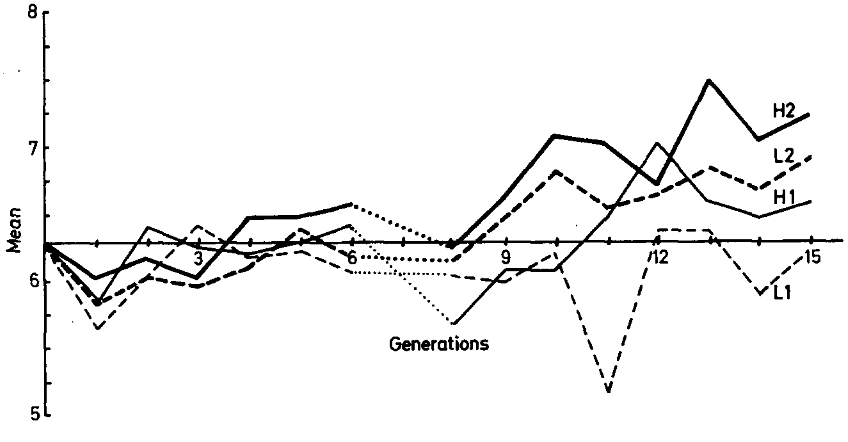

Fig. 3. Divergence under disruptive selection with mating-choice

Table 3. Means and variances of interocellar bristle number in MCh1 and MCh2

	MCh1		MCh2	
Generation	Mean	Variance	Mean	Variance
G 2	6.160±0.918	0.842±0.119	6.110±0.101	1.026±0.145
G 3	6.310±0.093	0.882±0.124	5.970±0.101	1.039±0.147
G 4	6.180±0.101	1.037±0.146	6.270±0.087	0.764±0.108
G 5	6.231±0.089	0.754±0.109	6.420±0.079	0.629±0.089
G 6	6.230±0.078	0.623±0.088	6.350±0.078	0.613±0.086
G 7	5.230±0.081	0.663±0.093	5.560±0.100	1.016±0.143
G 8	5.840±0.104	1.085±0.153	6.180±0.950	0.916±0.129
G 9	6.010±0.089	0.797±0.112	6.510±0.089	0.797±0.112
G 10	6.120±0.107	1.157±0.163	6.910±0.092	0.850±0.120
G 11	5.780±0.143	2.072±0.293	6.741±0.077	0.745±0.094
G 12	6.655±0.086	1.493±0.148	6.645±0.058	0.682±0.068
G 13	6.485±0.075	1.185±0.118	7.109±0.078	1.227±0.122
G 14	6.155±0.076	1.176±0.117	6.820±0.068	0.942±0.094
G 15	6.370±0.079	1.279±0.127	7.045±0.068	0.947±0.094

Table 4. Viability values of selected lines at generation 15

Line	No. eggs	No. adults	Viability (%)
QR1	400	258	64.5
QR2	400	248	62.0
MCh1	400	178	44.5
MCh2	400	288	72.0

Discussion

In this experiment, the response to disruptive selection practiced for number of interocellar bristles differs between the two mating systems used and also between the lines within mating systems. While the lack of repeatability found within the same mating system can be explained by the presence of a gene with a major effect which segregates in some replicates and not in others, the difference found between mating systems would means differences in the relative efficiency of "hybrid" crosses (L×H and H×L) against "non-hybrid" crosses (L×L and H×H).

The divergence obtained in QR, where "hybrid" crosses as well as "non-hybrid" crosses are found in each generation with the same frequency, will depend on the genetic variability. If this holds throughout many generations it will favour the fact that, in the selected sample, the low (L) and high (H) individuals will have a higher probability of descending from a "non-hybrid" cross than from a "hybrid" cross.

The low efficiency of the MCh system in producing divergence could mean that the probability of "hybrid" crosses is very high and/or their relative efficiency compared with "non-hybrid" crosses is significantly higher. According to Scharloo et al. (1967), Barker and Cummins (1969) and Robertson (1970), this last possibility is the best explanation. Thus, the reason for the absence of effect in MCh may reside in the fact that the progeny of "hybrid" matings are likely to be less inbred and therefore to have a higher viability, mating ability and egg production.

It is clear that in our experiment the disruptive random mating did not produce the expected results: significant increase of phenotypic variance and divergence of extreme mating groups.

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