EFFECTS OF DISRUPTIVE SELECTION

V. QUASI-RANDOM MATING

J. M. THODAY
Department of Genetics, Milton Road, Cambridge
and
T. B. BOAM
Department of Genetics, University of Sheffield

Received 8.iii.61

1. INTRODUCTION

THODAY (1958, 1959, 1960), Thoday and Boam (1959) and Millicent and Thoday (1961) have shown that disruptive selection can increase the variety of genotypes in a population. All their experiments were done with rather special systems involving either negative or positive assortative mating between the selected phenotypes. It therefore seemed worth while to run a brief pilot experiment to see what degree of variance could be maintained with a system simulating random mating, which (Thoday and Boam, 1959) is not to be confused with panmixia. Such a system was devised and an experiment started. It had to be stopped when the senior author moved to Cambridge, but the results seem sufficiently interesting to be worth reporting briefly.

2. METHODS

The character used was sternopleural chaeta number in *Drosophila melanogaster*. The system devised to give quasi-random mating is simple. It involved selecting from a population a number of flies of each sex (8) with high and the same number with low chaeta number. The resulting four groups of flies were each divided at random into two lots of four flies each. They were then set up for 24 hours in four mating tubes. The first contained four high females with four high males. The second contained four high females with four low males. The third contained four low females with four high males, and the last contained four low females with four low males. Twenty-four hours later the flies were removed from the mating tubes and the males were discarded. The sixteen females were then placed together in a single culture bottle for 72 hours. The progeny were collected as virgins and forty of each sex were assayed for chaeta number, and the selection and mating process was repeated. The degree to which this system simulates random mating will depend of course upon the degree to which the four different classes of mating produce equal numbers of offspring. The system could easily be arranged so as to ensure that equal numbers were included in the sample assayed by placing the four groups of females in separate cultures and taking equal numbers of progeny from the four cultures. However, the authors were at the time by themselves already maintaining too many selection lines, and time, particularly for virgin collecting, was limiting, so that it was decided to use the easier system for the present pilot experiment. As will be seen, the evidence suggests that, except in the first generation, the system produced adequate results.

3. MATERIAL

The material used was the same as that used by Thoday (1960), namely the high sternopleural chaeta number line homozygous for *vg* (vg 6 of Thoday and Boam, 1961), and the low chaeta number stock homozygous for *se cp* and *e*. The experiment

was started by setting up the four possible matings between vg 6 and the *sepe* stock as described above.

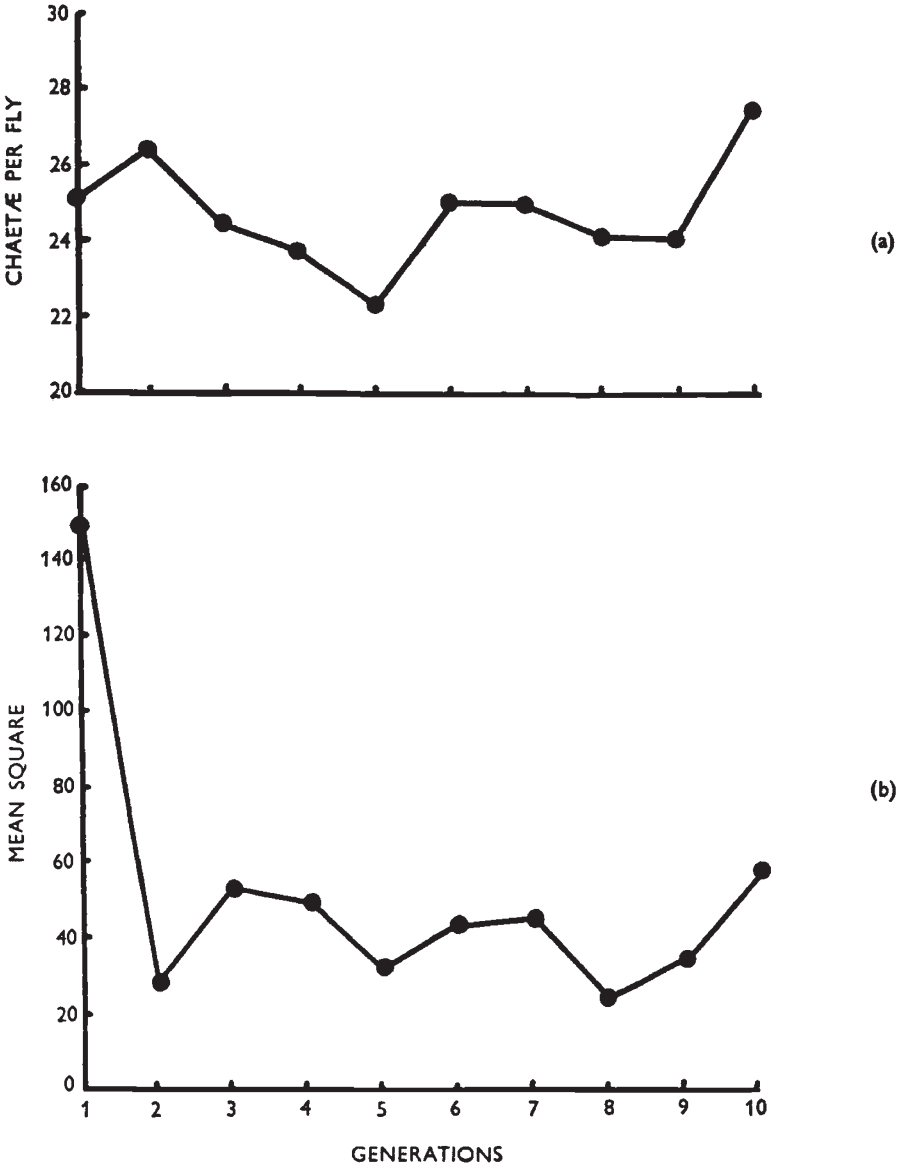

FIG. 1.—Means (*a*) and Mean Squares (*b*) for sternopleural chaeta number in each generation.

4. RESULTS

(i) *Means and variances*

The means and variances of chaeta number are illustrated in fig. 1. The mean remained around 25 chaetæ which is rather below the mid value between the vg6 and *sepe* means which were 42 and 16 respectively

when the experiment was started. The variance was very high in the initial generation but fell straight away to about 40, round which value it fluctuated thereafter. That the mean is lower than the mid parent value is explained by the fact that, in the foundation generation, the vg6 flies were less successful than *se cp e* flies. The very high variance in the foundation generation is caused by a deficiency of hybrid flies in this generation.

The mean variance from generation 2 to the end of the experiment is 41, and is higher than in the F_2 of the cross between vg6 and the *se cp e* stock described by Thoday (1960), which was 30. Disruptive selection with negative assortative mating in Thoday's (1960) lines derived from that F_2 stabilised this variance at about 15, whereas in his stabilising selection line variance was reduced to 5.

The maintenance of variance in the present line at so high a value clearly suggests that under the present system disruptive selection can be very effective. It may well be, indeed, that disruptive selection

TABLE 1

The number of vg/vg *and of* se/se *flies (80 flies assayed per generation)*

Generation	1	2	3	4	5	6	7	8	9	10	Total
se/se	38	24	14	22	33	18	13	3	12	12	150
vg/vg	22	14	17	19	22	16	14	13	8	5	128

will prove more effective with random mating, for the selection pressures used in this experiment are very much lower than in our earlier work. Twenty per cent. of the flies assayed were selected in the present experiment, whereas all the earlier work reported in this series of papers has involved selecting only 5 per cent. of the flies in each generation.

(ii) *The marker genes*

It is known that two powerful chaeta number factors distinguishing vg6 and the *se cp e* stock are linked to *se* and that interacting factors are present on Chromosome II (Thoday, 1960; and unpublished), though it is not yet known how closely linked the interacting factors are to the locus *vg*. It is therefore of interest to follow the behaviour of the loci *vg* and *se* in the present line. The numbers of *vg* homozygotes and of *se* homozygotes in each generation are listed in table 1. χ^2s have been calculated for the data, excluding the foundation generation, on the basis of expectation of one quarter of the population being homozygous for a mutant marker. For *vg*, the overall $\chi^2_{(1)}$ is 20·0296 showing that *vg* homozygotes form significantly less than a quarter of the population, but the heterogeneity $\chi^2_{(7)}$ is 5·0371 ($P = 0{\cdot}7-0{\cdot}5$), showing that the frequency of *vg* has not changed significantly over the generations, though the later generations seem to show *vg/vg* in lower

frequency. For *se* the overall χ^2 is 6·2296 and there is therefore significant, but much less, deviation from one quarter. The heterogeneity χ^2 is 46·3333, showing significant variation in proportion of *se/se* flies between generations, and there is some evidence of a trend in *se/se* frequency.

These data serve two purposes. In the first place they suggest that in this experiment, as in the experiment of Thoday (1960), disruptive selection helped to maintain the frequencies of the marker genes *vg* and *se*. *vg* frequencies can be very rapidly reduced by natural selection. Dinsley and Thoday (1961), for example, ran 6 populations heterozygous for *vg* and by the tenth generation natural selection had completely eliminated the *vg* gene from all of them.

Second they show that, since *vg/vg* and *se/se* flies together comprise less than half the flies in the population, more than half were hybrid genotypes, and hence that the extremely high variance maintained was not due to hybrid inviability or infertility of hybrid crosses despite the deficiency of hybrids in the first generation. Hence it is not unreasonable to apply the term quasi-random mating to the population.

5. CONCLUSIONS

It would be unwise to attach too much significance to this experiment. There was only one small line, it was only maintained for ten generations, and there were no stabilising selection or natural selection controls.

Nevertheless the variance maintained in the population was so large that it seems fair to regard the experiment as supporting the conclusion, suggested by Thoday and Boam (1959) and Millicent and Thoday (1961), that random mating would not prevent disruptive selection from maintaining (or even establishing) a wide variety of genotypes in a population. This conclusion is the more justifiable since the proportion of flies selected in this experiment (20 per cent.) is so much higher than the 5 per cent. selected in previous experiments on disruptive selection.

6. SUMMARY

1. A system is described for simulating random mating in a population under disruptive selection.

2. A system approaching this was used in a pilot experiment involving sternopleural chaeta number.

3. Though the selection pressure was low, so high a variance was maintained that it seems likely that disruptive selection will prove to have powerful effects despite random mating.

7. REFERENCES

DINSLEY, M. AND THODAY, J. M. 1961. Fitness and responses to selection. *Heredity*, *16*, 113-122.

MILLICENT, E., AND THODAY, J. M. 1961. Effects of disruptive selection. IV. Divergence and gene flow. *Heredity*, *16*, 199-217.

THODAY, J. M. 1958. Effects of disruptive selection: the experimental production of a polymorphic population. *Nature*, *181*, 1124-1125.

THODAY, J. M. 1959. Effects of disruptive selection. I. Genetic flexibility. *Heredity*, *13*, 187-203.

THODAY, J. M. 1960. Effects of disruptive selection. III. Coupling and repulsion. *Heredity*, *14*, 35-49.

THODAY, J. M., AND BOAM, T. B. 1959. Effects of disruptive selection. II. Polymorphism and divergence without isolation. *Heredity*, *13*, 205-218.

THODAY, J. M., AND BOAM, T. B. 1961. Regular responses to selection. I. Description of responses. *Genetical Research* (in the press).