Genet. Res., Camb. (1967), 9, *pp.* 119–120
Printed in Great Britain

The general importance of disruptive selection
(A comment on Waddington and Robertson's recent paper)

By J. M. THODAY

Department of Genetics, Cambridge University, England

(*Received* 5 *July* 1966)

In their recent paper, Waddington & Robertson (1966) discuss the general importance of disruptive selection and make various points that call for comment.

First, their statement that 'It is most desirable that Thoday's results . . . should be repeated, with special attention to the strict virginity of the flies used, . . .' appears to some readers as a scarcely veiled imputation that my experiments, especially that of Thoday & Gibson (1962), were executed without technical competence, though Waddington has informed me such imputation was not intended.

In view of this it is perhaps well that I should now state that though I made no mention of virginity in the paper of Thoday & Gibson (1962) this was because I thought it a factor to be taken for granted since no experimental *Drosophila* worker would take less than the necessary care to control this factor in an experiment to which it is obviously of crucial importance. It was in fact evident from the results given in the first paper that the flies were virgin or that any non-virginity was irrelevant. Had non-virginity been the explanation of the results in the selection line, the tests of hybrids would have given results similar to those obtained in the line itself but they did not. Further the separated sexes were stored for up to 4 days in vials with food between collection and selection. The vials in which the virgins were stored were regularly kept. They sometimes contained eggs but no larvae ever developed in any of them.

Second, Waddington and Robertson state that 'Thoday claims that in his experiments a considerable degree of mating preference was developed'. I made this claim, injudiciously perhaps, and would take this opportunity of qualifying it while restating that the experiments show unequivocally that a pronounced degree of reproductive isolation occurred in these lines. They do not unequivocally show that any of this isolation was a consequence of mating preference. The data, which are given in Table 1 of Thoday, 1964, might be explained either by relative lack of hybrid mating due to preference, or by relative lack of success of hybrid matings supposing mating occurred at random. The latter hypothesis seems unlikely for there would have to be many double matings which only gave rise to progeny from the component positive assortative matings. There are insufficient females failing to produce progeny for the data to be explained by random single matings with infertility of the hybrid matings. Mating preference therefore, remains the preferred hypothesis though it has not been directly observed in experiments made for the purpose. Whether or no mating preference is involved is not however a key point. The key point for population genetics (as distinct from behaviour genetics) is that the experiments prove that disruptive selection, in appropriate conditions, can give rise to a considerable degree of reproductive isolation, as Mather (1955) predicted.

Third, I cannot agree with Waddington and Robertson's statement that 'there is . . . no major generalization to be drawn from the results of the disruptive selections; . . .' The following generalizations, some of which I would regard as major, can be made from the experimental results I and my colleagues have obtained:

1. Disruptive selection can increase the phenotypic and genetic variance of a population.
2. Disruptive selection can maintain linkage disequilibrium in a population.
3. Disruptive selection can establish polymorphisms some of which are very similar in genetic principle to sex dimorphisms and mimicry polymorphisms in possessing switching supergenes and modifying (enhancing) genetic backgrounds.
4. Disruptive selection can produce and maintain divergence between two populations between which there is a very high rate of gene flow.
5. Disruptive selection can split a population into two parts between which there is considerable reproductive isolation.

These are, of course, restricted generalizations. None of them, of course, is incompatible with the finding that other experiments fail to produce these results, for no one expects to make generalizations about effects of selection in the form 'Selection procedure A will always have consequence B no matter what the genetic content of the population exposed to selection'. Not enough experiments have been done for us to know how often, how quickly, under what selection intensities, with which characters, with what organisms, to what extent etc., does what we know can happen actually happen in such experiments. The generalizations state what we know can sometimes happen, though they require quantitative qualification, as Waddington and Robertson's results help to show.

Finally, I feel Waddington and Robertson in saying 'As Thoday has often pointed out laboratory experiments on disruptive selection owe their main interest to the light they may throw on the conditions under which sympatric species divergence may occur in nature', may have introduced an undue bias into our interest in disruptive selection. This is not *the* main interest though it may be *a* main interest. I have equally regularly stressed generalizations 1 to 4 above. The origin of segregational polymorphisms is just as 'main' an interest, and generalization 4 is as relevant to our understanding of populations as is generalization 5.

REFERENCES

MATHER, K. (1955). Polymorphism as an outcome of disruptive selection. *Evolution, Lancaster, Pa.* **9**, 52–61.

THODAY, J. M. (1964). Effects of selection for genetic diversity. *Genetics Today*, pp. 533–540. *Proc. XI Int. Congr. Genet.*

THODAY, J. M. & GIBSON, J. B. (1962). Isolation by disruptive selection. *Nature, Lond.* **163**, 1164–1166.

WADDINGTON, C. H. & ROBERTSON, E. (1966). Selection for developmental canalisation. *Genet Res.* **7**, 303–312.